The Fossil Record 2
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### CONTENTS

**List of contributors** vii  
**Acknowledgements** x  
**Preface** xi

#### BASAL GROUPS

1. Monera (Bacteria, Blue-green Algae)  
   D. Edwards  
   3
2. Fungi  
   T. N. Taylor  
   9
3. ‘Algae’  
   15

#### ANIMALS: INVERTEBRATES

4. Protozoa  
   M. B. Hart and C. L. Williams  
   43
5. Porifera  
   J. K. Rigby, G. E. Budd, R. A. Wood and F. Debrenne  
   71
6. Coelenterata  
   J. R. Nudds and J. J. Sepkoski Jr  
   101
7. Mollusca: Amphineura and ‘Monoplacophora’  
   M. J. Benton and D. H. Erwin  
   125
8. Mollusca: Gastropoda  
   S. Tracey, J. A. Todd and D. H. Erwin  
   131
9. Mollusca: Cephalopoda (Nautiloidea)  
   A. H. King  
   169
10. Mollusca: Cephalopoda (pre-Jurassic Ammonoidea)  
    189
11. Mollusca: Cephalopoda (Ammonoidea: Phylloceratina, Lytoceratina, Ammonitina and Ancyloceratina)  
    K. N. Page  
    213
12. Mollusca: Cephalopoda (Coleoidea)  
    P. Doyle  
    229
13. Mollusca: Rostroconchia, Scaphopoda and Bivalvia  
    P. W. Skelton and M. J. Benton  
    237
14. ?Mollusca incertae sedis  
    M. A. Wills  
    265
15. Annelida  
    M. A. Wills  
    271
16. Arthropoda (Trilobita)  
    279
17. Arthropoda (Aglaspidida, Pycnogonida and Chelicerata)  
    P. A. Selden  
    297
18. Arthropoda (Crustacea, excluding Ostracoda)  
    D. E. G. Briggs, M. J. Weedon and M. A. Whyte  
    321
19. Arthropoda (Crustacea: Ostracoda)  
    R. C. Whatley, David J. Siveter and I. D. Boomer  
    343
20. Arthropoda (Euthycarcinoidea and Myriapoda)  
    A. J. Ross and D. E. G. Briggs  
    357
21. Arthropoda (Hexapoda; Insecta)  
    A. J. Ross and E. A. Jarzembowski  
    363
22. Brachiopoda  
    427
23. Phoronida  
    P. D. Taylor  
    463
24. Bryozoa  
    P. D. Taylor  
    465
25. Echinodermata  
    M. J. Simms, A. S. Gale, P. Gilliland, E. P. F. Rose and G. D. Sevastopulo  
    491
26. Basal Deuterostomes (Chaetognaths, Hemichordates, Calcichordates, Cephalochordates and Tunicates)  
    M. J. Benton  
    529
27. Graptolithina  
    R. B. Rickards  
    537
28. Problematica  
    M. A. Wills and J. J. Sepkoski Jr  
    543
29. Miscellania  
    M. A. Wills  
    555
ANIMALS: VERTEBRATES

30. Conodonta  
   R. J. Aldridge and M. P. Smith  
   563
31. Agnatha  
   L. B. Halstead  
   573
32. Placodermi  
   B. G. Gardiner  
   583
33. Acanthodii  
   J. Zidek  
   589
34. Chondrichthyces  
   H. Cappetta, C. Duffin and J. Zidek  
   593
35. Osteichthyes: Basal Actinopterygians  
   B. G. Gardiner  
   611
36. Osteichthyes: Teleostei  
   C. Patterson  
   621
37. Osteichthyes: Sarcopterygii  
   H.-P. Schultze  
   657
38. Amphibian-Grade Tetrapoda  
   A. R. Milner  
   665
39. Reptilia  
   M. J. Benton  
   681
40. Aves  
   D. M. Unwin  
   717
41. Mammalia  
   R. K. Stucky and M. C. McKenna  
   739

PLANTS

42. Bryophyta  
   D. Edwards  
   775
43. Pteridophyta  
   C. J. Cleal  
   779
44. Gymnospermophyta  
   C. J. Cleal  
   795
45. Magnoliophyta (‘Angiospermae’)  
   M. E. Collinson, M. C. Boulter and P. L. Holmes  
   809

Index  
   843
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PREFACE

The present volume had its origin in 1987, when Michael Whyte and the editor approached the Palaeontological Association with the idea of an update of *The Fossil Record* published by the Geological Society of London in 1967. That volume had resulted from discussions between the Geological Society of London and the Palaeontological Association, and followed a meeting held in 1965. The most valuable part of the original publication had been the extensive documentation of families, and we decided to focus on that aspect, and not to include any analytical or commentary papers in the present volume, or to hold a meeting.

The 1967 *Fossil Record* was produced by nine editors and 125 contributors, and amounted to 827 pages. The 1993 edition was produced by one editor and 90 contributors, and amounts to 845 pages: a sure sign of increasing efficiency by the palaeontological community! Of the original 125 contributors, only eight have been involved in the present edition (P. Copper, W. T. Dean, B. G. Gardiner, L. B. Halstead (= L. B. H. Tarlo), M. R. House, C. Patterson, R. B. Rickards and A. W. A. Rushton). Of the 1967 contributors, 105 are listed with UK addresses, nine from the United States of America, four from Australia, three from France, two from the Republic of Ireland, and one each from Canada and The Netherlands (i.e. 84% of the authors were British). Comparative figures for the present edition are that 61 of the 90 contributors are based in the UK, 12 in the United States, four in each of France and the Republic of Ireland, two in each of Australia and Canada, and one in each of China, Germany, Jamaica, the former USSR and Sweden. The British contingent represents 68% of the total of authors. The rise in non-British authors from 16% in 1967 to 32% in 1992 could be interpreted as a laudable move to internationalize the project: equally, the fall from 84% to 68% could indicate the relative decline of palaeontology in Britain over the past 25 years (indeed, many of the British contributors to the present edition, 18 of the 61) are graduate students, postdoctoral scientists or essentially unemployed.

RATIONALE

To many palaeobiologists, of course, this kind of enterprise is highly suspect. The reasons for this view are not hard to find. For example, it will be possible for experts to criticize nearly every entry since the authors have had to make difficult decisions concerning which taxa to include in a family and which to exclude, how to deal with questionable and incomplete material, how to treat specimens of uncertain age, and how to divide up the families. However, the scope of this publication has allowed authors to comment on all of these kinds of complex issues. Hence, users of the data will be able to decide how to code the information, whether to include families represented by single species or not, how to deal with incomplete and poorly defined early records, how to interpret uncertain stratigraphical assignments and so on.

One of these problems may be insurmountable for many critics: the validity of families, or indeed of any other higher taxon. How are families to be determined and how are they to be rendered comparable between bacteria and mammals, or between trilobites and birds? There is no counter-argument other than practicality. Our view has been that, if it is worth studying large-scale evolutionary patterns, palaeobiogeographical distributions, and other macro-evolutionary phenomena, one has to have some raw data to work with. Better to have a 1993 database, shot through with errors as it may be, than to continue to use a 1967 listing *faute de mieux*. The critics might have been partially disarmed by a generic-level listing, or even a species-level listing, but these would have entailed other kinds of scientific problems, as well as the practical ones of finding authors with the stamina to complete the task, and a publisher with the generosity to deal with such a monster.

There have also been criticisms that the stratigraphical stage (or epoch for the Precambrian, Cambrian, Ordovician, Silurian, Carboniferous, Miocene and Pleistocene) is too crude and can be improved upon for many groups. While this is doubtless true for certain marine fossils used in biostratigraphy, it would have been impossible to go to substages or zones for most groups. Indeed, it was hard enough to achieve stage-level accuracy for many terrestrial groups! Hence, the family and the stage (or epoch, as noted) were chosen as the most appropriate working units for this volume. None the less, where possible, many authors have used stage-level terminology for the Palaeozoic and Cainozoic erathems.

DATA COMPILATION

The editor decided to follow broadly the chapter divisions used in *The Fossil Record* (1967), and to commission authors/editors who would oversee each major group. Each of these was to use their specialist knowledge of the phylum – or other major group – in question, to select and commission portions of the text, and then to compile the whole chapter, plugging gaps and providing an overview. The first letters inviting contributions went out in mid-1988, and several chapters were successfully allocated in this way.

As time went on, it became clear that it would not be possible to complete the book in such a simple fashion: in many cases, appropriate authors did not exist, or they had other commitments that prevented them from completing the work on time. Early in 1990, Chapman & Hall agreed to publish the book and, later that year, generous grants were received from the Linnean Society (administering the NERC Taxonomic Publications Grant), the Royal Society (a Scientific Publications Grant), and the Palaeontological Association. This money was used to pay for the completion of certain chapters and parts of chapters (1, 3–6, 8, 10, 11, 13–16, 18–21, 28, 29, 42, 45) that otherwise could not
<table>
<thead>
<tr>
<th>Eono-them</th>
<th>Era-them</th>
<th>Sub-erathem, System, Sub-system</th>
<th>Series</th>
<th>Stage</th>
<th>Alternative stage Designations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quaternary</td>
<td>Holocene</td>
<td>HOL</td>
<td>Pliocene</td>
<td>PLE</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Pliocene</td>
<td>PLI</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Zancian</td>
<td>ZAN</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Messinian</td>
<td>MES</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Serravallian</td>
<td>SRV</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Langhian</td>
<td>LAN</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Burdigalian</td>
<td>BUR</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Aquitanian</td>
<td>AOT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Chattian</td>
<td>CHT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Rupelian</td>
<td>RUP</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Priabonian</td>
<td>PRB</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Bartonian</td>
<td>BRT</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Lutetian</td>
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<td>Quaternary</td>
<td>Holocene</td>
<td>Ypresian</td>
<td>YPR</td>
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<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Thanetian</td>
<td>THA</td>
<td></td>
</tr>
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<td></td>
<td>Quaternary</td>
<td>Holocene</td>
<td>Danian</td>
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Fig. P.1 The geological time scale used in *The Fossil Record*, Permian to Recent.
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Fig. P.1 The geological time scale used in *The Fossil Record 2*, Ordovician to Carboniferous.
have been produced in time, and to assist with editorial costs.

Chapman & Hall paid for the production of the stratigraphical range charts, which were generated during 1991 and early 1992 from authors' texts by Ms Rachael Walker in Bristol, using the graphics software Canvas 2.1 on a Macintosh personal computer. The diagrams are on disc, and may be updated readily, or adapted for various uses.

**STRATIGRAPHICAL FRAMEWORK AND OTHER STANDARDS USED**

Authors were invited to use any stratigraphical scheme that they thought was appropriate, but to use those summarized in Harland et al. (1990) if they could. This was an attempt to standardize the stratigraphical periods and stages used, as well as the abbreviations, and of course involved no consideration of the exact ages in millions of years given by those authors. The relevant features of the stratigraphical scheme of Harland et al. (1990) are summarized in Fig. P.1, and some equivalent divisions of time used by some authors are also given. In addition, authors who used different schemes from the Harland et al. (1990) standard, have commented on this in their chapter introductions.

Other standards used in recording data are broadly as they were in the 1967 *Fossil Record* (see pp. 158–9 therein). The First and Last records of each family are given, based on published and unpublished data. Living families are indicated as Extant, although families with no fossil record are not always listed. For some groups, Intervening records are indicated, at stage level, to allow assessment of the gappiness (proportion of stages lacking fossils to stages with fossils) of the ranges quoted. Indeed, the measure of gappiness of intervening values can help to assess the likelihood of accuracy of the first and last records on a range bar, since error bars may be calculated (Strauss and Sadler, 1989).

An attempt was made to minimize the number of bibliographic references listed for each chapter, by referring to recent monographs and volumes of the *Treatise on Invertebrate Paleontology*, where available, for range records. Fuller documentation is presented where no such overview publications exist. Authors and dates of establishment of all taxa are also noted fairly completely, another great advance over the 1967 edition, but bibliographic data are not given for such authorships.

In the diagrams, all families, or family-equivalent taxa, are represented as noted by the author(s) of the chapters. Certain ranges are indicated by a solid line, and uncertain range terminations by a dashed line. No attempt is made in the charts to indicate gaps in the intervening range. Taxa with no fossil representatives are not shown on the charts.

In view of the shifting geography of eastern Europe and the former Soviet Union, the following terms are used throughout: 'former USSR', 'former Yugoslavia' and 'Germany'. Former Soviet regions revert to their former titles, e.g. 'Buryat SSR' becomes 'Buryatia'.
Fig. P.2 The number of families per chapter of *The Fossil Record* 2, compared to numbers in *The Fossil Record* (1967). Chapter 21 is Insecta.
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<td>27. Graptolithina</td>
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<td>31. Agnatha</td>
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<td>36. Osteichthyes: Teleostei</td>
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<td>39. Reptilia</td>
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<td>45. Magnoliophyta ('Angiospermae')</td>
<td>167</td>
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**TOTALS** 2924 7186

Fig. P.3 Numbers of families recorded in the 1967 and 1993 editions of *The Fossil Record*. Key: *some taxa not divided to family level; **most taxa not divided to family level.
CHANGES SINCE 1967

Since 1967, a number of factors have combined to enhance the value of an updated second edition. Firstly, many more palaeobiologists than in 1967 are involved in research that requires accurate documentation of the fossil record, especially in the study of patterns of diversification, mass extinction, rates of evolution, clade shapes, completeness measures and phylogenetic bases of the data. Secondly, of course, much work has been done that will tend to change the nature of the family entries: systematic revisions of major groups, reassessments of numerous ‘first’ and ‘last’ taxa, discoveries of new fossils and revisions of stratigraphical schemes. All of these have resulted in a remarkable change in the database within 25 years: for example, Maxwell and Benton (1990) found that 416 out of 718 families of tetrapods (58%) listed in The Fossil Record (1967) had changed their durations in a 1987 compilation of data, and indeed most of these 416 changed families (57%) showed increased durations. Comparison of the independently compiled lists of marine animal families produced by Sepkoski (1982, 1992) shows similar large-scale changes in the database, here in the course of only ten years. It will be interesting to compare the 1967 and 1992 databases in similar ways in order to discover how much, and why, they have changed.

The Figs P.2 and P.3 indicate the numbers of families, or family-level equivalents identified for each major group in the 1967 and the 1992 editions of The Fossil Record. The overall increase in numbers of families listed, from 2924 to 7186, superficially reflects the effects of new finds and some taxonomic splitting in the intervening 25 years. However, much of the increase is a result of the fact that more groups in 1967 were covered at ordinal level than in the present volume. Also, of course, in many cases, families have been lost as a result of taxonomic revisions. Hence, there has been a particular advance in the coverage of the sponges, molluscs, annelids, arthropods (especially insects, chelicerates and crustaceans), brachiopods, bryozoans, echinoderms, conodonts, vertebrates and angiosperms. Much of the increase in taxon numbers within these groups has been the result of the more consistent effort to identify families in 1992 than in 1967. However, for some groups, such as insects, chelicerates, teleosts and angiosperms, detailed documentation had not been attempted previously in the way presented here. The composition of family lists for certain groups has also been heavily affected by the introduction of a cladistic methodology. Classifications of vertebrates and of some major groups of sponges, gastropods, arthropods, echinoderms and angiosperms in the present work are wholly, or largely, cladistic. This should mean that most, or all, taxa listed in those chapters are monophyletic; further details are given in individual chapter introductions.

Features of The Fossil Record 2 (1993) that represent advances over the 1967 version include, in summary:

1. consistent family-level coverage for all groups, except Monera;
2. consistent coverage to the stratigraphical stage level for most records, epoch level for most Precambrian, Cambrian, Ordovician, Silurian, Carboniferous, Miocene and Pliocene, records. For some groups, such as ammonoids, substage designations are given;
3. presentation of ‘Intervening’ data for many groups;
4. standardized presentation of details for ‘First’ and ‘Last’ records;
5. monophyletic, cladistically determined, families within many groups.

REFERENCES

Cordosphaeridium cantharellum (Brosius) Gocht, 1969, the benthic resting cyst of a planktonic dinoflagellate from the Bisciaro Formation (Miocene, Burdigalian) of Marche, Italy. The youngest member of the Cordosphaeridium Complex. The central body measures about 50μm across, and the specimen is viewed in mid-focus. Photograph courtesy of A. J. Powell.
Monera (Bacteria, Blue-Green Algae)

D. Edwards

Perhaps the most momentous developments in palaeontology since the publication of the first Fossil Record relate to direct evidence for life in the Precambrian. More than three hundred publications describing micro-organisms from the Archaean and Proterozoic have now been published. The time interval has also seen a biological revolution in the acceptance of the fundamental division of living organisms at the cellular level into eukaryotes and prokaryotes. This has resulted in major changes in classification. Thus in 1967, fossil bacteria from Phanerozoic and only two Precambrian occurrences were merely listed below an introduction citing the problems relating to the compilation. The Schizophyceae (oxygen-producing blue-green algae) were included in the algae, whereas here they are reported under Cyanobacteria.

In the euphoria of the first phases of research into Precambrian biotas there was a tendency to assign the microfossils, particularly of putative cyanobacteria, uncritically to extant families, in some cases incorporating into their names those of extant genera. A somewhat more unbiased approach was employed on the earliest eukaryotes. However, increasing awareness among palaeontologists of the striking morphological resemblances between various groups of prokaryotes, e.g. between sulphur and iron bacteria and oscillatoracean cyanobacteria resulting from their simplicity of organization, plus the realization of the enormous metabolic versatility of the prokaryotes (Knoll and Bauld, 1989) and its role in their classification, have necessitated a more cautious approach. With the exception of the more highly differentiated cyanobacteria, the morphology of prokaryotes is of limited value in inferring affinity and physiology. Such caution has been combined with a considerably heightened scepticism towards claims of biogenicity (see e.g. terminology suggested by Hofmann, 1972), and the appreciation that, while the records documented below demonstrate the presence of a taxon at that time, because of sampling deficiencies it may well have existed earlier. Further, more detailed examination of assemblages and comparisons with modern cultures have shown that some taxa may be based on features produced by post mortem degradation of cells and on mucilage sheaths. The analyses presented here reflect these changes of attitude, and are based on re-evaluations of Schopf and Walter (1983) on Archaean records and Mendelson and Schopf (1992) from c. 3500 Proterozoic and earliest Cambrian occurrences gleaned from 316 papers published before August 1988. DE is exceedingly grateful to these authors for access to this information, and to Andrew Knoll for further advice. However it should be appreciated that this section has been compiled by a non-expert and readers are advised to consult the primary sources.

The earliest generally accepted evidence for life on this planet comes from carbonaceous stromatolitic sediments in the Warrawoona Group, North Pole Dome, Western Australia (3.3–3.5 Ga) and from cherts in the Onverwacht Group, Barberton Mountain Land, South Africa (3.5 Ga). The status of spheroidal and filamentous structures associated with the stromatolites was assessed by Schopf and Walter (1983) for the Australian records and more recently by Schopf and Packer (1987) on the discovery of new fossils. For the South African records, although the biogenicity of the spheroids can be debated (Knoll and Barghoorn, 1977; Schopf and Walter, 1983), abundant filaments (of two kinds) are far more compelling evidence for life in the early Archaean (Walsh and Lowe, 1985).

Kingdom MONERA Haeckel, 1866 (see Fig. 1.1)
Phylum BACTERIA sensu lato
Subphylum COCCOID FORMS PC. (HUR)-Rec. Mar./FW

First: 'coccoid microfossils' (Lanier, 1986), Monte Cristo Formation, Chuniespoort Group, Transvaal Supergroup, South Africa (c. 2330 Ma).
Extant

Comments: Certain spheroids in the Archaean are assessed as dubiofossils by Schopf and Walter (1983), these authors finding no unequivocal evidence for coccoid micro-
organisms in that period. Their coccolid dubiofossils (i.e. possibilities) include some of the smaller carbonaceous spheroids (cf. Archaeosphaeroides barbertonensis) described by Muir and Grant (1976) from carbonaceous cherts and shales in the Onverwacht Group (3.540 ± 0.030 Ga) and A. barbertonensis from the Fig Tree Group (?3.5–3.1 Ga). Spheres called Isuasphaera isua Pflug from the Isua Supracrustal Belt, southwestern Greenland (3.770 ± 0.042 Ga) and described as yeast-like micro-organisms (e.g. Pflug and Jaeschke-Boyer, 1979) are considered to be non-fossils being interpreted as 'metamorphically produced multi-phase inclusions possibly containing organic fluids'.

**Subphylum ELLIPSOIDAL FORMS**

**P.C. (FHUR)–Rec. Mar./FW**

First: ellipsoidal (rod-shaped) microfossils (Lanier, 1986), Monte Cristo Formation, South Africa (c. 2330 Ma). **Extant Comments**: The earliest colonial ellipsoidal bacteria are described together with solitary examples as Eosynechococcus moorei by Hofmann (1976) in an extensive assemblage of prokaryotes from the Kasegalik Formation, Belcher Group, Canada. Rod-shaped structures (Eobacterium isolatum) from the Onverwacht Group (SA) examined ultrastructurally by Barghoorn and Schopf are now considered to be modern.
contaminants of preparation and provide a good example of the pitfalls when researching into fossil bacteria.

**Subphylum FILAMENTOUS FORMS**

PC (ANI) – Rec. Mar./FW

**First:** *Bioticatenoides sphaerula* Schopf, 1968 (septate filamentous bacterium) Kasegalik Formation, Belcher Group, Canada (c. 2150 Ma) (Schopf, 1968; Hofmann, 1976).

**Comments:** The oldest unequivocal fossils accepted by Schopf and Walter (1983) and called ‘filamentous Archean micro-organisms’ occur in the carbonaceous stromatolitic cherts in the Warrawoona Group, North Pole Dome, Western Australia. They were originally described as ‘filamentous fossil bacteria’ by Awramik et al. (1983), but it is also possible that they are partially degraded cyanobacterial filaments (as indeed may be the first record!). More recently collected cherts of undoubted provenance (i.e. Apex Basalt, 3.3 Ga) contain clasts with sinuous unbranched filaments (c. 3.0 μm diameter, 30–40 μm long) composed of uniseriate more-or-less equant cells. These are compared with the trichomes of extinct and extant prokaryotes with modern analogues among the oscilatoraceans, beggiatoaceans and chloroflexaceans (Schopf and Packer, 1987). Groups of radiating filaments from the same locality (Awramik et al., 1983) were assessed as dubiofossils, while similar structures (*Eoastrion*) in the
Gunflint Formation were accepted as prokaryotes, but of uncertain affinity (Mendelson and Schopf, 1992).

**Phylum CYANOBACTERIA** Stanier et al., 1978

**Order CHROOCOCCALES** Wettstein, 1924

F. CHROOCOCCACEAE Nágeli, 1849 (solitary fossils) PC. (ANI)—Rec. Mar./FW

**First:** *Huroniospora* sp. and type 2 of solitary coccoid bacteria in Hofmann and Jackson (1969), the latter determined as cf. *Leptoteichos* by Mendelson and Schopf (1992), Belcher Group, Canada (c. 2150 Ma).

**Extant**

F. CHROOCOCCACEAE (colonial) PC. (SWZ)—Rec. Mar./FW

**First:** Carbonaceous or iron-stained three-dimensionally preserved colonies of few to many sheath-enclosed spheroidal cells (Schopf and Packer, 1987), Towers Formation (3.4 Ga), Warrawoona Group.

**Extant Comments:** Globular colonies contain cells in two size ranges, c. 8 μm and c. 21 μm diameter. The latter are enclosed within a multilamellated sheath, and this, together with their size, is strongly suggestive of chroococcacean affinity. The oldest chroococcacean prefixed by ‘?’ in Mendelson and Schopf is *Polyprosphaeridium bullatum* Timofeev, 1966 from the Ikabisk Formation, Siberia (c. 2200 Ma) (Timofeev et al., 1976) and the oldest unequivocal Proterozoic exoskeletal form *Favososphaeridium bothnicum* Timofeev, 1966 from the Bothnia Formation, Siberia (c. 1770 Ma). The earliest cuboidal colonial coccoid cyanobacteria, were described as *Eucapsis?* in Licari et al. (1969) and Licari and Cloud (1972) from the Paradise Creek Formation, Australia (c. 1650 Ma).

F. ENTOPHYSALIDACEAE Geitler, 1925 (colonial) PC. (ANI)—Rec. Mar./FW

**First:** *Eoentophysalis belcherensis* Hofmann, 1976 Kasegalik Formation (c. 2150 Ma), Belcher Supergroup, Hudson Bay, Canada.

**Extant**

**Order PLEUROCAPSALES** Geitler, 1925

F. PLEUROCAPSAEAE Geitler, 1925 PC. (STU)—Rec. Mar./FW

**First:** *Palaeotheurocapsa wopfneri* Knoll, 1975, Skillogalee Dolomite, Australia (770 Ma) (Knoll et al., 1975).

**Extant Comments:** Older possible colonial coccoid pleurocapsaleans are *P. kelleri* Krylov and Sergeev, 1987, in the Satka Formation, Eurasia (c. 1550 Ma) or *Myxomorpha janeceki* Muir, 1976 in Oehler (1978) from the Nathan Group, Balbirini Dolomite (c. 1483 Ma), Northern Territory which is interpreted as a putative dromocarpaeceae or pleurocapsalean colonial coccoid cyanobacterium. *Pleurocapsa?* sp. from the Kasegalik Formation, Belcher Supergroup (c. 2150 Ma) (Hofmann, 1975) would be the oldest representative if the assignment is correct.

F. HYELLACEAE Borzi, 1914 PC. (ANI/BUZ)—Rec. Mar./FW

**First:** *Eothyella campbelliae* Zhang and Golubic, 1987, Dahongya Formation, Hebei Province, China (c. 1650 Ma) (Zhang and Golubic, 1987).

**Extant Comments:** Far better-preserved endoliths of ooids (cf. *Hyella gigas*) were described by Green et al. (1988) from the Eleonore Bay Group, Greenland (c. 750 Ma).

F. DERMOCARPACEAE Geitler, 1925 PC. (YUR)—Rec. Mar./FW


**Extant Comments:** *P. bipartitus* was recorded from the c. 750 Ma Eleonore Bay Group by Green et al. (1987) and identified as a benthic probable pleurocapsalean, producing a unidirectional secretion of extracellular mucilage.

**Order NOSTOCALES** Geitler, 1925

F. OSCILLATORIACEAE (S. F. Gray) Dumortier ex Kirchner, 1898 PC. (HUR)—Rec. Mar./FW

**First:** *Siphonophycus transvaalense* Beukes et al. (1987), Gamooha Formation, Ghaap Group, Transvaal Supergroup (2450–2250 Ma) (Klein et al., 1987).

**Extant Intervening:** Throughout Precambrian, but rare in Phanerozoic.

**Comments:** Mainly recorded as tubular sheaths. Oscillatoriaeans are important mat-forming organisms in stromatolites. However, there is no direct unequivocal evidence that they were involved in the stromatolitic sedimentary structures recorded from the Archaea.

F. NOSTOCAEAE Dumortier ex Engler, 1892 PC. (KAS)—Rec. Mar./FW

**First:** *Anaabaenium johnsonii* Schopf, 1968, *Veteranostocales* Schopf and Blacic, 1971, Bitter Springs Formation, Australia (c. 850 Ma) are both considered possible nostocaceans by Mendelson and Schopf (1992) (Schopf, 1968; Schopf and Blacic, 1971).

**Extant**

F. RIVULARIACEAE Kützing, ex Bornet and Flahault, 1887 PC. (KAR)—Rec. Mar./FW

**First:** *Caudiculophycus acuminatus* Schopf and Blacic, 1971 in Jankanskas (1982), Podinzer Formation, former USSR (c. 925 Ma) is considered to be a possible member. **Extant Comments:** This species, together with *C. rivularioides* Schopf, 1968 was first described from the Bitter Springs Formation, and again both are considered possible rivulariaceans. Knoll (1981) described *C. rivularioides* as sheathless trichomes of oscillatorian cyanobacteria, emphasizing problems of post-mortem degradation in recognition of affinity.

F. SCYTONEMATALES Kützing, 1843, ex Bornet and Flahault, 1886 D. (PRRA)—Rec. FW/Mar.

**First:** *Rhyniella vermiformis* Croft and George (1959) Rhynie Chert, Scotland; Croft and George (1966) Rhynie Chert, Scotland. Data from Tappan (1980). Extant

**Comments:** Most other records are in the Tertiary (earliest in Oligocene *Epivalvia* and *Encrusta* (Daley, 1975). However, Precambrian *Palaeoeyctonema* (Edhorn, 1975) is not accepted by Mendelson and Schopf (1992).

**Order STIGONEMATALES** Geitler, 1925

F. STIGONEMATAEAE Hassall, 1845 D. (PRRA)—Rec. FW/Mar.

**First:** *Langiella scourfieldi* Croft and George (1959); *Kástioniella frischii* Croft and George (1959), Rhynie Chert, Scotland.
REFERENCES


Although convincing examples of Precambrian fungi are not known, examples of the group can be documented throughout the rest of the geological record. Owing to the complexities of many fungal life histories, features used in taxonomy that cannot be demonstrated in fossils, and the often poor level of preservation, some of the earliest reports at the level of order and family were in error. By far the best record of the group is known from permineralized remains or epiphyllous types in which a sufficient suite of characters makes identification more reliable. In some instances, fungal spores have been useful in documenting some groups. New reports of fossil fungi are continually expanding the geological range of modern families, while at the same time demonstrating the existence of groups for which there are no modern analogues. In recent years, emphasis in palaeomycology has also centred on a variety of fungal interactions that can be demonstrated in the fossil record (Stubblefield and Taylor, 1988). Documenting interactions and fungal evolution will rely not only on past reports of fungi such as those listed by Tiffney and Barghoorn (1974), but also the discovery of additional forms from throughout the geological column (Taylor et al. 1992a,b,c).

The distribution of fungi in time and space, based on fossil evidence, together with rapidly accumulating molecular data, will provide the continuing impetus to characterize more accurately the phylogeny of the group.

### Class HYPHOCHYTRIDIOMYCETES

*Order HYPHOCHYTRIALES* C. (u.)-Rec. Terr.

**First:** *Milleromyces rhyniensis* (Taylor, Hass and Remy, 1992). (PRA). Together with *Lyonomyces pyriformis* and *Krispiromyces discoides* these aquatic fungi occur in the Rhynie Chert associated with the green alga *Palaeonitella*.

### Class CHYTRIDIOMYCETES


**First:** *Horneophyton lignieri* (Illman, 1984), Rhynie Chert bed, Aberdeenshire, Scotland, UK. This report is based on zoosporic fungal sporangia inside trilete spores of the taxon. Comparison is also made with oomycetes and hyphochytridiomycetes.

**Extant**

**Intervening:** VRK.


**First:** *Pleotrichelus askaulos* Bradley, 1967, Green River Formation, Wyoming, USA. Holocarpic zoosporangium with discharge tubes.

**Extant**


**First:** *Entophlyctis willoughbyi* Bradley, 1967, Green River Formation, Wyoming, USA. Sporangia with zoospore cyst and germ tube.

**Extant**

### Class OOMYCETES

*Order SAPROLEGNIALES* S. (GLE/GOR)-Rec. Terr.

**First:** *Palaeachlya perforans* (Duncan, 1876). Believed to have parasitized the coral *Goniophyllum pyramideale*. **Extant**

**Intervening:** SIG, C. (u.), T.

*Order PERONOSPORALES* C. (MOS)-Rec. Terr.

**First:** Unnamed (Stidd and Cosentino, 1975), Des Moines Series, Oskaloosa, Iowa, USA. Oogonia and disrupted tissues in the seed *Nucellangium* that are morphologically similar to the symptoms caused by the extant fungus *Albugo*. **Extant**

**Intervening:** RUP/CHT.

### Division AMASTIGOMYCOTA

*Class ZYGOMYCETES*

*Order MUCORALES*

**First:** *Paleobasidiospora taugourdeaui* Locquin, 1983. This new family was recently proposed to include the large number of vesicles and chlamydoospores found throughout...
the geological column that morphologically resemble the endogonaceous genus *Glomus* (Pirozynski and Dalpé, 1989). Included in this family are the chlamydospores from the Lower Devonian Rhynie Chert (Kidston and Lang, 1921) described as *Palaeomyces*, and numerous Carboniferous representatives termed *Glomus*-like (Wagner and Taylor, 1982). It is not known whether these fungi were biotrophic symbiotic endophytes. The most convincing evidence of endophytic mycorrhizal fungi come from the Triassic in the form of arbuscles in root cells (Stubblefield et al., 1987a,b). Also included in this family is the modern genus *Sclerocystis* which also dates from the Triassic (Stubblefield et al., 1987a,b). Some of the taxa placed in this family have previously been included within the Mucoraceae (Tiffney and Barghoorn, 1974). Extant

**Class TRICHOYMYCETES**

**Order ECCRINALES** Tr. (ANS) Terr.

**First and Last:** Unnamed (White and Taylor, 1989), Fremouw Formation, central Transantarctic Mountains,
Fig. 2.1

Antarctica. Fragment of what is interpreted as arthropod cuticle containing numerous fungal thalli and spores.

*Subdivision* ASCOMYCOTINA

*Class* LOCULOASCOMYCETES

*Order* DOTHIDEALES


First: Numerous genera of spores, hyphae and fructifications on various angiosperm leaves (Dilcher, 1965; Selkirk, 1974), Claiborne Formation, USA.  
Intervening: NG.

F. TRICHOPELTACEAE K. (MAA) Terr.

First: *Trichopeltinites* sp., Stromata (Sweet and Kalgutkar, 1989), Canada. Spores and hyphae assigned to this genus also reported (Dilcher, 1965; Selkirk, 1974).  
Extant


First: *Stomiopeltites cretacea* Alvin and Muir, 1976, Wealden, Isle of Wight, England, UK. Known from thyrothecia and hyphae.  
Last: *Dictyotopileos* sp., AQT–LAN1 (Selkirk, 1974).

*Class* PLECTOMYCETES

*Order* EROTIALES


First: *Cryptocolax clarnensis* Scott, 1956, Clarino Formation, Oregon, USA. Cleistothecia bearing asci and ascospores in dicotyledenous wood. A second species, *C. parvular*, also reported.  
Extant
Class PYRENOMYCETES
Order MELIOLALES
First: Meliolites dilcherii Daghlian, 1978, Rockdale Formation, Texas, USA. Known from hyphae, spores and perithecia. Extant
Intervening: T.

First: Unnamed (Currah and Stockey, 1991), British Columbia, Canada, based on spores that morphologically resemble teliospores of the extant genus Panus. Extant

Order ERYsiphaLES
F. ERYsipHACEAE T. (Ng.)–Rec. Terr.
First: ?Erysipites (Pampaloni, 1902), formation unknown, Neogene.

Order SPHAERIALES
F. HYPOcreaceae T. (Ng.)–Rec. Terr.
First: Polystigmites sp. (Massalongo and Scarabelli, 1858–1859), details unknown. Extant

Class DISCOMycetes
Order PEZIZALES
First: Pezizites sp. (Ettingshausen, 1868), details unknown. Extant

Subdivision BASIDiomyCOTINA
Class TELiomyCETES
First: Unnamed (Sherwood-Pike, 1988), Clarkia Locality, Idaho and Oregon, USA. Large helicoid spores that are similar to the extant aquatic hyphomycetes Helicoon plurisepatum and Helicodendron giganteum. Also numerous helicoid spores from the Upper Cretaceous might be included in this form class.

Class HYMENOMycetes
Order APHYLLOPHораLES
F. POLYPORACEAE J. (DOG/MLM)–Rec. Terr.
First: Phelinites digiusto Singer and Archangelsky, 1958, Matilda Formation, Patagonia, Argentina. Extant

Intervening: T.

Class GASTEROMycetes
Order Lycoperdаles T. (Ng.)–Rec. Terr.
First: Geasterites florissantensis Cockerell, 1908, Colorado, USA. Extant

Comments: Unnamed, branched and septate filaments with terminal and intercalary chlamydospores, from the Blackston Formation (FAM), Indiana, USA, are associated with decay patterns similar to those produced by modern white-rot fungi. Similar symptoms and clamp connections are seen in Permian and Triassic woods from Antarctica (Stubblefield and Taylor, 1986). Extant

F. UNNAMED C. (MOS) Terr.
First and Last: Palaeancistrus martini Dennis, 1970, Carbondale Formation, Illinois, USA. Named for a mycelium with clamp connections and chlamydospores, and compared with extant genus Panus. Extant

Form UNNAMED C. (MOS) Terr.
First and Last: Palaeosclerotium pusillum (Rothwell, 1972), Carbondale Formation, Illinois, USA. Cleistothecium-like structure with asci containing spores and hyphae with clamp connections (Dennis, 1976). Interpretations include: a fungus intermediate between ascomycete and basidiomycete; ascomycete parasitized by a basidiomycete; ascomycete closely related to the Eurotiales (Singer, 1977).

Form SUBDIVISION DEUTEROMycOTINA
Class UNKNOWN
F. UNNAMED S. (GOR/LDF)–Rec. Terr.
First: Unnamed (Sherwood-Pike and Gray, 1985), Burgsvik Sandstone, Gotland, Sweden. Multicellate spores, some with scar suggestive of those found in conidial fungi with holoblastic development; branched hyphae that resemble a conidiophore also suggest Ascomycetes. Extant

Intervening: Mesozonic, Cainozoic.

Form Class HYPhomycetes
First: Unnamed (Sherwood-Pike, 1988), Clarkia Locality, Idaho and Oregon, USA. Large helicoid spores that are similar to the extant aquatic hyphomycetes Helicoon plurisepatum and Helicodendron giganteum. Also numerous helicoid spores from the Upper Cretaceous might be included in this form class.

REFERENCES


Kidston, R. and Lang, W. H. (1921) Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire,


Recent major changes in the classification of protists involve the photosynthesizing, non-embryophyte, non-archegoniate, green plants previously grouped as the algae. In the ‘five kingdoms’ approach, they were included along with unicellular animals in the Protocista or the Protista, but recent research based particularly on molecular phylogenies (e.g. rRNA) (Fernholm et al., 1989) has prompted a reassessment by protozoologists (see Chapter 4) and the incorporation of certain groups, e.g. the dinoflagellates into the Protozoa, a subkingdom of Animalia. In that there as yet appears to be no consensus on the treatment of the former photosynthesizing protists, a more traditional scheme is adopted here, considering them as phyla within the eukaryotes. The classification is based on Round (1973, 1980), as modified from Engler (1954) and includes twelve phyla in all, subdivision being based on pigments present, type of food reserves, cell and flagellum ultrastructure, type of cell division and life cycles as well as morphology.

Recognition of these organisms in the fossil record, in the absence of biochemical and ultrastructural information and with a dearth of anatomical data, is often impossible. Exceptions are calcified forms and phytoplankton with resilient walls. Problems are compounded by convergence in evolutionary trends in organization (e.g. coccoid to filamentous forms) and in gross morphology in frondiose thalli. Thus it may be difficult to identify filaments even when preserved as permineralizations, and impossible to assign coalified compressions differentiated into holdfast, stipe and blade to reds, browns or even greens in the Palaeozoic (see e.g. Fry and Banks, 1955; Fry, 1983; Leary, 1986). Particularly intriguing are carbonaceous residues or impressions of presumed metaphytes in Precambrian rocks. The oldest structured carbonaceous filaments were described by Hofmann and Chen (1981) from the 1800Ma Changcheng System, China, while ribbon-like structures in the 1300Ma Belt Supergroup, Montana, were compared by Walter et al. (1976) with red, green and brown algae. It is, however, possible that they are aggregated sheaths of bacteria, an interpretation recently applied to the strap-shaped vendotaenids, common in the late Proterozoic (570–650 Ma) and considered to be allied to the Phaeophyta (Gnilovskaya, 1983). Vidal (1989) interprets them as the abandoned sheaths of sulphide-oxidizing organotrophic beggiatoacean bacteria. More compelling evidence for multicellular thallophytes derives from the longfengshaniids and tawuiids, widespread in the mid to late Proterozoic (1000 to 700 Ma) and splendidly illustrated in the Middle Proterozoic Little Dal macrobiota, Canada (Hofmann, 1985).

Coverage here is patchy, concentrating on unicellular forms with resilient walls (e.g. Dinophyta, Bacillariophyta, Haptophyta) or those with skeletons (e.g. Charophyta, calcified algae). Major calcified groups are indicated by*, and non-calcified members (if any) have usually not been included. For the remainder of the ‘algae’, the reader is referred to the original, The Fossil Record, although additional information on permineralized material of particularly early members of a group is given.

The systematic divisions used in this chapter cut across some commonly used micropalaeontological terms. Hence, the calcareous nannoplankton include the coccoliths (Phylum Haptophyta), some calcareous dinoflagellates (Phylum Dinophyta/Division Pyrrhophyta), and some Incertae sedis forms. Other well-known groups, such as the acritarchs, are of uncertain taxonomic position.

Contributions to this chapter were as follows: Chlorophyta (D. Edwards and R. Riding), Charophyta (M. Feist and N. Grambast-Fessard), Haptophyta (P. R. Bown and L. T. Gallagher), Bacillariophyta (J. G. Baldauf), Euglenophyta and Prasinophyta (M. B. Hart), Dinophyta/Pyrrhophyta (A. J. Powell), Acritarcha (K. J. Dorning), Rhodophyta (D. Edwards and R. Riding), Incertae sedis (P. R. Bown and L. T. Gallagher).

Acknowledgements – RR is indebted to the following colleagues for helpful advice: Juan Carlos Braga on corallines, Esmail Moussavian on corallines and peyssoneliaceans, and Andrey Zhuravlev on receptaculitids. KJD thanks S. G. Molyneux for assistance with the acritarchs.
**Fig. 3.1**

**Phylum** CHLOROPHYTA Pascher, 1914  
(see Fig. 3.1)

**Class** CHLOROPHYCEAE Kützing, 1833

**Order** CHLOROCOCCALES Marchand, 1985  
*orth. mut.* Pascher 1915  
P. C. (RIF)–Rec. FW/Mar.

This group probably includes the first coccoid green algae, possibly even the earliest eukaryotes, but unequivocal identification in the Precambrian is unlikely to be achieved. Thus, for example, *Carosphaeroides pristina* and *C. tetras* from the 850 Ma Bitter Springs Formation, Australia, are described as either coccoid algae of chlorophycean affinity or cyanobacterial, as are the coeval *Latistphaera wrightii* Licari, 1978 from the Pahrump Group, Beck Spring Dolomite, California, *Glenobotrydion majorinum* Schopf and Blacic, from c. 740 Ma Min’yar Formation, former USSR, and an unnamed diverse assemblage of solitary coccoids from c. 750 Ma Chichkan Formation, former USSR (Schopf et al., 1977). The last two records are also compared with rhodophytes, as are the putatively meiotically produced ?spores of *Ambiguaspora parula* Volkova, 1976 from the 560 Ma Kotlin Formation, former USSR. The earliest botryococcoids are possibly the colonies described by Mendelson and Schopf (1992) as *Pila*-like colonial algae from the c. 615 Ma, Post-Spilitic Group, Czechoslovakia (Konzalova, 1973). Knoll et al. (1991) argued that there is reasonable, if not compelling, evidence to use the name *Myxococcoides chlorelloidea* for coccoids in the Neo-proterozoic Draken Conglomerate Formation, Spitsbergen.

**Extant**

**Order** ULOTTRICHALES Borzi, 1895

*F. ULOTTRICHACEAE* Kützing *orth. mut.* Haulk, 1883  
P. (?PRA)–Rec. FW

**Comment:** Record is based on silicified filaments and attribution to the Ulotrichaceae on their general morphology, the typical chloroplasts not being preserved in the mat-like filaments. A similar reasoning was also used in naming filaments with relatively broad cells from an Upper Devonian chert as *Palaeogeminella folkii* Fairchild et al., 1979. *Archaeoellipsoides conjunctivus* Zhang, 1985 from the c. 1325 Ma Wumishan Formation, China, is described as a 'broad septate (ulotrichalean?) filament with elongate cells' in Mendelson and Schopf (1992).

**Order CHAETOPHORALES** West, 1904
PC. (RIF)—Rec. FW/Mar.

Butterfield *et al.* (1988) in a preliminary account of an Upper Riphean (700–800 Ma) biota from the Svanbergfjellet Formation, found a close structural analogue for some unnamed, repeatedly branched, non-cellular fibroids in the holdfasts of certain heterotrichous chaetophoraleans.

**Extant**

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<td>CHLOROPHYTA</td>
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<td>2. Ulotrichaceae</td>
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<td>3. Order CHAETOPHORALES</td>
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<td>29. Coccolithaceae</td>
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<td>36. Podorhabdaceae</td>
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<td>37. Pontosphaeraceae</td>
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<td>38. Prodiscosphaeraceae</td>
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**Class BRYOPSIDOPHYCEAE** Round, 1971

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**Fig. 3.1**
*Order DASYCLADALES Pascher, 1931


First: Possibly Yakutina aciculata (Korde, 1973), first recorded as *Siberiella aciculata* Korde, 1957 from the Middle Cambrian, Anga River, SE Siberia, former USSR (Korde 1957, p. 69, text-fig. 1). See Riding (1991, p. 327) for comments. Definitely *Rhabdoporella bacillum* Stolley, 1983, probably from the ‘Leptaena Limestone’, Upper Ordovician (also see Hoeg, 1932, p. 75).

Comment: The above records refer to strongly calcified forms. Weakly calcified representatives include *Primocorallina trentonensis* Whitfield, 1894 from the Middle Ordovician (Trenton Limestone) of New York, USA; and *Archeobatophora typa* Nitecki, 1976 from the Upper Ordovician (Richmondian) of Michigan, USA. Extant

*Order CAULERPALES Setchell, 1929

F. HALIMEDACEAE Hillis-Colinvaux, 1984
T. (Eoc./RUP)—Rec. Mar./FW


Order CLADOPHORALES West, 1904
PC. (KAR)—Rec. Mar./FW

First: In a preliminary account of a late Riphean (700–800 Ma) biota from the Svanbergfjellet Formation, Spitsbergen, Butterfield *et al.* (1988) compared some filamentous thalli of large cylindrical cells with distinctive thickened septal plates, and intercalary branching with cladophoralean greens (Ulvyophyceae).

Extant

Class ZYGNEMAPHYCEAE Round, 1971

Order ZYGNEMATALES Round, 1963


Extant

Intervening: Eoc. (Spirogyra: Wyoming, USA [FR]).

Comment: Earliest record is based on filaments preserved in chert.

Order DESMIDIALES Round, 1963


Extant

Comment: The record is based on single crescentic cells preserved in chert, which may be more realistically assigned to the acritarchs.

Class OEDOGONIOPHYCEAE Sarma, 1964

Order OEDOGONIALES Blackman and Tansley ex West, 1904

F. OEDOGONIACEAE (Thuret) de Bary, 1900 D. (EIF)—Rec. Mar./FW

First: *Paleoedogonium micrum* Baschnagel, 1966, Onondaga Formation, New York State, USA. Extant

Comment: Record based on silicified filaments with arguably typical apical cells.

Phylum CHAROPHYTA

Class CHAROPSIDA

Order SYCIDIALES Mädler, 1952

F. SYCIDIAEAE Karpinsky, in Peck, 1934 S. (PRD)—C. (?TOU)?Mar. FW

First: *Praesycidium siluricum* T. and A. Ishchenko, 1982, Shalsky Formation, Podolia, Ukraine, former USSR (Ishchenko and Ishchenko, 1982).

Last: *Sycidium foveatum* Peck, 1934 and *S. clathratum* Peck, 1934, Sylamore Formation, basal Mississippian, Missouri, USA.

F. CHOYANELLEAEEAE Grambast, 1962 D. (LOK—FAM) FW

First: *Choanella* sp. Li and Cai, 1978, Xiaishanchun and Xitun Formations, southern China.


F. PINNPUTAMENACEAE Z. Wang and Lu, 1980 D. (GIV) FW


Order TROCHILISCALS Mädler, 1952


First: *?Primochara calvata* Ishchenko and Saidakovski, 1975, Shalsky Formation, Podolia, Ukraine, former USSR.


Comment: *Primochara* is described as carbonaceous remains with an unknown number of dextral spiral cells, thus questionably assigned to the family (Feist and Grambast-Fessard, 1990).

Order CHARALES Lindley, 1836

F. EOCHARACEAE Grambast, 1959 D. (EIF/GIV) FW

First and Last: *Eochara wickendeni* Choquette, 1956, Elk Point Group, Alberta, Canada (Grambast, 1962).

F. PALEOCHARACEAE Pia, 1927 C. (BSK) FW

First and Last: *Paleochara acadica* Bell, 1922, lower part of Coal Measures, Nova Scotia, Canada (Peck and Eyer, 1963b).

F. POROCHARACEAE Grambast, 1962 C. (MOS)—T. (DAN) FW

**Last:** Porochara sp. (Feistella sp.?), Willow Creek Formation, Member E, Alberta, Canada.

**Comment:** Porocharaceae were the main components of the Triassic and Jurassic charophyte floras. They gave rise to the three post-Palaeozoic families.

F. **CLAVATORACEAE** Pia, 1927

J. (Oxfordian) – K. (Maastrichtian) FW


**Last:** Septorella ultima Grambast, 1971, Rognacian, Provence, France.

**Comment:** The main development of the family occurred during the early Cretaceous (Grambast, 1974).

F. **RASKYLLACEAE** Grambast, 1957

K. (Cretaceous) – T. (Aquitanian) FW

First: *Saportanella maslovi* Grambast, 1962, Begudien, Provence, France.

**Last:** Ranzieniella nitida Grambast, 1962, Calcaire blanc de l’Agenais, Paulhiac, Aquitaine, France.

**Comment:** The main genus is *Raskylia* Grambast, 1954, Eocene (Grambast, 1967).

F. **CHARACEAE** Agardh, 1824

J. (Oxfordian) – Rec. FW


**Extant**

**Comment:** Characeae played a very unobtrusive part during the Jurassic and Lower Cretaceous (Grambast, 1974). The number of genera and species increased, after the regression of Porocharaceae and Clavatoraceae, during the late Cretaceous (CMP–MAA). From the Miocene onward, the family regressed to the present state, with only six genera, which include all the extant charophyte species.

**Phylum** XANTHOPHYTA Polyansby and Hollerbach, 1951

**Order** VAUCHERIALES Bohlin, 1901

F. **VAUCHERIACEAE** T. (Miocene) – Rec. FW

First: *Vaucheria antiqua* Ludwig, Miocene Braunkohle (from Tappan, 1980).

**Extant**

**Comment:** Botryococcus, cited as the oldest genus in the first *Fossil Record*, is now considered to be a green alga. *Palaeovaucheria clavata* Hermann [Peck, 1981, Zürcher Formation, Bederysh Member, former USSR (c. 1000 Ma) is described as branched, septate *Vaucheria*-like, possibly eukaryotic filaments by Mendelson and Schopf (1992), while *Palaeosiphonella claudi* Li, 1978, Beck Spring Dolomite is interpreted as possibly a branching filamentous eukaryotic alga (as in original description) or a cyanobacterial sheath by Mendelson and Schopf. Butterfield et al. (1988) described some solitary filaments as resembling and possibly representing germinating zoosporae of filamentous protists with modern analogues including the xanthophycean algae from the 770–800 Ma Svanbergfjellet Formation, Spitsergenen.

**Phylum** HAPTOPHYTA Hibberd, 1972

**Division** PRYMNESIOPHYTA Hibberd, 1976

**Class** PRYMNESIOPHYCEAE Hibberd, 1976

**Order** COCCOSPHAERALES Parke and Dixon, 1976

The Order Coccosphaerales includes all coccolith-bearing prymnesiophytes. First and last occurrences have not been referred to a particular locality and horizon due to the vast amount of biostratigraphical data which exists in the literature. In the late Mesozoic and Cainozoic, in particular, many of the stratigraphical ranges are based upon data gathered by the Deep Sea Drilling Project and Ocean Drilling Program.

F. **ARKHANGELSKIELLACEAE** Bukry, 1969


First: *Acaenolithus vimineus* Black, 1973

**Last:** Arkhangelskiella cymoformis Vekshina, 1959, Upper Maastrichtian.

**Intervening:** CEN–CMP.

F. **BISCUTACEAE** Black, 1971


First: *Biscutum novum* (Goy, 1979), lower Pleistocene.

**Last:** *Biscutum harrisionii* (Varol, 1989).

**Intervening:** TOA–DAN.

F. **BRAARUDOSPHAERACEAE** Deflandre, 1947


First: *Braarudosphaera regularis* Black, 1973

**Extant**

**Intervening:** BER–HOL.

F. **CALCIOSELENIAE** Kamptner, 1927


First: *Scapholithus fossilis* Deflandre, 1954

**Extant**

**Intervening:** BRM–HOL.

**Comments:** Rare sporadic throughout its range.

F. **CALYCLUSACEAE** Noel, 1973

J. (Pleistocene) – Bajocian Mar.

First: *Calyculus crinum* Noel, 1973, lower Pleistocene.

**Last:** *Calyculus crinum* Noel, 1973, lower Bajocian.

**Intervening:** TOA, AAL.

F. **CALYPTROSPHAERACEAE** Boudreaux and Hay, 1969


First: *Anfractus harrisionii* Medd, 1979, lower Bathonian.

**Extant**

**Intervening:** CLV–HOL.

**Comment:** A strictly morphological taxonomic grouping which embraces coccolithophorids which secrete holococcoliths. Almost certainly includes taxa which also secrete heterococcoliths and are then included in other family groupings (for further explanation, see e.g. Mantow and Leedale, 1969; Wind and Wise, 1978).

F. **CERATOLITHACEAE** Norris, 1965


First: *Mesozoic Ceratolithina hamata* Martini, 1967

**Cainozoic Amaurolithus primus* (Bukry and Percival, 1971)

**Extant**

**F.** CERATOLITHACEAE **Norris, 1965**


First: *Mesozoic Ceratolithina hamata* Martini, 1967

**Cainozoic Amaurolithus primus* (Bukry and Percival, 1971)

**Extant**

**Intervening:** CEN–Maastrichtian; TOA–HOL.

**Comment:** The Mesozoic representatives of this extant family are comparable to, but distinct from, the Cainozoic
forms. An extremely long stratigraphical interval separates the ranges of the two groups (Perch-Nielsen, 1985).

**F. COCCOLITHACEAE Poche, 1913**


Intervening: THA–HOL.


Intervening: VLG–CMP.

**F. CRETARHABDACEAE Thierstein, 1973**


First: *Retecapsa incompta* Bown and Cooper, 1989, upper TOA.

Last: *Cretarhabdus crenulatus* Bramlette and Martini, 1964, upper MAA.

Intervening: AAL–CMP.

**F. EIFFELLITHACEAE Reinhardt, 1965**


Intervening: THA–HOL.
### Algae

| Period  | CRN | LAD | ANS | SCY | TAT | KAZ | UFI | KUN | ART | SAK | ASS | GZE | KAS | MOS | BSK | SPK | VIS | TOU | FAM | FRS | GIV | EIF | EMS | PRA | LOK | PRD | LUD | WEN | LLY | ASH | CRD | LLO | LLN | ARG | TRE | MER | STD | CRF | EDI | VAR | STU | RIF | ANI | HUR | RAN | SWZ | ISU | HDE |
|---------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|

**Fig. 3.2**

F. PARHABDOLITHACEAE Bown, 1987
Tr. (NOR) J. (BAJ) Mar.
Intervening: RHT–AAL.

F. PODORHABDACEAE Noel, 1965
First: *Axopodorhabdus atavus* Grun et al., 1974.

Intervening: TOA–CMP.

F. PONTOSPHAERACEAE Lemmermann, 1908
Intervening: YPR–HOL.

Extant
Comments: The Upper Cretaceous species *Prolatipatella multicarinata* (Gartner, 1968) has very similar morphology to Upper Cainozoic forms and is considered by some to be the first representative of this family.

F. PREDISCOSPHAERACEAE Rood et al., 1971
First: *Prediscosphaera* cf. *P. stoveri* Perch-Nielsen, 1968, upper APT.
Last: *Prediscosphaera grandis* Perch-Nielsen, 1979, upper MAA.
Intervening: CEN–CMP.
F. RHBADOSPHAERACEAE Lemmermann, 1908
First: *Rhagodiscus spinosus* (Deflandre and Fert, 1954), upper YPR.
Intervening: LUT–HOL.

F. RHAGODISCACEAE Hay, 1977
First: *Rhagodiscus asper* Stradner, 1963, upper TTH.
Last: *Rhagodiscus splendens* (Deflandre, 1953), upper MAA.
Intervening: BER–CMP.
F. STEPHANOLITHIACEAE Black, 1968
First: *Stradnerlithus catriatus* (Rood et al. 1973)?
Last: *Rotelapillus crenulatus* (Stover, 1966), upper MAA.
Intervening: TOA–CMP.
F. WATZNAUERIAEAE Rood et al., 1971
Intervening: TOA–MAA.
F. ZYGODISCACEAE Hay and Mohler, 1967
Tr. (NOR)–T. (RUP) Mar.
First: *Archaeozygodiscus koessensis* Bown, 1985, upper NOR.
Intervening: RHT–PRB.

Phylum BACCILLARIOPHYTA

Class BACCILLARIOPHYCEAE (Diatoms)
The diatom classification of Simonsen (1979), used here, subdivides the diatoms into two orders, five suborders, and twenty-one families, based predominantly on the presence, position and arrangement of various processes. Recent studies of Aaptian–Albian diatoms by Harwood and Gersonde (1990) and Gersonde and Harwood (1990), as well as others, indicate the need for revision of Simonsen’s classification, but revision awaits completion of additional studies. The recently proposed classification of Round et al. (1990) is not used here as detailed discussions are required to evaluate the merit of this classification.

Families are used here as discussed in Simonsen (1979) with the following exceptions: the genus *Azpeitia* Peragallo emend. Sims is included in the family Hemidiscaceae; the genera *Crucidenticula* Akiba and Yanagisawa, and *Neodenticula* Akiba and Yanagisawa are included in the family Nitzschiaeae; and numerous new genera proposed by Harwood and Gersonde (1990) and Gersonde and Harwood (1990) are included here because these new genera comprise one of the earliest diatom floras documented to date, but these genera are not assigned to a specific family until further analysis can be completed.

F. THALASSIOSIRACEAE Lebour, 1930 emend.
Hasle, 1973 K. (TUR)–Rec. Mar./FW
First: *Thalassiosira* Cleve (most likely *Thalassiosiropsis*), Turonian, Czechoslovakia (Wiesner, 1936) and France (Deflandre, 1941). Extant

F. MELOSIRACEAE Kutzning, 1844 J. (u.)–Rec. Mar./FW
First: *Stephanopyxis parentes?,* Upper Jurassic, western Siberia, former USSR (Vekshina, 1960): *Pyxidicula bollensis?,* Jurassic (Rothpletz, 1896). Extant

F. COSCINODISCACEAE Kutzning, 1844
K. (ALB)–Rec. Mar./FW
First: *Coscinodiscus* Ehrenberg, Albian clays of the Penza region, western Siberia, former USSR (Jouse, 1949). Extant

F. HEMIDISCACEAE Hendey, 1937 emend.
Simonsen, 1975 T. (PRB)–Rec. Mar./FW
First: *Azpeitia tuberculata* (Greivile) Sims (as *Coscinodiscus tuberculatus*), Oamaru Formation, South Island, New Zealand, Upper Eocene (Fryxell et al., 1986). *Azpeitia oligocenica* (Jouse) Sims recorded by Fenner (1977, 1981) as *Coscinodiscus oligocenicus* from Eocene and Oligocene sediments from the equatorial and South Atlantic (Sims et al., 1989). Extant

F. ASTEROLAMPRACEAE Smith, 1872
T. (YP)–Rec. Mar./FW
First: *Bergonia primitiva* Gombos, uppermost Lower Eocene sediments, DSDP Site 384, western North Atlantic (Gombos, 1980). Extant

F. HELIOPELTACEAE Smith, 1872
K. (ALB)–Rec. Mar./FW
First: Aulacodiscus Deby, Albian clays, Penza region, western Siberia (Jouse, 1949).


F. PYXILLACEAE Schutt, 1896 K. (APT/ALB)–Rec. Mar./FW

First: Gladius antiquus Forti and Schulz and Gladius perfectus Gersonde and Harwood (and numerous other Gladius), Aptian–Albian sediments, Ocean Drilling Program (ODP) Site 693, Weddell Sea: Gladius sp., Albian clays, Penza region, western Siberia (Strelnikova, 1975). Extant


F. RHIZOSOLENIACEAE Petit, 1888 K. (ALB)–Rec. Mar./FW

First: Dactyliosolen sp., Lower Cretaceous, ‘Phosphorite des Gaunts’ (Forti and Schulz, 1932); Rhizosolenia Ehrenberg, Campanian, western Siberia (Strelnikova, 1975); Rhizosolenia cretacea Hajas and Studr, Upper Campanian, DSDP Site 275 (Hajas and Studr, 1975) and of Seymour Island (Hartwood, 1988).

Includes genera: Rhizosolenia Ehrenberg, Dactyliosolen Castracane and Guinardia Paragallo.

F. BIDDULPHIACEAE Kutzing, 1844

Subfamily HEMIAULOIDEAE Jouse et al., 1949 K. (ALB)–Rec. Mar./FW

First: Hemiaulus fragilis Jouse, Albian clays, Penza region, western Siberia, former USSR (Jouse, 1949). Extant

Includes genera: Attheya West, Baxteriopsis Karsten, Campylosira Grunow, Cerataulina Peragallo, Climacioidum Ehrenberg, Cymatosira Grun, Encampia Ehrenberg, Goniohteicum Ehrenberg, Hemiaulus Ehrenberg, Monobrachia Schrader, Odontotripus Gran, Pseudorutilaria Grove and Sturt, Pseudotrigonum Grun, Ralfsia Jouse and Scheschykova-Poretzka and Trinacies Ehrenberg.

Subfamily BIDDULPHIOIDEAE Schutt, 1896 K. (TUR)–Rec. Mar./FW

First: Biddulphia Gray, upper Turonian, near Usti and Labem, Czechoslovakia (Wiesner, 1936). Extant


Subfamily STICTODISOIDEAE Simonsen K. (ALB)–Rec. Mar./FW

First: Stictodiscus punctata Jouse, Albian clays, Penza region, western Siberia (Jouse, 1949). Extant

Includes genera: Anthodiscus Grove and Sturt, Arachnooidiscus Deane, ex Pritch, Chrysanthemodiscus Mann, Ethmodiscus Castratance, Pleurodiscus Barker and Meakin, Stictocycleus Mann, and Stictodiscus Greville.

F. CHAETOCERACEAE Smith, 1872

T. (?Eoc.)–Rec. Mar./FW

First: Chaetoceros clavigerium Grunow, Eocene, Franz Josef’s Land and Ulyanovsk Province, former USSR. Extant

Includes genera: Acanthoceras Honigmann, Bacteriastrum Shadbolt, Chaetoceros Ehrenberg.

F. LITHODESMIACEAE H. and M. Peragallo, 1897–1908 K. (ALB)–Rec. Mar./FW

First: Ditylum sp., Lower Cretaceous, ‘Phosphorite des Gaunts’ (Forti and Schulz, 1932). Extant


F. EUPODISCACEAE Kutzing, 1849

Subfamily RUTILARIOIDEAE Pantocsek, 1889 K. (CMP)–Rec. Mar./FW

First: Synedroctys Ralfs and Rutilaria Greville, Campanian, western Siberia (Strelnikova, 1975). Extant

Includes genera: Rutilaria Greville, Synedroctys Ralfs, and Synedtoenies Gru.

Subfamily EUPODISCIOIDEAE Kutzing, 1849 K. (ALB)–Rec. Mar./FW

First: Triceratium schulzii Jouse, Albian clays, Penza region, western Siberia (Jouse, 1949). Extant


F. DIATOMACEAE Dumortier, 1823

K. (CMP)–Rec. Mar./FW

First: Rhaphonous Ehrenberg and Sceptroneis dimorpha Strelnikova, Campanian, western Siberia (Strelnikova, 1975) and Arctic Ocean, CEASER 6 cores (Barron, 1985); Rhaphonous elliptica Jouse and Sceptroneis witii Jouse, and Sceptroneis grunowii Anissimova, upper Campanian, DSDP Sites 275, South Pacific (Hajas and Studr, 1975). Extant


F. PROTORAPHIDACEAE Simonsen, 1970

Extant Mar./FW

First: Protaraphis was described by Simonsen (1970) from the modern flora. Further studies are required to ascertain its chronological range.

Includes genera: Protaraphis Simonsen and Pseudohimantidium Hustedt and Krasske.

F. EUNOTIACEAE Kutzing, 1844 T. (Eoc.)–Rec. Mar./FW

First: Eunotia striata (Grove and Sturt) Grunow recorded as Eudodia striata Grove and Sturt, Waiaereka Volcanic Formation, Oamaru, South Island, New Zealand. Extant
Includes genera: Actinella Lewis, Eunotia Ehrenberg, Peronia Brebisson and Arnott, and Semiiorbis Patrick.

F. ACHNANTHACEAE Kutzing, 1844
T. (PRB)–Rec. Mar./FW
First: Cocconeis costata Gregory and Cocconeis greville Smith (and others), Upper Eocene, Waiareka Volcanic Formation, Oamaru, South Island, New Zealand. Extant
Includes genera: Achnanthes Bory, Anarthriteis Grun, Campyoneis Grun and Cocconeis Ehrenberg.

F. NAVICULACEAE Kutzing, 1844 T. (PRB)–Rec. Mar./FW
First: Navicula hennedyi Smith and Navicula pratexta Ehrenberg, Upper Eocene, Ulyanovsk Province, former USSR (Witt, 1885). Extant

F. AURICULACEAE Hendey, 1964 Extant
Mar./FW
First: Described from the Isle of Lesina. Further studies are required to determine its chronological range.
Includes genera: Auricula Castracane and Hustedtia Meister.

F. EPITHEMIACEAE Grunow, 1860 T. (AQT)–Rec. Mar./FW
First: Epithema argus Kutzing (and others), Lower Miocene (Aquitaine), Lozere, France (Lauby, 1910).
Includes genera: Epithemia Brebisson and Rhopalodia Muller.

F. NITZSCHIACEAE Grunow, 1860 T. (LMI)–Rec. Mar./FW
First: Nitzschia male interpretatia and several Crucidentula species are common to abundant in the Lower Miocene sediment of the Pacific (Yanagisawa and Akiba, 1990; Barron, 1985). Extant

F. SURIRELLACEAE Kutzing, 1844 T. (CHT)–Rec. Mar./FW
First: Campylopus thureti Brebisson, Surirella brunii Heribaud, and Surirella striatula Turpin, Upper Oligocene, Puy-de-Mur, France (Lauby, 1910). Extant
Includes genera: Campylopus Ehrenberg, Cymatopleura Smith, Hydrocellina Brun, Stenopterobia Breb. and Surirella Turpin.


Phylum EUGLENOPHYTA Pascher, 1931
One of the earliest classifications (Klebs, 1883) was based on nutritional characteristics, although this is now recognized as somewhat artificial. Leedale (1967) has proposed a classification based on the flagellar characteristics and other cytological features; this was adopted by Tappan (1980).

Order EUTREPTIALES Leedale, 1967
A Holocene group characterized by Eutreptia Perty, 1852, Eutreptiella de Cunha, 1913, and Distigma Ehrenberg, 1838. Extant

Order EUGLEANAE Engler, 1898 T. (Eoc.)–Rec. FW
First: Phacus cf. cordata Huber, Eocene, Colorado. Extant
Comment: Bradley (1929) described fossil material from the Green River Formation of Colorado, but applied the name of an extant taxon, hence the ‘cf.’ in the above record.

Order RHABDOMONADALES Leedale, 1967
A monogeneric (Rhodomonas Fresenius, 1858) group of Holocene euglenophytes. Extant

Order SPHENOMONADALES Leedale, 1967
A Holocene group characterized by Anisomena Dujardin, 1841, Petalomonas Stein, 1878 and Sphenomonas Stein, 1878. Extant

Order HETERONOMATALES Leedale, 1967
A Holocene group characterized by Heteronema Dujardin, 1841, Peranema Dujardin, 1841 and Urceolus Mereschkowsky, 1879. Extant

Order EUGLENAMORPHALES Leedale, 1967
A monogeneric (Euglenamorpha Wenrich, 1924) group of Holocene euglenophytes. Extant

Phylum PRASINOPHYTA Round, 1971
A distinctive group (first recognized as such by Chadeau, 1950) of non-cellulosic green algae. They are closely related
to the Chlorophyta, to which they are probably ancestral. Some have been included previously within the acritarchs or the dinoflagellates. One of the most recent summaries of the group is that of Tappan (1980).

**Order PEDINOMONADALES**

F. PEDINOMONADACEAE Korshikov, 1938
A monogenic (*Pedinomonas* Korshikov, 1923) family of Holocene prasinophytes. **Extant**

**Order PYRAMINOMONADALES** Chadeauf, 1950

F. PYRAMINOMONADACEAE

F. HALOSPHAERACEAE
A Holocene group characterized by *Halosphaera* Schmitz, 1878 and *Hyalophysis* Cleve, 1900. **Extant**


**Order PRASINOCLADALES**

F. PRASINOCLADACEAE
A Holocene group characterized by *Platymonas* Belcher, 1966, *Prasinoclados* Kuckuck, 1894 and *Tetraselmis* Stein, 1878. **Extant**

**Order PTEROSPERMATALES** Schiller, 1925

F. NEPHROSELMIDACEAE Pascher, 1913

F. PTEROSPERMAEACEAE Lohmann, 1904
A Holocene group characterized by *Hexasterias* Cleve, 1900, *Pachysphaera* Ostenfeld, 1899, *Pterosperma* Pouchet, 1894 and *Sphaeropsis* Meunier, 1910 (non Saccardo, 1880). **Extant**

Tappan (1980) quotes a range of Precambrian to Recent, and cites a list of typical genera. **Extant**

Tappan (1980) quotes a range of Ordovician to ?Holocene, and cites a list of typical genera. **Extant**

**Extant**

Tappan (1980) cites a range of Precambrian to Holocene, and lists typical genera.

**Division PYRRHOPHYTA Pascher, 1914**

**Class DINOPHYCEAE** Fritsch, 1929 (see Fig. 3.3)

This review concerns the stratigraphical record of dinoflagellates that have produced fossilizable cysts. To state the obvious, it does not include those dinoflagellates that do not, and have not, produced fossilizable cysts. This factor is stressed at the outset because the dinoflagellate fossil record is open to dangerous misinterpretation; it is ‘an ambiguous record of dinoflagellate evolution’ (Evitt, 1985, p. 276).

The Division Pyrrhophyta is divisible into three classes on the basis of nuclear structure. These are Dinophyceae, Syndiniophyceae and Oxyrrhidiophyceae. The great majority of dinoflagellate taxa are contained within the Dinophyceae (see Fensome et al., 1989).

Dinoflagellates are unicellular, aquatic, biflagellate algae. During the motile, vegetative, thecate, planktonic stage in the life cycle (contributing to biocoenoses), most dinoflagellates exist within the photic zone of surface waters. Various representatives of the class can be either autotrophic or heterotrophic. The distribution and productivity of dinoflagellates in a biocoenosis depends upon a number of factors: water temperature, salinity, nutrient levels, sunlight and the nature of water-mass movements and currents. As part of their life cycle, some dinoflagellate thecae encyst. As a result, benthic resting cysts (dinoflagellate cysts) are produced. These contribute to thanatocoenoses and stand a chance of fossilization, depending upon the nature of the cyst wall. Almost all fossil dinoflagellates in palynological preparations are sporopollenin (organic-walled) cysts. Fossil thecae (i.e. tests as opposed to cysts) are also known, as are calcareous and siliceous dinoflagellates. The term ‘dinocsy’ is a commonly used abbreviation for a dinoflagellate resting cyst.

Dinoflagellates have a fossil record stretching back to at least the Middle Triassic, and possibly to the late Silurian. However, because not all dinoflagellates produce fossilizable cysts, and presumably have not done so in the geological past, it is impossible to state with any confidence the age when the first dinoflagellates evolved. Unfortunately, potential preservability as a fossil is not an adaptation that favours evolution.

Since Sarjeant and Downie (1967) produced their review of the stratigraphical distribution of fossil dinoflagellates, there has been a considerable expansion in the levels of published taxonomic information concerning this class. In 1967, according to the data in Bujak and Williams (1979), there were just over 1000 validly described species assigned to 200 genera. By 1989 (Lentin and Williams, 1989) nearly 3000 species and over 500 genera were valid, representing increases of 200% and 150% respectively. A review of the suprageneric classification of fossil dinoflagellates is therefore long overdue. In addition, the unresolved question of the suprageneric distribution of dinoflagellates is therefore long overdue. In addition, the unresolved question of the suprageneric classification of fossil dinoflagellates, and its relationship to the classification of modern dinoflagellates in particular, makes the present review problematic.

Earlier attempts at suprageneric classification have generally lost favour, because either they were developed before the realization that fossil dinoflagellates were cysts; they ignored existing classifications of modern dinoflagel-
lates; they did not incorporate morphological evidence from the thecae; they made insufficient allowance for the fact that not all dinoflagellates produce fossilizable cysts; or they overemphasized the importance of the archaeopyle (excystment aperture). Work is in progress (Fensome et al., 1989) to formulate a comprehensive phylogenetic classification for fossil and living dinoflagellates.

In their review, Sarjeant and Downie (1967) subdivided the Class Dinophyceae on the grounds of general morphology (proximate, chorate, cavate, etc.), and then on archaeopyle style (precingular, apical, intercalary, etc.). I have adopted a generally similar approach here in that I have not employed a phylogenetic suprageneric scheme. Instead, I have used the phenetic groupings of Evitt (1985) for sporopollenin dinoflagellate cysts, together with additional categories for calcareous and siliceous forms. Evitt’s scheme, in which paratabulation plays the major role in categorization, is not based upon biological grounds. Rather, the categories ‘are intended principally as a convenience for organizing extensive observational or descriptive data that have been reduced to identifications at the generic and specific level without requiring a commitment to any formal suprageneric scheme’ (Evitt, 1985, p. 174).

The generic and specific taxonomy of Lentin and Williams (1989) is applied without question, because their Index serves as a useful single reference point; it is the only source where all fossil dinoflagellates are treated, ostensibly in equal fashion. It would have been inappropriate to have strayed from their judgements for the purposes of the present review.
**Fig. 3.3**


**First:** *Dinogymnium cretaceum* (Deflandre) Evitt et al., 1967, Silex du Turonien supérieur (sommet), Ruyaulcourt, Pas-de-Calais, France (Foucher, 1974).


Category of N-cysts J. (PLB)–K. (VLG) Mar.

**First:** *Nannoceratopsis senex* van Helden, 1977, Wilkie Point Formation, Emerald Island, North-west Territories, Canada (van Helden, 1977).

**Last:** *Nannoceratopsis* spp., Upper Barrow Group, Barrow-25 well, Carnarvon Basin, offshore western Australia (Helby et al., 1987).

**Comments:** Helby et al. (1987) indicated that in offshore Australia, undifferentiated *Nannoceratopsis* species range inconsistently above the top of the Tithonian succession to within the lower Valanginian.

Category of S-cysts Tr. (CRN)–J. (SIN) Mar.


**Last:** *Suessia* sp., Upper Barrow Group, Barrow-25 well, Carnarvon Basin, offshore western Australia (Helby et al., 1987).

**Comments:** Helby et al. (1987) indicated that in offshore Australia, the last occurrence of *S. swabiana* coincides with that of *B. langii*.

Category of P-cysts

Category of Pq-cysts


**First:** *Wetzeliella astra* Denison in Costa et al., 1978, lower London Clay, Bean, England, UK (Costa et al., 1978).

**Last:** *Wetzeliella asymmetrica* Weiler, 1956, Untere Graffenberger Schichten, Tönisberg Borehole, Krefeld, Germany (Benedek, 1972).

**Comments:** The records of *W. symmetrica* by Benedek (1972) include *W. gochtii* Costa and Downie, 1976 as 'W.
Apectodinium Complex  


Comments: In their compiled range chart, Costa and Downie (1979) indicate that A. homomorphum ranges up to calcareous nonnoplankton Biozone NP23 of Martini (1971). If verified, this would give an Oligocene (Rupelian) last appearance for the Apectodinium Complex.

Category of Pp-cysts

Deflandrea Complex  

First:  Isabelidinium glabrum (Cookson and Eisenack) Lentin and Williams, 1977, subsurface Balclattica, Western Australia (Cookson and Eisenack, 1969).

Extant Comments: Liassidium variabile Drugg, 1978, originally described from Sinemurian material (Balingen, Swabia, Germany), would be the first representative if confidently assigned to the Deflandrea Complex. There are no unequivocal records of the complex between the Sinemurian and the Albian/Cenomanian. Species of Leipokatiium Bradford, 1975 and Omanodinium Bradford, 1975 are known from Recent sediments.

Spinidinium Complex  

First:  Spinidinium denticulatum Pothe de Baldis and Ramos, 1983, Rio Fosiles, Provincia de Santa Cruz, Argentina (Pothe de Baldis and Ramos, 1983).

Extant Comments: Some living species of Protoperidinium Bergh, 1882 are included within the Spinidinium Complex, e.g. P. divaricatum (Meunier) Parke and Dodge, 1975.

Selenopemphix Complex  


Extant Comments: Cysts of the extant species Protoperidinium subinerme (Paulsen) Loeblich III, 1970 are referable to S. nephroides (see Harland, 1982).

Palaeoperidinium Complex  
K. (?VLG/BRM)—Rec. Mar./FW


Extant Comments: Luxadinium? dabeirodense (Alberti) Bujak and Davies, 1983 was described originally from subsurface Valanginian material from Dabendorf near Berlin, Germany. However, Bujak and Davies (1983) only questionably included this species in the genus Luxadinium Bridgeaux and Mchtyre, 1975, and as a result it cannot be confidently referred to as the first representative of the Palaeoperidinium Complex. The genus Palaeoperidinium Deflandre, 1935, emend. Sarjeant, 1967 last appeared during Thanetian times (e.g. Holmehus Formation, Jutland, Denmark; Heilmann-Clausen, 1985). The genus Saeptodinium Harris, 1974 is known from Palaeogene and Neogene sediments, while Protoperidinium limbaun (Stokes) Lemmermann, 1900, and several other freshwater species which belong to the complex, are extant.

Ascodinium Complex  

First:  Oovidinium waltontii (Pocock) Lentin and Williams, 1976, Lower Member, Watrous Formation, Saskatchewan, Canada (Pocock, 1972).


Comments: The early stratigraphical record of the Ascodinium Complex is erratic. Pocock (1972) recorded O. waltontii from the PLB Lower Member of the Watrous Formation of Saskatchewan. There are no intervening occurrences between this record and the younger post-KIM Upper Member of the Vanguard Formation. The range of O. waltontii given by Jansonius (1986) is ‘Toarcian’ (Bajocien?). Members of the complex are known to occur fairly regularly through the APT to CEN succession. Foucher (1974, 1979) recorded Ascodinium cf. parvum (Cookson and Eisenack) Cookson and Eisenack, 1960 from ‘Silex du Turonien superieur (sommet) de Ruyaulcourt’, Pas-de-Calais, France, which would make it the last representative stratigraphically. However, there is a Cainozoic form, Oovidinium granulatum Z.-C. Song in Z.-C. Song et al., 1985, described from the Shelf Basin of the East China Sea (Donghai) region. Furthermore, Evitt (1985) indicated that the extant species Protoperidinium claudicans (Paulsen) Balech, 1974, P. oblongum (Aurivillius) Parke and Dodge, 1976 and Peridinium weissnosiensis Eddy, 1930 are also attributable to the Ascodinium Complex.

Phthanoperidinium Complex  

First:  Phthanoperidinium crenulatum Heilmann-Clausen, 1985, Holmehus Formation, Jutland, Denmark (Heilmann-Clausen, 1985).


Comments: Nagy (1966) stated that P. lambdoideum was recovered originally from Pannonian sediments. A Tortonian age is indicated therefore for the last representation of the Phthanoperidinium Complex. Stover and Evitt (1978) considered P. lambdoideum to be a problematic species and only questionably allocated it to the genus Phthanoperidinium Drugg and Loeblich, 1967 (sic.). There are also stratigraphical difficulties because there are no known early or middle Miocene records of the species. The next oldest species is P. polytrix Benedek, 1972, emend. Benedek and Sarjeant, 1981, which ranges into the Upper Oligocene (Untere Lintforter Schichten, Germany; Benedek, 1972).

Category of Px-cysts  
?J. (?KIM)/K. (HAU)—T. (Mio.) Mar./FW

First:  Subtilisphaera terrula (Davey) Lentin and Williams,
ever, because this species is only questionably referred to Subtilisphaera? inaffecta (Drugg) Bujak and Davies, 1983, is known to be restricted to the KIM. However, because this species is only questionably referred to Subtilisphaera Jain and Millepied, 1973, emend. Lentin and Williams, 1976, it cannot be said confidently to be the first representative of the genus. Apart from the KIM species S.? paeminosa (Drugg) Bujak and Davies, 1983, there are no other known records of the genus between the KIM and HAU. Both Geiseldinium Krutsch, 1962 and Teneridinium Krutsch, 1962, are freshwater representatives.

Category of R-cysts
Category of Rp-cysts

Comments: Morbey (1975) indicated that P. ceratophora ranges into upper Lias (TOA) sediments of north-west Europe.

Miscellaneous genera of Rr-cysts

First: Sahulidinium ottii Stover and Helby, 1987, unnamed unit, Sahul Shoals-1 Well, Bonaparte Basin, offshore northwestern Australia (Helby et al., 1987).
Last: Valvoedinium aquilimum (Dörhöfer and Davies), emend. Below, 1987, Lower Savik Formation and Jaeger Member, Ellef Ringnes Island, Northwest Territories, Canada (Dörhöfer and Davies, 1980).
Comments: The problematic species Apylorus antiquus Calandra, 1964, emend. Sarjeant, 1978 is known from Upper Silurian (LUD) subsurface sediments from Mechequig, Tunisia (see discussion in Sarjeant, 1978 and Evitt, 1985 for details concerning the nature and assignation of this species). There are no unequivocal dinoflagellate cyst species known between the Upper Silurian and the Middle Triassic. Stover and Evitt (1978) discredited the Permian dinoflagellate cysts records of Tasch (1963), while those of Jansonius (1962) are believed to be the result of contamination by younger material (Evitt, 1985).

Category of G-cysts
Category of Gc-cysts

Odontochitina Complex K. (BRM-MAA) Mar.

Pseudoceratium Complex
First: Pseudoceratium spiniense Jain and Garg in Jain et al., 1984, Spiti Shale (Formation), Malla Johar, Himalaya, India (Jain et al., 1984).

Comments: M. simplex sensu Gitmez and Sarjeant (1972) is most usually referred to as Muderongia sp. A of Davey (1979).

Category of Gv-cysts

Last: Chiroteridium mespilanum (Maier) Lentin and Williams, 1973, Atlantic Shelf Corehole 5/5B, Blake Plateau, offshore South Carolina, USA (Stover, 1977).
Comments: The oldest possible representative of the Areoligera Complex is the allegedly Upper Triassic Cyclonephelium granulatum (Horowitz) Stover and Evitt, 1978. However, there is doubt not only concerning the age of the sediments from which the type material was derived (see Conway and Cousminer, 1983) but also about its allocation to the genus Cyclonephelium. Deflandre and Cookson, 1955, emend. Stover and Evitt, 1978. The type species of Glaphyrocysta Stover and Evitt, 1978, G. retintexta (Cookson) Stover and Evitt, 1978, is the only representative of that genus within the Areoligera Complex; the other species belong to the Areosphaeridium Complex of Gi-cysts.

First: Senonia sphera jurassica (Gitmez and Sarjeant) Lentin and Williams, 1976, baylei Zone, Staffin Bay, Skye, Scotland, UK (Gitmez and Sarjeant, 1972).
**Canningia Complex**  
*j. (KIM/TTH)—K. (CMP/MAA)*  
**Mar.**

**First:** *Canningia apiculata* Jain and Garg, *in Jain et al.*, 1984, Spiti Shale (Formation), Malla Johar, Himalaya, India (Jain et al., 1984).

**Last:** *Canningia xinjiangensis* Chen et al., 1988, Western Xinjiang, China (J.-X. Yu and W.-P. Zhang, 1980).

**Comments:** Lentin and Williams (1989) give a TUR to CMP, e.g. Basin, France (Foucher, 1979).

**First:** Spiti Shale (Formation), Malla Johar, Himalaya, India (Jain et al., 1984).

**Last:** *Eocladopyxis peniculata* Mclean (1976) considered E. *Clay, Whitecliff Bay, Isle of Wight, England, UK (Bujak et al., 1984).*

**Comments:** This is a group of species having partiform hypocyts but not necessarily other features in common. Evitt (1978, p. 232) that Paragonyaulacysta Johnson and Hills, 1973, may be synonymous with *Carpathodinium* Drugg, 1978, and (p. 234) that Lacrymodinium Albert et al., 1986 may be congenic with *Pluriarvalium* Sarjeant, 1962.

**Category of Gq-cysts**

**Homotryblium Complex**  
*T. (YPR)—Rec. Mar.*


**Comments:** Mclean (1976) considered *E. peniculata* to be an ancestor to the extant *Pyrodinium bahamense* Plate, 1906. This dinoflagellate, whose cysts are referred to as *Polysphieridium zoharyi* (Rossignol) Bujak et al., 1980, is a member of the *Homotryblium Complex*.

**Heteraulacacysta Complex**  
*J. (OXF)/K. (ALB)–T. (SRV)*  
**Mar.**

**First:** *Dinopterygium bicuneatum* (Deflandre) Lentin and Williams 1981, Les Marines de Villers-sur-Mer, Calvados, France (Deflandre, 1938).

**Last:** *Heteraulacacysta cf. campanula* Drugg and Loeblich, 1967, Cassinisco Formation, Langhe, Piemonte, Italy (Powell, 1986a).

**Comments:** There is an apparent gap in the stratigraphical record of the *Heteraulacacysta Complex* between the KIM and ALB. Gitmez and Sarjeant (1972) recorded *D. bicuneatum* ranging into the KIM rotunda Zone, while the first occurrence of *Dinopterygium cladooides* Deflandre, 1935 is not known until the ALB (e.g. Foucher, 1981).

**Category of Gp-cysts**

**Microdinum Complex**  
?J. (?CLV)/K. (BRM/APT)–T. (THA/?Oli.)  
**Mar.**

**First:** *Fibradinium variculum* Stover and Helby, 1987, unnamed greensand unit, Warnbro Group, Houtman-1 Plate, Western Australia (Stover and Helby, 1987).

**Last:** *Cladopyxidium saeptum* (Morgenroth) Stover and Evitt, 1978, Holmehus Formation, Viborg 1 borehole, Jutland, Denmark (Heilmann-Clausen, 1985).

**Comments:** Lentin and Williams (1989) questionably transferred *Phanerodinium foliis Below, 1987 and P. diatretiforme Below, 1987* to the genus *Fibradinium* Morgenroth, 1968. If confidently accepted within the genus, the *Microdinum Complex* would first appear within the CLV and range to the Oligocene. The type species of *Microdinum* Cookson and Eisenack, 1960, emend. Stover and Evitt, 1978, *M. ornatum* Cookson and Eisenack, 1960, alone is placed within the complex; the other species of *Microdinum* belong to the *Phanerodinium Complex*. ‘*Microdinum* veligerum’ (Deflandre) Davey, 1969, another member of the complex, now lies within the monospecific genus *Rhiptocorys* Lejeune-Carpentier and Sarjeant, 1983.

**Phanerodinium Complex**  
*J./K. (TTH/VLG)–T. (DAN)*  
**Mar.**

**First:** *Druggidinium apicopaucicum* Habib, 1973, DSDP Site 105, Hatteras Abyssal Plain, offshore North Carolina, USA (Habib, 1973).

**Last:** *Glyphanodinium facetum* Drugg, 1964, Dos Palos Shale Member, Moreno Formation, Escarpado Canyon, California, USA (Drugg, 1964).


**Miscellaneous Complex of Gp-cysts**

**J. (PLB)—K. (BER)*  
**Mar.**


**Last:** *Paragonyaulacysta capitella* (Bradeaux and Fisher) Stover and Evitt, 1978, Lower Sandstone Division, Buff Sandstone Unit, *Buchia volgensis* Zone, Martin Creek, Arlavik Range, District of Mackenzie, Canada (Bradeaux and Fisher, 1976).

**Comments:** This is a group of species having partiform hypocyts but not necessarily other features in common. Evitt (1985, p. 232) intimated that *Paragonyaulacysta* Johnson and Hills, 1973, may be synonymous with *Carpathodinium* Drugg, 1978, and (p. 234) that *Lacrymodinium* Albert et al., 1986 may be congenic with *Pluriarvalium* Sarjeant, 1962.

**Category of Gs-cysts**

**Spiniferites Complex**  
?J. (?OXF)/K. (BER)–Rec.  
**Mar.**

**First:** *Spiniferites ramosus* (Ehrenberg) Loeblich and Loeblich, 1966, Les Marines de Villers-sur-Mer, Calvados, France (Deflandre, 1938).

**Extant Comments:** Although Deflandre (1938, p. 186) recorded *S. ramosus*, as *Hystrichosphaera furcata* (Ehrenberg) O. Wetzel, 1933, from OXF sediments (and as also reported by Sarjeant, 1960 and 1962), it is questionable whether or not this represents the first occurrence of the genus *Spiniferites*. Davey (1979, Fig. 6), for example, placed this event within the VLG. Duxbury (1977) recorded both *Achomosphaera? neptuni* (Eisenack) Davey and Williams, 1966 and *Avellidinium falsicum* Duxbury, 1977 from the Blue Beds, D6 division of the Speeton Clay (Speeton, Yorkshire, England, UK). Although both are only tentatively attributable to the *Spiniferites Complex*, they are the two next oldest records. Included within the *Spiniferites Complex* are some living species of *Gonyaulax spinifera* (Claparède and Lachmann) Diesing, 1886.

**Ctenidodinium Complex**  
*J. (BAJ)—K. (APT)*  
**Mar.**


**Last:** *Ctenidodinium elegantulum* Milloud, 1969, *Scapites*

Wanea Complex  J. (BAJ)–K. (VLG) Mar.
First:  
Last:  

Leptodium Complex  J. (BAJ)–Rec. Mar./FW
First:  
Comments:  
Although R.? regalis is only provisionally accepted in the genus Rhynchodiniopsis Deflandre, 1935, emend. Jan du Chêne et al., 1985, this does not preclude its allocation to the Leptodium Complex. A possible older representative is the undescribed Leptodium sp. 1 of Fenton and Fisher (1978) which first occurs within the humphriesianum Zone of eastern England. Living representatives of the complex include Gongaulax spp. indet. which produce cysts referable to Impagidinium Stover and Evitt, 1978 and the freshwater species Gongaulax apiculata (Penard) Entz, 1904.

First:  
Last:  
Comments:  
Foucher (1979) indicated that the last occurrence of H. pulchrum has been observed in MAA sediments from Belgium, The Netherlands, Denmark, and Sweden.

Category of Gi-cysts
First:  
Last:  
Comments:  
The Areosphaeridium Complex excludes the type species of Glaphyrocysta Stover and Evitt, 1978, G. retinexa (Cookson) Stover and Evitt, 1978, which is allocated to the Areoligera Complex of Gv-cysts.

First:  
Cordosphaeridium senegalense Jain and Millepied, 1975, subsurface, Borehole CM-1, offshore Senegal (Jain and Millepied, 1975).
Last:  
Cordosphaeridium cantharellum (Brosius) Gocht, 1969, Bisciaro Formation, Montebello d’Urbino, Marche, Italy (Biffi and Manum, 1988).

Hystrichosphaeridium Complex  J. (BTH)–Q. (PLE) Mar.
First:  
Adnatosphaeridium caulleryi (Deflandre) Williams and Downie, 1969, Lower Fuller’s Earth, zigzag Zone, vicinity of Bath, England, UK (Riding et al., 1985).
Last:  
Hystrichokolpoma rigaudiae Deflandre and Cookson, 1955, Utahime Member (Ma1 Member), Sao Formation, Osaka Group, northern Utahime, Nara City, Japan (Matsuoka, 1976).
Comments:  
Matsuoka (1976, 1979) indicated that H. rigaudiae last occurs stratigraphically below the normal Jaramillo Event within the Matsuyma Reverse Epoch; an early Pleistocene age is thus indicated.

First:  
Last:  

First:  
Last:  

Category of Gn-cysts
First:  
Last:  

Opeculodinium Complex  J. (BAJ)–Rec. Mar.
First:  
Cleistosphaeridium polytrichum (Valensi) Davey et al., 1969, Truellei Bed, Burton Limestone, parkinsoni Zone, Burton Bradstock, Dorset, England, UK (Fenton et al., 1980).
Comments:  
Woollam and Riding (1983) indicated that members of the C. polytrichicum Group do not range higher than the Jurassic, as least in England. There is, therefore, an apparent break in the stratigraphical distribution of the Opeculodinium Complex between the TTH and HAU, when Kiokansium polypes (Cookson and Eisenack) Below, 1982 first occurs (e.g. Division C8 of the Speeton Clay, Speeton, Yorkshire, England, UK, Duxbury, 1977). The extant dinoflagellates Gongaulax grindleyi Reinecke, 1967 and G. polyhedra Stein, 1883 produce cysts referable to Opeculodinium centrocarpum (Deflandre and Cookson) Wall, 1967 and Lingulodinium machaerophorum (Deflandre and Cookson) Wall, 1967, respectively.

Miscellaneous Complex of Gn-cysts
First:  
Last:  
Stenopyxium grassei Deflandre, 1968, Cretaceous (Senonian) flint (Deflandre, 1968).
Comments:  
Members of the Miscellaneous Complex of Gn-cysts are characterized by spinose projections which are
apparently distributed according to the general outline of the cyst, but not evenly and not in association with paratabulation. *Caucatia telata* (W. Wetzel) Sarjeant, 1984 was described originally from a DAN flint from drift deposits near Kiel, Germany. However, Sarjeant (1984) only attributed it provisionally to the genus *Caucatia* Davey and Verdier, 1971, and as a result in cannot be taken confidently as the last representative of the complex.

**Category of Gx-cysts**

*Batioladinium* Complex J. (u.)–K. (ALB) Mar.

**First:** *Batioladinium imbatodinense* (Vozzhennikova) Lentin and Williams, 1985, Verkhe-Imbatskoi, Well 1, western Siberia, former USSR (Vozzhennikova, 1967).


**Prolixosphaeridium** Complex J. (BAJ)–Rec. Mar.

**First:** *Ellipsoidictyum reticulatum* (Valensi) Lentin and Williams, 1977, Bajocian, Normandy, France (Valensi, 1953).

**Comments:** There is an apparent stratigraphical break in the distribution of members of the *Prolixosphaeridium* Complex between the Middle Miocene, when *Distotadinium fusiforme* (Matsuoka) Bujak and Matsuoka, 1976 last appeared (e.g. Toyoda Formation, Fujiwara Group, Nara Complex between the Middle Miocene, when Toyoda Formation, Fujiwara Group, Nara City, Japan; Matsuoka, 1974), and the late Pliocene. The extant *Prolixosphaeridium* are extant. Aside from these occurrences, the next youngest representative of the complex is *Prolixosphaeridium* *imbatodinense* (Vozzhennikova) Lentin and Williams, 1985, *Verkhe-Imbatskoi, Well 1, western Siberia, former USSR* (Vozzhennikova, 1967).

**Apteodinium** Complex J. (PLB)–Q. (HOL) Mar./FW


**Comments:** Fossil (Flandrian) freshwater dinoflagellate cysts belonging to the *Apteodinium* Complex have been reported from Victoria and Western Australia (see Harland and Sarjeant, 1970). It is unclear whether or not these forms are extant. Aside from these occurrences, the next youngest representative of the complex is *Apteodinium mceksense* (Nagy) Heleneis, 1984, described from upper Pannonian (i.e. Upper Miocene) sediments from Hungary (Nagy, 1969).

**Scriniophorella** Complex J. (CLV)–T. (AQT?PIA) Mar.

**First:** *Dingodinium harsveldii* Herrgreen et al., 1984, Achterhoek, eastern Netherlands (Herrgreen et al., 1984).

**Last:** *Lophocysta sulcolimata* Manum, 1979, DSDP Site 338, Vöing Plateau, Norwegian Sea (Manum, 1979).

**Comments:** Aside from *D. harsveldii*, *Scriniophorella crystallinum* (Deflandre) Klement, 1960 is also known from CLV sediments (e.g. Woolam and Riding, 1983). Harland (1979) recorded "*Thalassiphora delicata* auct. non Williams and Downie, 1966, emend. Eaton, 1976 in sediments as young as late Pliocene from the Bay of Biscay. According to Edwards (1984), these records are referable to *Invertocysta lacrymosa* Edwards, 1984. This record may represent the last appearance of the *Scriniophorella* Complex.

**Chlamydophorella** Complex J. (TOA)–T. (RUP) Mar.

**First:** *Scriniocassis weberi* Goth, 1964, Ziegeleigrube Frommern, near Balingen, Württemberg, Germany (Gocht, 1964).

**Last:** *Samlandia chlamydophora* Eisenack, 1965, Walsumer Schichten, Tönising borehole, Krefeld, Germany (Benedek, 1972).

**Miscellaneous Complex of Gx-cysts** J. (BAJ)–Rec. Mar.

**First:** *Aldorfa aldorfeni* (Gocht) Stover and Evitt, 1978, Upper Inferior Oolite, garantiana Zone, Dorset (Woolam and Riding, 1983).

**Comments:** Members of this varied catch-all complex do not fit into any of the other categories of Gx-cysts. Cysts referred to as *Tectatodinium pellitum* Wall, 1967 are produced by the extant *Gonyaulax* sp. indet.

**Category of M-cysts** J. (KIM)/K. (CEN/CON)–Rec. Mar.

**First:** *Cryptarchaeodinium calcaratum* Deflandre, 1939, emend. Gitmez, 1970, Schistes bitumineux d’Orbagnoux, Jura, France (Deflandre, 1939).

**Comments:** The category of M-cysts is a catch-all grouping which includes cysts with discernibly non-gonyaulacid paratabulations. There is a stratigraphical gap between the KIM, after which *Cryptarchaeodinium* Deflandre, 1939, emend. Sarjeant, 1984 is unknown, and the CEN, when *Caligidinium aceras* (Manum and Cookson) Lentin and Williams, 1973 first appeared (Hassel Formation, Ellef Ringnes Island, Northwest Territories, Canada; Manum and Cookson, 1964). The extant *Pyrophacus* Stein, 1883 produces cysts referable to *Tuberculodinium* Wall, 1967. Evitt (1985) indicated that the extant forms *Diplopsalis* Bergh, 1882 and *Zygabikodinium* Loeblich and Loeblich, 1970 are also referable to this category.

**Category of calcareous dinoflagellates** J. (KIM)–Rec. Mar.

**First:** *Schizosphaeraella punctulata* Deflandre and Dangeard, 1938, HET–KIM (Lentin and Williams, 1969).

**Comments:** Kalin and Bernoulli (1984) suggested that microfossil forms assigned to *Schizosphaeraella* Deflandre and Dangeard, 1938 may be dinoflagellates (and not calcareous nannoplankton). Extant calcareous dinoflagellate cysts include those referable to *Scrippsiella* Balech, 1959, ex Loeblich III, 1965. An alternative arrangement of this groups is to divide it into two families, the *Schizosphaeraceae* Deflandre, 1939, with a range from HET–OXF, and the *Thoracosphaeraceae* Schiller, 1930, with a range of NOR–Rec.

**Category of siliceous dinoflagellates** T. (Pal.)–Rec. Mar.

**First:** *Peridinates parvulus* Lefevre, 1933, Lower Tertiary, Barbados, Caribbean (Lefevre, 1933).

**Comments:** Lefevre (1933) described a number of species of *Peridinates* Lefevre, 1933 from Lower Tertiary sediments of Barbados. Representatives of the genus *Actiniscus* Ehrenberg, 1840 are extant.
The acritarchs are organic-walled microfossils of unknown and uncertain affinity. They are unicellular or apparently unicellular, although they may be found in clusters. The acritarchs are an informal, polyphyletic, organic-walled microfossil group, conceived as a holding category for a varied collection of incertae sedis. It is anticipated that as the affinities of certain acritarchs become firmly established, transfers can be made to the appropriate biotic classes. Many acritarchs are considered to be cysts or temporary resting stages of marine planktonic algae, although some are recorded in apparently lacustrine and terrestrial environments. A few have clear affinities with the Prasinophyta and Chlorophyta (Tappan, 1980). Fensome et al. (1990) note forms with questionable dinoflagellate affinity. A few have morphological similarities with amoeboid cysts, copepod eggs and masuelloids. To date, little progress has been made with the possible affinities of most acritarchs. At present, published and unpublished records suggest that well over 10,000 acritarch species are preserved in the fossil record. Fensome et al. (1990, 1991) list over 7000 in an index. Acritarchs are regularly recorded in abundance in routine palynological preparations, particularly in marine Palaeozoic sediments. Owing to their abundance and diversity, they are of particular importance in biostratigraphical correlation and palaeoenvironmental studies.

Authors have varied considerably in the adoption of possible biological affinities. Herein, acritarch records of forms considered by some workers to have affinities with known biotic groups are cross-referenced. Downie et al. (1963) divided the acritarchs into informal morphological subgroups, and parts of the scheme have been used by some other workers. Subsequent observations have noted that there is gradation between the spherical to subspherical vesicles of some acanthomorph acritarchs and the subpolygonal vesicles of some three-dimensional polygonomorph acritarchs, with the polygonal outline produced as a result of crushing during sediment compaction. A few species of both acanthomorph and herkomorph acritarchs have been observed enclosed within an outer laevigate sphaeromorph-type vesicle. Downie (1973, 1984) reviewed the classification of the acritarchs, and noted groupings on the basis of overall morphology, wall type and excystment openings. The inclusion of the sphaeromorph acritarchs in the informal group Cryptarcha, Diver and Peat, 1979 has not been generally adopted. The transfer of non-marine algal cysts, such as Chlorella, to the aneterma Cryptosponges, Richardson et al., 1984 by Strother (1991) on the basis of an ecological subdivision is not seen as appropriate. Alete spores may be distinguished from acritarchs in having significant variations in wall thickness and colour within an individual. Generally, at low geothermal alteration, cryptospores are noticeably darker in overall coloration than acritarchs with equivalent wall thickness.

None of the subdivision schemes for the acritarchs is entirely satisfactory, at least in terms of possible biological affinities, and many workers currently list all acritarchs, algal cysts and colonial algae together alphabetically when describing palynological assemblages.

The first record of acritarchs has been taken where possible from reference sections with independent age evidence. The last record of acritarchs, in common with most palynomorphs, is difficult to establish with certainty. Acritarchs are readily recycled during the erosion of significantly older sediments, and may prove particularly resistant to degradation if subjected to geothermal alteration (Dorning, 1986). In modern sediments, it is often difficult to distinguish with certainty between modern cysts and recycled forms derived from low-thermal alteration Mesozoic and Cainozoic sediments.

Most acritarchs fall into three main morphological categories; acritarchs without flanges or processes, acritarchs with flanges but no processes, and acritarchs with processes, with or without flanges. Taxonomic references may be found in Fensome et al. (1990).

1. Acritarchs without Processes or Flanges

This category includes the subgroup Sphaeromorphitae Downie et al., 1963, the sphaeromorph acritarchs, together with the Navifusa group of Downie (1973). This grouping is almost certainly polyphyletic, including forms possibly attributable to the Chlorophyta, Prasinophyta, Cyanophyta and other algal and faunal groups. Moyeria Thusu, 1973 is considered by Gray and Boucot (1989) to be a euglenoid cyst.

Subgroup SPHAEROMORPHITAE Downie et al., 1963

First: Sphaeromorphs, 20–200 μm in diameter, from the Chuanlinggou Formation (1800 Ma), Jixian, China, are compared with later Precambrian Kildinosphaera, Leiosphaeridium, and Chuaaria, and are considered to be the cysts of marine planktonic algae, the first possibly prasinophycean (see above) (Z. Zhang, 1986).

Extant

2. Acritarchs with Flanges, but without Processes

This category includes most forms in the subgroups Herkomorphitae Downie et al., 1963 and Pteromorphitae Downie et al., 1963. Some of these forms, including Cymatosphaera and Pterospheromopsis are related to the Prasinophyta (Tappan, 1980).

Subgroup HERKOMORPHITAE Downie et al., 1963


Extant

Subgroup PTEROMORPHITAE Downie et al., 1963


First: Pterospheromopsis sp., Cheney Longville Flags, Marshbrook Quarry, Shropshire, England, UK (Dorning, unpubl.).

Extant

3. Acritarchs with Processes, with or without Flanges

This category includes many forms in the subgroups Acanthomorphitae Downie et al., 1963, Diacromorphitae Downie et al., 1963, Netromorphitae Downie et al., 1963, Oomorphitae Downie et al., 1963, Polygonomorphitae Downie et al., 1963 and Prismatomorphitae Downie et al.,
1963. This group is almost certainly polyphyletic. Despite superficial resemblances of some to dinoflagellate cysts, the absence of consistent process-centred reflected tabulation and lack of stratigraphical continuity merely provides evidence of probable affinities of some within the marine microflora. The *Baltisphaeridium, Micrhystridium–Veryhachium, Leiojusa, Acanthodiacrodian and Visbysphaera* groups of Downie (1973) and the *Estiastra and *Tunisphaeridium* groups of Dorning and Bell (1987) are in this category. A few of the very large forms may have affinities with the masuelloids (Order Muellerisphaerida Kozur, 1984).

Subgroup **ACANTHOMORPHITAE** Downie et al., 1963 PC. (EDI)-Rec. Mar.


**Comment:** Extant form is 'Baltisphaeridium' from the Mediterranean (Rossignol, 1964).

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**Phylum** RHODOPHYTA Wettstein, 1901

**Class** RHODOPHYCEAE Ruprecht, 1831

**Subclass** BANGIOPHYCIDAE de Toni, 1897, orth. mut. L. M. Newton, 1953

**Order** BANGIALES Engler, 1892

F. BANGIACEAE (Gray) Någeli, 1847 PC. (YUR/STU)-Rec. Mar.

**First:** Unnamed multiseriate filaments preserved in chert, Hunting Formation, Somerset Island, Arctic Canada (1250–750 Ma: Butterfield et al., 1990).

**Extant**


**First:** *Palaeonchocelis starmachii* Campbell et al., 1979 in Widowo core, Bielsk Podlaski, eastern Poland, Lower Ludlow. Formation not given (Campbell et al., 1979).

**Extant**
Comment: Conchocelis stage of an endolithic microalga was compared with the modern bangiacean rhodophyte Porphyra nereocystis. Tappan (1980) cited several probable Precambrian cf. Porphyridaceae, the earliest being Clono­phycus J. Oehler 1977 from the 1500–1600Ma McArthur Group, although Oehler (1977) himself and Mendelson and Schopf consider it to be a colonial coccoid (?chroococc­acean) cyanobacterium.

Subclass FLORIDEOPHYCIDAE (Lamouroux, 1813)
Engler, 1892

Record is centred on calcified forms, there being insufficient characters to permit identification of foliose forms (e.g. Fry, 1983 for Ordovician problematica). However phosphatized Thal­lep­hy­ca ramosa Zhang, 1989 from the 680Ma Doushantuo Formation, South China, shows...
remarkable fountain-type cellular preservation compared with that in modern florideophyceans (Y. Zhang, 1989).

*Order CRYPTONEMIALES* Schmitz, in Engler, 1892

F. SOLENOPORACEAE Pia, 1927

**First:** Petrophyton kiaeri Høeg, 1932, Kalstad Limestone, Upper or upper Middle Ordovician, Meldal, Trondheim area, Norway (Høeg, 1932, p. 82).

**Last:** Neosolenopora patrini Mastorilli, 1955, Middle Miocene (Helvetic), Pavia area (Mastorilli, 1955). Originally described as Lithophyllum vinassai by Patrini (1932). Also see Elliott (1965).

**Comment:** Unlike Solenopora, Petrophyton has well-developed cross-partitions and lacks septa-like projections, and is on this basis more likely to be an alga. The larger cells and absence of sporangia distinguish it from corallinaceans. See Johnson and Høeg (1961, pp. 22, 113).

F. PEYSSONELIACEAE Denisot, 1968

**First:** Pseudolithothamnium album Pfender, 1936, Lower Cretaceous (Barremian) (Moussavian, 1988).

**Comment:** Some Pennsylvanian phylloid algae have been compared with Squamariaceae (=Peyssoneliaceae) (Wray, 1977, p. 53). Also see Corallinaceae below.

**First:** F. CORALLINACEAE (Lamouroux) Harvey, 1849

**First:** Sporolithon rude Lemoine, 1925, Lower Cretaceous (Barremian), southern France.

**Comment:** Several coralline species appear for the first time in the Barremian. In addition to S. rude, these are Kymalithon belgicum Foslie, 1909 (Lemoine, 1970) and Parakymalithon phylloidum Bucur and Dragastan, 1985 (Moussavian, 1987; E. Moussavian pers. comm., 1992). Published reports of Jurassic (Johnson, 1961, p. 48; Johnson 1962, p. 19) and even Upper Triassic (Zankl, 1969; Elliott, 1979), corallinaceans appear to be misidentifications of Thaumatoporella (as Lemoine, 1970 suggests), or of solenoporaceans or Marinella. However, there are undescribed Upper Triassic red algae which resemble corallines and peyssonneliaceans (E. Moussavian pers. comm., 1992). The phylloid alga (see below) Archaeolithophyllum from the Pennsylvanian is likely a rhodophyte but is not a coralline.

**Phylum RHODOPHYTA**

F. MONILIPORELLACEAE Gnilovskaya, 1972

**First:** Contexta binata Gnilovskaya, 1972 and Ansporella ansa Gnilovskaya, 1972, Bestamalskaya Suite (upper part), (upper part of lower Caradoc), eastern Kazakhstan, Chingiz, right bank of the River Chagan, former USSR (Gnilovskaya, 1972, pp. 110–12, 117–19, and table p. 166).

**Last:** Moniliporella halysitoides Gnilovskaya, 1972, (Llandovery), eastern Kazakhstan, Chingiz, Kokaiykir Mountain, former USSR (Gnilovskaya, 1972, pp. 106–8). Chuvashov and Riding, 1984 (Fig. 1) show Moniliporellaceae ranging to end-Devonian, but do not give details.

**INCERTAE SEDIS 1**

F. GYMNOCODIACEAE Elliott, 1955

**First:** Lower Permian Permocalculus cf. P. ienellus (Pia), Upper Pseudoschwagerina Limestone, Rattendorf Stage, Austria (Flügel, 1966, p. 16).

**Last:** Permocalculus iagifuensis Simmons and Johnston, 1991, Lower Miocene (Burdigalian), Darai Limestone Formation, Papua New Guinea (Simmons and Johnston, 1991).

**Class RECEPTACULITAE** Sushkin, 1962
O. (TRE/ARG)—P. Mar.

**First:** Calathella Rauff, 1894; Calathella sp., Pogonip Group (TRE—ARG), Nevada, USA (Nitecki and Debrenne, 1979, pl. 4); and Calathium Billings 1863: Calathium sp., El Paso Group (ARG), West Texas, (Toomey, 1970, pp. 1323–4, Fig. 10).

**Last:** Unidentified genus, Permian, Sicily (Parona, 1933). Also see Rietschel and Nitecki (1984, p. 415).

**INCERTAE SEDIS 2**

The groups included here are generally extinct taxa which had calcite tests within the size limits of calcareous nanoplankton but with morphologies which are distinct from members of the Coccosphaerales.

F. CONUSPHAERACEAE (informal) Tr. (NOR)—K. (APT) Mar.

**First:** Exconusphaera zambachensis Jafar, 1983, Upper NOR.

**Last:** Conusphaera rothii (Thierstein, 1971), lower APT.

**Intervening:** RHT, SIN—lower TOA, U. KIM—BRM.


**First:** Discoasteroides brazilei Bukry and Percival, 1971.

**Last:** Discoaster browaeri (Tan, 1927), upper PIA.

**Intervening:** YPR—ZAN.


**First:** Fasciculithus magnus Bukry and Percival, 1971.

**Last:** Fasciculithus thomasii Perch-Nielsen, 1971.

**Intervening:** THA.


**First:** Goniolithus fluckigeri Deflandre, 1957 (Stradner, 1959).

**Last:** Goniolithus fluckigeri Deflandre, 1957.

**Intervening:** DAN—RUP.

**Comments:** Rare and sporadic stratigraphical distribution.


**First:** Heliolithus elegans (Roth, 1973).

**Last:** Heliolithus megastypus (Bramlette and Sullivan, 1961).


**First:** Trochoaster simplex Klumpp, 1953.

**Last:** Trochoaster deflandrei (Stradner, 1959).

**Intervening:** BRT—MES.


**First:** Pseudolithraphidites multibacillatus Keupp, 1976?

**Last:** Lithraphidites kennethii Perch-Nielsen, 1984, upper MAA.
Intervening: BER–CMP.

F. NANNOCONACEAE Deflandre, 1959

First: Nannoconus compressus Bralower and Thierstein, in Bralower et al., 1989, upper TTH.

Last: ?Nannoconus elongatus Bronnimann, 1955, upper CMP.

Intervening: BER–SAN.

Genus PRINSIOSPHAERA Jafar, 1983
Tr. (CRN–RHT) Mar.


Last: Prinsiosphaera triassica Jafar, 1983, upper RHT.

Intervening: NOR.

Genus SCAMPANELLA Forchheimer and Stradner, 1973 and Genus LAPIDECASSIS Black, 1971

First: Lapideacassis mariae Black, 1971?

Last: Scampanela bispinosa Perch-Nielsen, 1977

Intervening: CEN–LUT.

Comments: Extremely rare and sporadic stratigraphical distribution.

F. SPHENOLITHACEAE Deflandre, 1952


Last: Sphenolithus neoabies Bukry and Bramlette, 1969.

Intervening: YPR–ZAN.

F. TRIQUETRORHABDULACEAE Lipp, 1969


Last: Triquetrorhabdulus striatus Muller, 1974.

Intervening: AQT–TOR.

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du Sud de la France. Memoires du Museum Nationale d'Histoire 
Naturelle, Paris, 7 (10), 127–240.


Manton, I. and Leedale, G. F. (1969) Observations on the micro-
apatology of Coccolithus pelagicus and Criocapsa carterae, with 
special reference to the origin and nature of coccoliths and 
scales. Journal of the Marine Biological Association of the UK, 49,
1–16.

nannoplankton zonation, in Proceedings of the 2nd Planktonic 


Powell, A. J. (1986a) A dinoflagellate cyst biozonation for the late Miocene to middle Miocene succession of the Langhe region, northwestern Italy. Revue de Palaeontologie, 38, 9, 238–44.


**NOTE ADDED IN PROOF**

Hans and Runnegar (1992) extended the range of *Grypania,* a spirally coiled, carbonaceous cylindrical filament with transverse markings (1 mm wide and 90 mm long) from 1.800 Ma (Zhang, 1986) to 2.100 Ma and interpreted it as a non-calcified dasycladacean alga. Although such an affinity is equivocal, these fossils have been accepted as eukaryotic, with major implications for the composition of the coeval atmosphere previously considered anoxic (Riding, 1992).

Animals: Invertebrates

Sanctacaris uncata Briggs and Collins, 1988 from the Burgess Shale (Middle Cambrian) of Mount Stephen, British Columbia, Canada. The oldest chelicerate arthropod. The specimen is about 70 mm long. Photograph courtesy of D. E. G. Briggs; published with thanks to the Royal Ontario Museum.
The Protozoa embrace a wide and diverse group of organisms, regarded by many as a separate phylum and regarded by others as a taxonomic dustbin. Since the publication of the original *Fossil Record* in 1967, scanning electron microscopy and transmission electron microscopy have revolutionized the study of these minute organisms. This group, more than the majority of the groups represented in the fossil record, has received a great deal of attention from biologists and zoologists. It is therefore proposed that, for the purpose of this chapter, a biological classification should be adopted. The Protozoa are now regarded as a Subkingdom of the Kingdom Animalia – at least by the Society of Protozoologists, whose classification proposals were published in 1980 (Levine *et al.*, 1980). Unfortunately, while solving many of the micropalaeontological problems of the ‘animal-based’ workers, it separates out the botanically oriented forms. For micropalaeontologists, therefore, there are still problems, but at least many of the common groups (Foraminifera, Radiolaria, thecamoebians, dinoflagellates, etc.) can now be described in terms of their biological affinities.

The botanically related protistids have been dealt with in a separate chapter as, at the present time, this is probably the most logical grouping. The algae, dinoflagellates, acritarchs, diatoms, haptophytes and charophytes are to be found, therefore, in Chapter 3.
Fig. 4.1

First: Amphitrema Archer, 1867 (Europe) and Archerella Loeblich and Tappan, 1961 (Europe; North America).

**Extant**

Superfamily EUGLYPHACEA Wallich, 1864

F. EUGLYPHIDAE Wallich, 1864

T. (LUT/BRT)–Rec. FW

First: Euglypha Dujardin, 1840; cosmopolitan. Extant

Class GRANULORETICULOSEA De Saedeleer, 1934

Order FORAMINIFERIDA Eichwald, 1830

Alcide d’Orbigny (1826) was the first author to use the name ‘foraminifères’ for this group of protozoans. He regarded them as a subdivision of the Cephalopoda and, as such, only placed them in an informal classificatory position. This, in the opinion of many workers, invalidated his use of the word ‘foraminifera’, at least in the higher levels of classification. Many of the species he described at the same time are still used as valid taxa. This would appear to be slightly inconsistent and there may be some justification for attributing the Foraminiferida to d’Orbigny. Current accepted usage, however, dictates that Eichwald (1830) be regarded as the origin of the Order. Range data are from Loeblich and Tappan (1964, 1988) and other sources.

Suborder ALLOGROMIINA Loeblich and Tappan, 1961

F. MAYLISORIIDAE Bykova, 1961 C. (CRF)–S. FW

First: Chitinodendron Eisenack, 1938; USA; Estonia, former USSR; Germany.

Last: Silurian: same genus.

F. ALLOGROMIIDA Rhumbler, 1904

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**Fig. 4.1**

**First:** Chitinolagena Bykova, 1961 and Labyrinthochitinia Bykova, 1961; Kazakhstan, former USSR.  
**Extant**

F. HOSPITELLIDAE Loeblich and Tappan, 1984  
T. (Eoc.)—Rec. FW

**First:** Thalamophaga Rhumbler, 1911; France.  
**Extant**

Suborder TEXTULARIINA Delage and Hérouard, 1896

**Superfamily** ASTRORHIZACEA Brady, 1881

F. ASTRORHIZIDAE Brady, 1881  

**First:** Astorhiza Sandahl, 1858; cosmopolitan.  
**Extant**

F. BATHYSIPHONIDAE Avnimelech, 1952  

**First:** Platysolenites Eichwald, 1860; former USSR; Poland; Norway; USA: California.  
**Extant**

F. RHABDAMMINIDAE Brady, 1884  

**First:** Psammotadendron Norman, 1881; Romania.  
**Extant**

F. DRYORHIZOPSIDAE Loeblich and Tappan, 1984  

**First:** Dryorhizon Henbest, 1963; USA: Texas.  
**Extant**

F. SILICOTUBIDAE Vyalov, 1968  
Animals: Invertebrates

First: Silicotuba Vyalov, 1966; Poland; Germany; Czechoslovakia.  
Last: Upper Cretaceous (Senonian); same genus.

First: Hippocrepinella Heron-Allen and Earland, 1932; South Atlantic.  
Extant

First: Cellonina Kristan-Tollmann, 1971 (Austria); Psammosphaera Schulze, 1875 (cosmopolitan); Pseudostrophiza Eisenack, 1932 (Estonia, former USSR); Raibosammina Moreman, 1930 (USA: Oklahoma).  
Extant

First: Amphitremoida Eisenack, 1938 and Ordovicina Eisenack, 1938; Baltic region.  
Extant

First: Middle Ordovician (Trenton): Genus Kerionammina Moreman, 1933; USA: Oklahoma.  
Extant

Superfamily HIPPOCREPINACEA Rhumbler, 1895  
First: Arenosiphon Grubbs, 1939; Baltic region.  
Extant

First: Sansabaina Loeblich and Tappan, 1984; USA.  
Last: Kechenotiske Loeblich and Tappan, 1984; former USSR, western Siberia.  
Extant

Superfamily AMMODISCACEA Reuss, 1862  
First: Spirosolenites Glaessner, 1979; Norway: Finmark.  
Extant

Superfamily RZEHAKINACEA Cushman, 1933  
First: Miliammina Heron-Allen and Earland, 1930 (cosmopolitan) and Rothina Hanzliková, 1966 (Czechoslovakia: Carpathians).  
Extant

Superfamily HORMOSINACEA Haeckel, 1894  
First: Aschemocella Vyalov, 1966; Romania; former USSR.  
Extant

First: Reophax de Montfort, 1808; cosmopolitan.  
Extant

First: Thomasinella Schlumberger, 1893; Algeria; Tunisia; Egypt; India.  
Extant

First: Cribratina Sample, 1932; USA: Texas, Oklahoma.  
Last: Upper Cretaceous (lower Cenomanian); same genus; USA.

Superfamily LITUOLACEA de Blainville, 1827  
Last: same genus; USA.

First: Ammosiphonia He, 1977; China: Yunnan Province.  
Extant

First: Ammoscalaria Höglund, 1947; Asiatic former USSR; North and South Atlantic; North and South Pacific; Gulf of Mexico.  
Extant

Superfamily LITUOLIDAE de Blainville, 1827  
First: Plagiophythe Kristian-Tollmann, 1973; Late Ladinian, northern Alps; Germany; Bulgaria.  
Extant

First: Nautiloculina Mohler, 1938; former USSR; Egypt; Middle East; France; Switzerland; former Yugoslavia.  
Last: Murgeina Bilote and Decrouez, 1979; Italy; Greece; former Yugoslavia; Lebanon.

First: FabellocyColina Gendrot, 1964 (France; Israel).  
Last: GendrotellaMaync, 1972 (France) and FabellocyColina Gendrot, 1964 (France; Israel).  
Extant

First: Flabellocyclus Endr., 1964; Israel; France.  
Last: Endr. 1972 (France) and Flabellocyclus Endr., 1964 (France; Israel).  
Extant
First: Recurvoides Earland, 1934; former USSR. Extant

F. AMMOBACULINIDAE Saidova, 1981

First: Bulbobaculites Maync, 1952; Colombia; Germany; former USSR: Ukraine. Extant

F. HAPLOPHRAGMIIDAE Eimer and Fickert, 1899

First: Haplophragmium Reuss, 1860; Europe. Last: same genus.

F. LABYRINTHIDOMATIDAE Loeblich and Tappan, 1988


F. NEZZAZATIDAE Hamaoui and Saint-Marc, 1970

First: Nezzazatinella Darmoian, 1976; Iraq; Romania; France. Last: Antalyna Farinacci and K6yluoglu, 1985; Turkey.

F. BARKERINIDAE Smout, 1956

First: Barkerina Frizzell and Schwartz, 1950; USA: Texas; Greece; Sardinia. Last: same genus.

Superfamily BIOKOVINACEA Gusic, 1977

F. CHARENTIIDAE Loeblich and Tappan, 1985
J. (CLV)–K. (MAA) Mar.

First: Praekaraisella Kurbatov, 1972; Uzbekistan, former USSR. Last: Praepeneroplis Hofker, 1952; The Netherlands; France.

F. LITUOLIPORIDAE Gusic and Velic, 1978
J. (L.) Mar.


F. BIOKOVINIDAE Gusic, 1977


Superfamily COSCINOPHRAGMATACEA Thalmann, 1951

F. HADDONIIDAE Saidova, 1981

First: Haddonia Chapman, 1898; Cuba; Germany. Extant

F. COSCINOPHRAGMATIDAE Thalmann, 1951
Tr. (L.)–Rec. Mar.

First: Alpinophragmium Flugel, 1967; Germany. Extant

Superfamily CYCLOLINACEA Loeblich and Tappan, 1964

F. CYCLOLINIDAE Loeblich and Tappan, 1964


F. ORBITOPSELLIDAE Hottinger and Caus, 1982
J. (L.–KIM) Mar.

First: Cyclorbitopsella Cherchi, Schroeder and B. G. Zhang, 1984 (Tibet), Labyrinthina Weynschenk, 1951 (Spain; Morocco; former USSR; Italy; former Yugoslavia) and Orbitopsella Munier-Chalmas, 1902 (Italy; Cyprus; former Yugoslavia; Greece; Mallorca; Morocco; Iran; Oman; Arabia; China).

Last: Labyrinthina Weynschenk, 1951; as above.

Superfamily LOFTUSIACEA Brady, 1884

F. MESOENDOTHYRIDAE Voloshinova, 1958
Tr. (LAD)–J. (TT) Mar.

First: Mesoendothyra Dain, 1958; Bulgaria; former Yugoslavia; former USSR: Ukraine. Last: Audienusina Bernier, 1985; France.

F. HOTTINGERITIDAE Loeblich and Tappan, 1985

First: Alveosepta Hottinger, 1967; Switzerland; France; Portugal; Morocco. Last: Hottingerita Loeblich and Tappan, 1985; Switzerland.

F. CYCLAMMINIDAE Marie, 1941
J. (L.)–Rec. Mar.

First: Amijiella Loeblich and Tappan, 1985; Iraq; Turkey; Italy; France; Switzerland; former Yugoslavia. Extant

F. ECOUGELLIDAE Loeblich and Tappan, 1985

First: Genus Ecougella Arnaud-Vanneau, 1980; France. Last: same genus.

F. SPIROCYCLINIDAE Munier-Chalmas, 1887
J. (L.)–T. (Eoc.) Mar.

First: Haurania Henson, 1948; (Morocco, Iraq, China) and Streptocyclammina Höttinger, 1967; (Morocco, Italy, former Yugoslavia)

Last: Saudia Henson, 1948; Saudi Arabia; Iraq; former Yugoslavia.

F. LOFTUSIIDAE Brady, 1884

First: Praereticulinella Deloffre and Hamaoui, 1970; Spain. Last: Loftusia Brady, 1870 (Iran, Turkey, Sumatra) and Reticulinella Cuvillier, Bonnefous, Hamaoui and Tixier, 1970 (Algeria, Libya).

Superfamily SPIROPLECTAMMINACEA Cushman, 1927

F. SPIROPLECTAMMINIDAE Cushman, 1927

First: Spiroplectammina Cushman, 1927; cosmopolitan. Extant

F. TEXTULARIOPSIDAE Loeblich and Tappan, 1982

First: Textulariopsis Banner and Pereira, 1981; cosmopolitan.
**Animals: Invertebrates**

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**Fig. 4.2**

**Last:** *Plectinella* Marie, 1956 (Egypt, France, Belgium, former USSR: Belorussia, Australia, USA: Texas) and *Pleurostomelloides* Majzon, 1943 (Hungary).


**First and Last:** *Plectorecurvoides* Noth, 1952; Austria; Czechoslovakia; former USSR; Eastern Atlantic.


**First:** *Abdullaevia* Suleymanov, 1965; former USSR: Uzbekistan, Kyzyl Kum.

**Superfamily** *PAVONITONACEA* Loeblich and Tappan, 1961


**First and Last:** *Hensonia* Marie, 1954 (France, Spain) and *Marieita* Loeblich and Tappan, 1964 (France, Spain).


**First:** *Pavonitina* Schubert, 1914; France; Poland; Austria; former Yugoslavia; Africa: offshore Cabinda (Angola).

**Last:** *Spiropsammia* Seiglie and Baker, 1984; Italy; Cameroon; Cabinda, Angola.

**Superfamily** *TROCHAMMINACEA* Schwager, 1877

**F. TROCHAMMINIDAE** Schwager, 1877 **C.** (u.)–Rec. Mar.
**Protozoa**

**Superfamily** VERNEUILINACEA Cushman, 1911

**F. CONOTROCHAMMINIDAE** Saidova, 1981

*First:* *Conotrochammina* Finlay, 1940; New Zealand.

*Last:* *Riyadhella* Redmond, 1965; Saudi Arabia; western India.

**Superfamily** ATAXOPHRAGMIACEA Schwager, 1877

**F. ATAXOPHRAGMIIDAE** Schwager, 1877

*First:* *Agglutisolena* Senowbari-Daryan, 1984 (Italy: Sicily) and *Kaeveria* Senowbari-Daryan, 1984 (Turkey, Italy: Sicily, Austria)

*Last:* *Arenobulimina* Cushman, 1927 (Europe, USA: Arkansas, Texas) and *Ataxophragmium* Reuss, 1860 (France, Germany, England, UK, Sweden, former USSR).

**F. GLOBOTEXTULARIIDAE** Cushman, 1927

*First:* *Remesella* Vašek, 1947; Czechoslovakia; Switzerland; Austria; Romania; former USSR: Crimea; New Zealand.

*Last:* *Mooreinella* Cushman and Waters, 1928; USA: Texas; Australia.

*First:* *Riyadhella* Redmond, 1965; Saudi Arabia; western India.

*Last:* *Mooreinella* Cushman and Waters, 1928; USA: Texas; Australia.

*First:* *Conotrochammina* Finlay, 1940; New Zealand.

*Last:* *Riyadhella* Redmond, 1965; Saudi Arabia; western India.

*First:* *Agglutisolena* Senowbari-Daryan, 1984 (Italy: Sicily) and *Kaeveria* Senowbari-Daryan, 1984 (Turkey, Italy: Sicily, Austria)

*Last:* *Arenobulimina* Cushman, 1927 (Europe, USA: Arkansas, Texas) and *Ataxophragmium* Reuss, 1860 (France, Germany, England, UK, Sweden, former USSR).

*First:* *Remesella* Vašek, 1947; Czechoslovakia; Switzerland; Austria; Romania; former USSR: Crimea; New Zealand.

*Last:* *Mooreinella* Cushman and Waters, 1928; USA: Texas; Australia.

*First:* *Conotrochammina* Finlay, 1940; New Zealand.

*Last:* *Riyadhella* Redmond, 1965; Saudi Arabia; western India.

*First:* *Agglutisolena* Senowbari-Daryan, 1984 (Italy: Sicily) and *Kaeveria* Senowbari-Daryan, 1984 (Turkey, Italy: Sicily, Austria)

*Last:* *Arenobulimina* Cushman, 1927 (Europe, USA: Arkansas, Texas) and *Ataxophragmium* Reuss, 1860 (France, Germany, England, UK, Sweden, former USSR).

*First:* *Remesella* Vašek, 1947; Czechoslovakia; Switzerland; Austria; Romania; former USSR: Crimea; New Zealand.

*Last:* *Mooreinella* Cushman and Waters, 1928; USA: Texas; Australia.

First: Guppyella Brönnimann, 1951; West Indies; Costa Rica; Venezuela. Extant


First: Palaeolitulonella Bérczi-Makk, 1981; Hungary; Italy; former Yugoslavia; Austria; Bulgaria. Last: Cuneolina d'Orbigny, 1839; China; USA; Europe.


First: Dicyclina Munier-Chalmas, 1887; France; Spain; former Yugoslavia. Last: same genus.


First: Conorhinella Poroshina, 1976; France; former USSR: Azerbaijan SSR. Last: Dictyopsella Munier-Chalmas, 1900; France; Spain.


First: Pseudolitulonella Marie, 1955; France; Spain; Israel; Turkey. Last: Coleiconus Höttinger and Drobné, 1980 (West Indies, USA; Florida), Coskinolina Stache, 1875 (former Yugoslavia, France) and Coskinon Höttinger and Drobné, 1980 (former Yugoslavia, Czechoslovakia, USA: Florida).

Superfamily ORBITOLINACEA Martin, 1890

F. ORBITOLINIDAE Martin, 1890 J. (m.)–T. (RUP/CHT) Mar.

First: Gutniciella Moullade, Haman and Huddleston, 1981 (Spain: Balearic Islands), Kilianina Pfender, 1933 (France) and Meyendorfina Aurouze and Bizon, 1958 (France). Last: Dictyococcus Blanckenhorn, 1900; cosmopolitan.

Superfamily TEXTULARIACEA Ehrenberg, 1838


First: Pseudomarssonella Redmond, 1965; Saudi Arabia; western India. Extant


First: Textularia De France, 1824; cosmopolitan. Extant


First: Clavulinopsis Banner and Desai, 1985 (USA: Texas, Arkansas), Pseudoclavulina Cushman, 1936 (Mexico, West Indies: Trinidad, USA, England, UK, Denmark, Poland, Sweden, Germany, The Netherlands), Pseudogaudryina Cushman, 1936 (West Indies, USA: South Carolina, Australia, Gulf of Mexico, Atlantic, Germany) and Valvoreussella Hofker, 1957 (Czechoslovakia, Germany, The Netherlands). Extant


First: Arenagula Bourdon and Lys, 1955 (France, Greece, USA: Florida, Pacific: Marshall Islands), Discorinopsis Cole, 1941 (USA: Florida) and Valvulammina Cushman, 1933 (France, Cuba). Last: Arenagula as above.


First: Clavulina d'Orbigny, 1826; cosmopolitan. Extant


First: Arkaeocella Pronina, 1964 (former USSR) and Eoammosphaeroides Pronina, 1970 (former USSR). Last: Insolentitheca Vachard, 1979; former USSR: southern Urals, Donbas, Kazakhstan; Belgium; France; Spain; Algeria; Morocco; Libya; Afghanistan; Japan; northern Thailand.


F. URALINELLIDAE Chuvashov et al., 1984
Last: Sogdianina Saltovskaya, 1973; former USSR: Tadzhikistan.

F. AURORIIDAE Loeblich and Tappan, 1986
First: Aupertororia Sabirov, 1984 (former USSR) and Auroria Poyarkov, 1969 (former USSR: Kirgiz).
Last: same genera.

F. USLONIIDAE Miklukho-Maklay, 1963
First: Bisphaera Birina, 1948; former USSR.
Last: same genus.

F. EOVOVOLUTINIDAE Loeblich and Tappan, 1986
Last: Eovolutina as above.

F. TUBERITINIDAE Miklukho-Maklay, 1958
S. (LLY)–P. Mar.
First: Illigata Bykova, 1956; Lithuania, former USSR.
Last: Tuberitina Gallaway and Harlton, 1928; cosmopolitan.

Superfamily EARLANDIACEA Cummings, 1955
F. EARLANDIIDAE Cummings, 1955
First: Earlandida Plummer, 1930; USA: Texas; England, UK; former USSR: Poland.

F. PSEUDOAMMODOCIDAE Conil and Lys, 1970
First: Brusniia Mikhaylov, 1935 (former USSR, Belgium) and Pseudoglossospira Bykova, 1955 (former USSR: Urals, Russian Platform).

F. PSEUDOLITUOTUBIDAE Conil and Longerstaey, 1980
First: Pseudolituo tuba Vdovenko, 1971; western Europe; former USSR.
Last: same genus.

Superfamily ARCHAEDISCACEA Cushman, 1928
F. ARCHAEDISCIDAE Cushman, 1928
Last: Archaediscus and Asteroarchaediscus as above.

F. LASIODISCIDAE Reytinger, 1956
C. (VIS)–P. Mar.
First: Houchinia Cushman, 1927; England, UK; Belgium; former USSR; Iran; USA: Alaska; Canada.
Last: Glomotrocholina Nikitina, 1977 (former USSR), Lasiodiscus Reichel, 1946 (former USSR, Cyprus, Greece) and Lasiotrochus Reichel, 1946 (Greece, former USSR: Azerbajian).

Superfamily MORAVAMMINACEA Pokorny, 1951
F. CALIGELLIDAE Reytinger, 1959
First: Glubokoerve1a Pronina, 1970 (former USSR) and Paracaligella Lipina, 1955 (former USSR, USA).
Last: Baituganella Lipina, 1955 (former USSR) and Paracaligella as above.

F. MORAVAMMINIDAE Pokorny, 1951
D. (GIV–FRS) Mar. (see Fig. 4.3)
First: Kettnerammina Pokorny, 1951 (Czechoslovakia), Moravammina Pokorny, 1951 (Czechoslovakia, former USSR) and Saccorhina Bykova, 1955 (former USSR).
Last: Kettnerammina and Saccorhina as above.

F. PARATIKHINELLIDAE Loeblich and Tappan, 1984
First: Vasiczek Kokorny, 1951; Czechoslovakia.

Superfamily NODOSINELLACEA Rhumber, 1895
F. EARLANDINITIDAE Loeblich and Tappan, 1984
First: Tikkiniella Bykova, 1952; former USSR: Russian Platform; Canada.
Last: Earlandinita Cummings, 1955 (USA: Texas, Great Britain) and Lugtonia Cummings, 1955 (USA, UK).

F. NODOSINELLIDAE Rhumber, 1895
S. (LUD)–P. Mar.
First: Eolagena Lipina, 1959; former USSR: Siberia.
Last: Biparietata Zolotova, 1980 (former USSR: Urals) and Nodosinella Brady, 1876 (England, UK).

Superfamily GEINITZINACEA Bozorgnia, 1973
F. GEINITZINIDAE Bozorgnia, 1973
First: Frondilina Bykova, 1952; former USSR; USA: Alaska.
Last: Lunucammina Spandel, 1898; Europe; Asia; Australia; North America.
F. PACHYPHLOIIDAE Loeblich and Tappan, 1984

First: *Pachyphloia* Lange, 1925; Malay Archipelago; Sumatra; former USSR; Iran; Turkey.

Last: *Maichelina* Sosnina, 1977 (former USSR) and *Robustopachyphloia* Lin, 1980 (China).

**Superfamily** COLANIELLACEA Fursenko, 1959

F. COLANIELLIDAE Fursenko, 1959

First: *Multiseptida* Bykova, 1952; former USSR: Russian Platform; Canada: Alberta; USA: Alaska.

Last: *Colaniella* Likharev, 1939 (Vietnam, China, Japan, former USSR, Greece, Turkey), *Cylindrocolaniella* Loeblich and Tappan, 1985 (former eastern USSR) and *Pseudowanganella* Sosnina, 1983 (former USSR).

**Superfamily** PTYCHOCLADIACEA Elias, 1950

F. PTYCHOCLADIDAE Elias, 1950

First: *Shuguria* Antropov, 1950; former USSR: Russian Platform.

Last: * Ptychocladia* Ulrich and Bassler, 1904; USA: Illinois, Nebraska, Oklahoma).

**Superfamily** PALAEOTEXTULARIACEAE Galloway, 1933

F. SEMITEXTULARIIDAE Pokorny, 1956
D. (GIV)–C. (u.) Mar.

First: *Paratextularia* Pokorny, 1951; USA: Iowa; Czechoslovakia; Poland; former USSR: Russian Platform.

Last: *Koskinotextularia* Eickhoff, 1968; Germany; Belgium; France; USA: Oklahoma; Canada.

F. PALAEOTEXTULARIIDAE Galloway, 1933
C. (TOU)–P. Mar.

First: *Palaeotextularia* Schubert, 1921; cosmopolitan.

Last: *Climacammina* Brady, 1873 (cosmopolitan), *Cribrrogenerina* Schubert, 1908 (Sumatra, former USSR, USA) and *Palaeobigenerina* Galloway, 1933 (cosmopolitan).

F. BISERIAMMINIDAE Chernysheva, 1941

First: *Biseriammina* Chernysheva, 1941; former USSR: Urals, Bashkirian.

Last: *Globivalvulina* Schubert, 1921 (cosmopolitan), *Paraglobivalvulina* Reytingler, 1965 (former USSR, Turkey, Iran, India, Thailand, China), *Paraglobivalvulinoides* Zaninetti and Jenny-Deshusses, 1985 (Iran), *Dagmarita* Reytingler, 1965 (former USSR, India, Iran, Turkey, China), *Paradagmarita* Lys, 1978 (Turkey, Iran, Oman, Afghanistan) and *Louisettita* Altiner and Brönnimann, 1980 (Turkey).

**Superfamily** TOURNAYELLACEA Dain, 1953

F. TOURNAYELLIDAE Dain, 1953


Last: *Chernobaculites* Conil and Lys, 1977; former USSR: Europe: Pyrenees.

F. PALAEOSPIROPLECTAMMINIDAE Loeblich and Tappan, 1984


### Protozoa

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<thead>
<tr>
<th>Permian</th>
<th>1. Moravaminidae</th>
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<tbody>
<tr>
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<td>3. Earlandinitidae</td>
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<tr>
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<td>7. Colaniellidae</td>
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<td>24. Schwagerinidae</td>
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*Fig. 4.3*
**Superfamily ENDOTHYRACEA Brady, 1884**

F. ENDOHYRIDAE Brady, 1884


**First:** Klubovella Lebedeva, 1956 (former USSR) and Quasendothyra Rauzer-Chernousova, 1948 (former USSR, Turkey).

**Last:** Endothyranella Galloway and Harloton, 1930; former USSR; USA; Texas, Oklahoma, Indiana.

F. BRADYINIDAE Reytinger, 1950


**First:** Bradyina von Möller, 1878; former USSR; Iran; Mongolia; China; UK: England, Scotland; Belgium; USA.

**Last:** Pseudobradyina Reytinger, 1950; former USSR; Moscow Basin, central Asia; USA: Kansas.

**Superfamily TETRATAXACEA Galloway, 1933**

F. PSEUDOTAXIDAE Mamet, 1974


**First:** Pseudotaxis Mamet, 1974; Europe; Asia; North America; Australia.


F. TETRATAXIDAE Galloway, 1933


**First:** Tetrataxis Ehrenberg, 1854; UK: England, Scotland; Belgium; Spain; Poland; Algeria; Iran; former USSR; China; India; Australia; USA.

**Last:** Tetrataxis as above and Polytaxis Cushman and Waters, 1928 (USA, Austria, Algeria).

F. VALVULINELLIDAE Loeblich and Tappan, 1984


**First:** Valvulinella Schubert, 1908; England, UK; Scotland, UK; Belgium; Germany; former Yugoslavia; Turkey; former USSR; North America.

**Last:** Same genus.

F. ABADEHILLIDAE Loeblich and Tappan, 1984


**First and Last:** Abadehella Okimura and Ishi, 1975; Iran; India; Malaysia: Japan; Cambodia; former USSR.

**Superfamily FUSULINACEA von Möller, 1878**

F. LOEBLICHIIDAE Cummings, 1955


**First:** Rhenothyra Beckman, 1950; Germany.

**Last:** Seminovella Rauzer-Chernousova, 1951; former USSR.

F. OZAWAINELLIDAE Thompson and Foster, 1937


**First:** Millerella Thompson, 1942 (North America, former USSR, North Africa, China, Japan), Chomatomediciods Vdovenko, 1973 (former USSR), Eostaffelia Rauzer-Chernousova, 1948 (North America, Europe, Asia), Mediciods Rozovskaya, 1961 (USA, Canada), Ninella Malakhova, 1975 (former USSR), Plectomediciods Brazhnikova and Vdovenko, 1983 (former USSR) and Pseuendo-thyra Mikhaylov, 1939 (former USSR, Mongolia, China, Japan, North America, Europe).

**Last:** Eostaffeloides Mikulko-Maklay, 1959 (former USSR), Parareichelina Mikulko-Maklay, 1959 (former USSR), Pseudokahlerina Sosnina, 1968 (former USSR), Reichelina Erk, 1942 (former USSR, China, SE Asia, Greece, Turkey, North America), Sichonetella Tumanskaya, 1953 (former USSR), Kangvarella Saurin, 1962 (Cambodia) and Primorina Sosnina, 1981 (former USSR).

F. SCHUBERTELLIDAE Skinner, 1931


**First:** Eoschubertella Thompson, 1937 (North and South America, Europe, Asia), Fusella Lee and Chen, 1930 (former USSR, North America, China, Japan) and Neo fusulinellina Deprat, 1912 (Laos).

**Last:** Neooschubertella Saurin, 1962 (Cambodia, Laos), Codonofusiella Dunbar and Skinner, 1937 (USA, Canada, Japan, Cambodia, Pakistan, former Yugoslavia, Greece, Turkey, former USSR), Dunbarula Ciry, 1948 (former Yugoslavia, former USSR, China, Japan, North Africa, North America), Gallowaiina Chen, 1934 (former USSR, southern China), Miniojapanella Fujimoto and Kanuma, 1953 (Japan, China, Inner Mongolia, Sumatra, former Yugoslavia, former USSR), Nanlingella Rui and Sheng, 1981 (southern China), Palaeofusulina Deprat, 1912 (Vietnam, China, Japan, Timor, former USSR, former Yugoslavia), Paradoxiella Skinner and Wilde, 1955 (USA, Japan), Parandumbarula Skinner, 1969 (Turkey, southern China, former USSR), Parananlingella Rui and Shen, 1981 (southern China), Russiella Mikulko-Maklay, 1957 (southern China, former USSR), Tewoella Sun, 1979 (northern China) and Ziguelli Lin, 1980 (China).

F. FUSULINIDAE von Möller, 1878


**First:** Verella Dalmatskaya, 1951 (former USSR), Eowedekindellina Ektova, 1977 (former USSR).

**Last:** Yangchienia Lee, 1934; southern China; Japan; Korea; former USSR; former Yugoslavia; Sicily; Greece; Turkey; Afghanistan; Algeria.

F. SCHWAGERINIDAE Dunbar and Henbest, 1930


**First:** Moniparus Rozovskaya, 1948; former USSR, China.

**Last:** Darasites Mikulko-Maklay, 1959 (former USSR, China, Japan), Nipponitella Hanzawa, 1938 (Japan, former USSR) and Rugososchwagerina Mikulko-Maklay, 1959 (Sicily, Iran, Iraq, Afghanistan, China, former USSR).

F. STAFFELLIDAE Mikulko-Maklay, 1949


**First:** Reitlingerina Rauzer-Chernousova, 1985; Europe; Asia; Canada.

**Last:** Eoverbeekina Lee, 1934; former USSR; China; Japan; former Yugoslavia; USA; Beliz; Guatemala; Mexico.

F. VERBEEKINIDAE Staff and Wedekind, 1910


**First:** Brexia Schenck and Thompson, 1940 (Laos, Japan, southern China, former USSR) and Miselina Schenck and Thompson, 1940 (former USSR, Japan, China, Laos, Turkey, Sumatra, former Yugoslavia).

**Last:** Pseudodoliolina Yabe and Hanzawa, 1932; Japan; Vietnam; China; former USSR; USA.

First: Shengella Yang, 1985; China.
Last: Yabeina Deprat, 1914; Japan; China; Vietnam; Cambodia; New Zealand; former USSR; Canada; USA.

Suborder INVOLUTINA Hohenegger and Piller, 1977 F. INVOLUTINIDAE Butschli, 1880 P. (ROT)–K. (CEN) Mar. (see Fig. 4.4)

First: Neohemigordius Wang and Sun, 1973; China.
Last: Hensonina Moullade and Peybernes, 1974 (Qatar, northern Spain), Involutina Terquem, 1862 (Europe, Asia) and Trocholina Paalzow, 1922 (cosmopolitan).

F. HIRSUTOSPIRELLIDAE Zainetti et al., 1985 Tr. (NOR) Mar.

First and Last: Hirsutospirella Zainetti et al., 1985; former Yugoslavia; Sicily.


First: Archaeosepta Wernli, 1970; France; Sardinia.
Last: Protopenoperlis Weynschenck, 1950; Austria; Italy; France; former Yugoslavia; Switzerland; Israel; Turkey.


First: Brasiliella Troelson, 1978; Brazil.

Superfamily CORNUSPIRACEA Schultze, 1854 F. CORNUSPIRIDAE Schultze, 1854 T. (MMI)–Rec. Extant

First: Tuberochilus Lin, 1984; China; Sumatra.


First: Septagathammina Lin, 1984; China; Sumatra.

F. FISCHERINIDAE Millett, 1898 J. (BAJ)–Rec. Extant

First: Dolosella Danich, 1969; former USSR; England, UK.
Last: F. NUBECULARIIDAE Jones, 1875 Tr. (ANS)–Rec. Extant

First: Gheorghianina Loeblich and Tappan, 1986; Romania; Bulgaria.

F. OPHTHALMIDIIDAE Wiesner, 1920 Tr. (ANS)–Rec. Extant

First: Eoophthalmidium Langer, 1968; Turkey.
Last: F. DISCOSPIRINIDAE Wiesner, 1931 T. (MMI)–Rec. Extant

First: Discospirina Munier-Chalmas, 1902; Atlantic; Mediterranean.

Superfamily MILIOLACEA Ehrenberg, 1839 F. MILIOLECHINIDAE Zaninetti et al., 1985 Tr. (NOR)–Rec. Extant

First: Miliolechina Zaninetti et al., 1985; former Yugoslavia.
Last: F. SPIROLOCULINIDAE Wiesner, 1920 J. (BAJ)–Rec. Extant

First: Palaeomiliolina Antonova, 1959; former USSR.
Last: F. HAUERINIDAE Schwager, 1876 J. –Rec. Extant

First: Cycloforina Luczkowska, 1972; cosmopolitan.
Last: F. MILIOLIDAE Ehrenberg, 1839 T. (LUT)–Rec. Extant

First: Neaguites Andersen, 1984 (USA) and Miliola Lamarck, 1804 (France, Belgium, USA).

First: Pseudohauerina Ponder, 1972; Atlantic; Pacific.

F. RHAPYDIONINIDAE Keijzer, 1945 K. (CEN)–?Rec. Extant

First: Lacazina Munier-Chalmas, 1882 (France, Spain, Israel) and Periloculina Munier-Chalmas and Schlumberger, 1885 (France).
Last: Lacazinella Crespin, 1962; New Guinea; Indonesia; Turkey.
### Fig. 4.4

**First:** *Pseudedomia* Henson, 1948; Qatar; Kuwait; Tunisia; Lebanon; Iraq; Israel; Italy; Portugal; former Yugoslavia; Greece.  
**Extant**

**Comment:** The extant species may have been a reworked Cretaceous specimen.

**F. ALVEOLINIDAE** Ehrenberg, 1839  
**K. (APT)—Rec. Mar.**  

**First:** *Archealveolina* Fourcade, 1980; Spain; Italy; Algeria.  
**Extant**

**Superfamily** *SORITACEA* Ehrenberg, 1839  
**F. MILIOLIPORIDAE** Brönniman and Zaninetti, 1971  
**P. (DZL)—Tr. (RHT) Mar.**  

**First:** *Kamurana* Altiner and Zaninetti, 1977; Turkey; Bulgaria.  
**Last:** *Galeanella* Kristan, 1958 (Austria, former Yugoslavia, Iran). *Orthotrinacria* Zaninetti et al., 1985 (Turkey, Sicily, former Yugoslavia), *Cucurbita* Jablonsky, 1973 (Czechoslovakia, Sicily, Greece) and *Miliolipora* Brönniman and Zaninetti, 1971 (Austria, Czechoslovakia, Iran).

**F. SIPHONOFERIDAE** Senowbari-Daryan and Zaninetti, 1986  
**Tr. (NOR) Mar.**  

**First and Last:** *Siphonofera* Senowbari-Daryan, 1983; Sicily.  
**F. PENEROPLIDAE** Schultze, 1854  
**K. (CON)—Rec. Mar.**
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**Fig. 4.4**

**First**: Vandenbroeckia Marie, 1958; France.

**Extant**

F. MEANDROPSINIDAE Henson, 1948

**First**: Broeckina Munier-Chalmas, 1882 (France, Syria) and Pastrikella Cherchi, Radočić and Schroeder, 1976 (former Yugoslavia, France).

**Last**: Hottingerina Drobné, 1975; former Yugoslavia.


**First**: Edomiida Henson, 1948 (Iran, Israel) and Pseudohypridionina de Castro, 1971 (Italy, Israel, Algeria).

**Extant**


**First**: Genus Pavlovicina Loeblich and Tappan, 1988; France; Switzerland.

**Extant**

**Suborder** SILICOLOCULININA Resig et al., 1980

F. SILICOLOCULINIDAE Resig et al., 1980

**First**: Miliammulis Saidova and Burmistrova, 1978; Bering Sea; Antarctic; North and Central Pacific and Indian Oceans.

**Extant**

**Suborder** LAGENINA Delage and Hérouard, 1896

**Superfamily** ROBULOIDACEA Reiss, 1963

F. SYZRANIIDAE Vachard, 1981
S. (PRD)–P. (DZH) Mar. (see Fig. 4.5)

**First**: Tuborectina Pronina, 1980; former USSR.

**Last**: Rectostipulina Jenny-Deshusses, 1985; Turkey; Cyprus; Greece; Afghanistan; Iran; India; former USSR: Armenia.

**Extant**

F. ICHTHYOLARIIDAE Loeblich and Tappan, 1986

**First**: Protonodosaria Gerke, 1959; former USSR: China; Burma.
Fig. 4.5

Last: *Lingulonodosaria* Silvestri, 1903; cosmopolitan.

F. ROBULOIDIDAE Reiss, 1963 P. (‘m.’)–J. (KIM) Mar.

First: *Robuloides* Reichel, 1946; Greece; Italy; former Yugoslavia; Austria; former USSR; Sumatra.

Last: *Partitionulina* Pelissié and Peybernes, 1982; France.


First: *Xintania* Lin, 1984; China.

Last: *Partisania* Sosnina, 1978; former USSR.

Superfamily NODOSARIACEA Ehrenberg, 1838

F. NODOSARIIDAE Ehrenberg, 1838 Tr. (RHT)–Rec. Mar.

First: *Berthelina* Loeblich and Tappan, 1957; France; Austria; USA: Alaska. Extant


First: *Lenticulina* Lamarck, 1804 (cosmopolitan) and *Vaginulinopsis* Silvestri, 1904 (cosmopolitan) Extant


First: *Reussolina* Colom, 1956; cosmopolitan. Extant

F. POLYMORPHINIDAE d’Orbigny, 1839 Tr. (RHT)–Rec. Mar.
Protozoa

**Suborder** GLOBIGERININA Delage and Hérouard, 1896

**Superfamily** HETEROHELICACEA Cushman, 1927

**F. GUEMBELITRIIDAE** Montanaro Gallitelli, 1957


First: Guemebelitria Cushman, 1933; cosmopolitan. Extant

**F. HETEROHELICIDAE** Cushman, 1927


First: Spiroplecta Ehrenberg, 1844; cosmopolitan.

Last: Spiroplecta as above and Bipacina Parker and Jones, 1872 (Europe, North America, Africa).

F. CHILOGUENMELINIDAE Reiss, 1963


First: Chiloguembelina Loeblich and Tappan, 1956; cosmopolitan. Extant

**Superfamily** PLANOMALINACEA Bolli et al., 1957

F. GLOBIGERINELLOIDIDAE Longoria, 1974


First: Blowiella Kretzschmar and Gorbachik, 1971 (cosmopolitan) and Globigerinelloides Cushman and ten Dam, 1948 (cosmopolitan).

Last: Globigerinelloides as above.

F. PLANOMALINIDAE Bolli et al., 1957


First and Last: Planomalina Bertram and Kemper, 1982; Germany; USA: Texas, California; Atlantic; Caribbean.

F. SCHACKOINIDAE Pokorny, 1958


First: Leupoldina Bolli, 1957; Trinidad; Mexico; France; Tunisia. Extant

Last: Schackoina Thalmann, 1932; cosmopolitan.

**Superfamily** ROTALIPORIDAE Sigal, 1958

F. HEDBERGELLIDAE Loeblich and Tappan, 1961


First and Last: Hedbergella Brönnimann and Brown, 1958; cosmopolitan.

F. GLOBULIGERINIDAE Loeblich and Tappan, 1984


First: Conoglobigerina Morozova, 1961; former USSR: Caucasus, Crimea, Azerbaijan; Turkmenia; Poland; Bulgaria; Canada: Nova Scotia. Extant

Last: Globigerina Bignot and Guyader, 1971; former USSR: Lithuania, Komi, Turkmen, Dagestan, Caucasus, Azerbaijan, Crimea; Sweden; France; Germany.

F. FAVUSELLIDAE Longoria, 1974


First and Last: Favusella Michael, 1973; cosmopolitan.

F. ROTALIPORIDAE Sigal, 1958

Animals: Invertebrates

First and Last: *Clavihedbergella* Banner and Blow, 1959; Europe; North America.

**Superfamily** GLOBOTRUNCANACEA Brotzen, 1942

**F. GLOBOTRUNCANIDAE** Brotzen, 1942

**K.** (TUR-MAA) Mar.

**First:** Sigalitruncana Korchagin, 1982 (cosmopolitan) and Marginotruncana Hofker, 1956 (cosmopolitan).

**Last:** Gansserina Caron et al., 1984 (Trinidad, Spain, Turkey, Egypt, Tunisia, Mid-Pacific), Globotruncana Cushman, 1927 (cosmopolitan), Kassabiana Salaj and Brown, 1956 (Cuba, Trinidad), Globotruncanella Reiss, 1957 (cosmopolitan) and Abathomphalus Bolli et al., 1957 (cosmopolitan).

**F. RUGOGLOBIGERINIDAE** Subbotina, 1959

**K.** (CON-MAA) Mar.

**First:** Archaeoglobigerina Pessagno, 1967; cosmopolitan.

**Last:** Archaeoglobigerina as above, Bucherina Bronnimann and Brown, 1956 (Cuba, North and South Atlantic, Egypt), Klugerina Bronnimann and Brown, 1956 (Trinidad, Tunisia) and Trinitella Bronnimann, 1952 (cosmopolitan).

**Superfamily** GLOBOROTALIACEA Cushman, 1927

**F. EOGLOBIGERINIDAE** Blow, 1979

**T.** (DAN-THA) Mar.

**First:** Eoglobigerina Morozova, 1959 (cosmopolitan), Globoconusa Khalilov, 1956 (cosmopolitan), Parvularugoglobigerina Hofker, 1978 (Italy, Germany, Spain, former USSR: Caspian Sea, Pacific. Atlantic: off Florida, Caribbean) and Postrugoglobigerina Salaj, 1986 (NW Tunisia).

**Last:** Eoglobigerina as above.

**F. GLOBOROTALIIDAE** Cushman, 1927


**First:** Planorotalites Morozova, 1957; cosmopolitan. **Extant**

**F. TRUNCOROTALOIDIDAE** Loeblich and Tappan, 1961

**T.** (THA-PRB) Mar.

**First:** Morozovella McGowran, 1968; cosmopolitan.

**Last:** Murioglobigerina Blow, 1979; cosmopolitan.

**F. PULLENIATINIDAE** Cushman, 1927

**T.** (PRB-MMI) Mar.

**First:** Globigerinopsis Bolli, 1962; Venezuela; Dominican Republic. **Extant**

**F. CANDEINIDAE** Cushman, 1927

**T.** (LUT)-Rec. Mar.

**First:** Tenuitella Fleisher, 1974; cosmopolitan. **Extant**

**F. CATAPSYDRACIDAE** Bolli, Loeblich and Tappan, 1957


**First:** Subbotina Broten and Pozarsyska, 1961; cosmopolitan. **Extant**

**Superfamily** HANTKENINACEA Cushman, 1927

**F. GLOBANOMALINIDAE** Loeblich and Tappan, 1957

**T.** (DAN-RUP) Mar.

**First and Last:** Globanomalina Haque, 1956; cosmopolitan.
First: *Islandiella* Nørvang, 1959; cosmopolitan. Extant

F. *CASSIDULINITIDAE* Saidova, 1981

First and Last: *Cassidulinita* Suzin, 1952; former USSR: northern Caucasus.

**Superfamily** *EOUVIGERINACEA* Cushman, 1927

F. *LACOSTEINIDAE* Sigal, 1952

First: *Elhasaella* Hamam, 1976 (Jordan) and *Lacosteina* Marie, 1945 (Morocco; USA: Alaska, California).

Last: *Felsinella* Conato, 1964 (Italy) and *Spirobelivina* Hofker, 1956 (Ecuador, South Atlantic).

F. *EOUVIGERINIDAE* Cushman, 1927

First and Last: *Eouvigerina* Cushman, 1926; cosmopolitan.

**Superfamily** *TURRILINACEA* Cushman, 1927

F. *TURRILINIDAE* Cushman, 1927

First: *Praebulimina* Hofker, 1953; cosmopolitan.

Last: *Turrilina* Andreae, 1884; France; Denmark; The Netherlands; Poland.

F. *TOSAIIDAE* Saidova, 1981

First: *Tosaia* Takayanagi, 1953; Japan; Egypt; Pacific, off Panama.

Extant
First: Hopkinsina Howe and Wallace, 1932 (North America, Europe) and Stainforthisa Hofker, 1956 (cosmopolitan).

Superfamily BULIMINACEA Jones, 1875
First: Siphogenerinoides Cushman, 1927 (North and South America, Africa, Middle East) and Orthokarstenia Dietrich, 1935 (North and South America, Africa).
First: Bulimina d’Orbigny, 1826 (cosmopolitan) and Globobulimina Cushman, 1927 (cosmopolitan).
First: Quadratobuliminella de Klasz, 1953; Germany; France; USA: California.

First: Trifarina Cushman, 1923; Atlantic; Pacific; New Zealand; Egypt.

First: Chrysalidinella Schubert, 1908; Caribbean; Cuba; USA: Kerimba Archipelago; Pacific; Indonesia.
First: Finlayina Hayward and Morgans, 1981; Mexico; New Zealand.

Superfamily FURSENKOINACEA Loeblich and Tappan, 1961
First: Pleurostomella Reuss, 1860; cosmopolitan.

Superfamily STILOSTOMELLACEA Finlay, 1947
First: Nodogenerina Cushman, 1927; cosmopolitan.

Superfamily ANNULOPATELLINACEA Loeblich and Tappan, 1964
First: Annulopatellina Parr and Collins, 1930; Australia; Trinidad.

Superfamily DISCORBACEA Ehrenberg, 1838
First: Topalodiscorbis Neagu, 1970; Romania.
Last: Conorbina Brotzen, 1936; Europe; North America.
First: Trispirina Danich, 1977; former USSR: Azerbaijan, Moldavia; France.

Superfamily PLEUROSTOMELLIDAE Reuss, 1860
First: Pleurostomella Reuss, 1860; cosmopolitan.

Superfamily DISCORBIDAE Ehrenberg, 1838
First: Discorbis Lamarck, 1804 (cosmopolitan) and Trochulina d’Orbigny, 1839 (cosmopolitan).
First: Rosalina d’Orbigny, 1826; cosmopolitan.
F. PANNELAINIDAE Loeblich and Tappan, 1984
First: *Pannellainia* Seigle and Bermúdez, 1976; USA: Mississippi; NW Australia. Extant

F. BRONNIMANNIIDAE Loeblich and Tappan, 1984
First: *Bronnimannia* Bermúdez, 1952; Gulf of Mexico; Atlantic; Pacific. Extant

F. SPHAEROIDINIDAE Cushman, 1927
First: *Pullenoides* Hofker, 1951; The Netherlands. Extant

Superfamily GLABRATELLACEA Loeblich and Tappan, 1964
F. GLABRATELLIDAE Loeblich and Tappan, 1964
First: (Cuisian): Genus *Pseudoruttenia* Le Calvez, 1959; France; Belgium. Extant

F. HERONALLENIIDAE Loeblich and Tappan, 1986
First: *Heronallenia* Chapman and Parr, 1931; cosmopolitan.

F. BULIMINOIDIDAE Seiglie, 1970
First: *Buliminoides* Cushman, 1911 (cosmopolitan on shallow-water reefs) and *Elongobula* Finlay, 1939 (New Zealand, USA: Alabama). Extant

Superfamily SIPHONINACEA Cushman, 1927
F. SIPHONINIDAE Cushman, 1927
First: *Pulsiphonina* Brotzen, 1948; North America; Europe. Extant

Superfamily DISCORBINELLACEA Sigal, 1952
F. PARRELLOIDIDAE Hofker, 1956
First: *Cibicidoides* Thalmann, 1939 (cosmopolitan) and *Woodella* Haque, 1956 (Pakistan). Extant

F. PSEUDOPARRELLIDAE Voloshinova, 1952
First: *Alabaminoides* Gudina and Saidova, 1967 (cosmopolitan) and *Pseudoparella* Cushman and ten Dam, 1948 (cosmopolitan). Extant

F. PLANULINOIDIDAE Saidova, 1981
First: *Planulinoidea* Parr, 1941; Australia; Japan. Extant

F. DISCORBINELLIDAE Sigal, 1952
First: *Biapertorbis* Pokorny, 1956, Czechoslovakia; Poland; former USSR: western Ukraine. Extant

Superfamily PLANORBULINACEA Schwager, 1877
F. PLANULINIDAE Bermúdez, 1952
First: *Planulina* d’Orbigny, 1826; cosmopolitan. Extant

F. CIBICIDIDAE Cushman, 1927
First: *Epithemella* Sliter, 1968; Sweden; Germany; USA: California; former USSR: Ukraine, Crimea. Extant

F. PLANORBULINIDAE Schwager, 1877
First: *Planorbulina* d’Orbigny, 1826 (cosmopolitan) and *Planorbulinella* Cushman, 1927 (Atlantic, Mediterranean, Pacific, Australia, New Zealand, Cuba, Mexico, USA: North Carolina. Extant

F. Cymbaloporidae Cushman, 1927
First: *Archaecyc1us* Silvestri, 1908; Italy. Extant

F. VICTORIELLIDAE Chapman and Crespin, 1930
First: *Haerella* Belford, 1960; Western Australia. Extant

Superfamily ACERVULINACEA Schultze, 1854
F. ACERVULINIDAE Schultze, 1854
T. (DAN/THA)–Rec. Mar. (see Fig. 4.7)
First: *Sphaerogypsina* Galloway, 1933; Western Europe; former USSR: Ukraine; Australia; New Guinea; Borneo; Caribbean; Jamaica; Costa Rica; San Domingo; Peru. Extant

F. HOMOTREMATIDAE Cushman, 1927
First: *Sporadotrema* Hickson, 1911; cosmopolitan in warmer waters. Extant

Superfamily ASTERIGERINACEA d’Orbigny, 1839
F. EPISTOMARIIDAE Hofker, 1954
First: *Nuttallinella* Belford, 1959; Western Australia; New Zealand. Extant

F. ALFREDINIDAE Singh and Kalia, 1972
First: *Alfredina* Singh and Kalia, 1972; India. Extant

F. ASTERIGERINATIDAE Reiss, 1963
First: *Eoeponidella* Wickenden, 1949; cosmopolitan. Extant

F. ASTERIGERINIDAE d’Orbigny, 1839
First: *Asterigerina* d’Orbigny, 1839; cosmopolitan. Extant

F. AMPHISTEGINIDAE Cushman, 1927
First: *Amphistegina* d’Orbigny, 1826; cosmopolitan. Extant

F. BORELOIDEDAE Reiss, 1963
Fig. 4.7

First and Last: *Boreloides* Cole and Bermúdez, 1947 (Cuba, Pacific: Eniwetok Atoll, Marshall Islands) and *Eocoruloides* Cole and Bermúdez, 1944 (Cuba, Leeward Islands, Barbados).

Extant

F. **LEPIDOCYCLINIDAE** Scheffen, 1932


First: *Eulinderina* Barker and Grimsdale, 1936 (Mexico), *Helicolepidina* Tobler, 1922 (North and South America), *Helicostegina* Barker and Grimsdale, 1936 (Trinidad, Mexico), *Nephrolepidina* Douvillé, 1911 (North and South America, North Africa, Europe, Indo-Pacific), *Caudriella* Haman and Huddleston, 1984 (Venezuela), *Lepidocyclus* Gümbel, 1870 (North and South America) and *Pseudo­lepidina* Barker and Grimsdale, 1937 (Mexico, Jamaica).

Last: *Nephrolepidina* as above.

Superfamily **NONIONACEA** Schultze, 1854

Extant

F. **NONIONIDAE** Schultze, 1854 K. (CON)–Rec. Mar.

First: *Nonionella* Cushman, 1926; cosmopolitan.

Extant


First: *Ganella* Aurouze and Boulanger, 1954; France.

Extant

Superfamily **CHILOSTOMELLACEA** Brady, 1881

Extant

F. **CHILOSTOMELLIDAE** Brady, 1881 K. (ALB)–Rec. Mar.

First: *Bagginoides* Podobina, 1975 (USA: South Dakota, Texas; Canada: Alberta; former USSR: western Siberia; Europe) and *Pallaimorphina* Tappan, 1957 (Greenland, USA: Alaska).

Extant


First: *Quadrimorphina* Finlay, 1939; cosmopolitan.

Extant


First: *Valvalabamina* Reiss, 1963; cosmopolitan.
F. GLOBOROTALIDAE Loeblich and Tappan, 1984
K. (BRM-MAA) Mar.  
First: Conorotalites Kaever, 1958; Europe.  
Last: Globorotaliinae Brotzen, 1942; cosmopolitan.  

F. OSANGULARIIDAE Loeblich and Tappan, 1964  
K. (ALB)–Rec.  
First: Charltonina Bermúdez, 1952 (Caribbean, Cuba, England, UK, Romania, Egypt, Australia) and Osangularia Brotzen, 1940 (cosmopolitan). Extant  

F. ORIDORSALIDAE Loeblich and Tappan, 1984  
T. (RUP/CHT)–Rec.  
First: Oridorsalis Andersen, 1961; North America; Caribbean; Japan. Europe. Extant  

F. HETEROLEPIDIDAE Gonzales-Donoso, 1969  
K. (ALB)–Rec.  
First: Anomalinites Brotzen, 1942; cosmopolitan. Extant  
F. GAVELINELLIDAE Hofker, 1956  
K. (BRM)–Rec.  
First: Gavelinella Brotzen, 1942; cosmopolitan. Extant  
F. KARRERIIDAE Saidova, 1981  
K. (APT)–Rec.  
First: Simionescella Neagu, 1975; Romania. Extant  

F. COLEITIDAE Loeblich and Tappan, 1984  
First: Coleites Plummer, 1934; USA: Texas, Alabama, New Jersey, California; Guatemala; Cuba; Haiti; Sweden; Pakistan.  
Last: (Lutetian): same genus.  

F. TRICHOHYALIDAE Saidova, 1981  
T. (RUP/CHT)–Rec.  
First: Buccella Andersen, 1952; cosmopolitan. Extant  
Superfamily ORBITOIDACEA Schwager, 1876  
F. LINDERINIDAE Loeblich and Tappan, 1984  
First: Eoannularia Cole and Bermúdez, 1944 (Cuba), Epianularia Caudri, 1974 (Venezuela) and Linderina Schlumberger, 1893 (France, Spain, Romania, Turkey, Somalia, North America, Indonesia).  
Last: Linderina as above.  

F. ORBITOIDIDAE Schwager, 1876  
First: Orbitoides d’Orbigny, 1848; Europe; North America; Caribbean; India.  
Last: Orbitoides as above, Pseudopomphalocyclus Meric, 1980 (Turkey), Simplorbites de Gregorio, 1882 (Sicily, France, Carpathians, Egypt), Simbra Sirel and Gündüz, 1978 (Turkey, Greece) and Omphalocyclus Bronn, 1853 (France, Netherlands, Switzerland, Italy, Greece, former Yugoslavia, Romania, Turkey, Iran, Syria, Tunisia, India, Tibet, Cuba).  

F. LEPIDORBITOIDIDAE Vaughan, 1933  
First: Sirtina Brönnimann and Wizr, 1962 (Iran, Libya, France) and Praesiderolites Wanner, 1983 (Spain, France).  
Last: Daviesina Smout, 1954 (Qatar, Egypt, East Africa, Spain, France) and Penoperculoides Cole and Gravel, 1952 (Cuba).  

Superfamily ROTALIACEA Ehrenberg, 1839  
F. PSEUDORBITOIDIDAE M. G. Rutten, 1935  
First: Pseudorbitoides Douvillé, 1922 (Jamaica, Cuba, Haiti, USA: Texas, Louisiana), Rhabdorbitoides Brönnimann, 1955 (Cuba), Sulcorbitoides Brönnimann, 1954 (Cuba, USA: Texas, Louisiana, Florida), Asterorbis Vaughan and Cole, 1932 (Cuba, Guatemala, Central Pacific, USA: Mississippi, Louisiana, Florida) and Orbitocyclina Vaughan, 1929 (Mexico, Cuba, USA: Florida, Louisiana).  
Last: Historbitoides Brönnimann, 1956 (Cuba), Pseudorbitoides as above, Vaughanina Palmer, 1934 (Cuba, Venezuela, Guatemala, Mexico, USA: Florida), Asterorbis as above and Orbitocyclina as above.  

F. ROTALIIDAE Ehrenberg, 1839  
K. (CON)–Rec.  
First: Pararotalia Le Calvez, 1949 (cosmopolitan), Oritkathina Höttinger, 1966 (Spain) and Rotalia Lamark, 1804 (cosmopolitan). Extant  
F. CHAPMANINIDAE Thalmann, 1938  
First: Sherbornina Chapman, 1922; cosmopolitan in warm water.  
Last: Chapmania Silvestri, 1931 (Italy, France, Spain, Greece, Romania) and Sherbornina as above.  

F. CALCARINIDAE Schwager, 1876  
K. (MAA)–Rec.  
First: Siderolites Lamark, 1801; Europe; Middle East; India.  
Extant  
F. ELPHIDIIDAE Galloway, 1933  
T. (DAN/THA)–Rec.  
First: Elphidiella Cushman, 1936; cosmopolitan. Extant  
F. MIOPYGSINIDAE Vaughan, 1928  
First: Miopygsonoides Yabe and Hanzawa, 1928; Europe; North America; Indo-Pacific; India: Kutch.  
Last: Lepidosemicyclina Rutten, 1911 (Borneo, Saipan, Australia, New Zealand, India, Japan), Miopygsonida Sacco, 1893 (Europe, North and South America, Indo-Pacific), Miopygsonita Drooger, 1952 (Mexico, Trinidad, USA: Florida, Mississippi, Louisiana), Miopygsonoides as above and Miopleiodycylina Silvestri, 1907 (Mediterranean region, Mexico, Puerto Rico, Ecuador, Panama, East Indies, USA: California, Florida, Mississippi).  

Superfamily NUMMULITACEA de Blainville, 1827  
F. PELLATISPIRIDAE Hanzawa, 1937  
First: Miscellanea Pfender, 1935; Pakistan; Qatar; Saudi Arabia; Somalia; Nicaragua.  
**F. NUMMULITIDAE** de Blainville, 1827  
**T. (DAN/THA)** Mar.  
*First: Nummulites* Lamarck, 1801; tropical and subtropical cosmopolitan.  
*Extant*

**F. DISCOCYCLINIDAE** Galloway, 1928  
*First: Discocyclina* Gümbel, 1870; tropical and temperate cosmopolitan.  
*Last: Actinocyclina* as above and *Pseudophragmina* Douvillé, 1923 (North and South America).  
*Superclass* ACTINOPODA Calkins, 1909  
*Class* POLYCYSTINEA Ehrenberg, 1838  
*First: Asterocyclina* Gümbel, 1870; tropical and subtropical cosmopolitan.  
*Last: Asterocyclina* as above and *Pseudophragmina* Douvillé, 1923 (North and South America).

The classes Polycystinea and Phaeodarea are equivalent to the Radiolaria (Levine *et al.*, 1980). The classification of the radiolaria is in a state of flux, which was initiated when Haeckel's (1887) system was abandoned. In recent decades, most classifications have been based on the work of Riedel and Sanfilippo, 1977; Pessagno, 1977; Sanfilippo and Riedel, 1985; and Petrushevskaya, 1977 among others.
Range data are derived from these works and others, including Foreman (1973) and Campbell and Moore (1954).

Variations on these themes continue to be used, often with the addition of new families, as the phyletic relationships are elucidated. In some cases, family names are used without reference to their position in the overall classification and these are included under ‘Radiolaria incertae sedis’.

In general, this work uses Levine et al. (1980) down to Order, and Riedel and Sanfilippo (1977) and others for family designations. In view of the ongoing development of the classification, only family ranges are presented, together with some relevant reference(s).

**Order SPUMELLARIDA Ehrenberg, 1875**

**F. ENTACTINIIDAES** Riedel, 1967 S. (LLY)–C. Mar. (see Fig. 4.8)

**Range:** Lower Silurian to Carboniferous; Nazarov and Ormiston (1986).


**Range:** Eocene to Recent; Riedel and Sanfilippo, 1977. Extant

**F. COLLOSPHAERIDAE** Müller, 1858 T. (LMI)–Rec. Mar.

**Range:** Lower Miocene to Recent; Anderson (1983). Extant

**F. ACTINOMMIDAE** Haeckel, 1862; *sensu* Riedel, 1967b Pz./Tr.–Rec. Mar.

**Range:** Palaeozoic/Triassic to Recent. Extant

**F. PHACODISCIDAE** Haeckel, 1881 Mz.–Rec. Mar.

**Range:** Mesozoic to Recent. Extant

**F. COCCODISCIDAE** Haeckel, 1862 Mz.–T. (Eoc.) Mar.
Range: Mesozoic to Eocene.

Range: Cenozoic; Riedel and Sanfilippo, 1977; Anderson (1983).
F. SPONGODISCIDAE Haeckel, 1862 emend.
D. Rec. Mar.

F. HAGIASTRIDAE Pz.-Mz./Cz. Mar.
Comment: Split into two families by Baumgartner (1980); the Hagiastriidae and the Patulibracchiidae Pessagno, 1971.

Range: Eocene to Recent; Anderson (1983).

Range: Middle Miocene to Recent; Riedel and Sanfilippo (1977).
Range: Carboniferous to Recent.

Order NASSELLARIDA Ehrenberg, 1875
Range: Upper Palaeocene to Recent; Riedel and Sanfilippo (1977).

F. ACANTHODESMIIDAE Hertwig, 1879 Cz. Mar.
Range: Cenozoic.

Comment: Also known as Trissocyclididae Goll, 1968.

Range: Eocene to Recent.
Range: Eocene to Recent.
Range: Tithonian to Upper Valanginian; Sanfilippo and Riedel (1985).
Range: Tithonian to Aiptian; Sanfilippo and Riedel (1985).
Range: Albian to Maastrichtian; Sanfilippo and Riedel (1985).

First: Specimens from the late TOR of Romanian eastern Predkaratje.
Class PHAEODAREA Haeckel, 1879
This class is very rare in the fossil record. Two families (Challengeridae and the Getticellidae) recognized by Dumitrica (1964 and 1965).

Protozoa

First: Specimens from the late TOR of Romanian eastern Predkaratje. Extant

RADIOLARIA INCERTAE SEDIS


Range: Silurian to Carboniferous.


Range: Upper Caradoc to Ashgill (Ordovician); Webby and Blom (1986); Renz (1990).


Range: Lower Ordovician to Upper Silurian (at least); Nazarov and Ormiston (1986); Renz (1990).

Comment: = the informal group Palaeoactinommids (Holdsworth, 1977).

F. CERATOIKISCIDAE S. (WEN)–? Mar.

Range: Middle Silurian to ?; Nazarov and Ormiston (1986).


Range: Lower Ordovician to Silurian–Permian; Nazarov and Ormiston (1986).


Range: Ordovician; Nazarov and Ormiston (1986).

Comment: Many other family names are to be seen in the literature; often survivors of the original Haeckelian classification.

Subphylum MASTIGOPHORA Diesing, 1866

Class PHYTOMASTIGOPHOREA Calkins, 1909

Order CRYPTOMONADIDA Senn, 1900 Extant

Order DINOFLAGELLIDA Butschli, 1885

These orders contain the normal members of the ‘Division’ DINOFLAGELLATA, which are included in Chapter 3.

Order PRYMNESIIDA Hibberd, 1976

This order contains the coccoliths and their relatives (see Chapter 3).

Order SILICOFLAGELLIDA Borgert, 1891


First: Corbisema Hanna, 1928 and Dictyocha Ehrenberg, 1837. Extant

Comment: This is based on data in Perch-Nielsen (1985), although Tappan (1980) does quote a range from early Cretaceous for the family.


First and Last: Vallacerta Hanna, 1928.


First and Last: Cornua Schulz, 1928.


First and Last: Lyramula Hanna, 1928.

Phylum CILIOPHORA Doflein, 1901

Class POLYMEMOPHOREA Jankowski, 1967

Subclass SPIROTRICHIA Butschli, 1889

Order OLIGOTRICHIDA Butschli, 1887

Suborder TINTINNINA Kofoid and Campbell, 1929

The Suborder Tintinnina are a group of organic-walled Recent ciliates. Their relationship with the calcareous-walled calpionellids is still under review. In accordance with normal practice, the latter group is placed in Incerta sedis.

Class Incerta sedis ‘calcispheres’

Spherical/elliptical bodies with a simple, circular aperture which are commonly encountered in pelagic successions. Masters and Scott (1978), while acknowledging that they may be of algal affinity, left them as Incerta sedis. They classified them on the basis of their wall ultrastructure. The size, shape and orientation of the calcite prisms that form the wall are used to define the family-level divisions.

Subsequently, Keupp (1984) has suggested that these planktonic ‘calcispheres’ should be regarded as calcified dinoflagellates. This suggestion has been taken up by Willems (1985, 1988, 1990) who has included them within the Dinophyceae on the evidence of internal features (see also Chapter 3 herein). Unfortunately, Willems (1985, 1988, 1990) does not refer to Masters and Scott (1978), and so it is almost impossible to reconcile the two classifications. Tappan (1980) appears to have a mixture of classifications for these fossils. Masters and Scott (1978) recognized three families, as follows:


First and Last: Bonetocardiella Dufour, 1968.


First: Stomiosphaera Wanner, 1940; Timor and cosmopolitan.


First: Cadosina Wanner, 1940, Timor and cosmopolitan.

Last: Cadosina is described from the CEN; later forms may be MAA.

Superfamily CALPIONELLIDEA

Recent tintinnids possess an organic lorica, while fossil calpionellids have a calcareous test. Mineralized tests
are completely unknown among ciliates in general, and
tintinnids in particular.

F. COLOMIELLIDAE Bonet, 1956

First and Last: Colomiella Bonet, 1956; Mexico; Cuba;
Tunisia; Aquitaine Basin, France.

F. CALPIONELLIDAE Bonet, 1956

First: Chitinoidea Dobren.
Last: Tintinnopsis Colom, 1948, top of lower VLG.

Phylum INCERTAE SEDIS ‘EBRIDIANS’

Class EBRIOPHYCEAE Loeblich, 1970

Order EBRIALES Honigberg et al., 1964

F. HERMESINACEAE Hovasse, 1943 T. (Pal.)–Rec.
Mar.

First: Spongeuria marthae Deflandre, 1951. Extant

First and Last: Ditripodium latum Hovasse, 1932, Miocene,
California, USA.


First and Last: Ammachium Hovasse, 1932.

F. EBRIACEAE Lemmermann, 1901 T. (Pal.)–Rec.
Mar.

First: Falsebria ambigua Deflandre, 1950. Extant

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The palaeontological record of the Porifera is mainly that of marine forms and extends in broken fashion from the early Cambrian to the Recent. Unlike the record of many phyla, our knowledge of sponges, in the historic sense, is still largely based on major monographic works. For example, such papers would include those by Walcott (1920), treating Cambrian forms, Rigby and Webby (1988) on Ordovician ones, Hall and Clarke (1899) and Rigby (1986) on Devonian ones, Finks (1960) and Senowbari-Daryan (1990) on Permian ones, Schrammen (1910, 1912, 1924, 1936), Moret (1926), Lagneau-Herenger (1962), and Hinde (1884, 1887–1893) on the Mesozoic faunas of Europe. The data are so limited that single studies still produce anomalies in any statistical treatments. Such papers show clearly in the ‘first and last’ occurrences compiled below. Assemblages of fossil sponges are generally localized, both in terms of geography and time. The record unduly emphasizes forms with calcareous skeletons or fused skeletons, in contrast to those with loose spicular skeletons or horny keratose skeletons, such as abound in modern seas, and which probably were equally common in ancient seas. The record is incomplete, and so the ranges given are generally only the minimum possible – all could be questioned.

For many years, the taxonomy of fossil Porifera appears to have been relatively stable, however, discoveries in the past two or three decades have prompted major revisions, many still under way. Spicule data have proved poriferan affinity for many stromatoporoids and chaetetids, and have also demonstrated that these formerly discrete systematic groups, together with the sphinctozoans, are polyphyletic. Hence, the higher systematic placing of sponges with an additional calcareous skeleton is still open to considerable interpretation. Archaeocyaths are also now considered as poriferans by several specialists (Debrenne et al., 1990). Similarly, classifications of major groups within Demospongia and Hexactinellida are undergoing major revisions. Some of those revisions are reflected in the lists below, as noted, but many changes are not reflected in the classifications used, for they are only in manuscripts still awaiting publication in the revision of the Treatise on Invertebrate Paleontology, Part E.

Here, non-calcified poriferans and the heteractinids have been documented by J. Keith Rigby and calcified forms (archaeocyaths, stromatoporoids, sphinctozoans and chaetetids) by Graham Budd, Rachel Wood and Francoise Debrenne.

**Class** DEMOSPONGIA Sollas, 1875

**Order** KERATOSA Grant, 1861


**First:** *Vauxia magna* Rigby, 1980, from the Glossopleura Zone, Spence Tongue, Lead Bell Shale, Wasatch Mountains, near Brigham City, Utah, USA. A Lower Cambrian (?) *V. gracilenta* has been reported from the Buen Formation of north Greenland (Rigby, 1986).

**Last:** *Vauxia gracilenta* Walcott, 1920 and several other species of *Vauxia*, Burgess Shale, Stephen Formation near Field, British Columbia, Canada.

**Order** MONAXONIDA Sollas, 1883

F. SPONGILLIDAE Gray, 1867  K. –Rec.  FW.

**First:** *Palaeospongilla chubutensis* Ott and Volkheimer, 1972, Chubut Group, near Cerro Condor, Patagonia, Argentina.  Extant

**Intervening:** Mio. – PLE.


**First:** *Hazelia grandis* Walcott, 1920, *Ogygopsis* Shale of Stephen Formation, Mount Stephen, near Field, British Columbia, Canada.

Fig. 5.1

F. HELIOSPONGIIDAE Finks, 1960
First: Coelocladia spinosa Girty, 1908, Gaptank Formation, Desmoinesian, Glass Mountains, Texas, USA.
Last: Heliospongia vokesi King, 1943, Bone Spring limestone, Leonardian, Sierra Diablo, north-west of Van Horn, Texas, USA.

First: Unnamed boring sponge, Forteau Formation, near Port Amour, Labrador, Canada (Kobluk, 1981); Clionolithes radicans Clarke, 1908, Devonian, New York is perhaps the oldest named species.

F. DYSTACTOSPONGIIDAE Miller, 1889
First: Dystactospongia minor Ulrich and Everett, 1890, Platteville Limestone, Dixon, Illinois, USA.
Last: Dystactospongia madisonensis Foerste, 1909, Saluda Limestone, near Madison, Indiana, USA. Batospongia spicata Miller, 1889 is questionably included in the family, from ‘near the base of the Coal measures,’ Seville, Illinois, USA.

First: Leptomitus teretiusculus, Leptomitella conica, Leptomitella confusa, Paraleptomitella dictyodroma, and P. globula, all described by J.-Y. Chen et al., 1989, Yuanshan Member, Chiungchussu Formation, near Chengjiang, Yunnan, China.
Last: Letomitella metta (Rigby, 1983), Bolaspiddela Zone, Marjum Formation, House Range, Utah, USA.

First and Last: Hamptonia bowerbanki Walcott, 1920,
Fig. 5.1

**Bathyuriscus–Elrathina Zone**, Burgess Shale, Stephen Formation, near Field, British Columbia, Canada.

**F. CHOIIDAE de Laubenfels, 1955**
€. (CRF–O.) (TRE?) Mar.

**First**: Choia hindei (Dawson, 1896), Buen Formation, north Greenland.

**Last**: Choia hindei (Dawson, 1896), black Levis(?) Shale, Tremadocian(?), Little Métis, south-eastern Quebec, Canada.

**Intervening**: STD.

**F. WAPKIIDAE de Laubenfels, 1955**
€. (STD) Mar.


**F. HALICHONDRIIDAE Rigby, 1986**
€. (STD)–O. (TRE?) Mar.


**Last**: Halichondrites confusus Dawson, 1889, black Levis(?) Shale, Tremadocian(?), Little Métis, south-eastern Quebec, Canada.

**F. PIRANIIDAE de Laubenfels, 1955**
€. (STD) Mar.


F. TAKAKKAWIIDAE de Laubenfels, 1955


Order CHORISTIDA Sollas, 1880

F. PLAKINIDAE Reid, 1968


First: *Plakina?* sp. Hinde, 1885, Upper Greensand, southern England, UK.

Intervening: Eoc.

F. THROMBIDAE Sollas, 1880


First: *Thrombus?* sp. or *Ortmannia* sp. Schrammen 1924, Upper Chalk (Mukronaten Kreide), Misberg, Germany.

Intervening: Eoc.

F. ACANTHASTRELLIDAE Schrammen 1924


First: *Acanthastrella?* sp., loose spicules only, Weissjura, southern Germany.

Last: *Acanthastrella panniculosa* Schrammen 1924, Upper Chalk (Mukronaten Kreide), Misburg, northern Germany.

F. HALINIDAE de Laubenfels, 1955


First: *Pachastrella etusuta* Hinde, 1883, Lower Limestone, Dalry, Ayrshire and other localities, Scotland, and Republic of Ireland.

Intervening: J. (I) APT, ALB, SEN, Eoc.

F. ANCORINIDAE Schmidt, 1870


First: *Oppligera clavaeformis* (Oppliger, 1921), Austria.

Intervening: ALB, TUR–SEN, Eoc.

F. GEOIDIIDAE Gray, 1867


First: *Geodites antiquus* (Hinde, 1883), and *G. deformis* Hinde, 1887, Lower Limestone, Dalry, Ayrshire and other localities, Scotland, UK.


F. CRANIELLIDAE de Laubenfels, 1955


First: *Crania?* sp., based on loose spicules only, Hinde and Holmes 1892, Plantagenet Beds, Western Australia.

F. CEPHALORAPHIDITIDAE Reid, 1968


First: *Cephaloraphides milleporatus* Schrammen, 1910, calcareous marls of Quadratenkreide at Oberg, Germany, co-occurring with *Megaloraphium auriforme* Schrammen, 1910 and *Polytreta seriaotopora* Schrammen, 1910.

Last: *Ophiraphidites infundibuliformis* Schrammen, 1899, Castle Hayne Limestone, Eocene, North Carolina, USA.

F. SCOLIORAPHIDIDAE Zittel, 1879


First: *Helminthopyllum feifeli* Schrammen, 1936, Weissjura γ, Schwabtal, Germany.

Last: *Scolioraphis cerebriformis* Zittel, 1878, sandy marls, Granulatenkreide, Sudmerberg, Germany.

Order LITHISTIDA Schmidt, 1870

Suborder ORCHOCLADINA Rauff, 1893

F. ANTHASPIDELLIDAE Miller, 1889


First: *Capsospongia undulata* Walcott, 1920, Burgess Shale, Stephen Formation, British Columbia, Canada. If *Fieldospongia* (Walcott, 1920), from the Mount Whyte Formation, Rocky Mountains, British Columbia, belongs here it extends the range of the family to near the base of the Middle Cambrian. Dendroclones such as characterize the family have been reported from the lower Middle Cambrian Tindall Limestone, near Tipperary, Northern Australia.

Last: *Timorella permica* Gerth, 1929, Amarass Formation, Timor.

Intervening: MER, TRE–LUD, GED–EIF, FRS–FAM, MOS, ART–KAZ. Family is major element in lower Palaeozoic faunas.

F. CHIASTOCLONELLIDAE Rauff, 1895


First: *Syltispongia ingemariae* Van Kempen, 1990, erratics containing probably CRD/ASH age sponges, in sediments on Island of Sylt, north-west Germany. *Chiastoclonea header* Rauff, 1894, Middle Silurian Brownsport Formation (WEN), Tennessee is the earliest species of the family with a certain provenance.

Last: *Actinocoelia maeandrina* Finks, 1960, San Andreas Formation Guadalupian, near Carlsbad, New Mexico, USA.

Intervening: WEN–LUD, FRS, ASS–ART.

F. ANTHRACOSYCONIDAE Finks, 1960


First: *Anthracosyon regulare* (King, 1943), Skinner Ranch Formation (Wolfcampian), Glass Mountains, Texas, USA.

Last: *Collatipora discreta* Finks, 1960, Rader Limestone Member, Upper Guadalupian Bell Canyon Formation, Guadalupe Mountains, Texas, USA.

Intervening: ART, KUN, UFI.

Suborder EUTAXICLADINA Rauff, 1893

F. ASTYLOSPONGIIDAE Zittel, 1877


First: *Caryospongia parvulum* (Billings, 1861), Cobourg Limestone, Trenton Group, Ottawa, Ontario, Canada.

Last: *Scheielloides?* sp., *Virgin Hills Formation* (FAM); all three *Scheielloides conica* Rigby, 1986 and *Sadleria pansa* Rigby, 1986 occur together in Sadler Limestone (FRS); all three in Devonian Canning Basin reef complexes of northern Western Australia.

Intervening: WEN, LUD, GED–EIF, FRS.
F. VETULINIDAE von Lendenfeld, 1904
First: Mastosia wetsleri Zittel, 1878, Weissjura ε, extends up to Weissjura δ, Sozenhausen and Gussenstadt, Germany.
Intervening: TUR–CMP.
Comment: Part of this family (Mastosidae Schrammen, 1924) was placed in the Anomocladina by de Laubenfels (1953, p. E64), but clearly belongs in the Eutaxicladina for, as de Laubenfels noted, the skeleton ‘is composed of sphaeroclines . . .’.

Suborder TRICRANOCLADINA Reid, 1968
First: Hindia sphaeroidalis Duncan, 1879, and species of Belubulaspongia, Palmatothina, Arborohindia, Mamelorhina and Fenestrospongia, all described by Rigby and Webby (1988), lower Malongulli Formation, Coppermine Creek breccias, New South Wales, Australia.
Last: Scheia tuberosa Tschneryschew and Stepanov, 1916, Amarassi Formation (Dzhulfian), Timor.
Intervening: LLN, ASH, SIG-EMS, VIS-KAZ.
Last: Laubenfels (1955). The suborder is being significantly re­vised in the new version of the Treatise on Invertebrate Paleontology.

Suborder RHIZOMORINA Zittel, 1895
Comment: Family classification follows that of de Laubenfels (1955). The suborder is being significantly revised in the new version of the Treatise on Invertebrate Paleontology.

F. HAPLISTIIDAE de Laubenfels, 1955
O. (CRD)–P. (KAZ) Mar.
First: Haplistion regularis Rigby and Webby, 1988, and species of Warrigaliu, Taplouvia, Lewinia and Boonderooia, all described by Rigby and Webby (1988), lower Malongulli Formation, Coppermine Creek breccias, New South Wales, Australia.
Last: Haplistion aestroglossa Finks, 1960, Word Formation, Glass Mountains, Texas, USA.
Intervening: LUD, EIF–FRS, TOU, VIS, MOS, ART, KUN.

F. CNEMIDIASTRIDAE Schrammen, 1924
First: Cnemidiastrum rimalusom (Goldfuss, 1833), Weissjura γ with C. granulosum (Quenstedt, 1878); C. stellatum (Goldfuss, 1833) occurs first in Weissjura β–γ; all at Hossingen, Tieringen and nearby localities, southern Germany.
Last: Lithostrobilis reticulatus Lagneau-Herenger, 1962, Aptian beds, Mas de Artis, Catalonia, Spain.
Intervening: KIM.

F. KALIAPSIDAE de Laubenfels, 1936
First: Seliscothon phlyctioides Moret, 1925, Aptian calcareous sandstone, Can Casanyas Castellet, Catalonia, Spain.

F. SCYTALIIDAE de Laubenfels, 1955
First: Yrrhiza immunata (Kolb, 1910), Weissjura ε, Son­theim, Germany.
Last: Scytalia terebrata (Phillips, 1835), Mukronatenkreide, Misburg area, north-western Germany.
Intervening: APT, CEN–CMP.

F. CHONEILLIDAE Schrammen, 1924
First: Platychonia brodiei Sollas, 1885, middle Lias, Ilminster, Somerset, England, UK.
F. ASTROBOLIIDAE de Laubenfels, 1955
J. (OXF)–T. (Mio.) Mar.
First: Cytoracia goldfussi (Quenstedt, 1878), Weissjura α, Streitberg and other localities, north-western Germany.
Last: Phlyctia expansa Pomel, 1872, Miocene, Cartennian terrain, DJebel Djambideia, Algeria.
Intervening: APT, CEN–CMP.

F. JEREOPSIIIDAE de Laubenfels, 1955
J. (OXF)–T. (Mio.) Mar.
First: Hyalotragos patella (Goldfuss, 1833), Weissjura α, Streitberg and other localities, Germany.
Last: Jereopsis inaequalis Pomel, 1872, and Moretispongia pyriformis (Pomel, 1872), Miocene, Cartennian terrain, DJebel Djambideia, Algeria.
Intervening: KIM, CEN–CMP.

F. LEIODORELLIDAE Schrammen, 1924
J. (OXF)–T. (Mio.) Mar.
First: Leiodorella pustulosa Schrammen, 1936, Weissjura α–ε, near Streitberg and Waldhlausen, southern Germany.
Pyrgochonia acetabula (Goldfuss, 1833) also in Weissjura α in southern Germany.
Last: Scythophymia crassa Pomel, 1872, and Plereophymia cotyle Pomel, 1872, along with several species of Verruculina., Miocene, Algeria.
Intervening: KIM, APT, CEN–CMP.

F. PLINTHODERMATIIDAE de Laubenfels, 1955
First and Last: Plinthodermatium exile Schrammen 1910, Mukronatenkreide, at Misberg, Germany.
First: Trachyspongia aquiluminata (Schrammen, 1912), Mukronatenkreide, Misburg, Germany.
Extant
F. SCLERITODERMATIDAE Sollas, 1888
J. (CLV)–Rec. Mar.
First: Azorica calloviensis Moret, 1928, La Voulte-Sur-Rhône (Ardèche), France.
Comment: Azorica was also quite logically and fairly?questionably reported from the SAN of France. Cretaceous record of Scleritoderma cited by de Laubenfels (1955, p. E49) not found. Otherwise recent forms known.

F. LECANELLIDAE Schrammen, 1924
First: Lecanella pateraeformis Zittel, 1878, Weissjura γ, Hossingen and ε–ζ, Heuchstein and Gersten, Germany.
Last: Regnardia lapparenti Moret, 1926, Cenomanian, yellowish Chalk, Coulonges-les-Sablon, France.

Suborder DICRANOCLADINA Schrammen, 1924
Comment: Usage of the suborder follows that of Reid (1968, p. 23) and, with some modification, follows the general family divisions recognized by Lagneau-Hérenger (1962).

F. ACROCHORDONIIDAE Schrammen, 1910


Last: *Acrochordonia ramosa* Schrammen, 1901 and *A. auricula* Schrammen, 1901, Quadratenkreide Olberg, Germany. Co-occurring *Gilbeitia catalaunica*, *Pycnoclonella dactyloformis*, and *P. ramosa*, also named by Lagneau-Hérenger (1962) for specimens from Can Casanyos Castellet.

Intervening: TUR–CMP.

F. PACHINIONIDAE Schrammen, 1924

First: *Pachinion scriptum* (Roemer, 1864) and *Pseudoveruculina globosa* Lagneau-Hérenger, 1962, Aptian calcareous sandstone, Can Casanyos Castellet, Catalonia, Spain. Co-occurring *Gilletia catalaunica*, *Pycnoclonella dactyloformis*, and *S. scytaforme* (Schrammen, 1910), Quadratenkreide, Misburg, Germany.

Intervening: SAN.

F. PHRISSOSPONGIIDAE Lagneau-Hérenger, 1962

First: *Kyphoclonella multiformis* Kolb, 1910, Weissjura e, Sontheim, Germany.

Last: *Schrammeniella scytaforme* (Schrammen, 1910), Quadratenkreide, Misburg, Germany.

Intervening: APT, SAN, TUR–CMP.

F. SPINOCLADIIDAE Lagneau-Hérenger, 1962
K. (APT) Mar.

**F. GIGNOUXIIDAE** de Laubenfels, 1955  
**J. (OXF)–K. (CMP) Mar.**  
**First:** *Dicranocloneella praecursor* Schrammen, 1936, Weissjura α, Streitberg, Germany.  
**Last:** *Gignouxia niciensis* Moret, 1926, CMP, blue marl, Saint-Ardre, near Nice, France.  
**Intervening:** KIM, APT, SAN–CMP.  
**Comment:** This family, as used by de Laubenfels (1955, p. E61–2), included sponges now placed in other families (Lagneau-Hérenger, 1962, pp. 161–74). Only those genera not included by her elsewhere are included here. Systematics of the Dicranoclada will be further revised in the new version of the *Treatise on Invertebrate Paleontology*. The reported Cretaceous occurrence of a species of the living *Cosinospingia* is questioned; the family appears to have a Jurassic–Cretaceous range.

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**F. PSEUDOVERRUCULINIDAE** de Laubenfels, 1955  
**K. (APT–SAN) Mar.**  
**First:** *Pseudoverruculina globosa* Lagneau-Hérenger, 1962, Aptan calcareous sandstone, Can Casanyas Castellet, Spain.
**Last:** Pseudoverruculina niciensis Moret, 1926, SAN, blue-grey marls, Nice, France.

**Suborder** DIDYMORINA Rauff, 1893

F. CYLINDROPHYMATIDAE Schrammen, 1936


**First:** Malinowskia actinomus Hurcewicz, 1985, upper FRS limestone, Kowala, Holy Cross Mountains, south-western Poland. The next record is Melonella ovata Sollas, 1883, Inferior Oolite, near Bristol, England, UK.

**Last:** Cylindrophyma milleporata (Goldfuss, 1833), Weissjura \( \xi \), Gerstetten and other localities, southern Germany.

**Intervening:** BAJ, OXF.

**Comment:** The Palaeozoic anthaspidellid Orchocladina, as that term was coined by Hinde, 1883, Upper Jurassic, in association with S. Evans, 1864, Upper Chalk, Flam­

**Suborder** MEGAMORINA Zittel, 1878


**First:** Megalithistida foraminosa Zittel, 1878, Weissjura \( \epsilon \) and \( \zeta \), Heuchstetten and other localities, southern Germany, and Switzerland.

**Intervening:** CEN–MAA.


**First:** Placonella perforata Hinde, 1883, Upper Jurassic, Nattheim, Germany.

**Last:** Doryderma ramosum ( Mantell, 1822), Upper Chalk, near Brighton and at Oare, Wiltshire, England, UK.

**Intervening:** ALB–CMP.


**First and Last:** Archaeodoryderma dalryense (Hinde, 1883), Dockra Limestone, Scotland, UK.

F. HELOBRACHIIDAESchrammen, 1910 K. (CMP) Mar. (see Fig. 5.2)

**First and Last:** Helobrachium consecutum Schrammen, 1910, Quaradenkreide, Oberg, Germany.


**First:** Heloraphinia arborescens Schrammen, 1936, Weissjura \( \delta \), Schwabtal, Germany.

**Last:** Isoraphinia texta (Roemer, 1864), Upper Chalk, Flamborough, Yorkshire, England, UK.

**Intervening:** APT–CEN–SEN.


**First:** Megaspiziza colungensis Moret, 1926, CEN, Upper Chalk, Coulonges-sur-Sablons, France.

**Last:** Megaspiziza dubia Schrammen, 1901, calcareous marl, Quaradenkreide, Misburg and Oberg, Germany.

**Suborder** DIDYMORINA Rauff, 1893


**First:** Saccospongia rudis and S. danvillensis Ulrich, 1889, Trenton Beds, the former near Lexington and Frankfort, and the latter near Danville, Kentucky, USA.

**Last:** Eochauanactis radiata and co-occurring Haplistionella garnieri and H. minitrola, described by Rigby and Dixon (1979), Read Bay Formation, Garnier Bay, Somerset Island, Arctic Canada.

**Intervening:** CRD, ASH.

**Suborder** TETRACLADINA Zittel, 1878

F. PROTETRACLIDATIDAE Schrammen, 1924 J. (KIM) Mar.

**First and Last:** Protetraclis linki Steinmann, 1881, Weissjura \( \epsilon \), Heuchstetten, Sontheim, Nattheim and Randen, Germany. Rhizotetraclis plana, Sontheimia parasitica and S. per­forata, all named by Kolb (1910, pp. 206–9), co-occur in the Weissjura \( \epsilon \) at Sontheim.

**Intervening:** BAJ, OXF.


**First:** Echinodiscus pyriformis (Goldfuss, 1833), Mas de Artis, Catalonia, Spain, in association with S. Evans, 1864, and Callopegma plana Lagneau-Hérenger, 1962, Spain.

**Last:** Siphonia konigi (Mantell, 1822) Upper Chalk, Flamborough, Yorkshire, and near Brighton, southern England, UK. The species has also been reported questionably from the Miocene of Italy.

**Intervening:** ALB, SAN, CMP.


**First:** Aulaxinia ventricosa Schrammen, 1910, 1912, APT, Mas de Artis and Can Casanyas Castellet, Catalonia, Spain.

**Last:** Aulaxinia sulcifera (Roemer, 1864), Upper Chalk, England, UK and Mukronaten- and Quadratenkreide, Misburg, Oberberg and other localities, north-western Germany, and in the Weiss Schreibkreide, Rügen, northern Germany.

**Intervening:** ALB, TUR–CMP.


**First:** Jerea sp. Trammer, 1982, Jasna Góra Beds, Niegowonice, Poland. Described species Jerea striata Lagneau-Hérenger, 1962, and Jerea excavata (Goldfuss, 1833) from APT, Mas de Artis, Catalonia, Spain.

**Last:** Placocystus jereiformis (Schrammen, 1901), Mukronatenkriede, Misburg and Oberberg, Germany.

**Intervening:** APT, CEN, TUR.


**First:** Ingelliottus ostreiformis Lagneau-Hérenger, 1962, APT calcareous sandstone, Can Casanyas Castellet, Catalonia, Spain.

**Last:** Myrmecheonium verrucosum Schrammen, 1910, calcareous marl of Quadratenkreide, Misburg, Oberberg and Biewende, Germany.

**Intervening:** CEN–TUR.

First: Phymaraphinia plana Lagneau-Hérenger, 1962, APT
calcareous sandstone, Can Canayas Castellet, Catalonia, Spain.
Last: (?)Compsaspis cretacea Sollas, 1880, MAA Trimming-
ham Chalk, England, UK, known only from isolated spicules.
Intervening: TUR-CMP.

F. CHENENDOPORIDAE Schrammen, 1910

First: Tretoechus coniformis Oppliger, 1915, Upper Jurassic,
Switzerland.
Last: Chenenopora fungiformis Lamoroux 1821,
Mukronatenkreide, Misburg, Germany, and Turonia cf. T.
aerebriformis Schrammen, 1910, Weiss Schreibkriede, Rügen,
northern Germany.
Intervening: APT, ALB, CEN, SAN.

Extant

Porifera

Intervening: NAM–WES.

F. PHERONEMATIDAE Gray, 1872 T. (?Eoc.)–Rec.
Mar.

First: Pheronema sp. Hinde and Holmes 1891, Tertiary
spicule, near Oamaru, Otago, New Zealand.

Extant

Mar.

First: Hyalonema sp. Hinde and Holmes, 1892, Tertiary
spicule, near Oamaru, Otago, New Zealand.

Order RETICULOSA Reid, 1958

Superfamily PROTOPONGIOIDEA Hinde, 1887

F. PROTOPONGIIDAE Hinde, 1887

First: Protopongia fenestrata Salter, 1864, as spicules; ear-
liest intact skeletons are P. fenestrata Salter, 1864, P. hicksi
Hinde, 1887 and Diagoniella hindei (Walcott, 1920), Burgess
shale, Stephen Formation, near Field, British Columbia,
Canada.
Last: Gabelia pedunculus Rigby and Murphy, 1987, un-
named Devonian shale, Roberts Mountains, Nevada, USA.
Intervening: STD, LLO, LLY–LUD, FRS.

Superfamily DIERESPONGIOIDEA Rigby and
Gutschick, 1976

F. DIERESPONGIIDAE Rigby and Gutschick, 1976

First: Dierespongia palla Rigby and Gutschick, 1976,
Pooleville Limestone Member, Bromide Formation, Criner
Hills, Oklahoma, USA.
Last: Polylophidium discus Finks, 1960, Road Canyon For-
mation, Glass Mountains, Texas, USA.


First and Last: Hydnodictya acantha Rigby, 1971, Cat Head
Member, Red River Formation, Lake Winnipeg, Manitoba,
Canada.

F. MULTIVASCULATIDAE de Laubenfels, 1955

First and Last: Multivasculatas ovatus Howell and Van
Houten, 1940, ‘Gallatin’ Formation, Bighorn Mountains,
Wyoming, USA.

F. TITUSVILLIDAE Caster, 1939

First: Prototarmstrongia thelachensis Caster, 1941, Enfield
Shale, Portage Formation, Ithaca, New York, USA.
Last: Titusvillia drakei Caster, 1939, Tidioute Shale,
Titusville, or Corry Sandstone, McKean and Warren Coun-
ties, Pennsylvania, USA.

Comment: If Annulispongia interrupta Rigby and Moyle,
1959, is a titusvillid, it would be the first, but its poriferan
nature is in question, Upper Manning Canyon Shale, near
Ophir, Oquirrh Mountains, Utah, USA.

F. AGLITHODICTYIDAE Hall and Clarke, 1899

First: Aglithodictya numulina Hall and Clarke,
1899, sandstones of Chemung Group, near Laurenceville, Pennsylvania, USA.

Superfamily DICTYOSPONGIOIDEA Hall and Clarke, 1899

F. DICTYOSPONGIIDAE Hall and Clarke, 1899

First: Tiddalickia quadrata Rigby and Webby, 1988, Sugarloaf Creek breccia, top of Malongulli Formation, Cliefden Caves area, New South Wales, Australia.

Last: Microstaura doliolum Finks, 1960, Road Canyon Formation, Glass Mountains, Texas, USA.

Intervening: ASH, LUD, SIG, FRS-FAM, TOU-NAM.

F. UPHANTENIDAE de Laubenfels, 1955

First: Uphantenia chemungensis Vanuxem, 1842, sandstone of Chemung Group, near Owego, New York, USA.

Last: Physospongia dawsoni Whitfield, 1881, calcareous shale of Keokuk Group, Crawfordsville, Indiana, USA.

Intervening: ART, KUN.

F. DOCODERMATIDAE Finks, 1960

First: Docodermia sp. Finks, 1960, spicules, Magdalena Formation, near Alamogordo, New Mexico, USA; oldest sponge with intact skeletons Docodermia rigidum Finks, 1960, which co-occurs with Carphites plectus Finks, 1960 and Acanthocoryna stauroma Finks, 1960 in the Road Canyon Formation, Glass Mountains, Texas, USA.

Last: Carphites diabloensis Finks, 1960, upper Bone Springs Limestone, Sierra Diablo, Texas, may be slightly younger than species listed above. Isolated spicules of Docodermia sp. Finks, 1960, Monos Formation, El Antimonio, Sonora, Mexico appear to be youngest evidence of the family (KAZ).

Intervening: Art, KUN.

F. STEREODICTYIDAE Finks, 1960

First: Stereodictyum proteron Rigby and Washburn, 1972, Diamond Peak Formation, Buck Mountain, near Eureka, Nevada, USA.
### Key for both diagrams

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Subfamily</th>
<th>Genus</th>
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<tbody>
<tr>
<td>1.</td>
<td>Farreidae</td>
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<td>Wewokellidae</td>
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<td>38.</td>
<td>Virgolidae</td>
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### Last: Stereodictyum orthoplectum Finks, 1960, Bone Springs Limestone, Guadalupe Mountains, Texas, USA.

**Superfamily** HINTZESPONGIOIDEA Finks, 1983

F. HINTZESPONGIOIDEAE Finks, 1983

First: Polyplectella mira Ruedemann, 1925, Frankfort Shale, Six Mile Creek, New York, USA.


Intervening: LLO–CRD.

F. TEGANIIDAE de Laubenfels, 1955


First: Teganium subsphaerica (Walcott, 1879), Utica Shale, Holland Patent, New York, USA.

Last: Teganium subsphaerica (Walcott, 1879), Utica Shale, Holland Patent, New York, USA.

Order HEMIDISCOSA Schrammen, 1924

F. HEMIDISCOSAE Kling and Reif, 1969


First: Microhemidiscia ortmanni Kling and Reif, 1969, Itarare Formation, Sausal de la Vuelta, north-eastern Uruguay.
Animals: Invertebrates

Subclass HEXASTEROPHORA Schultz, 1887

Order LYSSACINOSA Zittel, 1877

Superfamily EUPLECTELLOIDEA Finks, 1960

F. EUPLECTELLIDAE Gray, 1867


Intervening: SCY, SIN, CEN–SEN. Extant

F. PYRUSPONGIIDAE Rigby, 1971

First: Pyrusponsia ruga Rigby, 1971, Cat Head Member, Red River Formation, Lake Winnipeg, Manitoba, Canada.

Last: Wongsponsia minor and W. major, both named by Rigby and Webbey (1988), Sugarloaf Breccias, upper Malongulli Formation, Cliefden Caves area, New South Wales, Australia.

F. MALUMISPONGIIDAE Rigby, 1967


First: Malumispongia hartnageli (Clarke, 1924), La Vieille Formation, Black Cape Gaspé, Quebec, Canada.

Last: Oncosella catinum Rauff, 1894, Wenlock Limestone, Dudley, England, UK.

F. CAULOLOPHACIDAE Ijma, 1927


First: Caulophacus sp. Hinde and Holmes, 1891, spiculite Oamaru, Otago, New Zealand.

Last: Fossils known only as loose spicules.

F. STAURODERMATIDAE Zittel, 1877


First: Paleostauronema transversallas, co-occurring with Poriferella formosum and Protremadictyon kainos, all Hurcewicz, 1985, Upper FRS Limestone, Kowala, Holy Cross Mountains, south-western Poland. The next record is Stauroderma explanatum Hinde, 1893, Inferior Oolite, Burton Bradstock, Dorset, southern England, UK.

Last: Stauroderma lochensis (Quenstedt, 1858), Weissjura a–y, Streitberg and other localities, southern Germany.

Intervening: BAJ.

F. APHROCALLISTIDAE Gray, 1867


First: Aphrocallistes verrucosus and A. macroporus, both Lagneau-Herenger, 1962, ALB, Gourdon, Maritime Alps, southern France.


F. TRETODICTYIDAE Schulze, 1885

J. (OXF)–Rec. Mar.

First: Psiloscalyx nitidus (Schrammen, 1936), Weissjura a, Streitberg, southern Germany.
Intervening: TUR, SEN.


First and Last: Pileolites baccatus Finks, 1960, Skinner Ranch Formation, Glass Mountains, Texas, USA.


First and Last: Stromatidium typicale Girty, 1908, ranges from Getaway Limestone Member of Cherry Canyon Formation, to Pinery (?) and Rader Members, Bell Canyon Formation, Guadalupe Mountains, Texas, USA. Order LYCHNISCOSA Schrammen, 1903 Comment: Family usage follows de Laubenfels (1955), although extensive revision of the order will be done by Reid in the revision of the Treatise on Invertebrate Paleontology.


First: Calathicus variolatus Sollas, 1883, Inferior Oolite, Burton Bradstock, Dorset, southern England, UK.

Last: Rhizopoterion ceroxiricor (Goldfuss, 1826–1833), Upper Chalk, Bromberg Halden, Germany. Several species of Venticulites also co-occur in the Upper Chalk of England, along with several species of Sephalites; V. radiatus Mantell, 1822 occurs with Rhizopoterion tubiforme Schrammen, 1912 and Leiostracosa angustata (Roemer, 1841) in Weiss Schreiberkreide, Rügen, northern Germany.

Intervening: OXF, VAL—ALB, TUR—SEN.


First: Sestrocladia furcata Hinde, 1884, Grey Chalk of Lower Chalk, Dover, England, UK.

Last: Coeloscyphia sulcata Tate, 1865, Upper Chalk, Island Magee, near Belfast, Northern Ireland.


First: Phylosthenium coniforme Quenstedt, 1877, Weissjura γ—8, Oberdigisheim, and other localities, southern Germany.

Last: Polyblasticum luxurians Zittel, 1877, Upper Chalk, Hanover, Germany. The coeval Upper Chalk species P. tuberosum and P. racemosum Toulin-Smith, 1848, come from Kent and Sussex, England, UK.

F. COELOPTICYIDAE Zittel 1877 K. (ALB—?MAA) Mar.


Last: Celleoptychium agaricoides Goldfuss, 1833, and several other species, Upper Chalk (Mukronatenkreide), near Misburg and other localities, north-western Germany.


Last: Camerospongia pervia Schrammen, 1912, Quadratenkreide, Oberg, north-western Germany; several species of Camerospongia occur in the Upper Chalk of southern England, UK.

Intervening: VLG, ALB, TUR—SEN.


First: Cyplea prolifera (Quenstedt, 1878) and other species of the genus; Weissjura α, Lochem and Heuberg, southern Germany.

Last: Ophryostoma micromatum Roemer, 1864, Grey Chalk of Lower Chalk, Dover, England, UK.

Intervening: ALB, TUR.


First: Oncotoechus cavernosus Schrammen, 1912, Scaphitenpläner (Lower Chalk), southern Germany.

Last: Oncotoechus subrutes (Quenstedt, 1878), Cuvieri pläner (Middle Chalk), Grossen Heere, southern Germany, and Chalk Marl (Lower Chalk), Isle of Wight, England, UK.

F. CALLODICITYIDAE Zittel, 1877 K. (ALB—?MAA) Mar.

First: Callodicityon fragile (Roemer, 1841), ALB, Escragonelles, southern France, and TUR Scaphitenpläner, Oppeln, Germany. Sclerokalia cunningtoni Hinde, 1884, ALB Greensands near Devizes, Wiltshire, England, UK, was questionably included in the family by de Laubenfels (1955). Sporadiscina decheni (Goldfuss, 1826) and S. teutonicae Schrammen, 1912 were also found in ALB, Gourdon, southern France.

Last: Callodicityon infundibulum (Zittel, 1877), Upper Chalk (Mukronatenkreide), Mizberg, Oberg and Ohlten, north-western Germany; Marshallia tortuosa (Roemer, 1864) and Pleuroe lacunosa (Roemer, 1841), Mukronatenkreide, Misberg and/or Oberg. To these are added coeval Porochonia simplex (Toulin-Smith, 1848), Upper Chalk, Sussex and Kent, and Diplodicityon bayfieldi Hinde, 1884, Upper Chalk, Norwich, southern England, UK.

Intervening: ALB, SEN.


First: Cinclidella solitaria (Schrammen, 1912) and Coscinopora infundibuliformis (Goldfuss, 1826), Cuvieri pläner (Middle Chalk), Grosse Heere and Störmede, north-western Germany.

Last: Balantonella elegans (Schrammen, 1902), calcareous marls of Quadratenkreide, Misburg and Oberg, north-western Germany.


First: Ceriodicyon coniformis Oppliger, 1907, Birmendorferschichten, Most Rivel, Jura, Switzerland.

Last: Cyclostigma acinosa Schrammen, 1902 and C. mean-
F. C. CALYPTERELLIDAE Schrammen, 1912

First: Coscinula micropora Schrammen, 1936, Weissjura y-o, Erkenbrechtsweiler, southern Germany.

Last: Calyptella bertae Schrammen, 1912 and Saraphora armata Schrammen, 1912, calcareous marls of the Quadratenkreide, Oberg, north-western Germany, and Plectascus labrosus (Toulmin-Smith, 1848), Weiss Schreibenkreide, Rügen, northern Germany.

Intervening: APT, ALB, SEN.

F. DACTYLOCALYCIDAE Gray, 1867


Intervening: ALB, CEN-SEN.

Class CALCAREA Bowerbank, 1864

Comment: Extensive revision of classification of the Calcarea, and fossils traditionally included in the past, will be treated in the revision of Treatise on Invertebrate Paleontology, Part E.

Subclass CALCINEA Bidder, 1898

Order SOLENIDA de Laubenfels, 1955

F. CAMAROCLADIIDAE de Laubenfels, 1955

First: Protoscyon punctata (Goldfuss, 1833), Weissjura, Streitberg, Germany. Extant

F. LEUCONIIDAE Vosmaer, 1886

First: Leuconia walfordia (Hinde, 1883), Marlstone of middle Lias, Kings Sutton, Northampton, England, UK. Extant

Order LABETIDA de Laubenfels, 1955

F. GRANTIIDAE Dendy, 1892


Order HETERACTINIDA de Laubenfels, 1955

First: Precorynella crysanthenum (Parona, 1933), Palazzo d’Adriano, Sicily.

Last: Sestrostomella rugosa Hinde, 1882, Upper Greensand, near Le Havre, France. Extant

Intervening: CRN, OXF, KIM.

F. DISCOCOELIIDAE de Laubenfels, 1955


Order BACTRONELLIDAE de Laubenfels, 1955

First: Bactronella pusillum Hinde, 1883, Upper Jura probably from Thurnau, Bavaria, Germany. Extant

Intervening: PG.

Order HETERACTINIDA de Laubenfels, 1955

First: Peronidella beipeiensis Rigby et al., 1989, Maokou Formation, Xiangbo, Guangxi, China. Last: Peronidella ocellata (Hinde, 1883), Upper Chalk, Bromley, Kent, England, UK. Extant

Intervening: OXF–KIM.

F. PHARETROSPONGIIDAE de Laubenfels, 1955


Intervening: OXF–KIM.

F. LEELAPIIDAE Dendy and Row, 1913

First: Corynella penetrata Quenstedt, 1878, St Cassian Formation, Dolomite Alps, Italy. Extant

Intervening: OXF–KIM, NEO, APT, MAA.

F. DISCOCOELIIDAE de Laubenfels, 1955

First: Peronidella beipeiensis Rigby et al., 1989, Maokou Formation, Xiangbo, Guangxi, China. Last: Peronidella ocellata (Hinde, 1883), Upper Chalk, Bromley, Kent, England, UK. Extant

Intervening: OXF–KIM, NEO, APT, MAA.

F. BACTRONELLIDAE de Laubenfels, 1955

First: Bactronella pusillum Hinde, 1883, Upper Jura probably from Thurnau, Bavaria, Germany. Extant

Intervening: PG.

Order HETERACTINIDA de Laubenfels, 1955

First: Precorynella crysanthenum (Parona, 1933), Palazzo d’Adriano, Sicily.

Last: Sestrostomella rugosa Hinde, 1882, Upper Greensand, near Le Havre, France. Extant

Intervening: CRN, OXF, KIM.

F. STELLISPONGIIDAE de Laubenfels, 1955


Intervening: CRN, OXF–KIM.

F. ELASMOSTOMATIDAE de Laubenfels, 1955

First: Elasmostoma subpeziza (D’Orbigny, 1847), Upper Chalk, Bromley, Kent, England, UK. Extant

Intervening: OXF–KIM.
Classification, with minor modifications, follows Rigby (1983, 1986).

F. ASTRAEOSPONGIIDAE Miller, 1889
First: Jawonyia gurumal Kruse, 1987, and Wagima galbanyin Kruse, 1987, lower parts of the lower Middle Cambrian, Tindall Limestone, near Tipperary, Northern Territory, Australia.
Last: Astraeospongium (?) spicule, Sadler Limestone, Sadler Ridge, reef tract, Canning Basin, Western Australia.
Intervening: STD-D. (m).

First: Eiffelia araniformis (Mizzarzhevsky, 1981), Shabakty Formation, upper Atdabanian, Aktugay, former USSR, and coeval units from Europe, Mongolia, China and Australia.
Last: Zangerlispongia richardsoni Rigby and Nitecki, 1975, Carbondale Formation, Moscovian (Alleghenian), Fulton County, Illinois, USA.
Intervening: STD, O. (I., m.).

First: Asteractinella expansa Hinde, 1888, lower part of Lower Limestone, Ayrshire, Scotland, UK, and from upper TOU limestones, Neufvilles-Soignes, Belgium.
Last: Talpaspongia clavata King, 1943, Talpa Member, Clyde Formation, Runnels County, central Texas, or top of Neal Ranch Formation, Wolfcampian, Glass Mountains, western Texas, USA.
Intervening: VIS, NAM, WES, STE.

‘SPHINCTOZOANS’, ‘CHAETETIDS’, ‘STROMATOPOROIDS’

These three groups are maintained as separate entities here, in line with traditional views based on their skeletons. However, spicule and soft-tissue data suggest that all three are polyphyletic.

Class ‘SPHINCTOZOANS’

Families and references pertaining to them are taken from Senowbari-Daryan (1990).

Order VERTICILLITIDA Termier and Termier, 1977
Last: Stylothalamia lehmanni (Engeser and Neumann, 1986), Krappfeld-Gosau, Germany.
Intervening: KUN–SPA, HET–TOA, CON–SAN.

Order PERMOSPINCTA Termier and Termier, 1974
First: Amblysiphonella parvula Pickett and Jell, 1986, New South Wales, Australia.

Last: Phragmocelia endersi Ott, 1974, Northern Calcareous Alps, Italy.
Intervening: GIV.

First: Radiothalamos uniramosus Pickett and Rigby, 1983, Garra Formation, New South Wales, Australia.
Last: Phragmocelia endersi Ott, 1974, Northern Calcareous Alps, Italy.
Intervening: GIV.

First: Fania astoma (Seilacher, 1926), Luning Formation, Pilot and Cedar Mountains, Nevada, USA.
Intervening: NOR.

### Fig. 5.4

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<td>JURASSIC</td>
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**Key for both diagrams**

- **SPHINCTOZOANS**
  1. Verticillitiidae
  2. Sebargasiidae
  3. Colospongiidae
  4. Tebagathalamiidae
  5. Annaecoeliidae
  6. Cheilusporitiidae
  7. Salzburgiidae
  8. Cribrathalamiidae
  9. Anguloonidae
  10. Phragmocoeliidae
  11. Polysolothiidae
  12. Solenolmiidae
  13. Intrasporeocoeiliidae
  14. Cryptocoeliidae
  15. Palermocoeliidae
  16. Celyphiidae
  17. Spicidae
  18. Thaumastocoeliidae
  19. Polypedidae
  20. Olangocoeliidae
  21. Clefeneleniiidae
  22. Amphorithalamiidae
  23. Pisothalamiidae
  24. Glomocystospongiidae
  25. Cassianothalamiidae
  26. Alpinothalamiidae
  27. Ceotinelliaidae
  28. Guadalupiidae

**First:** *Hormospongia labyrinthica* Rigby and Blodgett, 1983, western central Alaska.
**Last:** *Paradeningera alpina* Senowbari-Daryan and Schäfer, 1979, Northern Calcareous Alps, Italy.
**Intervening:** GIV, ASS–TAT, ANS–NOR.

**F. INTRASPOROCOEILIIDAEO** Fan and Zhang, 1985

- **First and Last:** Intrasporeocoeiliidae Fan and Zhang, 1985, Pietro di Salamone, Sosio Valley, Sicily.
**Intervening:** KUN–KAZ.

**F. CRYPTOEOEIIDAEO** Steinmann, 1882

- **First:** Righeypogonia catenulata* De Freitas, 1987, Cornwallis Island, Arctic Canada.
- **Last:** *Sphinctonella tristini* Hurcewicz, 1975, Poland. The next youngest is Cryptocelia zitteli Steinmann, 1882, Mufara Formation, Sicily (RHT).
**Intervening:** ANS–RHT, OXF–KIM.

**F. PALERMOCOELIIDAEO** Senowbari-Daryan, 1990

- **First and Last:** Palermocoelia tubifera Senowbari-Daryan, 1990, Reef Carbonate, La Montagnola, Sicily.
**Intervening:** ?LLO–HIR, ART–KUN, ANS–NOR.

**F. CELYPHIIDAEO** Laubenfels, 1955

- **First:** Porefieldia robusta Rigby and Potter, 1986, north California, USA.
- **Last:** Celyphia submarginata (Münster, 1841), Cassian Formation, Italy.
**Intervening:** ?LLO–HIR, ART–KUN, ANS–NOR.

**F. SPICIDAE** Termier and Termier, 1977

- **First:** Glomocystospongiidae De Freitas, 1987, Cornwallis Island, Arctic Canada.
- **Last:** Russospongia lupensis (Senowbari-Daryan, 1980), Sicily.
Fig. 5.4

First: Girtyocoelia canna Rigby and Potter, 1986, eastern Klamath Mountains, northern California, USA.

Last: Thaumastocoelia cassiana Steinmann, 1882, Cassian Formation, Italy.

Intervening: LLO-HIR, ?KRE-NOG, ART-KUN, ANS-NOR.


Last: Polyedra tebagensis Termier and Termier, 1955, Djebel Tebag, southern Tunisia.

Intervening: LAD-NOR.

First and Last: Olangocoelia otti Bechstadt and Brandner, 1970, Dolomite Alps, Austria.

First and Last: Cliefdenella etheridgei Webby, 1969, New South Wales, Australia.

Intervening: HIR-RAW.
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<th>Class</th>
<th>Demospongiidae Sollas, 1875</th>
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<td>Order</td>
<td>HADROMERIDA Topent, 1928</td>
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<tr>
<td>First and Last</td>
<td>Cassianothalamia zardinii Reitner, 1987, Cassian Formation, Italy.</td>
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**Order INCERTAE SEDIS**

F. ALPINOTHALAMIIDAE Senowbari-Daryan, 1990  
P. (ART)–Tr. (RHT) Mar.

**First and Last:** Uvanella irregularis Ott, 1967, Guangxi, China.  
**Last:** Leinia schneebergensis Senowbari-Daryan, 1990, Pantokrator Chalk, Greece.  
**Intervening:** LAD–NOR.

F. CEOTINELLIIDAE Senowbari-Daryan, 1978  
Tr. (ANS–RHT) Mar.

**First and Last:** Coetinella mirunae Pantic, 1975, Montenegro, former Yugoslavia.  
**Intervening:** LAD–NOR.

**Order GUADALUPIIDA Termier and Termier, 1977**

F. GUADALUPIIDAE Termier and Termier, 1977  
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Fig. 5.5

**First and Last:** *Lemonea cylindrica* (Girty, 1908), Texas, USA.

**Intervening:** SAK–KAZ.

**‘CHAETETIDS’**

Data are from Hill (1981) unless otherwise stated.

**Class** DEMOSPONGIAE Sollas, 1875

**F. ACANTHOCHAETETIDAE** Fischer, 1970


**F. CERATOPORELLIDAE** Hickson, 1911

- First: *Ceratoporella* sp., Tunisia.

**Extant**

**F. CHAETETIDAE** Milne-Edwards and Haime, 1850

- First: *Chaetetella filiformis* Sokolov, 1962, former northeastern USSR.

**F. DESMIDOPORIDAE** Preobrazhenskiy, 1968

- First: *Desmopora* sp., Turfan, China.

**Extant**

- Last: *Desmopora* sp., Turfan, China.
Animals: Invertebrates

First: Schizolites floriformis Preobrazhenskiy, 1968, former north-eastern USSR.
Last: Desmidopora sp., Tien Shan, former USSR.
Intervening: SHE-GLE.
First and Last: Favosichaetetes multiporosus Yang, 1978, China.

Last: Tiverina vermiculata Sokolov and Tesakov, 1968, Podolia, former USSR.
Intervening: SHE-GLE.


Fig. 5.6

F. SYRINGOSTROMELLIDAE Stearn, 1980
Last: Parallelopora paucicanaliculata Lecompte, 1951, Belgium.
Intervening: S. (WHI)–D. (GIV) F.
F. SYRINGOSTROMATIDAE Lecompte, 1951
First: Syringostroma centrotum Girty, 1953, New York, USA.
Last: Syringostroma densa Nicholson, 1886, Belgium.
Intervening: GED–GIV.

MESOZOIC ‘STROMATOPOROIDS’

Data are from Lecompte (1956) unless otherwise stated.

**Class** DEMOSPONGIAE Sollas, 1875

**Order** AXINELLIDA Lévi, 1956

F. ASTROSCLERIDAE Lister, 1900 Tr. (NOR)–Rec. Mar.
First and Last: Actinostromarianina lecompti Hudson, 1955, Alam Abayadh, North Yemen. Intervening: OXF.
First: Murania sp., Italy (Wood, 1987).
Last: Murania lefeldi Kazmierczak, 1974, Slovakian-Tatra Mountains, Poland (Kazmierczak, 1974).
Intervening: KIM.

F. ACTINOSTROMARIIDAE Hudson, 1955
Last: Actinostromaria stellata Dehorne, 1915, L’Ile Madame, France.
Intervening: KIM, VLG–BRM.

Order HAPLOSCLERIDA Topent, 1928

Order INCERTAE SEDIS
First and Last: Ellipsactinia ellipsoida Steinmann, 1878, Australia. Intervening: KIM.
First: Lithopora sp., Europe (Grubic, 1961).
Last: Lithopora sp., Tunisia (Grubic, 1961).
Intervening: ?SIN–TOA, OXF.
F. DISJECTOPORIDAE Tornquist, 1901
P. (UFI)–Tr. (CRN) Mar.
First: Disjectopora japonica Yabe and Sugiyama, 1935, Japan.
Last: Balatonia kochi Vinassa, 1908, Hungary.
Intervening: KAZ–LAD.
F. BURGUNDIDAE Dehorne, 1920
First: Burgundia trinorchii Dehorne, 1916, France.
Intervening: KIM–VLC.
F. SPONGIOMORPHIDAE Frech, 1890
P. (?TAT)–J. (TTH) Mar.
First: Spongiomorpha sp. Frech, 1890, Tunisia.
Last: Heptastylis stromatoporoides Frech, 1890, Japan.
Division ARCHAEOCYATHA Bornemann, 1884
Class REGULARES Vologdin, 1937
Information is taken from Debrenne et al. (1990b), unless otherwise stated.
Order MONOCYATHIDA Okulitch, 1935
F. MONOCYATHIDAE R. Bedford and W. R. Bedford, 1934
First: Archaeolynthus porosus (Bedford and W. R. Bedford, 1934), western Sayan, former USSR.
Last: Kyarocyathus duplus Kruse, 1982, Cymbric Vale Formation, New South Wales, Australia.
Intervening: ATB.
F. PALAEOCONULARIDAE Tchudinova, 1959
First and Last: Sajanolynthus desideratus Vologdin and Kashina, 1972, eastern Sayan, former USSR.
F. GLOBOSOCYATHIDAE Okuneva, 1969
First: Propriolynthus sp., Far East of former USSR.
F. FAVILYNTHIDAE Debrenne, 1974
€. (BOT) Mar.
First and Last: Favilynthus mellifer (F. Bedford and W. R. Bedford, 1936), Ajax Limestone, South Australia.
Order CAPSULOCYATHIDA Zhuravleva, 1964
F. CAPSULOCYATHIDAE Zhuravleva, 1964
First: Capsulocysthus subcallosus Zhuravleva, 1964, eastern Sayan, former USSR.
F. CRYPTOPOROCYATHIDAE Zhuravleva, 1963
First: Cryptoporocyathus junicanensis Zhuravleva, 1960, north of Krasnoyask Region, Siberia, former USSR.
Last: Korshunovicyathus melnikovi Korshunov and Zhuravleva, 1967, northern Yakutia, Khara-Ulakh, former USSR.
F. FRANSUASAECYATHIDAE Debrenne, 1964
First: Fransusaecyathus subtumulatus Zhuravleva, 1960, southern Yakutia, Lena River, former USSR.
F. TYLOCYATHIDAE Zhuravlev, 1988
€. (BOT) Mar.
First and Last: Tylocyathus bullata (Zhuravlev, 1961), eastern Sayan, former USSR.
F. URALOCYATHIDAE Zhuravleva, 1964
€. (BOT) Mar.
First and Last: Rhabdoilyxus conicus Zhuravleva, 1960, southern Yakutia, Lena River, former USSR.
F. CALYPTOCOSCINIDAE Debrenne, 1964
First and Last: Calyptocoscinus cornucopiae (Bornemann, 1887), Nebida Formation, Sardinia.
F. CLATHRICOSCINIDAE Rozanov, 1964
First and Last: Clathricoscinus vologdini Bornemann, 1887, Nebida Formation, Sardinia.

First and Last: Mawsonicoscinus sigmoides Debrenne and Kruse, 1986, Shackleton Limestone, Antarctica, Nimrod Glacier.


First and Last: Coscinocyathella nikitini Vologdin, 1959, Kuznetsky Alatau, former USSR.


First: Crassicrinus repandus (Rozanov, 1964), Ajax Limestone, South Australia.
Last: Coscinocyathellus vulgaris Vologdin, 1940, Gorny Altay, former USSR.


First and Last: Anaptyctocyathus cribripora (R. Bedford and J. Bedford, 1934), Ajax Limestone, South Australia.


First: Erismacoscinus sp., Siberian Platform, former USSR.


First: Dokidocyathella incognita Zhuravleva, 1960, southern Yakutia, Lena River, former USSR.
Last: Incurvocyathus voronovae Rozanov, 1966, Tuva, former USSR.


First: Carinocyathus sp., Siberian Platform, former USSR.
Last: Porocyathellus boudii Debrenne, 1977, Jbel lhrourd, Morocco.


First and Last: Cordobicyathus deserti Perejon, 1975, Cordoba, Spain.


First: Coscinocyacta convoluta Taylor, 1910, Ajax Limestone, South Australia.


First: Heckericyathus heckeri (Zhuravleva, 1960), southern Yakutia, Lena River, former USSR.
Last: Diplocyathellus ritezona (Taylor, 1910), Ajax Limestone, South Australia.


First: Dokidocyathus sp., Siberian Platform, former USSR.
Last: Dokidocyathus simplicissimus Taylor, 1910, Ajax Limestone, South Australia.

Intervening: ATB.


First: Ladaecyathus limbatus (Zhuravleva, 1955), Kuznetsky Alatau, former USSR.
Last: Ercopyathus heterovallum (Vologdin, 1928), Kuznetsky Alatau, former USSR.


First: Ethmocoscinus papillipora (R. Bedford and J. Bedford, 1934) Ajax Limestone, South Australia.


First: Fauciscyathus ?taumatus Zhuravleva, 1963, southern Yakutia, Lena River, former USSR.
Last: Angaricyathus cyrenovi Zhuravleva, 1965, northern Transbaikalia, former USSR.

Intervening: BOT.
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<td>7. Lunulacyathidae</td>
<td>17. Putapacyathidae</td>
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Fig. 5.7

F. FALLOCYATHIDAE Rozanov, 1969

First: *Fallocyathus dubius* Rozanov, 1969, southern Yakutia, Lena River, former USSR.

Last: *Yukonocyathus francisci* Handfield, 1971, western Canada, Yukon Province.

F. GAGARINICYATHIDAE Debrenne et al., 1989

First and Last: *Gagarinicyathus ethmophylloides* Zhuravleva, 1969, north of Krasnoyarsk Region, Sukharikha River, former USSR.

F. GEOCYATHIDAE Debrenne, 1964

First and Last: *Geocyathus botomaensis* (Zhuravleva, 1955), southern Yakutia, Botoma River, former USSR.

F. GLORIOSOCYATHIDAE Rozanov, 1969

First: *Dupliporocyathus tumulosus* Jazmir, 1975, Transbaikalia, Vitim Ranges, former USSR.

Last: *Gloriosocyathus permutus* Rozanov, 1969, northern Yakutia, Olenek River Basin, former USSR.

F. HUPECYATHIDAE Rozanov et al., 1990


F. HUPECYATHELLIDAE Rozanov, 1973
C. (BOT) Mar.

First and Last: *Hupecyathellus chouberti* Rozanov, 1968, north of Krasnoyarsk Region, Sukharikha River, former USSR.

F. JAKUTOCARINIDAE Debrenne et al., 1989

First: *Jakutocarinus jakutenis* Zhuravleva, 1960, southern Yakutia, Mukhatta River, former USSR.

Last: *Rossocyathella niaekosti* Zhuravleva, 1960, southern Yakutia, Botoma River, former USSR.

F. JAPHANICYATHIDAE Rozanov, 1973

First and Last: *Japhanicyathus genurosus* Korshunov, 1969, southern Yakutia, Lena River, former USSR.

F. JEBILETICOSCINIDAE Debrenne et al., 1989
C. (BOT) Mar.

First and Last: *Jebileticoscinus huvelini* Debrenne, 1977, Jbel Irhoud, Morocco.

F. KALTATOCYATHIDAE Rozanov, 1964

First and Last: *Kaltatocyathus kaschinae* Rozanov, 1964, eastern Sayan, former USSR.

F. KASRYCYATHIDAE Zhuravleva, 1961

First: *?Agyreocyathus malovi* Konjuschkov, 1967, northeastern Kazakhstan, former USSR. Both familial assignment and age are questionable – may be Toyonian.

Last: *Kasryicyathus schirokovae* Zhuravleva, 1961, eastern Sayan, former USSR.

F. KIDRJASOCYATHIDAE Rozanov, 1964

First and Last: *Kidrjasocyathus uralensis* Rozanov, 1960, south Urals, former USSR.
F. KIJACIYATHIDAE Zhuravleva, 1964

First: Kijacyathus chomentovskii Zhuravleva, 1969, Kuznetsky Alatau, former USSR.


F. KISASACYATHIDAE Konjuschkov, 1972
€. (BOT) Mar. (see Fig. 5.7)

First and Last: Kisasacyathus microtumulatus Konjuschkov, 1972, western Sayan, former USSR.

F. KOLBCYATHIDAE Debrenne et al., 1988

First and Last: Kolbicyathus kolbiensis Zhuravlev, 1988, Kuznetsky Alatau, former USSR.

F. KORDECYATHIDAE Missarzhevsky, 1961
€. (BOT) Mar.

First and Last: Kordecyathus shiveligensis Missarzhevsky, 1961, Tuva, former USSR.

F. KYMBECYATHIDAE Debrenne et al., 1989
€. (BOT) Mar.

First and Last: Kymbecyathus avius Debrenne and Kruse, 1986, Shackleton Limestone, Byrd Glacier, Antarctica.

F. LENOCYATHIDAE Zhuravleva, 1956
€. (ATB) Mar.

First and Last: Lenocyathus lenaicus Zhuravleva, 1955, southern Yakutia, Lena River, former USSR.

F. LEPTOSOCYATHIDAE Vologdin, 1961

First: Temnericyathus malycanicus Rozanov, 1969, southern Yakutia, Lena River, former USSR.

Last: Ichnuosocyathus ichnusae (Meneghinin, 1881), Nebida Formation, Sardinia.

F. LUNULACYATHIDAE Debrenne, 1973
€. (BOT) Mar.

First and Last: Lunulacyathus minimiporus (R. Bedford and J. Bedford, 1934), Ajax Limestone, South Australia.

F. MOOTWINGEECYATHELLIDAE Rozanov, 1964

First: Robertocyathus sp., Rozanov, 1969, Altay Sayan, former USSR.

Last: Urcyathella tercyathoides Zhuravleva, 1961, eastern Sayan, former USSR.

F. ROZANOVICYATHIDAE Korshunov, 1969

First: Churanocyathus aculeatus Sundukov, 1984, southern Yakutia, Lena River, former USSR.

Last: Dentatocoscinus sektensis (Korshunov and Zhuravleva, 1967), northern Yakutia, Khara-Ulakh, former USSR.

F. RUDANULIDAE Debrenne et al., 1989
€. (BOT) Mar.

First: Rudanulus petersi (R. Bedford and J. Bedford), 1934, Ajax Limestone, South Australia.

Last: Pilodicoscinus yuani Debrenne and Jiang, 1989, Tsanglanpu Formation, Yunnan Province, China.

F. SAJANOCYATHIDAE Vologdin, 1956
Animals: Invertebrates

First: Chakassicyathus galinae (Zhuravleva, 1967), Tuva, former USSR.
Last: Siderocycathus duncanae Debrenne et al., 1990, Battle Mountains, Nevada (Debrenne et al., 1990).
Intervening: BOT.

F. SALAIROCYATHIDAE Zhuravleva, 1956
$\text{First}: \text{Kotuyicoscinus minaevae} \text{Sundukov, 1983, Anabar Region, former USSR.}$
$\text{Last}: \text{Salairocyathus zenkovae} \text{Vologdin, 1940, Salair, former USSR.}$

F. SANARKOCYATHIDAE Hill, 1972
$\text{First and Last}: \text{Ringifungia vavilovi} \text{Korshunov, 1969, southern Yakutia, Lena River, former USSR.}$

F. SCHUMNYICYATHIDAE Debrenne et al., 1989
$\text{First and Last}: \text{Schumnyicyathus validus} \text{Zhuravleva, 1968, north of the Krasnoyarsk Region, Sukharikha River, former USSR.}$

F. SIGMOSCINIDAE R. Bedford and J. Bedford, 1939
$\text{First and Last}: \text{Sigmocoscinus sigma} \text{R. Bedford and J. Bedford, 1937, Ajax Limestone, South Australia.}$

F. SIGMOCYATHIDAE Krasnopeeva, 1953
$\text{First and Last}: \text{Sigmocyathus didymoteichus} \text{Taylor, 1910, Ajax Limestone, South Australia.}$

F. SOANICYATHIDAE Rozanov, 1973
$\text{First and Last}: \text{Batschykicyathus angulosus} \text{Zhuravlev, 1983, southern Yakutia, Lena River, former USSR.}$

F. TUMULIFUNGIIDAE Rozanov, 1973
$\text{First}: \text{Arturocyathus borisovi} \text{Rozanov, 1973, Kuznetsky Alatau, former USSR.}$
$\text{Last}: \text{Sclerocyathus sp.}, \text{Tuva, former USSR.}$

F. TUMULOCYATHIDAE Krasnopeeva, 1953
$\text{First and Last}: \text{Sclerocyathus sp.}, \text{Tuva, former USSR.}$

Class IRREGULARES Vologdin, 1937 (see Fig. 5.8)

Comment: A major revision of Irregulars systematics has been completed recently (Debrenne and Zhuravlev, 1992), and this is the scheme of classification followed herein. This work is in press at the time of writing, and so its appearance before The Fossil Record cannot be guaranteed. Owing to this, it is deemed that this section on Archaeocyathida, Class Irregulares is invalid for taxonomic purposes.
### Taxonomy

#### Porifera

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**Fig. 5.8**


First and Last: *Anthomorpha margarita* Bornemann, 1884, Sardinia.

**F. DICTYOCYATHIDAE** Taylor, 1910 * (TOM-TOY) Mar.

First: *Dictocyathus translucidus* Zhuravleva, 1960, Lena River, Yakutia, former USSR.

Last: *Molybdocyathus juvenalis* Debrenne and Gangloff, 1990, Battle Mountain, Nevada, USA.

**Intervening:** ATB-BOT.


First: *Stevocyathus elictus* Debrenne et al., 1989, Caborca, Mexico.

Last: *Claruscocoscinus billingsi* (Vologdin, 1940), Altay Sayan, former USSR.


First and Last: *Altaicyathus notabilis* Vologdin, 1932, Altay Mountains, former USSR.

**F. ARCHAEOPHARETRIDAE** Bedford and Bedford, 1936 * (ATB-BOT) Mar.

First: *Sphinctocyathus (Dictyosycon) gravis* Zhuravleva, 1960, Lena River, Yakutia, former USSR.

Last: *Protopharetra junensis* Voronova et al., 1987, Mackenzie Mountains, Canada.

**F. ARCHAEOSYCONIIDAE** Zhuravleva, 1949 * (BOT-TOY) Mar.


Last: *Archaeosycon billingsi* Walcott, 1886, Labrador, Canada.

**F. METACYATHIDAE** Bedford and Bedford, 1934 * (BOT-TOY) Mar.

First: *Metaldetes cylindricus* Taylor, 1910, South Australia.

Last: *Metaldetes profundus* Billings, 1861, Labrador, Canada.


First: *Warriootacyathus wilkawillinensis* Gravestock, 1984, South Australia.

Last: *Warriootacyathus lucidus* Gravestock, 1984, South Australia.


First and Last: *Taeniacyathellus semenovi* Zhuravleva, 1960, western Sayan, former USSR.

**F. ARCHAEOSYCONIIDAE** Zhuravleva, 1949 * (BOT-TOY) Mar.

First: *Archaeosycon copulatus* (Debrenne and Gangloff, in Voronova et al., 1987).

Last: *Archaeosycon billingsi* (Walcott, 1886), Labrador, Canada.


First: *Beltanacyathus digitus* Gravestock, 1984, South Australia.

Last: *Beltanacyathus wirrialpensis* (Taylor, 1910), South Australia.
REFERENCES


Kazmierczak, J. (1974) Lower Cretaceous sclerosponges from the...


COELENTERATA

J. R. Nudds and J. J. Sepkoski Jr

The stratigraphical information for the first and last occurrences of each family has been extracted mainly from Harland et al. (1967), Sepkoski (1982) and from the various volumes of the Treatise on Invertebrate Paleontology which cover the coelenterates (Bayer et al., 1956; Glaessner, 1979; Hill, 1981). Evidence for the first occurrences of some of the very early members of the phylum is from Scrutton (1979, 1984). Bibliographical references to most of this information are given in these various works and are not repeated here. Additional references are included herein only when they offer newer data.

Acknowledgements – We are extremely grateful to Dr B. R. Rosen (Natural History Museum, London), Dr C. T. Scrutton (University of Durham) and Dr P. Wyse Jackson (Trinity College, Dublin) for their willing help in providing both literature references and specialist advice, often at very short notice. Sepkoski acknowledges partial support for research from NASA Grant NAGW-1693.

Class ‘PETALONAMAE’ Pflug, 1970a

Leaf-like structures, often with a median line (the ‘petal organisms’ of Pflug, 1970–1973); some appear to represent colonial organisms and many are considered to be pen­natulaceans, although Pflug (1970–1973) considered that they represent a separate phylum. Classification mostly follows Glaessner (1979).

Order ERNIIETTOMORPHA Pflug, 1972

Dickinsoniidae and Bomakellidae possibly belong in this order, but the former should more probably be assigned to the primitive phylum Proarticulata (Fedonkin, 1990), while the latter probably belongs to the Arthropoda (Fedonkin, 1990).


Glaessner (1979) declares most of these genera to be unrecognizable.

First and Last: Various genera, e.g. Ernietta, Erniofossa, Ernionorma, Erniobeta, Erniograndis, from the Nama Group, Namibia, SW Africa.


First and Last: Pteridinium simplex Gurich, 1933, Nama Group, Namibia, SW Africa.

F. UNCERTAIN V. (POU) Mar.

First and Last: Namalia villiersiensis Germs, 1968 and Naspeia altae Germs, 1972, Nama Group, Namibia, SW Africa; Bakaluna sessilis Sokolov, 1972, upper Vendian, southern Siberia.

Order RANGEOOMORPHA Pflug, 1972

The Sprigginidae possibly belongs in this order, but should more probably be assigned to the Polychaeta. It should be noted that Jenkins (1985) infers the Charniidae to be pen­natulaceans and places the remaining Rangeomorpha within the Octocorallia.


First and Last: Rangea schneiderhohni Gurich, 1930, Nama Group, Namibia, SW Africa.

Class CYCLOZOA Fedonkin, 1983

Classification follows Fedonkin (1985), and includes numerous Ediacaran medusoids, such as: Beltanelliformis, Cyclo­medusa, Ediacaria, Kaisalia, Kimberia, Lorenzinites, Medusinites, Nimbia, Paliella, Pseudorhizostomites, Rugoconites, Tirasiana and others. Glaessner (1979) describes these as ‘medusae of uncertain affinities’, while Harland et al. (1967) class them as ‘medusae incertae sedis’.


Sun (1986) places this family in the Scyphozoa, questionably in the order Coronatida. However, the specimens appear to be preserved in hyporelief, suggesting that they are ‘resting traces’ rather than medusoids. We place the family questionably with the Cyclozoa.

F. UNCERTAIN V. (POU) Mar.

First and Last: Mawsonites spriggi Glaessner and Wade, 1966, Ediacara Member, Rawnsley Quartzite, Pound Sub­group, Ediacara, South Australia.
**First and Last:** Various genera, including *Cyclomedusa*, Pound Quartzite Formation, upper Adelaide Series, Ediacara, South Australia.

**F. UNCERTAIN** V. (POU) Mar.

**First and Last:** Various genera, including *Medusinites*, Pound Quartzite Formation, upper Adelaide Series, Ediacara, South Australia.

**Class HYDROCONOZOA** Korde, 1963

Classification follows Korde (1963). The Tabulaconidae, included herein by Sepkoski and Kasting (in press), were referred to the Anthozoa by Debrenne et al. (1987).


**First and Last:** *Gastroconus venustus* Korde, 1963, Lower Cambrian, Bolshoy Shangan River, Tuva, former USSR.


**First and Last:** *Hydroconus mirabilis* Korde, 1963, Lower Cambrian, Bolshoy Shangan River, Tuva, former USSR.


**First and Last:** *Dasyconus porosus* Korde, 1963, Lower Cambrian, Bolshoy Shangan River, Tuva, former USSR.

**Class INCERTAE SEDIS**

Informal classification follows Sepkoski (1982) and Sepkoski and Kasting (in press).

**F. BONATIIDAE** Fedonkin, 1985  V. (POU) Mar.

**First and Last:** *Bonata septata* Fedonkin, 1980, Bed 1, Valdai Series, mouth of Yelovyy Stream, Zimniy coast of White Sea, northern Russian Platform.
### Class Coelenterata

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**Continued from Fig. 6.1 Part 1**

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### F. Hiemaloriiidae Fedonkin, 1985 V. (POU) Mar.

**First and Last:** *Hiemalora stellaris* Fedonkin, 1982 and *Evmiaksia aksionovi* Fedonkin, 1984, upper Vendian, former USSR.


**First and Last:** *Kimberella quadrata* Wade, 1972, Pound Quartzite Formation, upper Adelaide Series, Ediacara, South Australia.

### F. Pomoriidae Fedonkin, 1985 V. (POU) Mar.

**First and Last:** *Pomoria corolliformis* Fedonkin, 1980, Bed 11, Valdai Series, Medvezh'iy Stream, Zimnyi coast of White Sea, north Russian Platform.

### F. Uncertain V. (POU) Mar.

**First and Last:** *Stauriniidia crucicula* Fedonkin, 1985, upper Vendian, former USSR.

### F. Uncertain C. (MEN) Mar.

**First and Last:** *Cambromedusa furcula* Willoughby and Robison, 1979, *Bathyuriscus fimbriatus* Subzone, Wheeler Shale, upper Middle Cambrian, Wheeler Amphitheatre, House Range, Millard County, west-central Utah, USA.

### F. Uncertain C. (LEN) Mar.

**First and Last:** *Rosellatana jamesi* Kobuk, 1984, *Bonnia–Olenellus* Zone, Rosella Formation, Atan Group, Lenian, east of Dease River, 70 km SW of fork with Liard River, near Yukon–British Columbia boundary, Cassiar Mountains, northern British Columbia, Canada.

### Class Incertae Sedis

Bayer et al. (1956) and Harland et al. (1967) referred the following to the Class Protomedusae, but we suggest suppression of this ‘trash-can taxon’.

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**Fig. 6.1**
Class SCYPHOZOA Gotte, 1887

Classification follows Bayer et al. (1956) and Harland et al. (1967). Approximately 13 extant families without fossil representatives (including all in the Stauromedusida) are not listed.

Order CARYBDEIDA Claus, 1886

F. CARYBDEIDAE Gegenbaur, 1856


First: Anthracomedusa turnbulli Johnson and Richardson, 1968, Upper Moscovian, Pit Eleven, Mazon Creek, Essex, Illinois, USA. Extant

Intervening: Quadrimedusina quadrata (Haeckel, 1869), Solnhofen Limestone (TTH), Bavaria, Germany.

Order CORONATIDA Vanhoffen, 1892


First: ?Camptostroma’ germanicum Hundt, 1939, Phycodes-Schichten, upper Tremadoc, eastern Thuringia, Germany. (Harland et al., 1967, record C. roddyi from the Cambrian, but this is now referred to the Echinodermata.) Extant

Intervening: ?Cannostomites multircratus Maas, 1906, Solnhofen Limestone (lower TTH), Bavaria, Germany; ?Lorenzinizia, Cretaceous, Italy and Tertiary (Eocene) of Italy, Cyprus, Poland and Albania.

F. PERIPHyllIDAE Claus, 1886 J. (TTH)–Rec. Mar.

First: Epiphyllina distincta (Maas, 1906), Solnhofen Limestone, Bavaria, Germany. Extant

Intervening: None.

Order SEMAEOSTOMATIDA L. Agassiz, 1862


First and Last: Eulithota fasciculata Haeckel, 1869, Solnhofen Limestone, Bavaria, Germany.


First and Last: Semaeostomites zitteli Haeckel, 1869, Solnhofen Limestone, Bavaria, Germany.

Order LITHORHIZOSTOMATIDA von Ammon, 1886


First and Last: Rhizostomites admirandus Haeckel, 1869, Solnhofen Limestone, Bavaria, Germany.

Order RHIZOSTOMATIDA Cuvier, 1799

F. LEPTOBRACHIIDAE Claus, 1883 J. (TTH)–Rec. Mar.

First: Leptobrachites trigonobrachius Haeckel, 1869, Solnhofen Limestone, Bavaria, Germany. Extant


First and Last: Prothysanomostoma eleonorae Ossian, 1973, Wea Shale, Cherryville Formation, lower Stephanian, Limekiln Hollow, Pottawattamie County, western Iowa, USA.

Order ?CONULARIIDA Miller and Gurley, 1896

Considered by many to be unrelated to the coelenterates and often assigned to the Problematica.


First and Last: Quadrosiphonogumichites and Paranabarites, Lower Cambrian, Meishucun, China.

F. CIRCONULARIIDAES Bischoff, 1978b


First: Circularia eosiilurica Bischoff, 1978b, Garaconularia ‘n. sp. A.’ Bischoff, 1978b and ‘n.g. b. n. sp. b.’ Bischoff, 1978b all from Panuara Group, lower Llandovery, southern bank of Cobblers Creek, 30 km SW of Orange, New South Wales, Australia. Last: Garaconularia multicostata Bischoff, 1978a, basal Garra Formation, upper Lochkovian, New South Wales, Australia.

F. CONULARIELLIDAE Kiderlen, 1937

C. (TOM)–O. (ARG) Mar.

First: Arthrochites and Barbitositheca, lower Meishucun, China.

Last: Conulariella, Lower Ordovician, Europe.

F. CONULARIIDAE Walcott, 1886

C. (MER)–Tr. (RHT) Mar.

First: Conularia, Upper Cambrian, world-wide. Last: Conularia stromeri Osvald, 1918, oberen Kossener Mergel, Tegernsee, Bavaria, Germany.

F. CONULARIOPSISIDAE Sugiyama, 1942 Tr. (SCY) Mar.

First and Last: Conulariopsis quadrata Sugiyama, 1942, Triassic (Olenekian), Japan.

Order INCERTAE SEDIS

F. CONCHOPELTIDAE Moore and Harrington, 1956

V. (POU)–O. (CRD) Mar.

Considered by Oliver (1984) to be unrelated to the conularids; possibly sycphyzoan or hydrozoan.

First: Conomedesites lobatus Glaessner and Wade, 1966, Pound Quartzite Formation, upper Adelaide Series, Ediacara, South Australia. Last: Conchopeltis alternata Walcott, 1876, Trenton Limestone (upper third), Trentonian, Trenton Falls, New York, USA.
First and Last: Corumbella werneri Hahn et al., 1982, Corumba Group, Corumba–Ladario, Mato Grosso, SW Brazil.

Class HYDROZOA Owen, 1843
Classification follows Bayer et al. (1956), Glaessner (1979) and Harland et al. (1967). Stromatoporoida and Spongiomorpha are not listed as they are now considered to be Porifera (q.v.). An additional approximately 25 extant families without fossil representatives (including all in the Siphonophorida) are also not listed.

Order TRACHYLINIDA Haeckel, 1877
First: ?Beltanella gilesi Sprigg, 1947, Pound Quartzite Formation, upper Adelaide Series, Ediacara, South Australia. This taxon is considered to be doubtful and a possible synonym of Ediacaria (Cyclozoa) by Glaessner and Wade (1966). No other fossil records; numerous extant genera. Extant

First: Acalepha deperdita Beyrich, 1849, Solnhofen Limestone, Bavaria, Germany. Extant
First and Last: Velumbrella czarnockii Stasinska, 1960, Lower Cambrian, Poland.

Order HYDROIDA Johnston, 1836
The first six families cited here belong to the suborder Chondrophorina, which has previously been included in the Siphonophorida (Bayer et al., 1956; Harland et al., 1967). It is now widely accepted that this suborder belongs to the Hydroida (Glaessner, 1979).


F. PORPITIDAE Brandt, 1835 V. (POU)?–Rec. Mar.
First: Eoporpita medusa Wade, 1972, Pound Quartzite Formation, upper Adelaide Series, Ediacara, South Australia. Fedonkin (1985, 1990) assigns this genus to the Cyclozoa. The next oldest porpitid is Discophyllum petalum Hall, 1847, from the Middle Ordovician (Caradoc), New York, USA. Extant

Originally considered to be a monoplacophoran (Mollusca); placed in the Chondrophorina by Yochelson and Stanley (1981).

First: Palaeacmaea typica Hall and Whitfield, 1872, Potsdam Group, New York, USA. Last: Palaeophacmaea annulata (Yokoyama, 1890), upper Ishido Formation, Sanchu area, Japan (Stanley and Kanie, 1985).


First: Hydractinia sp. Records from Jurassic are tentative. Mainly from Lower Cretaceous and Lower Eocene onwards. Extant

Considered to be graptolites by Ruedemann (1947), but assigned to the Hydroida by Mierzejewski (1986).

First: Crucimedusina walcotti (Barbour, 1914), Stephanian, Burlington Quarries, South Bend, Nebraska, USA. Extant
The authors consider this to be a hydroid rather than a graptolite.
First: Rhabdohydra tridens Kozlowski, 1959, Ontikan Limestones, Oland, Sweden. Last: Rhabdohydra tridens Kozlowski, 1959, limestone erratic, Zegrze, Poland. Extant
First and Last: Mazohydra megabertha Schram and Nitecki, 1975, Francis Creek Shale, Westphalian C, upper Mos-
Fig. 6.2

Covian, Pit Eleven, Mazon Creek, Will-Kankakee Counties, NE Illinois, USA.

**Suborder** CALYPTOBLASTINA Allman, 1871


**Order** MILLEPORINA Hickson, 1901

The Heterastriidiidae were tentatively included in the
Hydroida by Bayer et al. (1956), and in the Sphaeractinida by Harland et al. (1967), but are herein assigned to the Milleporina.

**F. AXOPORIDAE** Boschma, 1951

*Last*: *Axopora michelini* Duncan, 1866, Oligocene, England, UK.

**F. MILLEPORIDAE** Fleming, 1828 T. (DAN)–Rec. Mar. (see Fig. 6.2)

*First*: *Millepora parva* Nielsen, 1919, Chalk, Faxe Quarry, Denmark. Extant

**F. HETERASTRIDIIDAE** Frech, 1890 Tr. (NOR) Mar.

*First and Last*: *Heterastridium conglobatum* Reuss, 1865, Upper Triassic, Europe and Asia (Timor).

**Order STYLASTERINA** Hickson and England, 1905


*First*: Unnamed stylasterines from White Chalk, Denmark (Floris, 1979). Extant

**Class ANTHOZOA** Ehrenberg, 1834

**Subclass CERIANTIPATHARIA** van Beneden, 1898


*First*: *Leiopathes glaberrima* Esper, 1792, Miocene, Italy. Extant

**Subclass OCTOCORALLIA** Haeckel, 1866

Classification mostly follows Bayer et al. (1956). Approximately 27 extant families without fossil representatives (including all in the Telestacea) are not listed.

**Order STOLONIFERA** Hickson, 1883
The Clavulariidae, included herein by Bayer et al. (1956), have been reassigned to the Coenothecalia by Bayer (1979).


**Order ALCYONACEA** Lamouroux, 1816

**F. ALCYONIIDAE** Lamouroux, 1812 S. (LLY)–Rec. Mar.

*First*: *Atractosella cataractaca* Bengtson, 1981, lower and upper Visby Beds and Hogklint Beds, upper Llandovery to lower Wenlock, Gotland, Sweden. Extant

**F. NEPHTHEIDAE** Gray, 1862 J. (HET)–Rec. Mar.

*First*: *Nepthea*, Lower Jurassic, Europe. Extant


*First*: *Nepthya*, upper Turonian, Bohemia, Czechoslovakia (Sokolov, in Orlov, 1958–1964). Extant

**Order COENOTHECALIA** Bourne, 1895

**F. CLAVULARIIDAE** Hickson, 1894 K. (BER)–Rec. Mar.

These were assigned to the Stolonifera by Bayer et al. (1956), but reassigned to the Coenothecalia by Bayer (1979).

*First*: *Bayer (1981) lists the only definite fossil here as Scyphopodium ingolfi (Madsen), Upper Pleistocene, dredged sample off Oregon, USA. However, Bayer et al. (1956) list Ephiphaxum autoporoides Lonsdale, 1850, Cretaceous, England, UK. Extant

**F. HELIOPORIDAE** Moseley, 1876 K. (BRM)–Rec. Mar.

*First*: *Pseudopolytremastrum hanagaensis* Kuz'micheva, 1975, Lower Cretaceous, Zeyva River, David-Bek village, Kafan District, Armenia, former USSR. Extant

**Order GORGONACAE** Lamouroux, 1816


*First*: *Kaluginella turkmenensis* Kuz'micheva, 1980, Chaaldzha Formation, western Kopet Dag, Turkmenia, former USSR. Extant

**F. CORALLIIDAE** Lamouroux, 1812 K. (BER)–Rec. Mar.

*First*: *Corallium*, Lower Cretaceous, California, USA. Extant


*First*: *Nicella bursini* Kuz'micheva, 1980, lower Maastrichtian, Mount Besh-Kosh, Bakchisaray, SW Crimea, former USSR. Extant

**F. GORGONIIDAE** Lamouroux, 1812 T. (EOC)–Rec. Mar.

*First*: *Gorgonocephalum banniti* Giammona and Stanton, 1980, Stone City Formation, Claiborne Group, Middle Eocene, south bank of Brazos River, west of College Station, Texas, USA. Extant

**F. ISIDIDAE** Lamouroux, 1812 K. (CEN)–Rec. Mar.

*First*: *Moltkia faveolata* (Reuss, 1865) and *Moltkia solida* (Stol.), Upper Cretaceous, Czechoslovakia (see Kuz'micheva, 1980). Extant


*First*: *Krimella klikusini* Kuz'micheva, 1980, lower Maastrichtian, Mount Besh-Kosh, Bakchisaray, SW Crimea, former USSR. Extant


*First*: *Parisis steenstrupi* Nielsen, 1917, lower Campanian, Denmark (see Kuz'micheva, 1980). Extant
First: Primnoa costata Nielsen, 1913, Upper Cretaceous, Poland (Malecki, 1982).  
Extant  
First and Last: Pragnellia arborescens Leith, 1952, Upper Ordovician, Manitoba, Canada.  
Order PENNATULACEA Verrill, 1865  
F. PENNATULIDAE Ehrenberg, 1828 Tr.—Rec. Mar.  
First: Prographularia, Triassic, Germany (Sokolov, in Orlov, 1958–1964). Extant  
First: Pteroeides, Tertiary, Sumatra. Extant  
First: Virgularia, Cretaceous, world-wide. Extant  
Order?SEPTODAEARIA Bischoff, 1978a  
Conti and Serpagli (1984) regard this taxon as a bryozoan.  
Subclass ZOANTHARIA de Blainville, 1830  
A number of extant families without fossil representatives (including all in the Zoanthiniaria and Corallimorpharia) are not listed.  
Order KILBUCHOPHYLLIDA Scrutton and Clarkson, 1991  
All details from Scrutton and Clarkson, 1991.  
First and Last: Kilbuchophyllia discoidea Scrutton and Clarkson, 1991, Kirkcolm Formation, middle Caradoc (Soudleyan–Actonian), Kilbucho, near Biggar, Southern Uplands, Scotland, UK.  
Order SCLERACTINIA Bourne, 1900  
The classification of the scleractinian corals has always been controversial and is presently the subject of major revision. In the absence of any strong alternatives, the classification herein follows Bayer et al. (1956), but no suprafamily grouping has been attempted.  
F. ASTROCOENIIDAE Koby, 1890 Tr. (ANS)—Rec. Mar.  
First: Koilocenia decipiens (Laube, 1865), Middle Triassic, Europe. Extant  
F. THAMNASTERIIDAE Vaughan and Wells, 1943 Tr. (ANS)—Rec. Mar.  
First: Thamnasteria, Middle Triassic, Europe. Extant  
First: Madracis, Upper Cretaceous, Europe, North America. Extant  
First: Astreopora, Upper Cretaceous, Europe. Extant  
F. STYLINIDAE d’Orbigny, 1851 Tr. (ANS)—T. (PRB) Mar.  
First: Procyathophora furstenbergensis (Eck, 1880), Middle Triassic, Germany. Last: Phylosperis rugosa Tomes, 1882, Middle Jurassic, England, UK.  
F. PROCYCLOLITIDAE Vaughan and Wells, 1943 Tr. (ANS)—J. (BAJ) Mar.  
First: Triadophyllum posthumum Weissermel, 1925, Middle Triassic, Austria. Last: Phylloseris rugosa Tomes, 1882, Middle Jurassic, England, UK.  
F. CALAMOPHYLLIIDAE Vaughan and Wells, 1943 Tr. (CRN)—K. (MAA) Mar.  
F. PROCYCLOLITIDAE Vaughan and Wells, 1943 Tr. (CRN)—K. (MAA) Mar.  
First: Funginella, Lower Cretaceous, France. Last: Cyclolitopsis patera d’Achiardi, 1867, Middle Eocene, Italy.  
First: Cycloseris escosurae Mallada, 1887, Lower Cretaceous, Spain. Extant
**Fig. 6.3**

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|    | 1. Micrabaciidae |
|    | 2. Microsolenidae |
|    | 3. Actinacididae |
|    | 4. Poritidae |
|    | 5. Stylophyllidae |
|    | 6. Amphiastreidae |
|    | 7. Montlivaltiidae |
|    | 8. Favidiidae |
|    | 9. Rhizangiidae |
|    | 10. Oculinidae |
|    | 11. Meandrinidae |
|    | 12. Merulinidae |
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|    | 15. Caryophylliidae |
|    | 16. Rhipidogyridae |
|    | 17. Flabellidae |
|    | 18. Guyniidae |
|    | 19. Dendrophylliidae |
|    | 20. Cufiastraeniidae |
|    | 21. Distichophyllidae |
|    | 22. Donacosmilidae |
|    | 23. Intersmilidae |
|    | 24. Pachythecalidae |
|    | 25. Pamiroseniidae |
|    | 26. Zardinophylliidae |
|    | 27. Carolastraeidae |

**F. MICRABACIIDAE** Vaughan, 1905  
**First:** *Micrabacia beaumonti* Milne Edwards and Haime, 1851, Lower Cretaceous, France.  
**Last:** *Actinacis*, Lower Oligocene, Eurasia, North America, South America, West Indies, Africa.

**F. MICROSOLENIDAE** Koby, 1890  
J. (HET)—K. (SAN) Mar.  
**First:** *Chomatoseris*, Lias, Europe.  
**Last:** *Gesaviarea*, Upper Cretaceous, Austria.

**F. ACTINACIDIDAE** Vaughan and Wells, 1943  
**First:** *Actinarea*, Lower Jurassic, no locality given (Roniewicz and Morycowa, 1989).

**F. PORITIDAE** Gray, 1842  
**First:** *Goniopora*, Upper Jurassic, NW of former Yugoslavia (Turnsek, 1989).  
**Last:** *Protoheterastrea leonardi* (Volz, 1896), Middle Triassic, Europe.

**F. STYLOPHYLLIDAE** Volz, 1896  
Tr. (LAD)—J. (BAJ) Mar.  
**First:** *Protoheterastrea leonardi* (Volz, 1896), Middle Triassic, Europe.  
**Last:** *Lepidophyllia*, Middle Jurassic, UK, South America and *Heterasastrea*, Middle Jurassic, Europe.
Animals: Invertebrates

F. AMPHIASTREIDAE Ogilvie, 1896
First: Discocenia ruperti (Duncan, 1867), angulata Zone, lower Liassic, Down Yatherly, Gloucestershire, England, UK (Negus, 1983).
Last: Budaia travensis Wells, 1933, Upper Cretaceous, Texas, USA Amphiastrea and Axosmilia, Upper Cretaceous, Italy.

F. MONTIVALTIIDAE Dietrich, 1926
Tr. (NOR)–T. (LUT/BRT) Mar.
First: Palaeastraea, Upper Triassic, Europe (Roniewicz and Morcyowa, 1989).
Last: Placosmilia, Middle Eocene, Europe and Alabama, USA and Elasmophyllia, Middle Eocene, Europe, South America.

First: Goniocora concina Tomes, 1882, Middle Jurassic, Jebel Bou Dahar, Morocco (Beauvais, 1986).

F. RHIZANGIIDAE d’Orbigny, 1851
First: Arctangia nathorsti (Lindstrom, 1900), Lower Cretaceous, King Charles Island, Arctic.

First: Harland et al. (1967) cite Pseudogatheria hiraigensis Eguchi, 1951 from the Aptian Miyako Group of Japan, but this genus is considered by Bayer et al. (1956) to belong to the Stylinidae. Archohelia occurs in the Middle Cretaceous of North America, Central America and the West Indies.

First: Dendrogyra, Lower Cretaceous, Mexico, Spain, Italy.

F. MERULINIDAE Verrill, 1866 T. (UMI)–Rec. Mar.
First: Merulina ampliata (Ellis and Solander, 1786), Upper Miocene, Indonesia (Chevalier and Beauvais, 1987).

F. MUSSIDAE Ortman, 1890 J. (OXF)–Rec. Mar.
First: Palacomussa, Rauracian, Europe.

First: Pectinia pseudeamandrites d’Archicardi, 1867, Middle Eocene, Italy.

First: Thecocystthus, Lower Jurassic, Europe.

Last: Aplosmilia, upper Santonian, Austria and France and Fromentelligyra, upper Santonian, France.

First: Adkinsella edwardsensis Wells, 1933, Lower Cretaceous, Texas, USA.

First: Microsmilia sp. Mariotti et al., 1979, Middle Jurassic, Sasso di Pale, Foligno, Umbria, Italy.


F. CIUFASTREIDAE Mel’nikova, 1983
Tr. (NOR–RHT) Mar.
First: Ciufastastra granulata Mel’nikova, 1983, Bor-Tepa Formation, upper Norian, Karakul’-Ashu Pass, SE Pamir, Tajikistan, C. tenuiseptata (Mel’nikova, 1967), Bor-Tepa Formation, upper Norian, Bor-Tepa Gorge, SE Pamir, Tajikistan and Gillastraera delicata Mel’nikova, 1983, Bor-Tepa Formation, upper Norian, between Khan-Yuly and Beik Gorges, SE Pamir, Tajikistan.
Last: Ciufastastra incurva Mel’nikova, 1983, Chichkaute Formation, Bezmyanny Gorge, left bank of Karauldyn-Dana Valley, SE Pamir, Tajikistan.

F. DISTICHOPHYLLIDAE Cuif, 1976
Tr. (CRN–RHT) Mar.
First: Distichophyllia, Upper Triassic, no locality given (Roniewicz and Morcyowa, 1989).
Last: Distichophyllia, Upper Triassic, no locality given (Roniewicz and Morcyowa, 1989).

First: Prodonacocsmilia ronovii in Mel’nikova and Roniewicz, 1976, Churumdinskaya Member, mouth of Djangi-davan saj, SE Pamir, Tajikistan.
Last: Prodonacocsmilia sp. Mel’nikova and Roniewicz, 1976 and Donacocsmilia corallina de Fromentel, 1861, both from Upper Jurassic, Strambert, western Carpathians.

First: Intersmilia dijartyrabatica Mel’nikova, in Mel’nikova and Roniewicz, 1976, Ghurumdinskaya Member, Djarty-Rabat Mountain, SE Pamir, Tajikistan.
Last: Intersmilia, Upper Jurassic, Eurasia (Mel’nikova and Roniewicz, 1976).

First: Pachysolenia mardjinaica (Mel’nikova), Upper Triassic, Katta-Mardzhinay River, SE Pamir Range, Tajikstan (Il’ina, 1983).
Last: Pachysolenia cylindrica, Mardzhinay River, SE Pamir, Tajikistan.

F. PAMIROSERIIDAE Melnikova, 1984
Tr. (ANS–RHT) Mar.
First: Pamirosersis silesiacus (Beyrich, 1852), Gorazde Beds, lower Anisian, Upper Silesia, Poland (Malinowska, 1986).
Last: Pamirosersis rectilamellosa (Winkler, 1861), Sub-tiatric
**Order** ACTINIARIA R. Hertwig, 1882

**F. ZARDINOPHYLLIIDAE** Montanaro Gallitelli, 1975

**First:** *Zardinophyllum zardinii* Montanaro Gallitelli, 1975, Cassiani Beds, Middle Triassic, near Cortina, northern Italy.

**Last:** *Zardinophyllum zardinii* Montanaro Gallitelli, 1975, Cassiani Beds, Upper Triassic, near Cortina, northern Italy.

**F. CAROLASTRAEIDAE** Eliasova, 1976

**First:** *Carolastraea* sp. Mel’nikova and Roniewicz, 1976, Koltshakskaya Member, middle Callovian, Koltshak Mountains, Kuntej saj, SE Pamir, Tajikistan.

**Last:** *Carolastraea fraji* Eliasova, 1976, Upper Jurassic, west Carpathians.

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**Order** ACTINIARIA R. Hertwig, 1882

**F. UNCERTAIN** E. (STD) Mar.

**First and Last:** *Mackenzia costalis* Walcott, 1911, Burgess Shale, Middle Cambrian, British Columbia, Canada.

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**Subclass** TABULATA Milne Edwards and Haime, 1850

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Fig. 6.4

Series, Upper Triassic, Tatra Mountains, Poland (Malinowska, 1986).

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**Series, Upper Triassic, Tatra Mountains, Poland (Malinowska, 1986).**
Classification follows Hill (1981), but excludes the Chaetetidae, Desmidoporididae, Tiverinidae and Acanthochaetetidae (Order Chaetetida), which are now assigned to the Porifera (q.v.). Other families referred to the Chaetetida by Hill (1981) are herein included with the Lichenariida and the Tetradiida, following Laub (1984).

**Order LICHENARIIDA Sokolov, 1962**

First and Last: *Lamottia heroensis* Raymond, 1924, Day Point Limestone, Top of Lower Chazyan, upper Llanvirn, W. C. Hall's Pasture, 2 miles SW of South Hero, Vermont, USA.

**F. LICHENARIIDAE Okulitch, 1936**

First: *Lichenaria claudi* Bassler, 1950, upper Tremadoc, Texas, Missouri, USA. Laub (1984) doubts that these early forms are true Lichenaria and regards the earliest undisputed example to be *Lichenaria prima* Okulitch, 1936 from the Chazyan (Llanvirn) of Tennessee, USA.

Last: *Lichenaria typa* Winchell and Schuchert, 1895, Guttenberg Member, Decorah Formation, Blackriverian, upper Caradoc, St Paul, Minnesota, USA.

Order TETRADIIDA Okulitch, 1936

Several workers have expressed doubt that the tetradiids are true tabulate corals, and perhaps they should be considered as Problematica.

First: *Phytopsis cellulosum* Hall, 1847, base of Middle Ordovician, New York, USA.


First and Last: *Paleoalveolites*, lower Caradoc, Tennessee, Indiana, USA.


First: *Cryptolichenaria miranda* Sokolov, 1955, upper Arenig, River Moyero, northern Siberian Platform, former USSR.

Last: *Cryptolichenaria*, upper Ashgill, Estonia, former USSR, and *Porkunites amaloides* (Dybowski, 1873), upper Ashgill, Porkuni, eastern Estonia, former USSR.

Order SARCINULIDA Sokolov, 1950


First: *Billingsaria parva* (Billings, 1859), Valcour Limestone, Sloop Island, New York, USA; Minegan Formation, Quebec and Aylmer Limestone, Ontario, Canada.


First: *Thecia swindernaria* (Goldfuss, 1829), upper Llandovery, widespread, UK, and *Romingerella major* Rominger, 1876, upper Clintonian, Indiana, USA.

Last: *Fossopora devonica* Leleshov, 1965, Middle Devonian, southern slope of Gissar Range, upper reaches of River Sorbukh, basin of River Kafirnigan, Kazakhstan, former USSR.

Order FAVOSITIDA Wedekind, 1937


Last: *Sutherlandia*, lower Artinskian, Europe (Urals).


First and Last: *Pseudafoxosites stylifer* Gerth, 1921 and *Stylonites porosus* Gerth, 1921, upper Kazanian, Timor.


First: *Syringolites huronensis* Hinde, 1879, Brassfield-Sexton Creek Limestone, middle Llandovery, near Hamburg and Cluster Park, western Illinois, USA.

Last: *Syringolites*, Middle Silurian, Gotland, Sweden, Estonia, former USSR.


First: *Priscosolenia priscus* (Sokolov, 1951), Porkuni Stage, upper Ashgill, Estonia, former USSR.

Last: *Mesosolenia festiva* (Chernyshev, 1951), Upper Silurian, Kuzbas, left bank of River Chumysh, Mount Glyaden, Siberia, former USSR.


First: *Agetolites mirabilis* Sokolov, 1955, Upper Ordovician, SW foothills of Chingiz Range, Kazakhstan, former USSR, and *Agetolitella prima* Kim, 1962, Upper Ordovician, Zeravshan-Gissar Range, Tien Shan, China.

Last: *Somphopora daedalea* Lindstrom, 1883, Middle Silurian, Shan-Tien, Szechwan, China.


First: *Pleurodictyum*, upper Ludlow, Kentucky, Tennessee, USA; New South Wales, Australia.

Last: *Michelinia*, lower Tatarian, Europe, Asia.


Last: *Donetzites milleporoides* Dampel, 1940, lower Ordovician, Kuzbas, left bank of River Chumysh, Mount Glyaden, Siberia, former USSR.
Moscovian, Europe (Donbas), Asia (Iran, Vietnam, Kweichow).

First and Last: Vaughania cleistoporoides Garwood, 1913, upper Tournaisian, UK.

First: Palaeacis enorme (Meek and Worthen, 1860), Louisiana Limestone and Saverton Shale, upper Famen­
nian, eastern Missouri, USA.
Last: Palaeacis regularis Gerth, 1921 and Palaeacis tubifer Gerth, 1921, Middle Permian, Timor.

First: Striatopora flexuosa Hall, 1851, Brassfield Formation, middle Llandovery, Cincinnati Arch region, Cincinnati,
Ohio, USA (Laub, 1979).
Last: Gertholites curvata (Waagen and Wentzel, 1886), Salt Range, Pakistan; lower Tatarian, Timor, yakutia, Australia.

First: Kolymopora irjadiensis Preobrazhenskiy, 1964, upper Caradoc, River Kolym, NE of former USSR.
Last: Fomichevia salairica Dubatolov, 1959, Shanda Beds, Kuzbas, former USSR.

First: Archypora tuvella Chekhovich, 1975, lower part of upper Chergak subhorizon, western Tuva, Khondelen.
Last: Various genera, e.g. Alveolites, Crassialveolites, Kitakami, upper Frasnian, cosmopolitan.

First: Planoecinites, upper Llandovery, Estonia, former USSR.
Last: Planoecinites, Middle Devonian, Asia and New South Wales, Australia.

Order HELIOLITIDA Frech, 1897
First: Heliolites inordinatus (Lonsdale, 1839), Middle Ordovician, Robeston Walthen, Pembrokeshire, Wales, UK.
Last: Heliolites porosus Goldfuss, 1826, Upper Devonian, Torquay and Plymouth, England, UK; Ron, Annam, Indo­
China.

First: Wormsiopora hirsuta (Lindstrom, 1899), middle Caradoc, Tasmania.
Last: Boginibilites sytovae Bondarenko, 1966, Nadaynasu Horizon, 5 km NE of ruins of Bogimba, Kazakhstan, former USSR.

First: Parastelliporella columella Lin and Chow, 1977, Upper Ordovician, Kiangsi, China.
Last: Podollites, Middle Devonian, Kazakhstan, former USSR.

First: Visbyolites stella (Lindstrom, 1899), Dulankar Horizon, upper Caradoc, Tarbagatau Range, Kazakhstan, former USSR.
Last: Pachyhelioplasma kettnerovae Kim, 1966, Middle Devonian, Zeravshan-Gissar Range, basin of River Kashkadari, Khodza-Kurgan Gully, Kazakhstan, former USSR.

First: Propora tubulata (Lonsdale, 1839), lower Caradoc, Bala Limestone, Gwynedd, Wales, UK.
Last: Innapora incredula (Chernova, in Kovalevskiy et al., 1960), Dalian Horizon, left side of River Isfara, north slopes of Turkestan Range, southern Tien Shan, China.

First: Mongoliolites paradoxides Bondarenko and Minzhin, 1977, lower Ashgill, southern foot of Khangay Range, Central Mongolia.
Last: Sibiriolitella, Middle Silurian, China.

First: Plasmaporella, middle Caradoc, New South Wales, Australia.
Last: Camptolitusa papillata (Romer, 1876), upper Wenlock, Michigan, USA.

Last: Asticmis ascalphata Leleushus, 1974, lower part of Dalian Horizon, Southern Tien Shan, China.

First: Cyrtophylum densum Lindstrom, 1882, middle Caradoc, Middle Tunguska River, Siberia, former USSR.
Last: Karagemia altaica Dzubo, 1960, upper Ashgil, right side of River Karagym, Altay Mountains, former USSR, and Rhiphylum constellatum Lindstrom, 1882, upper Ashgil, middle Tunguska river, above last rapids before River Chuna, Siberia, former USSR.

First: Coccoseris, low in Fauna 1, lower mid-Mohawkian, New South Wales, Australia.
Last: Acidolites lower Wenlock, locality unknown.


First and Last: Pycnolithus bifidus Lindstrom, 1899, upper Llandovery or lower Wenlock, lower Visby shore, Gotland, Sweden. [Not in situ.]


First: Trochiscolithus microaster (Lindstrom, 1899), middle Caradoc, Norway, Sweden and Estonia, former USSR.
Last: Various genera, e.g. Halytites, Catenipora, Acanthohalytites, Cystihalytites, Falsicatenipora, Solenihalytites, Upper Chasmosps Beds, upper Ashgill, Norway.


First: Queopora quebecensis (Lambe, 1899), Chaumont Limestone, Blackriveran (lower Caradoc), 2 miles south of Blue Point, Lake St John, Quebec, Canada.
Last: Various genera, e.g. Halytites, Catenipora, Acanthohalytites, Cystihalytites, Falsicatenipora, Solenihalytites, Upper Silurian, cosmopolitan.

Order Auloporida Sokolov, 1947


First: Aulopora, Lower Ordovician, Europe (Baltic), Asia (Irkutsk).
Last: Aulopora timorica Gerth, 1922, Basleo Limestone, Timor.


First: Bajgolia altaica Dzyubo, 1962, lower Caradoc, Tasmania, New South Wales, Australia.
Last: Bajgolia altaica Dzyubo, 1962, lower Ashgill, Bay-gol Creek, 1 km above junction with River Kayna, Altay, former USSR.


First: Kozlowskiozziidae (Stasinska, 1958), Middle Devonian, Grzegorzowice, Poland.


First: Eofletcheriella primitioa Lin and Chow, 1977, Upper Ordovician, Kiangsi, China.
Last: Pseudofletcheriella furanhbula Chi, 1976, lower Middle Devonian, Dong Uijimqin Qi, NE Inner Mongolia.


First: Bainbridgia typicalis Ball, 1933, lower Ludlow, Missouri, USA.
Last: Cladochonus, lower Tatarian, cosmopolitan.


First: Oculinella gerthi Yakovlev, 1939, upper Artinskian, Oufimskoe Plateau, Donbas-Krasnojarsk, Urals, former USSR.

Last: Trachypysamma dendroides Gerth, 1922, Basleo Limestone, upper Kazanian, Timor.


First and Last: Auloheilla irregularis Gerth, 1921 and Auloheilla laevis Gerth, 1921, Basleo Limestone, upper Kazanian, Timor.


First: Romengeria, upper Llandovery, Estonia, former USSR.
Last: Protopora cystoides (Grabau, in Greene, 1901), upper Mississippian, Indiana, USA.


First and Last: Palaeofavosipora clausa (Lindstrom, 1866), Middle Silurian, Gotland, Sweden.


First: Aulocystus, Lower Silurian, Estonia, former USSR.
Last: Adaterina acritos Webby, 1977, Top of Malachi’s Hill Beds, middle to upper Cincinnatian (Richmondian), New South Wales, Australia.

Last: Pseudoromingeria kotoi Yabe and Hayasaka, 1915, Yabeina Zone, upper Kazanian, Kinsyozan, Gifu Prefecture, Fuwa-gun, Japan.


First and Last: Khmeria problematica Mansuy, 1914, lower Artinskian, Cambodia, Japan, Armenia, Sicily, Kazan, Donbas, Urals, Tunisia, etc.

F. Syringoporidae de Fromentel, 1861 O. (ASH)–P. (KAZ) Mar.

First: Sinopora, lower Silurian, Estonia, former USSR, and Sinoporella fenggangensis Kim and Yang, in Yang et al., 1978, Shiniulan Formation, Feng-gang, Guizhou, Kweichow, China.
Last: Sinopora dendroides (Yoh, in Yoh and Huang, 1932), Chihsia Limestone, lower Artinskian, Chi-lung-shan, near Ho-chou, SE Anhui, China.


First and Last: Khmeria problematica Mansuy, 1914, lower Artinskian, Cambodia, Japan, Armenia, Sicily, Kazan, Donbas, Urals, Tunisia, etc.

F. Syringoporidae de Fromentel, 1861 O. (ASH)–P. (KAZ) Mar.

First: Syringopora, upper Ashgill, Urals, former USSR.
Last: Enigmilites lectus Dzyubo, 1962, upper Tastuba subhorizon, right bank of River Kosva, western slopes, central Urals, former USSR.


First and Last: Periphaeolinaeidae exornata Dethier and Pel, 1971, lower Givetian, Hampleau, Belgium.


First: Labyrinthis chidlensis Lambe, 1906, middle Caradoc, shore of west central Lake Manicouagan, Quebec, Canada.
Last: Hayasaka aequitabulata (Huang, 1932), H. eleganella (Yabe and Hayasaka, 1915) and H. lanchangensis (Huang,
1932), all from Wushan Limestone, lower Tatarian, Hupei and northern Szechwan, China.

**F. MULTITHECOPORIDAE** Sokolov, 1950

First: *Multithecopora*, Lower Silurian, Norway.
Last: *Multithecopora*, Upper Permian, China, Japan, Iran, Afghanistan, former Yugoslavia; Urals, former USSR; Yukon, Canada.

**F. ROEMERIIDAE** Pocta, 1904

First: *Roemerolites*, ?Lower Silurian, Kweichow, China.
Last: *Bayhaium merriamorum* Langenheim and McCutcheon, 1959, McCloud Limestone, Lower Permian, Shasta County, California; Nevada, USA.

**F. THECOSTEGITIDAE** de Fromentel, 1861

First: *Thecostegites*, Upper Silurian or Lower Devonian, Polar Urals, former USSR.
Last: *Duncanopora duncaneae* Sando, 1975, Moffat Trail Limestone Member, ?lower Namurian, Wyoming, USA; ?lower Namurian, Idaho, Utah, USA.

**F. CHONOSTEGITIDAE** Lecompte, 1952

First and Last: *Chonostegites*, Lower–Middle Devonian, eastern North America.
First:  Meitanopora convexocystosa Yang, 1973, Shiniulan Formation, Lower Silurian, Meitan, Guizhou, Kweichow, China.
Last:  Neozyringspora, Lower Permian, Spitsbergen; Urals, former USSR; Devon Island, Nevada, USA.

Order UNCERTAIN
First and Last:  Lipopora lissa Jell and Jell, 1976, Coonigan Formation, lower Middle Cambrian, western New South Wales, Australia.

Subclass RUGOSA Milne Edwards and Haime, 1850
Classification follows Hill (1981).
Order CYSTIPHYLLIDA Nicholson, 1889
First:  Primitophyllum primum Kaljo, 1956, lower Caradoc, Estonia, former USSR.
Last:  Bojocyclus bohemicus Prantl, 1939, Hlucobycey Limestone, ‘White Bed’ at top, Quarry at Holyne, west of Prague, Czechoslovakia.

First:  Hillophyllum priscum Webby, 1971, Ciefden Caves Limestone (lower part), lower Caradoc, Booneroo, New South Wales, Australia.
Last:  Aphyllylum, Middle Devonian, Tajikistan, former USSR.

Stasinska (1967) suggests that this genus belongs instead to the Tabulata (?Auloporida).
Last:  Fletcheria tubifera Milne Edwards and Haime, 1851, Middle Silurian, Gotland, Sweden.

First:  Holmophyllum, Lower Silurian, New South Wales, Australia.
Last:  Holmophyllum uralicum (Zhavoronkova, 1972), Middle Devonian, western slopes of South Urals, River Maly Ik, former USSR.

First:  Goniophyllum pyramidalis (Hisinger, 1831), upper Llandovery; UK; Gotland, Sweden; Ontario; Canada; Iowa, USA and Araepomopra prismatica (Lindstrom, 1868), upper Llandovery, Gotland, Sweden.
Last:  Calceola sandalina (Linnaeus, 1771), upper Givetian, Europe, Africa, Asia, Australia.

First:  Cystiphyllum, Upper Ordovician, cosmopolitan.
Last:  Cystiphyllum (Zonophyllum), ?Upper Devonian, Poland, western Australia. Definitely known from the Givetian – e.g. C. (Z.) thomasi (Taylor, 1951), upper Middle Devonian, Richmond Walk Quarry, Stonehame, Plymouth, England, UK; Cystiphyllodes (Lythophyllum) excertricum (Borchers MS, in Wedekind, 1925), Berndorf, Germany; Diplochone striata Frech, 1886, upper Stringocephalus Beds, Rhinelan, Germany.

First:  Digonophyllum and Mesophyllum, both from Zlicchovian, Western and Arctic Canada and Alaska (Oliver and Pedder, 1979).
Last:  Various genera, e.g. Digonophyllum (Digonophyllum), D. (Mochophyllum), Mesophyllum (Mesophyllum), M. (Dialytophyllum), M. (Hemicosmophyllum), M. (Lekanophyllum), M. (Zonodigonophyllum), all from Givetian of Germany, etc.

Order STAURIIDA Verrill, 1865
First:  Fauvistina undulata (Bassler, 1950), Platteville Limestone, Blackriverian, lower Caradoc, Beloit, Wisconsin, USA.
Last:  Columnaria, Upper Devonian, Altai–Sayan, former USSR (Oliver and Pedder, 1979).

First:  Protopilophyllum, upper Llandovery, Siberian Platform, former USSR.
Last:  Cyithopaedium paucitabulatum (Schluter, 1880), Stringocephalus Limestone, Hebborn, Bergisch–Gludad, Germany; Depasophyllum adnetum Grabau, 1936, bioherm in Four Mile Dam Formation, Traverse Group, Four Mile Dam, Thunder Bar River, Alpena County, Michigan, USA, and Fletcherina simplex (Yabe and Hayasaka, 1913), Middle Devonian, Queensland, Australia.

First:  Neocolumnaria vagranensis Soshkina, 1949, Eifelian, Krasnaya shapochka no. 19, northern Ursals, former USSR.
Last:  Neocolumnaria, ?Givetian, NW Territories, Canada.

First and Last:  Centristela fasciculata Tsyganko, 1967, Middle Devonian, Pay–Khoy, Belovskaya River, former USSR and C. anavarensis (Goryanov, in Bulvankver et al., 1968), Middle Devonian, southern Fergana, Katran Range, former USSR.

First:  Amplexoides severnensis (Parks, 1915), lower Llandovery, Limestone rapids, Severn River, northern Ontario, Canada.
Last:  Gorskyella tschigariensis (Fomichev, 1935), Donbas Limestone, C23, Upper Bashkiran, right bank of Zheleznyaya ravine, former USSR.
F. KIZILIIDAE Degtyarev, 1965
First: Kizilia concavitabulata Degtyarev, 1965, Kizilian Suite, upper Viséan, Kizil, southern Urals and Melanophyllidium latiosculus Kropacheva, 1966, lower part of Puma Suite, upper Viséan, southern Fergana, southern slopes of Katran Range, former USSR.
Last: Kizilia, upper Serpukhovian, Urals, former USSR (Semenoff-Tian-Chansky and Sutherland, 1982).

F. STREPTELASMATIDAE Nicholson, 1889
First: Streptelasma corniculum (Hall, 1847), N. gracilis Zone, Blackriver Formation, lower Caradoc, New York, Michigan, USA.
Last: Altaiophyllum belgebaschicum Ivaniya, 1955, upper Givetian, right tributary of River Chi, River Belgebash, Altay and Xenophyllum thenofordense (Stewart, 1936), Hamilton-Arkona beds, upper Givetian, Dam on Aus Sables River at mouth of Rock Glen, Arkona, Ontario, Canada.

F. DITOECHOLASMATIDAE Sutherland, 1965
S. (LUD) Mar.
First and Last: Ditoechasomas fanninganum (Safford, 1869), Brownsport Formation, Tennessee, USA and D. lawrencense Sutherland, 1965, Henryhouse Formation, Oklahoma, USA.

F. PALIPHYLLIDAE Soshkina, 1955
First: Various genera, e.g. Paliphyllum, Protocyathactis, Sumsarophyllum, all from Upper Ordovician of Asia.
Last: Neopaliphyllum soshkinae Zheltonogova, 1961, Baskuskan Suite, left bank of River Baskuskan, Salair Mountains, former USSR.

F. KODONOPHYLLIDAE Wedekind, 1927
First: Kodonophyllum, ?Upper Ordovician, Estonia, former USSR. Schlothoimophyllum paetellatus (Schlotheim, 1820), definitely occurs in the upper Llandovery of the UK, Sweden and Norway.
Last: Sinochlamydophyllum crassiseptatum Guo, 1976, lower Middle Devonian, Inner Mongolia and Zelophyllia tabulatum (Soshkina, 1937), Middle Devonian, left bank of River Vagran, Urals, former USSR.

F. MUCOPHYLLIDAE Soshkina, 1947
First: Kunjeophyllum ajaguseense Sultanbekova, 1971, upper Llandovery, River Ayaguz, Chingiz Range, Kazakhstan, former USSR.
Last: Biomphoza repleta Barrois, 1889 and Pseudamplexus ligeriensis (Barrois, 1889), Calcaire d’Erbray, Chateau-Briant, France.

F. ACROPHYLLIDAE Stumm, 1949
D. (EMS) Mar.
First and Last: Acrophyllum onoidaeense (Billings, 1859), Ooondaga Limestone, Ontario, Canada, and Scenophyllum conigerum (Rominger, 1876), Coral Zone in Jeffersonville Limestone, Falls of the Ohio, Indiana, USA.

F. AMSDENOIDIDAE Hill, 1981
First: Amsdenoides acutianumlatum (Amsden, 1949), Brownsport Formation, Tennessee, USA.
Last: Multicarinophyllum multicarinatum Spasskiy, 1965, Middle Devonian, River Kyzylagach, Dzungarian Alatau, former USSR.

F. CALOSTYLIDAE Zittel, 1879
First: Various genera, e.g. Calostylis, Ningnanophyllum, Yohophyllum, all from Middle Ordovician of Szechwan and Kweichow, China.
Last: Calostylis, Aynas Horizon, Kazakhstan, former USSR.

F. LAMBELASMATIDAE Weyer, 1973
First: Lambeophyllum profundum (Conrad, 1843), Platteville Limestone, Black River Group, lower Caradoc, Mineral Point, Wisconsin, USA.
Last: Prototryplasma oromianiv Ivanovskiy, 1963, upper Llandovery, basin of River Imanga, Norilsk district, Siberian Platform, former USSR.

Last: Cyathaxonia, Upper Permian, Cambodia.

F. PETRAIIDAE de Koninck, 1872
Last: Petraiella kielcensis Rozkowska, 1969, lower Famen­nian, Kielce, Poland.

F. METRIOPHYLLIDAE Hill, 1939
S. (WEN)–P. (KAZ) Mar.
First: Duncanella borealis Nicholson, 1874, ‘Lower’ Silurian, Waldron, Indiana, USA.
Last: Asserculinia prima Schoppe and Stacul, 1959, lower Kazanian, Basleo, Timor.

F. LACCOPHYLLIDAE Grabau, 1928
S. (WEN)–P. (TAT) Mar.
First: Laccophyllum acuminatum Simpson, 1900, lower Wenlock, Perry County, Tennessee, USA.
Last: Ampelocarina, Palaeofusulina Zone, upper Tatarian, Salt Range, Timor (Flügel, 1970).


First and Last: Lindstroemia columnaris Nicholson and Thomson, 1876, lower Givetian, North America.
F. HADROPHYLLIDAE Nicholson, 1889
First: Hadrophyllum orbignyi Milne Edwards and Haime, 1850, Jeffersonville Limestone, Indiana or Kentucky, USA; Speeds Limestone, Charlestown, Indiana, USA.
Last: Microcyclocus discus Meek and Worthen, 1868, St Laurens Limestone, Hamilton Group, Grand Tower, northern end of Backbone Ridge, Illinois, USA.

Last: Combophyllum osismorum Milne Edwards and Haime, 1850, lower Eifelian, Brest roadstead, Le Fret, France.

First: Petrozium dewateri Smith, 1930, Pentamerus Beds, upper Llandovery, Morrell's Wood Brook, near Buildwas, UK.
Last: Kysylagathophyllum michnevitichi Kaplan, 1971, lower part of Pribalkhash Horizon, near Kyzyl-Akat, Kazakhstan, former USSR and Scyphophyllum, Lower Devonian, northern Urals, central Kazakhstan, former USSR.

Last: Micula simplex (Strelnikov, 1968) and Contortophyllum tchernovi Strelnikov, 1968, Dnencamuiskiy Horizon, River Kozhim, Polar Urals, former USSR.

First: Arachnophyllum, upper Llandovery, Europe, North America and Angulophyllum varissi McLean, 1974, Lower Limestone Horizon, upper Llandovery, Cobblers' Creek, Angullong District, near Orange, central New South Wales, Australia.
Last: Cranerophyllum, Onondaga Limestone, Kentucky, Indiana, USA; Ontario, Canada.

First: Dentilasma honorabilis Ivanovskiy, 1962, upper Llandovery, River Mogokta, western Siberian Platform and Heterolasma foerstei Ehlers, 1919, Manistique Formation, upper Llandovery (or lower Wenlock), half a mile south of Gould City, Michigan, USA.
Last: Chasakia chasaktiensis Lavrusevich, 1959, Pholidophyllum Beds, Khvasak Gully, Zeravshan-Gissar Range, Tajikistan, former USSR and Natalieiella poslavskijae Sytova, in Sytova and Ulitina, 1966, upper part of Aynasu Horizon, Nurin Syncline, left bank of River Medine, central Kazakhstan, former USSR.

First: Donacophyllum, Upper Ordovician, Estonia, former USSR.
Last: Various genera, e.g. Bouvierophyllum, Mikkawphyllum, Wapitiophyllum, Parasamiphyllum, Taraphyllum, Kakasiphyllum, all from upper Frasnian, western Alberta, eastern British Columbia and southern District of Mackenzie, western Canada (McLean and Pedder, 1984).

First: Mictocystis endophylloides Etheridge, 1908, Quarry Creek Limestone, upper Llandovery, central New South Wales, Australia.
Last: Smithiphyllum, Upper Devonian, Poland. May also occur in Carboniferous of Timan.

First: Heterospongophyllum simplex (He MS in Kong and Huang, 1978), Shiniulan Formation, Shiqian, Guizhou, Kweichow, China.
Last: Neoeupresiphyllum immersum (Hill, 1942), Middle Devonian, Arthur's Creek, Burdekin Downs, Queensland, Australia.

First: Cymatela phylloidea Hill and Butler, 1936, Woolhope Limestone, Woolhope, near Hereford, UK.
Last: Hankaxis tinostis (Frech, 1885), Iberger Kalk, upper Frasnian, Grund, Germany.

First: Fasciphyllum sp., Pragian, western and Arctic Canada and Alaska, former USSR, eastern Australia and New Zealand (Oliver and Pedder, 1979).
Last: Fasciphyllum conglomeratum (Schloter, 1881), Middle Devonian, Eifel, Germany, and Crista compacta Tsyganko, 1971, Middle Devonian, River Nadota, Polar Urals, former USSR.

First: Rhegmaphyllum, Lochkovian, Tien Shan, China and former USSR (Oliver and Pedder, 1979).
Last: Stringophyllum, Parasociophyllum and Sociophyllum, common in upper Givetian, Germany and Belgium.

Last: Camurophyllum camurum Kravtsov, 1966, Lower, Zone of Valnevsk Horizon, Tsiolvo Bay, Novaya Zemlya.

First: Kobeha walcotti Merriam, 1974, Coral Zone B, Nevada
Formation, southern Sulphur Springs Range, Nevada, USA.

Last: Various genera, e.g. Hallia, Aulacophyllum, Odontophyllum, all from Middle Devonian of North America and Aspasmophyllum from Middle Devonian of Germany.

F. ACERVULARIIDAE de Fromentel, 1861
First: Acervularia and Diplophyllum, Middle Silurian, Europe, North America.
Last: Oliveria planotabulata Sutherland, 1965, Henryhouse Formation, Lawrence Uplift, Oklahoma, USA.

F. COLUMNARIIDAE Nicholson, 1879
D. (GED–FRS?) Mar. (see Fig. 6.6)

First: Circumtextiphyllum annulatum Kaplan, 1971, lower part of Pribalkhash Horizon, near Kyzel-Agat, Kazakhstan, former USSR.
Last: Columnaria sulcata Goldfuss, 1826, lower Frasnian (or upper Givetian), Paffrather Mulde, near Bensberg, 10 miles east of Cologne, Germany.

First: Radiastraea, Upper Silurian, Canadian Arctic.
Last: Temnophyllum, Upper Devonian, Urals, former USSR.

First: Phillipastrea, Lower Devonian, Victoria, New South Wales, Australia; France.


F. ERIDOPHYLLIDAE de Fromentel, 1861

First: Campophyllum heliundii Sutherland, 1965, Henryhouse Formation, Lawrence Uplift, Oklahoma, USA.

Last: Cylindrophyllum elongatum Simpson, 1900, Onondaga Limestone, upper Givetian, Clarksville, New York and Asterobillingia confluenta (Vanuxem, 1842), Onondaga Limestone, upper Givetian, quarry south of Chittenango, near Perryville, New York, USA.

F. ZAPHRELLIDAE Milne Edwards and Haime, 1850

First: Heliophyllum, Lower Devonian, Victoria, Australia.

Last: Heliophyllum, upper Givetian, eastern North America, Morocco, Spanish Sahara (NW Africa), Spain.

F. CYATHOPHYLLIDAE Dana, 1846

First: Radiophyllum, Lower Devonian, Kuzbas, former USSR.

Last: Commutatifyllum cincinnatum Kaplan, 1971, C. sulcifer beds, northern Cis-Balkhash, Kazakhstan, former USSR.

F. ?BETHANYPHYLIDAE Stumm, 1949

First and Last: Bethaniphyllum and Tortophyllum, Middle Devonian, North America, e.g. B. robustum (Hall, 1876), Hamilton Group, western New York, USA and T. cysticum (Winchell, 1866), Upper Blue Shale, Gravel Point Formation, Traverse Group, Bell Quarry, Michigan, USA.

F. CAMPOPHYLLIDAE Wedekind, 1992

First: Campophyllum flexuosum (Goldfuss, 1826), upper Famennian, and Campophyllum cylindricum (Onoprienko, 1979), lower Elrgetekhyn Suite, upper Famennian, Omolon Massif, NE of former USSR (Sorauf and Pedder, 1986).

Last: Campophyllum, lower Serpukhovian, locality unknown.

F. PTEROSPADAEAE Dybowski, 1873

First: Ptychodermophyllum, Lower Silurian, Michigan, USA: Ontario, Canada; Siberian Platform, Altay, Sayan, Tajikistan, former USSR; New South Wales, Queensland, Australia.

Last: Impliciphylum vesiculosum Sytova, in Sytova and Uli­tina, 1966, Zone of Nataliella poslavskajae, Aynasu Horizon, south flank of Karaganda Basin, central Kazakhstan, former USSR.

F. STEREOLOMATIDAE Fomichev, 1953
D. (GIV)—C. (MOS?) Mar.

First: Stereolasma rectum (Hall, 1876), Amplexiphyllum hamiltoniae (Hall, 1876), Lopholasma carinatum Simpson, 1990 and Stewartophyllum intermittens (Hall, 1876), all from Hamilton Shale, New York, USA.

Last: Lopholasma, ?lower Moscovian (or upper Viséan), China.

F. ANTIPHYLLIDAE Illina, 1970


Last: Lytvolasma asymmetricum Soshkina, 1925, Lower Permian, 6 km below Alexandrovskiy Works, River Lytva, central Urals, former USSR.

F. HAPSIPHYLLIDAE Grabau, 1928


Last: Duplophyllum zaphrentoides Koker, 1924, upper Kazanian, Basleo, Timor.

F. ZAPHRENTOIDIDAE Schindewolf, 1938

First: Zaphrentoides (?) ecavatus Hill, 1954, P. (?or Upper Silurian), Shishkat ravine, north slope of Zeravshan Range, Tajikistan, former USSR.

Last: Basleophyllum indicum (Koker, 1924), Upper Permian, Basleo, Timor.

F. POLYCLEITIDAE de Fromentel, 1861

First: Amandaria prima Lavrusevich, 1968, Kunzhak Horizon, Lower Devonian (?or Upper Silurian), Shishkat ravine, north slope of Zeravshan Range, Tajikistan, former USSR.

Last: Callophyllum donatianum (King, 1848), Magnesian Limestone, lower Tatarian, Hambledon Hill, County Durham, UK; Gerthia angusta (Rothpletz, 1892), Upper Permian, Ajer Mati River, near Kupang, Timor; Groenlandophyllum teicherti (Flügel, 1973), Productus Limestone, Kap Stosch, eastern Greenland; Hexalasma, Upper Permian, Timor, NE of former USSR; Tetralasma, Upper Permian, Greenland; Prosmitia cyathophyllum (Gerth, 1921), Upper Permian, Basleo, Timor.

F. ANISOPHYLLIDAE Ivanovskiy, 1965

First: Anisophyllum agassizi Milne Edwards and Haime, 1850, 30–45 feet (c. 11–16 m) above Dixon-Brownsport contact, Brownsport Formation, Blue Mount Glade, Perryville Quadrangle, Tennessee, USA.

F. PLEROPHYLLIDAE Koker, 1924

First: Ufimia, upper Emsian, Germany.

Last: Plerophyllum radiciforme Gerth, 1921 and Pleroplexus simulis Schindewolf, 1940, lower Tatarian, Basleo and Olimasi, Timor and Barbarella stelliforma (Flügel, 1972), Lower Jamul Formation, Kuk-e-Bagh-e-Vang, eastern Iran.

F. ENDOTHECIDAEN Schindewolf, 1942
P. (KAZ) Mar.

First and Last: Endothecia, upper Devonian, Timor.

Last: Endothecium apertum Koker, 1924, upper Kazanian, Basleo, Timor.
F. ADAMANOPHYLLIDAE Vasilyuk, 1959

First: Tachyphyllum artyshtense Dobrolyubova, in Soshkina et al., 1962, lower Terei Horizon, River Artyshta, Kuzbas, former USSR.

Last: Adamanophyllum incertum Vasilyuk, 1959, Namurian, right bank of River Berestovaya, opposite Obiliine, Donbas, Ukraine, former USSR.

F. PENTAPHYLLIDAE Schindewolf, 1942

First: Oligophyllum quinqueseptatum Pocta, 1902, Dvorce Limestone, Lower Devonian, Dvorce, Czechoslovakia.

Last: Pentamplexus, Palaeofusulina Zone, upper Tatarian, Iran (Flügel, 1970).

F. LOPHOPHYLLIDAE Grabau, 1928


Last: Lophophyllidium, Cadonofusiella Zone, lower Tatarian, North America (Flügel, 1970).


First and Last: Timorphophyllum wanneri Gerth, 1921, upper Kazanian, Timor.


First: Cravenia rhyoides Hudson, 1928, lower Viséan, Haw Crag Lower Quarry, Bell Busk, Yorkshire, England, UK.

Last: Verbeekiella cristata (Gerth, 1921), upper Kazanian, Basle, Timor.

F. CYATHOPSIDAE Dybowski, 1873

First: Caninia cornucopiae Michelin, 1840, Upper Devonian, no locality given (Sorauf and Pedder, 1986).

Last: Paracaninia sinensis Chi, 1937, upper Wumaling Series, Yungsins District, Wumahuitou, Kiangsi, China, Arctophyllum intermedium (Toula, 1875), lower Artinskian (? or Upper Carboniferous), Belsub, Spitsbergen and Fomichevella, ?lower Artinskian, Urals, former USSR.

F. BOTHROPHYLLIDAE Fomichev, 1953

First: Bothrophyllum sp. a, Bothrophyllum sp. b and Caninophyllum sp. a, all Sorauf unpubl., Box Member, Percha Formation, upper Famennian, SW New Mexico, USA and Caninophyllum adaptum (Onoprienko, 1979), lower Erlegetekheyn Suite, upper Famennian, Omolon Massif, NE USSR (Sorauf and Pedder, 1986).

Last: Caninophyllum, Lower Permian, Spitsbergen; Urals, former USSR; Carnic Alps and Hornsundia latespeta Fedorowski, 1965, 5th coral limestone Horizon, upper Treskeledden Beds, Hornsund, Vestspitsbergen.

F. URALINIIDAE Dobrolyubova, 1962


Last: Byfossularia ussowii (Gabuniya, 1919), Podyakov Horizon, upper Viséan, River Tom, Kuzbas, former USSR, Keypserlingophyllum, Viséan, Iran, Kuzbas, ?France and Liardiphym hager Sutherland, 1954, middle Mississippian, Liard Range, North-west Territories, Canada.


First and Last: Endamplexus dentatus Koker, 1924 and Spineria diplochone (Koker, 1924), upper Kazanian, Basle, Timor.

F. AULOPHYLLIDAE Dybowski, 1873

First: Various genera from upper Famennian, various localities (Sorauf and Pedder, 1986).


F. EKVASOPHYLLIDAE Hill, 1981

First: Zaphryphyllum sp. a, Sorauf unpubl., Box Member, Percha Formation, upper Famennian, SW New Mexico, USA (Sorauf and Pedder, 1986).

Last: Ekvasophyllum inclinatum Parks, 1951, Faberophyllum occultum Parks, 1951 and Turbophyllum multicoronum Parks, 1951, all from Brazer Limestone, Meramecian, lower upper Mississippian, Wasatch Mountains, Utah, USA.

F. PALAESMIILIDAE Hill, 1940

First: Palaeosmia, upper Famennian, Belgium, Germany, Western Australia.


First: Naoides ranganiensis Pickett, 1967, Rangari Limestone, upper Tournaian, Parish Rangari, County Nandewar, New South Wales, Australia.

Last: Various genera, e.g. Aphrophyllum, Aphrophylloides, Coenaphrodia, Merlewoodia, Nothaphrophyllum, Symplectophyllum, all from Viséan, New South Wales and Queens­land, Australia.

F. LITHOSTROTIONIDAE D’Orbigny, 1852

First: Stelechophyllum alferovi (Gorskiy, 1935), Stelecho­phyllum naliikini (Gorskiy, 1935) and Stelechophyllum plativiculocus (Gorskiy, 1935), all from upper Famennian, Stroganova Gulf, southern island of Novaya Zemlya, former USSR (Sorauf and Pedder, 1986).

Last: Yatsengia, lower Tatarian, ?locality.

F. DURHAMINIDAE Minato and Kato, 1965
C. (TOU)–P. (KAZ) Mar.

First: Protoxolosdaleastra atbasarica Gorskiy, 1932, ?Tournaian, Atbasarsky region, River Dzhezky, Kirghiz Steppe, Western Kazakhstan, former USSR.

Last: Tanbeilla izuruhense (Sakaguchi and Yamagiwa, 1958), Neoschusterina Zone, lower Kazanian, Osaka Prefec­ture, Takatsuki City, Izuruha-Shimojo, Japan.
F. AXOPHYLLIDAE Milne Edwards and Haime, 1851

**First:** Axophyllum sp. a, Sorauf unpubl., Box Member, Percha Formation, upper Famennian, SW New Mexico, USA (Sorauf and Pedder, 1986).

**Last:** Lonsdaleia, II Member, Tagnana Formation, upper Serpukhovian, Bechar Basin, NW Sahara, Algeria (Semenoff-Tian-Chansky and Sutherland, 1982).

F. PETALAXIDAE Fomichev, 1953

**First:** Paralithostroton podborei (Dobrolyubova, 1958), upper Viséan, Lyobytin district, Podbore, NW Russian Platform, former USSR.

**Last:** ?Lithostrotonella unica (Yabe and Hayasaka, 1915), Lower Permian, Hui-tso-hsien, Kungshan, Yunnan, China.

F. HETEROCORALLIA Bayer, 1941

**First:** Hexaphyllia, upper Namurian, Europe, Asia, North America.

**Order:** COTTHONIIA Oliver and Coates, 1987

**First:** F. ?COTHONIIA Jell and Jell, 1976

**Last:** COTHONIIA Jell and Jell, 1976, E. (SOL) Mar.

**First and Last:** Cotonon symposium Jell and Jell, 1976, lower Middle Cambrian, New South Wales, Australia.

**Order:** UNCERTAIN

F. ?NUMIDIAPHYLIDAE Flugel, 1976


**Last:** Various species of Diffingia and Turgidiffia, Skinner Ranch Formation and Hess Formation, upper Wolfcampian, western Texas, USA.

**Order:** UNCERTAIN

F. TABULACONIDAE Debrenne et al., 1987

**First:** Tabulaconus kordeae Handfield, 1969, Sekwi Formation, Mackenzie Mountains, District of Mackenzie, North-west Territories, Canada.

**Last:** Tabulaconus kordeae Handfield, 1969, Sekwi Formation, Mount Field, British Columbia, Canada.

**Subclass:** UNCERTAIN

F. TABULACONIDAE Debrenne et al., 1987

**First:** Tabulaconus kordeae Handfield, 1969, Sekwi Formation, Mackenzie Mountains, District of Mackenzie, North-west Territories, Canada.

**Last:** Tabulaconus kordeae Handfield, 1969, Sekwi Formation, Mount Field, British Columbia, Canada.

**Subphylum:** CTENOPHORA Eschscholtz, 1829

**First:** F. UNCERTAIN, C. (LEN-SOL) Mar.

**Last:** F. UNCERTAIN, C. (LEN-SOL) Mar.

Collins et al. (1983) compare this taxon to ctenophores, but full description is needed (Briggs and Conway Morris, 1986).

**First and Last:** Fasciculus vesanus Simonetta and Delle Cave, 1978, Stephen Formation, locality 9, Mount Stephen, British Columbia, Canada.

**Last:** Fasciculus vesanus Simonetta and Delle Cave, 1978, Burgess Shale, Stephen Formation, Mount Field, British Columbia, Canada.

**Order:** HETEROCORALLIA Schindewolf, 1941

F. HETEROPHYLLIDAE Dybowski, 1873

**First:** Pseudopetraia devonica Soshkina, 1951, Middle Devonian, near Pokrovsk Egoshin, eastern slopes of central Urals, former USSR.

**Last:** Hexaphyllia, upper Namurian, Europe, Asia, North America.

**Order:** COTTHONIIA Oliver and Coates, 1987

**First:** F. ?COTHONIIA Jell and Jell, 1976

**Last:** COTHONIIA Jell and Jell, 1976, E. (SOL) Mar.

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**First:** Pseudopetraia devonica Soshkina, 1951, Middle Devonian, near Pokrovsk Egoshin, eastern slopes of central Urals, former USSR.
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MOLLUSCA: AMPHINEURA AND ‘MONOPLACOPHORA’

M. J. Benton and D. H. Erwin

The Amphineura and ‘Monoplacophora’ are of uncertain phylogenetic position within the Mollusca. The database on Amphineura is based on Smith (1960, 1973), Van Belle (1981) and Smith and Hoare (1987), and updated according to cited references. The familial revisions in Smith and Hoare (1987), in particular, gave quite different range data from previously published accounts.

Untorted univalved molluscs with multiple muscle scars have traditionally been placed in the Class Monoplacophora. Peel (1991a,b) has reviewed the various arguments concerning the class, and concluded that the class is best rejected completely in favour of two classes, the Class Tergomya Horny, 1965 and Helcionelloida Peel, 1991. Unfortunately, the assignment of many problematic Cambrian univalves is unknown, as are the precise limitations of each class. Peel’s recommendations as to membership are followed here.

The Amphineura and Aplacophora were compiled by MJB and the ‘Monoplacophora’ by DHE. The stratigraphical nomenclature of Harland et al. (1990) is used throughout this chapter.

Acknowledgements – MJB thanks Richard Hoare (Bowling Green, Ohio), David Jablonski (Chicago) and Ben McHenry (South Australian Museum) for their extensive and invaluable help in updating the coverage of Amphineura and Aplacophora.

Class AMPHINEURA von Ihering, 1876

Subclass POLYPLACOPHORA de Blainville, 1816

Superorder PALAEOLORICATA Bergenhayn, 1955

The Yangtzechitonidae, noted by W. Yu (1984) as possible palaeloricate chitons, have been assigned to the Para­carinachitidae, an unassigned family of Problematica (see Chapter 28).

Order CHELODIDA Bergenhayn, 1943

F. CHELODIDAE Bergenhayn, 1943

First: Eochelodes bergenhayni Marek, 1962, lower part of Cernin Beds, central Bohemia, Czechoslovakia.

Last: Probolaeum corrugatus Sandberger and Sandberger, 1856, Stringocephalen Kalk, Hesse-Nassau, Germany.

Intervening: D. (l.).

Comment: The Chelodidae, according to Smith and Hoare (1987), excludes the numerous species of Chelodes, which are mainly placed in Mattheviidae.

F. MATTHEVIIIDAE Walcott, 1886

First: Matthevia variabilis Walcott, 1885, Hoyt Limestone Member, Theresa Formation, ?upper Franconian and lower Trempealeauan, Saratoga Springs, New York, USA; Matthevia walcotti Runnegar et al., 1979, Black Earth Member, St Lawrence Formation, lower Trempealeauan, Eikey Quarry, Wisconsin, USA (Runnegar et al., 1979).

Last: Chelodes bohemicus (Barrande, 1867), Upper Silurian, Bohemia, Czechoslovakia, and C. calceoloides Etheridge, 1897, Series of Yass, Upper Silurian, King County, New South Wales, Australia.

Intervening: TRE-LLO, WEN.

Comment: A younger record may be Chelodes? sarthacensis (Oehlert, 1881) from the Lower Devonian of Sarthe, France, but its affinities are not clear (Smith and Hoare, 1987, p. 48).

F. GOTLANDOCHITONIDAE Bergenhayn, 1955

First: Gotlandochiton hami Smith, in Smith and Toomey, 1964, Kindbladochiton arbuckensis (Smith, in Smith and Toomey, 1964), and Paleochiton kindbladensis Smith, in Smith and Toomey, 1964, all Kindblade Formation, Arbuckle Mountains, Oklahoma, USA.


Intervening: none.

F. PREACANTHOCHITONIDAE Bergenhayn, 1960


Last: Preacanthochiton cooperi Bergenhayn, 1960 and P. depressus Bergenhayn, 1960, Gasconade Formation, Madison
**Fig. 7.1**

County and Reynolds County respectively, Missouri, USA (Bergenhayn, 1960).

**F. SCANOCCHITONIDAE** Bergenhayn, 1943  
**O.** (TRE/ARG)–**K.** (CMP)  Mar.

**First:** *Ivoechiton calathicolus* Smith, *in* Smith and Toomey, 1964 and *I. oklahomensis* Smith, *in* Smith and Toomey, 1964, both Kindblade Formation, Arbuckle Mountains, Oklahoma, USA.


**Intervening:** None.

**F. SEPTEMCHITONIDAE** Bergenhayn, 1955  
**O.** (LLO/CRD–ASH)  Mar.

**First:** *Solenocaris elongata* (Hadding, 1913), LLO/CRD, Aakirkeby, Sweden.

**Last:** *Septemchiton grayiae* (Woodward, 1885) and *S.? thrairensis* (Reed, 1911), both Starfish Bed, Drummuck Group, near Girvan, Ayrshire, Scotland, UK.

**Intervening:** CRD.
Superorder PHOSPHATOLORICATA Bischoff, 1981

Order PHOSPHATOLORICATIDA Bischoff, 1981

F. COBCREPHORIDAE Bischoff, 1981
Intervening: LLY, WEN.

Superorder NEOLORICATA Bergenhayn, 1955

Order LEPIDOPLEURIDAE Thiele, 1910

F. ACANTHOCHITONIDAE Pilsbry, 1893
First: Acanthochiton (Notoplax) ashbyi (Laws, 1932), Duntroonian, upper CHT, New Zealand (Beu and Maxwell, 1990).
Extant

F. ACUTICHITONIDAE Hoare, Mapes, and Atwater, 1983
First: Soleachiton soleiformis (Etheridge, 1882) and Acutichiton etheridgei Smith and Hoare, 1987, both Main or Hurlet Limestone, Namurian A, Dalry, Ayrshire, Scotland, UK (Hoare et al., 1983; Hoare and Smith, 1984), and Elachychiton juxtaterminus Hoare and Mapes, 1985, Imo Formation, Chesterian, Searcy County, Arkansas, USA.
Last: Soleachiton yochelsoni Hoare and Smith, 1984, Leonard and Road Canyon formations, upper Leonardian, West Texas, USA (Hoare and Smith, 1984).
Intervening: BSH—ART.

F. AFOSSOCHITONIDAE Ashby, 1925
First and Last: Afossochiton cudmorei Ashby, 1925, Balcombian, Hamilton, Victoria, Australia.
Extant

Comment: This family is synonymized with the Acanthochitonidae by Gowlett-Holmes (1987).
First: Callistochiton maffaiensis Davis, 1954, Lower Miocene, Mafia Island, East Africa.

F. CALLOCHITONIDAE Plate, 1899
First: Callochiton chattonensis Ashby, 1929, Duntroonian, upper CHT, New Zealand (Beu and Maxwell, 1990).

Intervening: None.

F. CHAETOPLACIDAE Plate, 1899
First: Chaetopleura apiculata (Say, 1834). Camp Roosevelt Shell Bed, Calvert Formation, upper Burdigalian, Plum Point, Maryland, USA.

Extant: None.

F. CHITONIDAE Rafinesque, 1815
First: Chiton (Chiton) cretaceus Berry, 1940, Coon Creek Formation, lowermost MAA, Coon Creek, Tennessee, and Severn [formerly Monmouth] Formation, lower MAA, Brightseat, Maryland, USA; Chiton (Chiton) berryi Smith et al., 1968, Ripley Formation, lower to middle MAA, Quitman County, Georgia, USA (Smith et al., 1968).

Comment: The ages of the Coon Creek and Ripley Formations have been revised to fall entirely within the MAA (Pojeta and Sohl, 1987), instead of being partially, or wholly, upper CMP as in Smith et al. (1968).

Extant: None.

F. CHORIPLACIDAE Cotton and Weeding, 1939

F. CYMATOCHITONIDAE Sirenko and Starobogatov, 1977
First: Cymatochiton? kirkbyi (de Koninck, 1883), Lower Scar Limestone, Settle, Yorkshire, England, UK.

Last: Cymatochiton houseanus (Kirkby, 1857) and C. lofusiusan (King, 1850), upper Magnesian Limestone, Durham, England, UK.

Intervening: C. (u.), MOS, KUN, UFI.

F. GLYPTOCHITONIDAE Starobogatov and Sirenko, 1975
First: Glyptochiton cordifer (de Koninck, 1844), Tournai, Belgium.

Last: Glyptochiton kirkbyanus (Etheridge, 1882), G. quadratus (Etheridge, 1882), G. subquadratus (Kirkby and Young, 1867), and G. youngianus (Kirkby, in Young, 1865), all Main or Hurlet Limestone, Dalry, Ayshire, Scotland, UK.

Intervening: None.

First: Hanleya? multigranosa (Reuss, 1860), Korytica Clays, lower Tortonian, Holy Cross Mountains, Poland and Bohemia, Czechoslovakia (Baluk, 1971).

Extant: None.

F. HETEROCITONIDAE Van Belle, 1978
First: Loborachiton anomalous (Rowley, 1908), Louisiana Limestone (FAM), Missouri, USA or Öchmazochiton comptus Hoare and Smith, 1984

First: Allochiton gemellaroi Fucini, 1912, Lias inferiore, Montagna di Casale, Sicily (Hoare and Smith, 1984).

Intervening: KUN.

F. ISCHNOCHITONIDAE Dall, 1889

Extant: None.

F. LEPIDOPLEURIDAE Pilsbry, 1892
First: Helminthochiton? aquivoca Robson, 1913, Sára and Malé Prely, Bohemia, Czechoslovakia.

Intervening: LLY, D. (I., m.), TOU—KAS, SAK—KUN.

F. LLANDEILOCHITONIDAE Bergenhayn, 1955
O. (LLO) Mar.
First and Last: Llandeilochiton ashbyi Bergenhayn, 1955, Barr Group, Balclatchie, southern Scotland, UK.


Extant: None.

F. PERMOCITONIDAE Sirenko and Starobogatov, 1977
D. (EMS)—P. Mar.
First: Euleptochiton lebescontei (Barrois, 1889), EMS, Loire Inférieure, France.

Last: Permochiton australianus Iredale and Hull, 1926, upper Marine Series, Pérmo-Carboniferous beds of Bundanoon, New South Wales, Australia (DeBrock et al., 1984).

Intervening: SPK—KAS/GZE.

F. SCHIZOCITONIDAE Dall, 1889
First: Aulacochiton praecursor Smith et al., 1968, San German Formation, lower MAA, Sabana Grande, Puerto Rico (Smith et al., 1968).

Extant: None.

F. SCHIZOPLACIDAE Bergenhayn, 1955
Extant: None.

F. SUBTERENOCHITONIDAE Bergenhayn, 1930
Extant: None.

Subclass APLACOPHORA von Ihering, 1876

The only fossil aplacophoran recorded is an example suggested by Amelie Scheltema from the Mazon Creek locality, Illinois, USA (Francis Creek Shale, Carbondale Formation, upper Moscovian) (Lindberg, 1985, p. 236).
Order NEOMENIIDAE Simroth, 1893
F. NEOMENIIDAE von Ihering, 1876 Extant
F. PRONEOMENIIDAE Simroth, 1893 Extant
F. LEPIDOMENIIDAE Pruvit, 1890 Extant
F. GYMNOLOMENIIDAE Ohdner, 1921 Extant

Order CHAETODERMATIDA Simroth, 1893
F. CHAETODERMATIDA von Ihering, 1876 Extant

‘MONOPLACOPHORA’

Class TERGOMYA Horný, 1965
 Traditionally, all untorted molluscs have been placed in the Class Monoplacophora. As discussed by Peel (1991a,b), so many different groups have been assigned to the class that the term is virtually meaningless. Consequently, Peel has replaced the class with two new classes, the Tergomya and the Helcionelloydia, as followed here. The definition of these classes and constituent orders given here follows Peel (1991a,b) and Runnegar and Jell (1976), which should be consulted for details and references. In fact, neither the higher taxa nor the genera of Lower Palaeozoic cap-shaped molluscs are well understood.

Order TRYLIIDIDA Lemche, 1957
F. TRYBLIDIDAE Horný, 1965
€. (SOL)–Rec. Mar.
First: Helcionopsis sp. Runnegar and Jell, 1976, Coonigan Formation, New South Wales, Australia. Extant
First and Last: Archaeopraga pinnaeformis (Perner, 1903) noted in Horný (1963), Pfidolfi Beds near Prague, Czechoslovakia.

Order CYRTONELLIDIDA Horný, 1963
F. CYRTOLITIDAE Miller, 1889
First: Cyrtolitopsis sp. Runnegar and Jell, 1976, Coonigan Formation, New South Wales, Australia. Extant
F. CHAETODERMATIDAE Miller, 1889 (formerly SCENELLIDAE Wenz, 1938)
Yochelson and Gil Cid (1984) suggested that at least some species assigned to Scenella may be chondrophorine floats.

REFERENCES
Animals: Invertebrates


The higher-level classification of the Class Gastropoda is in a state of flux. The classification in the *Treatise on Invertebrate Paleontology* (Knight et al., 1960) is incorrect; several superfamilies recognized there actually represent convergent grades rather than monophyletic clades. Several people, including one of us (DHE) are engaged in phylogenetic analyses of the Palaeozoic taxa in the hope of resolving these difficulties. Thus the classification outlined below is preliminary, but is the best current approximation. Moreover, since many Palaeozoic groups have not been restudied since the Treatise, it is generally far from clear whether a species is properly assigned to a genus or family. Hence, the first and last species listed below should be regarded as approximations only, and the data presented here should not be used for further analyses without additional study.

As a result of ongoing anatomical work on living species, the higher classification of caenogastropods and docoglossans has recently undergone a revolution and is still far from settled. The high degree of convergence of gross shell morphology between some distantly related groups has rendered difficult the placement of exclusively fossil taxa. Characters such as shell microstructure and protoconch morphology are now being used to attempt to construct a more robust phylogenetic system for fossil taxa.

We have based the classification of the caenogastropods, opisthobranchs and pulmonates on the schemes of Haszprunar (1988), Ponder and Waren (1988) and Vaught (1989), with a few small changes and additions due to recent work such as that of McLean (1990) and Bandel (1991, and other papers listed therein). Although several long-established neogastropod families were merged by Ponder and Warén (1988) owing to anatomical similarities, we have preferred to list all such families separately in view of their easily recognized shell characters.

Families known to be polyphyletic are marked with an asterisk (*). Where the superfamilial assignment of a family is uncertain it is marked with a question mark (?). If no source is listed for a record, the specimens are unpublished and housed in the collections of the United States National Museum (Palaeozoic groups) or the British Museum (Natural History) (other groups). DHE compiled the Palaeozoic data, while ST and JAT compiled the Mesozoic and Cainozoic records.

Acknowledgements – We are indebted to Ellis Yochelson, Smithsonian Institution, Peter Wagner, University of Chicago, Robert Blodgett, United States Geological Survey, and Noel Morris and John Cooper, Natural History Museum, London, for assistance in compiling these data.
order. The next youngest species is *Euomphalus leucocarinatus* Yochelson, 1956 from the Bell Canyon Formation, Texas, USA.

**Order HYPERSTROPHINA** Linsley and Kier, 1984

Linsley and Kier (1984) erected the class Paragastropoda for a number of apparently untorted molluscs, which superficially appear to be similar to the Gastropoda, including the *Euomphalina* and several other groups. Dzik (1983) proposed the suborder Mimospirina to separate the Clisospiridae and the Onychochilidae from the *Euomphalina*. Linsley and Kier’s more inclusive order is used here to include a variety of groups which are distinct from both the *Euomphalina* and Macluritina. The relationships between these three families are not clear, and the order may be polyphyletic.

**F. CLISOSPIRIDAE** S. A. Miller, 1887

*Clisospira curiosa* Billings, 1865, Beekmantown Limestone, Quebec, Canada.

**Last:** Progalerus concoides Holzapfel, 1895, Massenkalk, Frettermühle, Germany.

**F. OMPhALOCirRIdAE** Linsley and Kier, 1984

**First:** Liomphalus northi (Etheridge, 1890), Lilydale Limestone, Victoria, Australia (Philip and Talent, 1959).

**Last:** Omphalocirrus goldfussi (Archiac and Verneuil, 1842), Stringocephalus Beds, Germany (Linsley and Kier, 1984).

**F. ONYCHOCHILIDAE** Koken, 1925

*Omphalocirrus minutissimus* Yoo, 1988, Dangerfield Formation, New South Wales, Australia.

**Comment:** This species is considerably younger than the next youngest record of the family, and may not be correctly assigned. The next youngest record is *Sinistracirsa* sp. from Emsian-age rocks, Limestone Mountain, Alaska, USA (Blodgett *et al.*, 1988).
**Order** MACLURITINA Cox and Knight, 1960

F. MACLURITIDAE Fischer, 1885


Last: *Maclurites manitobensis* (Whiteaves, 1887), Bighorn Group, Wyoming, USA (Rohr, 1979).

**Order** BELLEROPHONTINA Ulrich and Schofield, 1897

Superfamily BELLEROPHONTOIDEA M'Coy, 1851

**Order** EUPHEMITIDAE Knight, 1956

D. (PRA)–Tr. (GRI) Mar.


F. BELLEROPHONTIDAE M'Coy, 1851
O. (TRE)—Tr. (SCY) Mar.


Last: Retispira asiatica (Wirth, 1936), Feixianguan Formation, Guizhou Province, China (Yochelson and Yin, 1985).

F. BELLEROPHONTIDAE M'Coy, 1851
O. (TRE)—Tr. (SCY) Mar.

?First: Lepetopsis ?petricola (Kittl, 1895), L. campannaeformis (Münster, 1841) and L. costulata (Münster, 1841), all St Cassian Formation, Italy (Yochelson, 1960).

F. BELLEROPHONTIDAE M'Coy, 1851
O. (TRE)—Tr. (SCY) Mar.

Last: Eobucania mexicana Yochelson, 1968, Tusin Formation, Oaxa, Mexico.

F. BELLEROPHONTIDAE M'Coy, 1851
O. (TRE)—Tr. (SCY) Mar.

Order ARCHAEOGASTROPODA Thiele, 1925
Superfamily PATELLOIDEA Rafinesque, 1815

F. ARCHINACELLIDAE Knight, 1956

First: Archinacella ? cf. elongata (Cullison, 1944), Poulsen Cliff Formation, Greenland. The next youngest is Floripatella rousseui Yochelson, 1988, Kanosh Shale, Utah, USA. Last: Guelphinacella canadense (Whiteaves, 1884), Guelph Formation, Ontario, Canada.

F. PATELLIDAE Rafinesque, 1815

First: Patella ? miyakoensis Kase, 1984, Hiraiga Formation, Oshima Island, Miyako area, Japan.

Comment: Triassic records from the St Cassian Formation, Italy, and earlier, are problematic.


Superfamily NACELLOIDEA Thiele, 1929


First: Cellana ampla Lindberg and Hickman, 1986, Middle Member, Keasey Formation, Oregon, USA.

Comment: This is the earliest definite occurrence. Others recorded from the Cretaceous of New Zealand and Australia are represented only by steinkerns and cannot be referred to this family with certainty (Lindberg and Hickman, 1986).

F. ACMAEIDAE Carpenter, 1857
Tr. (CRN)—Rec. Mar.

First: Scurriopsis cycloides Tichy, 1979, Raibl Group, Raibl, Italy.


First: Lepeta ? boutillieri (Cosman, 1888), Calcaire grossier, Parnes, Paris Basin, France (Dolin et al., 1980).

Suborder UNCERTAIN

F. METOPTOMATIDAE Wenz, 1938
O. (LLO)—P. (KUN) Mar.

First: Paleoscucrria ordovicana Horný, 1961, Dobrotiwa Beds, near Beroun, Czechoslovakia.

Last: Metoptoma Phillips, 1836, Guadalupian (Roadian), West Texas, USA.

Comment: The family is of uncertain affinities but is probably docoglossan. Lepetopsis Whitfield, 1882, is differentiated from Metoptoma by the muscle scar and position of the apex (Yochelson, 1960; McLean, 1990), and the Lepetopsidae are here retained as a separate family.

Suborder LEPETOPSINA McLean, 1990

Superfamily LEPETOPSOIDEA McLean, 1990

F. LEPETOPSIDAE McLean, 1990
C. (VIS)—Tr. (LAD) Mar.

First: Lepetopsis levectei White, 1882, Warsaw Formation, Sperrgen Hill, Salem, Indiana, USA.

Last: Lepetopsis ? petricola (Kittl, 1895), L. campannaeformis (Münster, 1841) and L. costulata (Münster, 1841), all St Cassian Formation, Italy (Yochelson, 1960).


This family was erected for extant species with similar shells to the Lepetopsidae and perhaps derived from them, but lacking radular mineralization, which was thought to have been lost (McLean, 1990).

Suborder VETIGASTROPODA Salvini-Plawen, 1980

Superfamily LEPETODRILIOIDEA McLean, 1988


Superfamily PLEUROTOMARIOIDEA Swainson, 1840


First: Sinuoea sweeti Whitfield, 1882, Norwalk Sandstone, Wisconsin, USA.


First: Clathospira sp., Smithville Formation, Arkansas, USA.

Last: Pycnophalus expansus (J. Sowerby, 1821), Bakony Mountains, Hungary, and in Pliensbachian deposits throughout Europe and North Africa (Szabó, 1980).


First: Clathospira typica (Ulrich and Bridge, 1931), Eminence Dolomite, Missouri, USA.

Last: Sisenna subturrita (Deslongchamps, 1849), Calvados, France and southern Germany, and S. turrita (Deslongchamps, 1849), Bakony Mountains, Hungary (Szabó, 1980).


First: Lophospira parangulata (Hall, 1847), upper Durness Limestone, Scotland, UK (Donald, 1902).

Last: Worthenia zhongshanensis Pan, 1982, Lower Jurassic, south-west China.

Comment: The Lophospiridae are considered here to
include most of the Trochonematidae, a polyphyletic assemblage of pleurotomarians, most of which are closely related to the Lophospiridae.

**F. LUCIELLIDAE** Knight, 1956

First: Rhombella umbilicata (Ulrich and Bridge, in Drake and Bridge, 1932), Deadwood Formation, USA.

Last: Luciella infrasinuata Koken, 1897, Ober-Rothelstein, Hallstatt, Austria (Ferenc, 1961).

**F. PHANEROTREMATIDAE** Knight, 1956

First: Brachytomaria baltica (Verneuil, 1845), Orthoceras Limestone, Estonia, former USSR (Koken, 1925).

Last: Phanerotrema ornatum Sayre, 1930, Drum Limestone, Kansas, USA (Forney and Nitecki, 1976).

**F. GOSSELETINIDAE** Wenz, 1938

First: Cataschisma typa Branson, 1909, Auburn Chert, Missouri, USA (Forney and Nitecki, 1976).


**F. EUOMPHALOPTERIDAE** Koken, 1896

First: Euomphalopterus sp. Rohr and Blodgett, 1985, Lone Mountain, Alaska, USA.

Last: Euomphalopterus sp. Blodgett et al., 1988, Limestone Mountain, Alaska, USA.

**F. PORTLOCKIELLIDAE** Batten, 1956

First: ??Agnesella aratula Perner, 1903, southern Urals, former USSR.


**F. CATANTOSTOMATIDAE** Wenz, 1938

First and Last: Catantostoma clathratum Sandberger, 1842, Stringocephalus Beds, Germany.

**F. RHAPHISCHISMATIDAE** Knight, 1956

First: Rhaphischisma planorbiformis de Koninck, 1843 (Knight, 1956). Extant

**F. TROCHOTOMIDAE** Cox, 1960


Last: Discotoma amata (d’Orbigny, 1850), Rauracian?, France (Knight et al., 1960).

**Superfamily SCISSURELLOIDEA** Gray, 1847

**F. SCISSURELLIDAE** Gray, 1847


Next oldest: Scissurella annulata Ravn, 1933, Calcaire de Faxe, Faxe, Denmark. Extant

**F. TEMNOTROPIDAE** Cox, 1960

First: Temnotropis carinata (Münster, 1841), St Cassian Formation, Cortina d’Ampezzo, Italy.

Last: Temnotropis carinata (Münster, 1841) and T. bicarinata Laube, 1869, Balaton Mountains, Hungary (Ferenc, 1961).

**F. HALIOTIDAE** Rafinesque, 1815

First: Haliotis sp. (Sohl, 1987), Maastrichtian, Puerto Rico.

Next oldest: Haliotis sp. (Sohl, 1987), Maastrichtian, Puerto Rico. Extant

**Superfamily FISSLEREOIDEA** Fleming, 1822

**F. FISSLEREOIDEA** Fleming, 1822

First: Flustra costata (Garavello-Spaetti) and F. cristata Zardini, 1978, all St Cassian Formation, Cortina d’Ampezzo, Italy (Zardini, 1978). Extant

**F. CYPEOSECTIDAE** McLean, 1989 Extant

**Superfamily TROCHOIDEA** Rafinesque, 1815

First: F. MICRODOMATIDAE Wenz, 1938

# Animals: Invertebrates

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**Fig. 8.2**

**First:** *Daidia cerithioides* (Salter, 1859), Leray-Rockland Beds, Allumette Island, Ottawa River, Canada.

**Last:** *Microdoma variegata, M. nodosa* and *Glyptospira?* sp. Batten, 1979, 1985, H. S. Lee Mine No. 8, Perak, Malaysia.

**F. ELASMONEMATIDAE** Knight, 1956

**First:** *Elasmonema?* sp., Racine Dolomite, specimens at Field Museum, Chicago, listed as *Callonema? elevatum* Wing nomen nudum.

**Last:** *Anematina?* sp. Batten, 1979, H. S. Lee Mine No. 8, Perak, Malaysia.

**F. ANOMPHALIDAE** Wenz, 1938

**First:** *Grantlandispira christiei* Peel, 1984, Offley Island Formation, Kap Tyson, Greenland. Wenz (1939) claimed a Middle Ordovician record for *Pycnomphalus*, but it is unclear to which species he referred.

**Last:** *Anomalhus helicoides* Münster, 1841 and *biconcavus* Haas, 1953, Pucará Group, Cerro de Pasco area, Peru (Haas, 1953).

**F. PELYCIDIIDAE** Ponder, 1983

**Extant** Mar.

**F. HOLOPEIDAE** Wenz, 1938

**O. (ARG)—P. (WOR) Mar.** (see Fig. 8.2)

**First:** *Straparollina pelagica* Billings, 1865, Quebec Group, Newfoundland, Canada.

**Last:** *Yunnania meridionalis* Mansuy, 1914, H. S. Lee Mine No. 8, Perak, Malaysia (Batten, 1979), and *Yunnania?* sp. Glass Mountains, Texas, USA.

**Comment:** There are more uncertain records of *Cinclidonema* and *Rhabdotocochlis* from Western Guizhou Province, China (Wang and Xi, 1980). Family uncertain.

**F. TROCHIDAE** Rafinesque, 1815

**Tr. (LAD)—Rec. Mar.**

**First:** *Diplochilus bistriatus* (Münster, 1841), *Pseudoclanculus cassianus* (Wissmann, in Münster, 1841), *P. nodosus* (Münster,
Mollusca: Gastropoda

Fig. 8.2

1841), *Solarioconulus nudus* (Münster, 1841), all from the St Cassian Formation, southern Tyrol, Italy (Ferenc, 1961).

**Comment:** There do not seem to be any valid Permian records for the family.

**F. ATAPHRIDAE** Cossmann, 1918

*Tr. (LAD)–K. (SAN/CMP) Mar.*

**First:** *Cirsostylus glandulus* (Laube, 1869), Ladinian, southern Tyrol (Knight et al., 1960).

**Last:** *Ataphrus compactus* Gabb, Chico Formation, Texas Flat, California, USA (Wenz, 1938).

**F. TURBINDAE** Rafinesque, 1815  *P. (WOR)–Rec. Mar.*

**First:** *Eucycloscala asiatica* Batten, 1985, H. S. Lee Mine No. 8, Perak, Malaysia.

**F. SKENEIDAE** Clark 1851  *T. (CHT)–Rec. Mar.*

**First:** *Skenea andersoni* and *S. radiostriata* R. Janssen, 1978, Kassel Meeressandes, Glimmerode, Niederhessen, Germany.

**Extant**

**F. CYCLOSTREMATIDAE** Fischer, 1885

*J. (?BAJ/OXF)–Rec. Mar.*

**First:** *Ataphropsis pygmaeus* Conti and Fischer, 1982, Case Canepine, Spoleto, Italy.

**Next oldest:** *Teinostomopsis saharae* Chavan, 1954, Upper Rauracian, France (Knight et al., 1960).

**Extant**

**F. PHASIANELLIDAE** Swainson, 1840

*T. (THA)–Rec. Mar.*

**First:** *Tricola laubrierei* (Cossmann, 1888), Sables de Chalons-sur-Vesle, Chenay (Marne), France (Cossmann and Pissarro, 1913).

**Extant**
F. TRACHYSMATIDAE Thiele, 1910

First: Trachysma sp. (Moisescu, 1982), Merisor, Haget Basin, Romania.

Extant

F. TROCHACLIDIDAE Thiele, 1928

Superfamily PLATYCERATOIDEA Hall, 1859

F. PLATYCERATIDAE Hall, 1859

First: Cyclonema montrealense Billings, 1865?, Ottawa Formation, St Lawrence Valley, Canada.

Last: Platytrochus (Orthonychia) bowsheri Yochelson, 1956, Cherry Canyon Formation, Texas, USA.

Comment: The subgenus Orthonychia is widely distributed in approximately coeval sediments.

F. PARATURBINIDAE Cossmann, 1916


First: Charronella unicolorata and C.? pagina Batten and Stokes, 1980, Sinbad Member, Moenkopi Formation, Windowblind Butte, Utah, USA.

Last: Paraturbo kusumaetani (Matsumoto, 1938), Goshonoura Group, Goshonoura Island, Kumamoto area, Japan (Hayami and Kase, 1977).

Superfamily AMBERLEYOIDAE Wenz, 1938

F. PLATYACRIDAE Wenz, 1938
Tr. (SCY) – J. (KIM) Mar.

First: Lepidotrochus perfectus Pan, 1982, Scythian, southwest China.

Last: Platyacra (Asperilla) longispina (Rolle), Kimmeridgian, Nattheim, Austria (Brosamlen, in Wenz, 1938).

F. CIRRIDA Cossmann, 1916

Tr. (APT) – K. (APT) Mar.

First: Sororcula gracilis and S. costata Haas, 1953, Pucará Group, Cerro de Pasco area, Peru.

Last: Shikamavirius nipponicus Kase, 1984, Tanoohata Formation, Koikorobe, Miyako, Japan.

F. AMBERLEYIDAE Wenz, 1938


First: Euenomias epaphus (Laube, 1869), Marmolod Mountains, Italy (Ferenc, 1961).

Last: Eucyclus bundensis (von Koenen, 1892), Lattorfian, Brandhorst, Germany (Cossmann, 1915).

F. NODODELPHINULIDAE Cox, 1960

Tr. (NOR) – K. (APT) Mar.

First: Metriomphalus textorius (Briotlii, 1907), Pachycardintuffe, Southern Alps, Italy (Ferenc, 1961).

Last: Hanaispira tabulata (Cossmann, 1903), Senonian, France, or Trochanthius tuberculatocinctus (Münster, in Goldfuss, 1844), Senonian, Germany (Knight et al., 1960).

?Superfamily PSEUDOPHOROIDEA Miller, 1889

Ponder and Warén (1988) placed these families in the Xenophoridea, but with little justification.

?F. PSEUDOPHORIDAE Miller, 1889


First: Pseudophorus sp. Rohr and Blodgett, 1985, Lone Mountain, Alaska, USA.

Last: Sallya linsa and S. striata Yochelson, 1956, Cherry Canyon Formation, Texas, USA and S. terendaka Batten, 1979, H. S. Lee Mine No. 8, Perak, Malaysia.

F. PLANITROCHIDAE Knight, 1956


First: Raphistomina inflata Cullison, 1944, Theodosia Formation, Missouri, USA.


Suborder UNCERTAIN

Superfamily MURCHISONIOIDEA Koken, 1896

F. MURCHISONIIDAE Koken, 1896

O. (ARG) – Tr. (NOR) Mar.

First: Hormotoma artensis Billings, 1865 Smithville Formation, Arkansas and Beekmantown Formation, New York State, USA. Hormotoma sp. Fortey and Peel, 1990 occurs in the Poulsen Cliff Formation, Lower Ordovician (TRE) of northern Greenland. Gascondia putilla (Sardeson, 1896), Gasconde Dolomite, Missouri, has been considered to be a murchisoniid, but the assignment is doubtful.

Last: Vestilia klipseini Koken, 1897, Sandling, Hallstatt, Austria.

F. PLETHOSPIRIDAE Wenz, 1938


Last: Wortheniopsis margaretae (Kittl, 1895), Hallstatt, Austria (Ferenc, 1961).

F. CROSSOSTOMATIDAE Cox, 1960

Tr. (LAD) – J. (BTH) Mar.

First: Palaeocollonia laevigata (Münster, 1841), St Cassian Formation, southern Tyrol, Italy (Ferenc, 1961).


F. ACANTHONEMATIDAE Wenz, 1938


First: Acanthonema newberryi (Meek, 1871), Upper Monroan, Ohio. Wenz (1938) records the genus from the Upper Silurian, but no such species can be identified.

Last: Orthonema paecide Erwin, 1988, Cathedral Mountain Formation, Texas, USA, and O. striatodontosum Chronic, 1952, Bone Spring Limestone, Kaibab Formation, Walnut Canyon, Arizona, USA (Erwin, 1988).

Comments: Acanthonema and Orthonema were assigned by Knight (1934) and Knight et al. (1960) to the Turritellidae. Acanthonematids have an orthocline outer lip with a slight inflection ab- and adapically which corresponds with a spiral angulation or carina. The central part of the whorl is rather smooth (Knight, 1934). In contrast, turritellids have a generally well-developed lateral sinus, its vertex not dependent on the position of spiral ornament and an overall orthoclone to strongly prosocline outer lip. The present family is tentatively placed in the Murchisonioidea.

Suborder UNCERTAIN

Animals: Invertebrates
Mollusca: Gastropoda

F. OMPHALOTROCHIDAE Knight, 1945

First: Bassotrochus angulatus Tassell, 1977, Bell Point Limestone, Victoria, Australia.
Last: Discotropis sp., Seven Devil's Formation, Idaho, USA.

Suborder UNCERTAIN

F. HELICOTOMIDAE Wenz, 1938

First: Prohelicotoma uniangularia (Hall, 1847), Smith Basin Limestone, New York, USA.
Last: Helicotoma patula Lamont, 1946, lower Drummuck Group, Scotland, UK.

Comment: Wenz (1938) and the Treatise (Knight et al., 1960) included two unrelated groups in the Helicotomidae. Here the family is restricted to the Lower Palaeozoic forms.

Suborder UNCERTAIN

Superfamily ORIOSTOMATOIDEA Wenz, 1938

F. ORIOSTOMATIDAE Wenz, 1938

First: Oriostoma bromidensis Rohr and Johns, 1990, Bromide Formation, Oklahoma, USA.
Last: Oriostoma aff. geraubIti Oehlert (Blodgett and Johnson, 1993), Dehay Formation, Nevada, USA.


Suborder COCCULINIFORMIA Haszprunar, 1987

Superfamily LEPETELLOIDEA Dall, 1882


First: Sablea minuta Allen, 1970, Middle Eocene, Red River, Grant Parish, Louisiana, USA.


F. PYROPELTIDAE McLean and Haszprunar, 1987 Extant Mar.


F. ADDISONIIDAE Dall, 1882 Extant Mar.

F. CHORISTELLIDAE Bouchet and Warén, 1979 Extant Mar.


Superfamily COCCULINOIDEA Dall, 1882


F. BATHYSCIADIIDAE Dautzenberg and Fischer, 1990 Extant Mar.

Suborder NERITIMORPHA Golikov and Starobogatov, 1975

Superfamily NERITOIDEA Rafinesque, 1815


First: Plagiothyra sp. Blodgett et al., 1988, Lowther Island, Canadian Arctic.


First: Naticopsis transversa (Lindstrom, 1884), Hogklinl Beds, Gotland.

Superfamily PALAEOTROCHOIDEA Knight, 1956


Last: Turbonopsis apachiensis Day and Bues, 1982, Martin Formation, Arizona, USA.

F. NERITIDAE Rafinesque, 1815 Tr. (NML)–Rec. Mar./Brackish/FW


F. CERESIDAE Thompson, 19807 (PLE)–Rec. Terr.

First: Linidiella (Staffola) derbyi Dall, 1905, Pleistocene, Brazil (Knight et al., 1960).


First: Deianira sp. 1 (Kollmann, 1980), Losenstein Formation, Losensten, Austria.
Last: Deianira bicarinata (Zekei, 1852) Daniian, Austria (Knight et al., 1960).


First: Plesiothyreus parmophoroides Cossmann, 1885, Auvers-sur-Oise (Val d'Oise), France (Cossmann and Pissarro, 1911).

Superfamily HELICINOIDEA Latreille, 1825
**Fig. 8.3**

F. HELICINIDAE Latreille, 1825  
First: *Dawsonella meeki* (Bradley, 1872), Carbondale Formation, Herrin Coal Member (lower Westphalian C), Petty's Ford, Little Vermillion River, Georgetown, Illinois, USA (Solem and Yochelson, 1979).  
*Extant*

Next oldest: *Dimorphoptychia* Sandberger, 1871, Turonian, Europe (noted by Wenz, 1938).

**Superfamily HYDROCENOIDEA** Troschel, 1856  
F. HYDROCENIDAE Troschel, 1856  
First: *Hydrocena troili* Schlickum, 1978, Upper Miocene, Germany.  
*Extant*

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**Superfamily TITISCANIOIDEA** Bergh, 1890  
F. TITISCANIIDAE Bergh, 1890  
*Extant* Mar.

**Superfamily SYMMETROCAPULOIDEA** Wenz, 1938  
F. SYMMETROCAPULIDAE Wenz, 1938  
First: *Phryx bilateralis* (Blaschke, 1905) St Cassian Formation, southern Tyrol, Italy (Knight et al., 1960).  
Last certain: *Symmetrocapulus hanaii* Kase, 1984, Tanohata and Hiraiwa Formations, Miyako area, NE Japan.  
Last: *Symmetrocapulus* sp. (Squires, 1989), Tejon Formation, Tehachapi Mountains, Great Valley, California, USA.  
**Comment**: The morphology of the protoconch of some symmetrocapulids supports their placement within the...
Neritomorpha, most closely related to the following superfamilies (McLean, 1988).

**Superfamily** PELTOSPIROIDEA McLean, 1989

F. PELTOSPIRIDAE McLean, 1989 **Extant** Mar.

The Triassic genus *Phryx* Blaschke, 1905 resembles this family but not enough is known of its shell characters to permit the assignment (McLean, 1989). Following Knight et al. (1960), it is here retained in the Symmetrocapulidae.

**Superfamily** NEOMPHALOIDEA McLean, 1981


**Suborder** SEGUENZIINA Salvini-Plawen and Haszprunar, 1987

F. SCHIZOGONIIDAE Cox, 1960 **Extant** Mar.

**First**: *Schizogonium scalare* (Münster, 1841), Ladinian, S. Tyrol, Italy (Ferenc, 1961).

**Last**: *Pseudoschizogonium turriculatum* Kutassy, 1937, Carnian, Hungary (Knight et al., 1960).

F. SEGUENZIIDAe Verrill, 1894 **Extant** Mar.


**Last**: *Pseudoschizogonium turriculatum* Kutassy, 1937, Carnian, Hungary (Knight et al., 1960).

F. LAUBELLIDAE Cox, 1960 **Extant** Mar.

**First and Last**: *Laubella delicata* (Laube, 1868) St. Cassian Formation, Stuoresmergel, St. Cassian, Italy (Wenz, 1938)

**Suborder** ARCHTAENIOGLOSSA Haller, 1892 (see Fig. 8.3)

**Superfamily** CYCLOPHOROIDEA Gray, 1847

F. CYCLOPHORIDAE Gray, 1847 **Extant** Mar.

**First**: *Pseudarminia sp.*, Bear River Formation, Bear River,
near Beartown, Wyoming, USA (Fürsich and Kauffman, 1984).

**Intervening**: BAR–PLE

**Extant**

**Comment**: The Carboniferous Dendropupinae, formerly included here, have been shown to be buliminid pulmonates (Solem and Ychelson, 1979).

**F. NEOCYCLOTIDAE** Kobelt and Moellendorff, 1897

**Extant** Terr.

**F. NEOPUPIDAE** Kobelt, 1902


**First**:

Megalomastoma? sp. (Poinar and Roth, 1991), preserved in amber, Upper Eocene–Upper Oligocene, Dominican Republic. An indeterminat shell with operculum, perhaps, represents this or a similar genus (Poinar and Roth, 1991).

**Next oldest**:

A few species of the endemic genera Hainesia L. Pfeiffer, 1856 and Acroplejha Crosse and Fischer, 1877 occur in the Pleistocene of Madagascar (Wenz, 1938).

**Intervening**:

C. (OCR)-Rec. Terr.

**Extant**

F. CRASPEDOSTOMATIDAE Kobelt and Moellendorff, 1897 T. (THA)–Rec. Terr.

**First**:

Craspedopoma conoideum (Boissy, 1848), and C. insuetum (Deshayes, 1863), both thanetian, chenay (Marne), France (Cossmann, 1888).

**F. DIPLOMATINIDAE** Pfeiffer, 1856

J. (TTH)–Rec. Terr.

**First**:

Diplomatopychia conulus Maillard, 1885, Sourse de l’Ain, Nozeroy, Jura, France (Wenz, 1938).

**Intervening**:

EoC.

**F. PUPINIDAE** H. and A. Adams, 1855

K. (SAN)–Rec. Terr.

**First**:

Cyclomastoma pachygaster Hrubesch, 1965, Gosau Group, Glanegg near Salzburg, Austria (Hrubesch, 1965a), and Rognac, Les Pennes (Bouches-du-Rhone), France (Weinz, 1889).

**Extant**

Superfamily AMPULLARIOIDEA Gray, 1824

**F. VIVIPARIDAE** Gray, 1847

2C. (VIS)/J. (BAJ)–Rec. FW/Brackish

**First**:


**Extant**

**Next oldest**:

Viviparus langtonensis (Hudleston, 1896), Inferior Oolite, Langton Bridge, England, UK (Cossmann, 1921), or V. wangjianshanensis Guo et al., 1982, Middle Jurassic, north-west China.

**F. AMPULLARIIDAE** Gray, 1824 J. (MLM)–Rec. FW/Semi-terr.

**First**:


**Suborder** UNCERTAIN

**Superfamily** UNCERTAIN

Ponder and Warén (1988) assigned these two families to the Suborder Archtaenioglossa. The two groups are very poorly known, at least in the Palaeozoic.
Mollusca: Gastropoda

Cossmann, 1913, Saintpuits (Yonne), France (Cossmann, 1913).

F. PALAEOZYGOPLEURIDAE Horný, 1955


First: Palaeozigopleura alinae (Perner, 1903), Dvorce Limestone, Czechoslovakia.

Last: Palaeozigopleura venusta and P. welleri Thein and Nitecki, 1974, Lower Okaw Group, Illinois, USA.

F. PSEUDOZYGOPLEURIDAE Knight, 1930


Last: Pseudozygopleura pleurozyga, P. obliqua, P. convexa and P. irata Batten, 1985, H. S. Lee Mine No. 8, Kampar, Perak, Malaysia.

Comment: Wang and Xi (1980) recorded two species of Pseudozygopleura from the Wuchiapinian Stage (DZH), China, but the information is insufficient.

F. ABYSSOCHRYSIDAE Tomlin, 1927

Extant Mar.

No fossil record as such, but Houbrick (1979) has provided convincing evidence that the modern deep-sea genus Abyssochrysis Tomlin, 1927 is a living representative of the Zygozpuleuridae/Pseudozygopleuridae.

Superfamily SUBULITOIDEA Lindström, 1884

F. SUBULITIDAE Lindström, 1884

O. (ARG)–Tr. (SCY) Mar.

First: Fusispira sp., Smithville Formation, Arkansas, USA.

Last: Strobeus paludinaformis (Hall, 1858), Moenkopi Formation, Utah, USA (noted in Batten and Stokes, 1986).

F. MEEKOSPIRIDAE Knight, 1956


First: Auripitygma fortior Perner, 1903, Band e, Lochkov, Czechoslovakia.

Last: Meekospira melanooides and Meekospira ligoni Batten, 1985, at H. S. Lee Mine No. 8, Kampar, Perak, Malaysia.

Comment: Meekospira sp. Ishii and Murata, 1974, from the upper Sisophon Limestone, Cambodia, may be a representative of the genus, and may be younger, but neither is clear.


First and Last: Ischnopygma archeis Erwin, 1988, Road Canyon Formation, Texas, USA.

Superfamily PSEUDOMELANIOIDEA Fischer, 1885

F. PSEUDOMELANIIDAE Fischer, 1885

Tr. (LAD)–T. (BUR) Mar.

First: Oonia subtortilis (Münster, 1841), Marmolatakalke, Marmola, Mountan, Italy.

Last: Bayania purpurilla (Degranges-Touzin, 1895), Burdigalian, Dax, France (Cossmann, 1909).

Comment: A poorly known and probably polyphyletic group of elongate, often rather featureless shells. Cenomanian Liscium and typically Palaeogene Bayania seem to be close relatives, but their relationship to other genera assigned here is problematic. Included here are the Trajanellidae Pachelintsev, 1853, K. (APT–SEN) which do not show enough distinguishing features to be recognized with confidence.

Superfamily CERITHIOIDEA Férussac, 1819

F. PROCERITHIIDAE Cossmann, 1906

Tr. (LAD)–K. (MAA)–? Rec. Mar.

First: Paracerithium subcerithiforme (Kittl, 1895), Marmolatakalke, Marmola, Italy.


Extant Comment: By the Norian the family was abundant, species-rich and diversified (Haas, 1953). Various Tertiary species placed in the Cerithiidae, e.g. Batillona amara Finlay, 1927 (Oligocene, New Zealand), have the shell morphology of the Procerithiidae. Also probably cofamilial with these is Argyropeza Melville and Standen, 1901 (e.g. A. scheipmaniana Melville, 1912) living in the Indo-Pacific (Houbrick, 1980). Cossmann (1906) classified his genera Metacerithium and Nerineopsis as procerithiids, but these seem to be Cerithiidae/Potamidae and Cerithiopsidae, respectively. Spaniomepha from the mid-Devonian of England, placed by Knight et al. (1960) in this family almost certainly does not belong here.


F. CASSIOPIDAE Kollmann, 1979

J. (TTH)–K. (CMP), ?T. (Eoc.) Mar./Brackish

First: Paraglauconia sp. nov. (Cleevely and Morris, 1988), Indotritygia danielli horizon, Sana'a, Yemen.


Comment: No undoubted species are known from the Tertiary. Pseudoglauconia Douville, 1921 from the Eocene of Negritos, Piura, Brazil, was included doubtfully by Cleevely and Morris (1988).


First: Modulus turbinate (Heilprin, 1887), Orthaulax Bed, Ballast Point, Tampa Bay, Florida, USA (Dall, 1915).

Extant Comment: The Maasachriistic genus, Turbinopsis Conrad, 1860 from the Ripley Formation of Tennessee, USA, has been included in the Modulidae, but Sohl (1964a) considered it to belong to the Trichotropidae.

F. DIASTOMATIDAE Cossmann, 1895

and P. affinities of most Tertiary genera, formerly regarded as convergent with the Vanikoridae, which is where the de Bracheux, Abbecourt near Beauvais, France (Cossmann, 1889).

Comment: Houbrick (1981) restricted the family to the typical genus, including one living representative.

F. MELANOPSIDAE H. and A. Adams, 1854 K. (TUR)–Rec. FW/Brackish

First: ?Diastoma arcotense (Stoliczka, 1867), Arivalur Group, south India. Extant

Comment: Houbrick (1981) restricted the family to the typical genus, including one living representative.

F. THIARIDAE Troschel, 1857 C. (SPK)–Rec. FW/Brackish


Intervening: MLM, TTH, SEN–PLE Extant

Comment: Considered likely to be polyphyletic by Houbrick (1988).

F. PACHYCHILIDAE Troschel, 1857 K. (BER)–Rec. FW

First: Pachychilus (Pachychiloides) manselli (de Loriol, 1866) and P. (P.) attenuatus (J. de C. Sowerby, 1836), Corbula Beds, Middle Purbeck Beds, Durlston Bay, Dorset, England, UK (Arkell, 1941).

Extant


First: Planaxis africana Adegoke, 1977, Ewekoro Formation, Ewekoro, Nigeria. Extant

Comment: The Albion species ‘P.’ simplex Mahmoud, 1956 from Egypt is unlikely to belong to this family.


First: Fossarus sp. Middle Eocene, Selsey Formation, Bracklesham, Sussex, England, UK (but not ‘Fossarus’ dixoni Wrigley, 1942, which is a trochocean from an earlier horizon at the same locality: S. Tracey, unpublished data), and ?Zeradina obliquicostata (Marshall and Murdoch, 1920)., Borontonian, New York, USA (Beu and Maxwell, 1990). Extant

Comment: The shells of this family are to some extent convergent with the Vanikoridae, which is where the affinities of most Tertiary genera, formerly regarded as fossarid, will probably prove to lie.

F. BATILLARIIDAE Thiele, 1929 T. (DAN)–Rec. Brackish

First: Batillaria (Vicinocerithium) inopinata (Deshayes, 1864), Calcaire de Mons, Mons, Belgium (Gilbert, 1973). Extant


First: Echinobathra vicina (Verneuil and Lorrièere, 1868) APT, Utrillas, Spain (Kollmann, 1979), Pyrazus ? scadariformis and P.? sp. (Nagao, 1934), Hiraiga Formation (APT), Hiraiga, Miyako, Japan, have a similar form and ornament to Pyrazus, but this assignation cannot be confirmed as details of the aperture and body whorl are missing (Kase, 1984).

Extant

Comment: The differentiation of potamidid from other cerithiform gastropods is problematic in the Mesozoic. Albion cerithiids such as Metacerithium trimonile (Michelin, 1838) from the Gault of Folkestone, Kent, England, UK (Abbass, 1973), have the shape and ornament of three beaded cords that is found in various Tertiary potamidids (Physopomatides, Eotymanotonus) and cerithiids (Serratocerithium).


First: Springvaleia? sp. Sohl, in Boucot, 1990, Owl Creek Formation, Ripley County, Mississippi, USA (Boucot, 1990).

Extant


First: Brachytremata labiosum Deslongchamps, 1866, Piensbachian, May, France.

Last: Brachytremata superbum Zittel, 1873, B. (Petersia) victrix and B. (P.) curvatum (Zittel, 1873), all Tithonian, Straberg, and B. (P.) costatum (Gemmellaro, 1870), Tithonian, Sicily, Italy, and B. lamberti Cossmann, 1913, Auxerre, France (Cossmann, 1906, 1913). Extant


First: Diatinostoma euterpe (d’Orbigny, 1852), Arthis, Calvados, France.

Last: Ditretus nodosostriatus (Peters, 1865) and D.? collotti Cossmann, 1913, Portlandian, Murles, Hérault, France (Cossmann, 1913).

Extant


(see Fig. 8.4)

First and Last: Faxis macrostoma Ravn, 1933, Calcaire de Faxe, Denmark (Wenz, 1939).


First: Sandbergeria antecedens and S. crispicans (Stoliczka, 1867), Arivalur Group, southern India (Cossmann, 1906; Wenz, 1939).

Extant


First: ?Siliquaria triadica Kittl, 1892, St Cassian Formation, Austria (Cossmann, 1912; Wenz, 1939).

Next oldest: Siliquaria (Agathiresis) lima (Lamarck, 1818) and S. (Pyxipoma) gracilis (Deshayes, 1861), Cuisian, Vregny, Paris Basin, France (Cossmann and Pissarro, 1910).

Intervening: MAA of Egypt (Quaas, 1902, noted by K. Bandel in MS) Extant
Fig. 8.4
F. TURRITELLIDAE Lovén, 1847
First: Torquiesia ? dupiniana (Orbigny, 1842), Valanginian, Marolles, France.
Extant
Comments: Phylogenetic analysis of the Cerithioidea (Houbrick, 1988) has shown the Turritellidae to be one of the most highly derived families. This supports the view that Palaeozoic genera sometimes placed in this family (and herein assigned to the Acanthonematidae) are probably turritellid homeomorphs. Supposed Triassic and Jurassic species often have heterostrophic apices preserved and can be referred to the Heterostropha.

F. PAREORIDAE Finlay and Marwick, 1937
First: Pareora sp. (Beu and Maxwell, 1990).
Last: Pareora striolata (Daday, 1885) Opisthobranchia, New Zealand (Beu and Maxwell, 1990).
Comment: Maintained as a separate family by Beu and Maxwell, but included in the Turritellidae by Ponder and Waren (1988).

Superfamily CAMPANILIOIDEA Douville, 1904
F. CAMPANILIDAE Douville, 1904
First: Procamanile sp. (Pan, 1990), lower Member, Kukebai Formation, South Xinjiang, China.
Extant

Section NEOTAENIAYSULUS Haller, 1892
Superfamily LITIORINOIDEA Gray, 1840
F. PURPURINIDAE Zittel, 1895
Tr. (LAD)–K. (SEN) Mar.
First: Angularia subpleurotomaria (Münster, 1841), Stuoresmergel, St Cassian, Italy, and Aristerostrophia gracilis Broili, 1907, Ladinian, southern Alps (Ferenc, 1961).
Last: Purpurina subcaucasia Dzhaliilov, 1977, Upper Cretaceous, Turkmenistan, former USSR.

F. LITITORINIDAE Gray, 1840
First: ?Lemmiscollitorina berryi (Wade, 1926), Ripley Formation, Mississippi, USA (Sohl, 1960). In form and ornament this is not close to later littorinids, and may be unrelated (Reid, 1989). The protoconch of a species from the Campanian Coffee Sand Formation of Mississippi, referred to this genus by D. T. Dockery (pers. comm.), shows it to belong to the Mathildidae.
Extant
Next oldest: Melaraphe rissoides (Deshayes, 1861) and M. mausseneti (Cossmann, 1907), both Sables de Chalons-sur-Vesle, Chenay (Marne), France (Cossmann and Pissarro, 1913), and Littorina ? sp. (Woods and Saul, 1986), Sepultura Formation, Baja California, Mexico (Reid, 1989).
Comments: Wenz's (1938) Cretaceous records of Litiorinopsis from Europe and East Africa were not corroborated by Reid (1989). Lacunina Kittl, 1899 and species referred to Lacuna Turton, 1827 from the Triassic St Cassian fauna from Italy do not appear to be littorinids and are of uncertain systematic position.

F. POMATIASIDAE Gray, 1852
K. (CON)–Rec. Terr.
Extant
F. ANNULARIIDAE Henderson and Bartsch, 1920
F. ACICULIDAE Woodward, 1854
T. (?Eoc.)/(CHT)–Rec. Terr.
First: Acicula (Platyla) sp. was indicated by Wenz (1939) from the Cretaceous of Europe, but the record could not be located.
Extant
F. SKENEOPSIDAE Iredale, 1915
Extant Mar.
Superfamily CINGULOPSISIDAE Fretter and Patil, 1958
F. EATONIELLIDAE Ponder, 1968
Extant
F. CINGULOPSISIDAE Fretter and Patil, 1958
Q. (PLE)–Rec. Mar.
First: Eatonina (Otatarata) subflavescens Iredale, 1915, Pleistocene, New Zealand (Beu and Maxwell, 1990).
Extant
F. RASTODENTIDAE Ponder, 1966
Extant Mar.
Superfamily RISSOIDEA Gray, 1847
F. HYDROBIIDAE Troschel, 1857
?P. (KUN)/J.(DOG)–Rec. FW/Brackish
First: Hydrobia gondwanica Cox, 1953, Ecca Beds, Karroo, Zimbabwe. Doubtfully hydrobid, described as having a slightly heterostrophic protoconch (Cox, 1953).
Next oldest: Pseudamnicola acuta, Amnicola kushiuixaensis and A. shuidonggouensis Pan, 1982, Middle Jurassic, China (Guo et al., 1982).
Extant
F. BITHYNIIDAE Gray, 1857
J. (MLM)–Rec. FW
First: Bithynia haizhouensis Yu, 1982, Fuxin Formation, western Liaoning, China.
Extant
Comment: The calcified opercula, characteristic of this family, first occur in the lower Ypresian Reading Formation, Harefield, Middlesex, England (Cooper, 1976).
F. HYDROCOCCIDAE Thiele, 1928
Extant Brackish
F. POMATIOPSIDAE Stimpson, 1865
T. (Mio.)–Rec. FW
First: Prosothenia spp. (Neumayr, 1869), Dalmatian Miocene, former Yugoslavia (noted in Davis, 1979).
Extant
Comment: Ponder (1985) implied a possible Cretaceous occurrence of the family.

First: Truncatella minor Briart and Cornet, 1887, Calcaire de Mons, Mons, Belgium (Glibert, 1973). Extant

F. STENOXYRIDAE Fischer, 1885 T. (DAN)–Rec. FW/Brackish

First: Stenoxyra pupiformis (Briart and Cornet, 1887), Calcaire de Mons, Mons, Belgium (Glibert, 1973). Extant

F. FALSICINGULIDAE Slavoshevskaya, 1975 Extant Mar.

F. IRAVADIIDAE Thiele, 1928 K. (CMP)–Rec. Brackish/Brackish

First: Nozedia sp. Coffee Sand Formation, Friendship near Chapelville, Lee County, Mississippi, USA (D. T. Dockery, pers. comm.) Extant

F. PYRGULIDAE Brusina, 1881 K. (NEO)–Rec. FW

First: Micromelania katoensis and Itonelania basicordata (Suzuki, 1943), Naktong Group, Kyongsang-namdo and Cane pine, Spoleto, Italy (Conti and Fischer, 1982). Extant


F. VITRINELLIDAE Bush, 1897

First: ?Teinostoma valfenense Loriol, 1886?, Calcaires blancs, Valfin, France (Cossmann, 1918). Extant

Next oldest: Cenomanella archiaciana (Orbigny, 1847), Cenomanian, Le Mans (Sarthe), France (Wenz, 1938). Extant

Comment: Teinostoma spp., showing little difference from living forms, were widespread by the late Cretaceous.


First: Tornus trigonostoma (Basterot, 1825) and T. quadrifasciatus (Grateloup, 1832), Laag van Miste, Winterswijk–Miste, The Netherlands (Janssen, 1984) and Naricava huttoni (Marwick, 1924), Altonian, New Zealand (Beu and Maxwell, 1990). Extant

Comments: The Tornidae are difficult to identify in the Tertiary as the shells are convergent with those of Vitrinellidae and related families. Aderoris bicanatus and A. spirorbis (Lamarck, 1806) of the French Ypresian resemble some tornids in shape but are connected to typical Aderoris (Vitrinellidae) by a range of intermediate forms.

Superfamily STROMBOIDEA Rafinesque, 1815


First: Anchura (Piettea) huddlestoni (Wilson, 1887), lower Lias, Bristol, Avon, England, UK (Cossmann, 1904). Extant

Comments: Wenz (1940) doubtfully suggested a Rhaetian age for Spinigeria Orbigny, 1850, but the species referred to is not certain. The family is considered to include the Harpagoida Pchelintsev, 1963.


First: ?Adiopsis clathrata Gemmellaro, 1878, Lias, Sicily, Italy.

Next oldest: Columbellaria bathomica Cossmann, 1913, St Gaultier, France.

Comments: This family is perhaps the stem group of the Cypraeoida and Tonnoida (Taylor and Morris, 1988).


First: Conchothyra parasitica Hutton, 1877, Waipara Formation, Waipara River, New Zealand (Beu and Maxwell, 1990). Extant


Next oldest: ‘Sipunculidae’ paliatus (Forbes, 1848), Trichinopoly and Arivalur Groups, south India (Stoliczka, 1868). Extant

Comments: The genus Pugnellia, dating from the Santonian, is now considered an aporrhaid (Popeneo, 1983).
First: Seraphs soperi (Solander, in Brander, 1766), l’Aude or l’Hérault, southern France (noted in Jung, 1974).

Extant

First and Last: Therisites gracilis (Coquand, 1862), Tunis, Tunisia, and T. ponderosa (Coquand, 1862), Tébessa, Constantine Province, Algeria (Wenz, 1943).

Superfamily VANIKOROIDEA Gray, 1840
First: Vanikoropsis decussata (Deshayes, 1842), Kimigahama Formation, Choshi area, Japan (Hayami and Kase, 1977). Extant


Superfamily CALYPTRAEOIDEA Lamarck, 1809
First: Galericulus altus (Seeley, 1861), Cambridge Greensand, Cambridge, England, UK (Wenz, 1938). Extant

First: Capulus verus (Bohm, 1885), Aachen Greensand, Vaals, The Netherlands and Königsthor, Germany (Holzapfel, 1888). Extant

Comments: This appears to be the first recognizable capulid. Most earlier records of capuliform gastropods are of uncertain affinities, including those figured by Zardini (1978) from the Triassic St Cassian Formation.

First: ?Atresius cornuelianus (Orbigny, 1843), Aptian, Vaucluse, France. Extant
Next oldest: Atresius lallierianus (Orbigny, 1843), Gault Yonne, Sainte Florentin, France.

Superfamily XENOPHOROIDEA Troschel, 1852
First: Lamelliphorus supraliasinus (Vacek, 1886), Aalienian, Tuscany, Calabria and Veneto, Italy. Last: Lamelliphorus torrillius (Peron, 1900), Neocomian, Yonne, France (Ponder, 1983).

Comment: The shell morphology resembles that of xenopids but lacks the attachment of foreign objects. Their systematic position is, however, still uncertain.


Superfamily VERMETOIDEA Rafinesque, 1815
First: ?Provermicularia circumcarinata (Stoppani), Esinokalk, Ca’ nova am Monte Croce, Esino, Italy (Kittl, 1899 noted in Wenz, 1939), and ?Pseudobrochidium germanicum Grube, 1907, lower Keuper, Hannover, Germany (Wenz, 1939). Extant

Next oldest: Burtinella damesi (Noetling, 1885), Cenomanian, Germany (Cossmann, 1912; Wenz, 1939).

Comment: The family, as presently understood, is probably a polyphyletic group featuring lax coiling. Convergence makes it difficult to identify Mesozoic vermetids from the adult shells.

Superfamily NATICOIDEA Forbes, 1838
First: Ampullospira adducta (Phillips, 1829), Dogger, Yorkshire coast, England, UK. Extant

Comments: This would appear to be one of the earliest records of an unequivocal naticid. Shells of Gyrodes spp. from the upper Albian Blackdown Greensand of Devon, UK, occur in association with drill holes, as made by living naticids (Taylor et al., 1983).

First: Ampullospira adducta (Phillips, 1829), Dogger, Yorkshire coast, England, UK (Hudleston, 1892). Extant

Comments: The simple morphology of the naticiform shell is seen to recur in distantly related groups. Earlier Mesozoic forms are of uncertain affinities. Bandel (1988b) has shown the larval shell morphology of genera such as Amauropsis to be neritoidean in character and he considers that there are no confirmed naticoids from the Triassic. Kase (1990) briefly notes that the sole surviving species, Cerinia fluctuata (G. B. Sowerby, 1825) is an archaeniglans. Pending a fuller investigation, the family is retained in the Naticoidea.

Superfamily CYPRAEOIDEA Rafinesque, 1815
First: Palaeocypraea titonica and Bernaya gemmellarii Stefano, 1882, Terminl Imere, Sicily, Italy (Schilder and Schilder, 1971).

Extant

First: Eocypraea pilulosa (Stoliczka, 1867), Cenomanian, India (Schilder and Schilder, 1971).

Extant

Superfamily LAMELLARIOIDEA d’Orbigny, 1841
First: Lamellaria inopinata Cossmann, 1907 Jonchery (Aisne), France (Cossmann and Pissarro, 1910). Extant

First: Johnstrupia faxensis Ravn, 1933, Calcaires à Coralliaires, Faxe, Denmark (Schilder and Schilder, 1971). Extant
F. **PSEUDOSACCULIDAE** Wenz, 1940  Extant  Mar.

**Superfamily** **TONNOIDEA** Suter, 1913


First: *Pseudocymia aurora* Popenoe and Saul, 1987, Frazier Silts tone, Salt Creek, Shasta County, California, USA.

Last: *Perissitys stewarti* (Zinsmeister, 1983), Lower Santa Susana Formation, Simi Hills, Ventura County, California, USA (Popenoe and Saul, 1987).

F. **TONNIDAE** Suter, 1913  K. (MAA)–Rec.  Mar.

First: *Protodolium speighti* (Trechmann), Maastrichtian, Waipara, New Zealand (Wenz, 1941). Extant


First: *?Protopirula capensis* (Rennie, 1931), Umzamba Beds, Pondoland, South Africa (Wenz, 1939).

Next: *Priscoficus bicarinatus* (Briart and Cornet, 1870), Calcaire de Mons, Mons, Belgium (Glibert, 1973) and *P. obtusus* (Marshall, 1917), Wangaloa Formation, Wangaloa, New Zealand (Beu and Maxwell, 1990). Extant

F. **CASSIDAE** Latreille, 1825  K. (CON/SAN)–Rec.  Mar.


F. **RANELLIDAE** Gray, 1854  K. (BRM)–Rec.  Mar. (pelagic)

First: *Eoranella kiliani* Sayn, 1932, Urgonian sables calcaires, Bogaris, near Barcelona, Spain. Extant

Comment: Considered by Sayn (1932) to have many ranellid features, this species also bears a strong resemblance to later Muricidae.


First: *?Hanaibursa aequilana* (Parona, 1909), Hiraiga Formation, Miyako area, Japan (Kase, 1977). Extant

Next oldest: *Bursa saundersi* Adegoke, 1977, Ewekoro Formation, Ewekoro, Nigeria. Extant

F. **LAUBIERINIDAE** Warén and Bouchet, 1990  Extant  Mar.

**Superfamily** **CARINARIOIDEA** Blainville, 1818

F. **ATLANTIDAE** Rang, 1829  T. (DAN)–Rec.  Mar. (pelagic)

First: *Eoatlanta* sp. novo (Rosenkrantz, 1960), Calcaire de Faxe, Denmark. Recorded by Ravn (1933) as *E. spiruloides* (Lamarck, 1824). Extant

F. **CARINARIIDAE** Blainville, 1818  J. (TOA)–Rec.  Mar. (pelagic)

First: *Celoliscus minutus* (Zieten, 1832) and *C. fluegeli* Bandel and Hemleben, 1987, *Posidonia* Shales, Germany (Bandel and Hemleben, 1987). Extant

F. **FIROLIDAE** Rang, 1829  J. (TOA)–Rec.  Mar. (pelagic)


F. **PTEROSOMATIDAE** Rang, 1829  Extant  Mar. (pelagic)

**Superfamily** **TRIPHOROIDEA** Gray, 1847


F. **SHERBORNIIDAE** Iredale, 1917  Extant  Mar.


First: *?Triphora cincta* (Kaunhowen, 1898), Chalk, Maastrichtian, The Netherlands (Cossmann, 1906).

Next oldest: *Triphora staadti* (Cossmann, 1907), Sables de Chalons-sur-Vesle, Chenay (Marne), France. Extant

**Superfamily** **JANTHINOIDEA** Lamarck, 1812

F. **EPITONIIDAE** S. S. Berry, 1910 (1812)  J. (BTH)–Rec.  Mar.

First: *Proacirsa inornata* (Terquem and Jourdy, 1869) Fuller’s Earth, Clapes, Lorraine, France (Cossmann, 1912).

F. **JANTHINIDAE** Lamarck, 1812  T. (MES)–Rec.  Mar. (pelagic)

First: *Hartungia typica* Bronn, 1861, Messinian, East Cape, New Zealand; Santa Maria Islands and Azores (Beu and Maxwell, 1990). Extant

Comment: Not *Janthina cimbrica* Sorgenfrei, 1958 (Miocene, The Netherlands) which was shown to be a juvenile cypraeid (Janssen, 1984).

**Suborder** **UNCERTAIN**

**Superfamily** **EULIMOIDEA** Troschel, 1853


First: *Graphis formosa* (Briart and Cornet, 1873), Calcaire de Mons, Mons, Belgium (Glibert, 1973). Extant

F. **EULIMIDAE** Troschel, 1853  K. (?CENIMAA)–Rec.  Mar.

First: *Eulima persimplica* and *E. laevigata* Wade, 1926, Ripley Formation, Tennessee, USA (Sohl, 1964a). Extant

Comments: These are among the earliest described species, although Sohl (1967) reported unspecified eulimids from the Cenomanian to Maastrichtian of New Mexico, Colorado and Wyoming, USA. Kier (1981) described an upper Albian spatangoid echinoid from Texas showing
the characteristic ambulacral 'perforation' of a parasitic eulimid.

**F. STILIFERIDAE H. and A. Adams, 1853**

First: *Semistylifer pellucidus* (Deshayes, 1824), Calcaire Grossier, Parnes, France (Cossmann, 1888).  
Extant Comments: The earliest stiliferid is listed here, although the group is now included in the Eulimidae (Warén, 1983). Also included in the Eulimidae by Warén (1983) are the families Thyridae Thiele, 1931, Asterophilidae Thiele, 1925, Paedophoropodidae Ivanov, 1933, and Entoconchidae Gill, 1871, all Recent, marine and without fossil records.

**F. WEEKSIIIDAE Sohl, 1960**

First: *Weeksia lubbocki* (Stephenson, 1941), Nacotch Sand, Navarro Group, Texas, USA (Sohl, 1960).  
Last: *Weeksia deplanata* (Johnson, 1905), Prairie Bluff Chalk, Alabama and Mississippi, USA (Sohl, 1960).  
Comments: Sohl included the Triassic genera *Discohelix* Dunker, 1848 and *Amphitomaria* Koken, 1897 in his family of supposed archaeogastropods. Bandel (1988a) showed *Discohelix* to be a trochoidean, *Amphitomaria* a hetero-
strophan and placed *Weeksia* in the Neogastropoda, although Batten (1984b) considered it a mesogastropod.

**Section NEOGASTROPODA** Thiele, 1929

**Superfamily** MURICOIDEA da Costa, 1776

**F. MURICIDAE** da Costa, 1776


**Comments:** The relationships of pre-Tertiary forms are unclear. If the Moreinae Conrad, 1860 are muricids (see Sohl, 1964a) then the above record is the oldest. The many species of supposed Rapaninae from the Albian Blackdown Greensand of England, UK (Taylor et al., 1983) may be rapanid homeomorphs and not closely related (N. J. Morris, pers. comm.).

**F. CORALLIOPHILIDAE** Chenu, 1859

*First: Lowenstamia funiculus* Sohl, 1964a, Coffee Sand Formation, near Ratliff, Lee Co., Mississippi, USA. **Extant**

**Comment:** *Lowenstamia* Sohl, 1964 and the contemporaneous *Sargana* Stephenson, 1923 are possibly neotaenioglossan muricoid homeomorphs.

**F. BUCCINIDAE** Rafinesque, 1815

*First: ‘Buccinum’ incertum* Orbigny, in Murchison, 1845,
Speeton Clay, Speeton, North Yorkshire, England, UK (N. J. Morris, pers. comm.).

F. COLUMBELLIDAE Swainson, 1840
First: Mitrella (Columbellopsis) edmondi (Briart and Cornet, 1870), Calcaire de Mons, Mons, Belgium (Glibert, 1973).

First: Buccinopsis sp. novo Sohl, 1964, Eutaw Formation, Alabama, USA.
Comment: Buccinopsis Conrad, 1857 is considered to represent the first recognizable nassariid (Nuttall, in Taylor et al., 1980).

First: Hydrotribulus nodosus Wade, 1916, Ripley Formation, Mississippi, USA (Soh!, 1964a).
Last: Strepsidura turgida (Solander, in Brander, 1766) Barton Clay Formation, Barton, Hampshire, England, UK. Comment: Three other species from Oligocene strata, formerly assigned to Strepsidura Swainson, 1840, have all proved to belong to the Nassariidae (Nuttall and Cooper, 1973).

First: Tantunia clathrata (J. de C. Sowerby), Blackdown Greensand, Blackdown, Devon, England, UK (Taylor et al., 1983).

First: ‘Fusus’ valanginiensis Pictet and Campiche, 1872, Auberson, St Croix, Switzerland. Comment: Such early fusiform gastropods may belong to a stem group of the paraphyletic Fasciolariidae and the Turridae (N. J. Morris, pers. comm.).

First: Carota pendula Stephenson, 1952, Lewisville Member, Woodbine Formation, Texas, USA. Extant

First: Eoharpa sinusua Stephenson, 1955, Owl Creek Formation, Missouri and Mississippi, USA (Soh!, 1964a).
Next oldest: Mesorhysis ripleyana (Wade, 1926), Ripley Formation, Coon Creek, Tennessee, USA (Cernohorsky, 1970).

First: ‘Tudicla’ monheimi (Müller, 1851), Aachen Greensand, Vaals, The Netherlands (Holzapfel, 1888). Extant
Comment: By the Maastrichtian the family was represented by about ten genera in the USA alone (Soh!, 1964a; Saul, 1988).

First: Columbarium heberti (Briart and Cornet, 1880), Tuffeau de Maastricht, Limburg, The Netherlands (Darragh, 1969). Extant
Comment: The columbariids are now generally considered a subfamily of the Vasiidae.

First: Popoeaeum subcostatum (Stoliczka, 1868), Arivalur Group, Ninnyoor area, south India (Squires et al., 1989), and Ptychosyca inornata Gabb, 1876, Ripley Formation, Mississippi, USA (Soh!, 1964a).

First: Imbricaria (Sohlia) conoidea Kollmann, 1976, Losenstein Formation, Losenstein, Austria. Extant
Comment: Ponder (1973) suggests that the cancellariids represent the sister group of all other living Neogastropoda. Their recognition earlier in the Cretaceous is difficult as the diagnostic shell characters were not fully developed.

First: Gibberula sp. nov. (Glibert, 1973), Calcaire de Mons, Mons, Belgium.

First: Conomitra glabra (Ravn, 1933), Calcaire de Faxe, Nez, Faxe, Denmark. Extant

First: Mesorhysis decorosa (Stephenson, 1952), Coffee Sand Formation, Texas, USA. Extant
Next oldest: Mesorhysis ripleyana (Wade, 1926), Ripley Formation, Coon Creek, Tennessee, USA (Cernohorsky, 1970).

Superfamily CANCELLARIOIDEA Gray, 1853
First: Palaeocancellaria hoelleitenensis Kollmann, 1976, Losenstein Formation, Losenstein, Austria. Extant
Comment: Ponder (1973) suggests that the cancellariids represent the sister group of all other living Neogastropoda. Their recognition earlier in the Cretaceous is difficult as the diagnostic shell characters were not fully developed.

Superfamily CONOIDEA Fleming, 1822
First: Hemiconus bicornatus (Melville, 1843), Sables de Chalons-sur-Vesle, Jonchery-sur-Vesle (Marne), France (Cossmann, 1913). Extant
Comment: All records of Conidae from the Cretaceous
appear to be based on doubtful forms or are mistakenly dated.

**F. TURRIDAE** Swainson, 1840

**First:** ?'Pleurotoma' subfusiformis d'Orbigny, 1831, Gosau Group, Austria (Stoliczka, 1867).

**Next oldest:** Struthiolariopsis ferrieri (Philippi, 1887), Quiriquina, Chile, and Berreta preclara Sohl, 1964b, Coffee Sand Formation, Mississippi, USA (Sohl, 1964b). *Extant*

**F. SPEIGHTIIDAE** Powell, 1942

**First:** Andicula occidentalis (Woods, 1922), Negritos of Peru (Powell, 1966).

**Last:** Speightia spinosa (Suter, 1917), Bortonian, Waihao River, South Island, New Zealand (Powell, 1966).

**Comment:** Although allowed familial status by some authors, some if not all of the speightiids may prove to belong in the Fasciolariidae.

**F. TEREBRIDAE** Mörch, 1852

**First:** Hastula (Terebrellina) plicatula (Lamarck, 1805), Blackheath Beds, Abbey Wood, London, England, UK (Wrigley, 1942). *Extant*

**Comment:** Wenz (1943) doubtfully extended the range of the family into the Cretaceous but this appears to be unsubstantiated.

**Suborder** HETEROSTROPHA Fischer, 1885

**Superfamily** VALVATOIDEA Gray, 1840 and Thompson, 1840

**F. VALVATIDAE** Gray, 1840 and Thompson, 1840
J. (DOG)–Rec. FW

**First:** Amplovalvata antiqua and A. obliqua Pan, 1982, Middle Jurassic, China (Guo et al., 1982). *Extant*

**F. CORNIROSTRIDAE** Ponder, 1990
Extant Shallow mar.

**F. ORBITESTELLIDAE** Iredale, 1917

**First:** Orbitestella (Omalogyrina) picatella (Cossmann, 1888) middle Lutetian, Villiers-St-Frédéric (Yvelines), France (J. Le Renard, unpublished data). *Extant*

**Comment:** The family is linked to the Architectonicidae by the intermediate genera, Amphitomaria Koken, 1897 and Neamphitomaria Bandel, 1988a, from the late Cretaceous of the eastern USA, and the Tertiary, respectively (Bandel, 1988a).

**Superfamily** GLACIDORBOIDEA Ponder, 1986

**Suborder and Superfamily** UNCERTAIN

**F. OMALAXIDAE** Wenz, 1938

**First:** Omalaxis sp. (Bandel, 1988), Marnes de la Tuilerie de Gan (Pyrenees Atlantiques), France, and O. deshayesi (Michaud, in Deshayes, 1863) and O. laudunensis (Defrance, 1828), Sables de Cuise, Cuise-Ia-Motte (Oise), France (Gougerot and Le Renard, 1980). *Extant*

**Comment:** The placement of this Eocene family is problematic.

**Superfamily** NERINEOIDEA Zittel, 1873

Pchelintsev (1965) considered the three families below to be superfamilies containing fifteen families. This scheme has not won general acceptance, and a more traditional system is used here.

**F. NERINEIDAE** Zittel, 1873

**First:** Prodiozyoptyxis permiana Batten and Stokes, 1986, Moenkopi Formation, Utah, USA. *Extant*

**F. ARCHITECTONICIDAE** Gray, 1850
Tr. (LAD)–Rec. Mar.

**First:** Rinaldoconchus ampezzanus (Zardini, 1980) and Amphitomaria cassiana (Koken, 1889), St Cassian Formation, Cortina d’Ampezzo, Italy (Bandel, 1988a). *Extant*

**Superfamily** RISSOELLOIDEA Gray, 1850

**F. RISSOELLIDAE** Gray, 1850 *Extant* Mar.

**Superfamily** OMALOGYROIDAE G. O. Sars, 1878

**F. OMALOGYRIDAE** G. O. Sars, 1878
?K. (SAN)/T. (LUT)–Rec. Mar./Brackish

**First:** ?Omalogyra sp. (Bandel, 1988), Amman Formation, Jordan. *Extant*

**Next oldest:** Omalogyra cf. atomus (Philippi, 1841), Thionville-sur-Opton (Yvelines), France (J. Le Renard, unpublished data). *Extant*

**Comment:** The family is linked to the Architectonicidae by the intermediate genera, Amphitomaria Koken, 1897 and Neamphitomaria Bandel, 1988a, from the late Cretaceous of the eastern USA, and the Tertiary, respectively (Bandel, 1988a).
to the Cretaceous genus *Diozoptyxis*, which according to Houbrick (1981), may not be a nerineid.

F. **NERINELLIDAE** Pchelintsev, 1960
**First:** *Nerinella noriigensis* (Tausch), HET, Alpes méridionales, France (Cossmann, 1896).
**Last:** *Multipityxis gissarensis* (Pchelintsev, 1960), Senonian, former ‘Soviet Central Asia’ (Pchelintsev, 1965).

**First:** *Itieria cabanetiana* (Orbigny, 1841), Oyonnax, near Nantua (Ain), France.
**Last:** *Itruvia carinata* (Reuss), Calcaire à Hippurites, Czechoslovakia (Cossmann, 1896; Kollmann and Sohl, 1980).

Subclass **EUTHYNEURA** Spengel, 1881

**Superorder** OPISTHOBANCHIA Milne-Edwards, 1848
**Order** CEPHALASPIDEA Fischer, 1883

**Superfamily** CYLINDROBULLINOIDEA Wenz, 1947
**First:** *Girty spies* sp. Yoo, 1988, Namoi Formation, New South Wales, Australia.
**Last:** *Acteocina obesa* Stoliczka, 1868, Arivalur Formation, southern India (Cossmann, 1895).

F. **CERITELLIDAE** Cossmann, 1895 J. (SIN)–K. (APT/ALB) Mar.
**First:** *Ceritella exilis* (Martens), Semur (Cossmann, 1895).
**Last:** *Pseudonerinea stantoni* and *P. sturtoni* Allison, 1955, Punta China, Baja California, Mexico.

**Superfamily** ACTEONELLOIDEA Zilch, 1959
**First:** *Acteonella baconia* Benköne-Czabalay, 1965, upper Aiptian/Albian, Hungary (Dzhailov, 1972).
**Last:** *Acteonella laevis* (J. de C. Sowerby, 1833), *A. elongata* and *A. (Sogdianella) zekei* Kollmann, 1965, all Gosau Group, Austria (Dzhailov, 1972).

**First:** *Cylindrites acutus* (J. de C. Sowerby, 1824), Lias, Europe (Akopyan, 1972).
**Last:** *Trochactaeon truncatus* and *T. minutus* (Stoliczka, 1868) Arivalur Formation, southern India (Stoliczka, 1868).
**Comment:** Zilch’s (1959) record of *Trochactaeon* from the Danian could not be substantiated.

**Superfamily** ACTEOIDEA Orbigny, 1842
**First:** *?Tornatella heberti* (Piette), lower Lias, France (Cossmann, 1895).
**Next oldest:** *Tornatella fontis* (Duméril, 1806), Charmouthian, eastern France (Cossmann, 1895). *Extant*
Mollusca: Gastropoda

Comment: Although usually placed here, the North American Upper Cretaceous genus, *Bullopsis* Conrad, 1858 contains globular shells with two strong columellar pleats, and is unlikely to belong in this family.

**F. HAMINOEIDAE** Pilsbry, 1895 K. (MAA)–Rec. Mar./Brackish

First: 'Cylichna' incisa Stephenson, 1941, Ripley Formation, Mississippi, USA (Sohl, 1964a).

Comments: This species appears to be congeneric with a number of Tertiary species, variously assigned to *Roxania* Gray, 1847, *Mnestia* H. and A. Adams, 1854, or *Atys* Montfort, 1810. The fossil forms more closely resemble *Aliculastrum* Pilsbry, 1896, and are better placed in this family.

**F. RETUSIDAE** Thiele, 1926 J. (BTH)–Rec. Mar./Brackish

First: Retusa sp. novo (Cossmann, 1895), Boulonnais, France. Extant

Intervening: CLV–PLI.

**Superfamily** RUNCINOIDEA Gray, 1857

F. RUNCINIDAE Gray, 1857 Extant Mar.

F. ILDICIDAE Burn, 1963 Extant Mar.

**Superfamily** HEDYLOPSOIDEA Bergh, 1896

This comprises the families Acochondiidae Küthe, 1935, Hedylopsidae Bergh, 1896, Platyhedylidae, ?Tantulidae and Microhedylidae Odhner, 1938, which have no shell. There is no fossil record of this superfamily, although calcareous spicules occur in the mantle of some groups and theoretically could be detected in micropalaeontological samples.

**Superfamily** ?HILINOGLOSSOIDEA

This comprises the Phelinoglossidae in which the shell is absent, and the Plusculidae with a vestigial shell. No fossil record.

**Order** SACOGLOSSA Ihering, 1876

**Superfamily** JULIOIDEA E. A. Smith, 1885

F. CYLINDROBULLIDAE Thiele, 1931 Extant Mar.

F. VOLVATELLIDAE Pilsbry, 1895 Extant Mar.


F. OXYNOIDAE H. and A. Adams, 1854 Extant Mar.


F. CALIPHYLLIDAE Clark, 1982 Extant Mar.

F. LIMAPONTIIDAE Gray, 1847 Extant Mar.

F. ELYSIIDAE H. and A. Adams, 1854 Extant Mar.

F. BOSELLIIDAE Marcus, 1982 Extant Mar.

**Order** APLYSIMOFORMA

**Superfamily** APLYSIOIDEA Rafinesque, 1815


First: Dolabella aldrichi Dall, 1890, Chipola Formation, Alum Bluff, western Florida, USA (Dall, 1915).

F. NOTARCHIDAE Eales, 1925 Extant Mar.

**Order** ANASPIDEA Fischer, 1883


**Order** NOTASPIDEA Fischer, 1883

**Superfamily** TYLODINOIDEA Gray, 1847


First: Umbraculum laudunense (Melleville, 1843), Sables de Pierrefonds, Laon, France (Cossmann and Pissarro, 1913), or *U. sylvaeviridis* (Harris) and *Eosinica elevata* (Aldrich), Bashi Mar! Member, Hachetigbee Formation, Woods Bluff, Alabama, USA (Jablonski and Bottjer, 1990).


First: Tylodina (Tylodinella) rafinesquei Philippi, 1844?, Pliocene, Sicily, Italy (Cossmann, 1895).

**Superfamily** PLEUROBRANCHIOIDEA Menke, 1828

F. PLEUROBRANCHIDAE Menke, 1828 Extant Mar.

**Order** PTEROPODA Cuvier, 1804

**Suborder** EUTHECOSOMATA Meisenheimer, 1905

**Superfamily** LIMACINOIDEA Blainville, 1823

F. LIMACINIDAE Blainville, 1823 T. (THA)–Rec. Mar. (pelagic)

First: Limacina mercinensis (Watelet and Lefevre, 1885), Tusahoma Sand Formation, Bear Creek Mar! Member, Bear Creek, Alabama, USA (S. Tracey, unpublished data).


**Suborder** PSEUDEUTHECOSOMATA Meisenheimer, 1905

F. PERACLIDAE C. W. Johnson, 1915 Extant Mar. (pelagic)

F. CUMBULIDAE Gray, 1840 Extant Mar. (pelagic)
Fig. 8.6

<table>
<thead>
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<th>F. DESMOPTERIDAE Chun, 1889</th>
<th>Extant</th>
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<td>Mar. (pelagic)</td>
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*Order* **GYMNOSOMATA** Blainville, 1824

Comprising the families Pneumodermatidae Latreille, 1825, Notobranchaeidae Pelseneer, 1886, Cliopsidae Costa, 1873, Thliptodontidae Kwietniewski, 1902, Hydromylidae Pruvo-Fol, 1942, Laginiopsidae and Clionidae Rafinesque, 1815, which have no shell in the adult phase. Protoconchs referable to the Gymnosomata have been found in Pleistocene samples from the northeast Atlantic (Van der Spoel and Diester-Haass, 1976).

*Superorder* **GYMNOMORPHA**

*Order* **SYSTELLOMMATOPHORA**

*Superfamily* **ONCHIDIOIDEA** Gray, 1824

F. **ONCHIDIIDAE** Gray, 1824  Extant  Mar.

*Order* **SOLEOLIFERA**

This comprises the families Veronicellidae Gray, 1840, Rhodopidae and Rathouisiidae Sarasin, 1899 which have no shells and are not recorded as fossils.  Extant

*Superorder* **PULMONATA** Cuvier, 1817

*Order* **ARCHAEOPULMONATA** Morton, 1955

F. **ACROREIDAE** Wenz, 1923  K. (SEN)-T. (YPR)  Probably brackish

This order contains 66 families of opisthobranchs without shells, and there are no reliable fossil records.  Extant
**Mollusca: Gastropoda**

### Key for both diagrams

1. Hydatinidae
2. Cylichnidae
3. Tornatinidae
4. Philinidae
5. Diaphanidae
6. Bulinidae
7. Haminoeidae
8. Retusiidae
9. Juliidae
10. Aplysiidae
11. Akeridae
12. Umbraculidae
13. Tylodinidae
14. Limacinidae

### PERMIAN

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### ORDOVICIAN

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**Fig. 8.6**

**First:** Acroreia (Vasculum) obliqua (White, 1889), Laramie Group, California, USA.  
**Last:** Acroreia baylei (Cossmann, 1885), Sables d’Hérouval, Hérouval, Paris Basin, France (Cossmann, 1895; Zilch, 1959).

**F. MELAMPIDAE** Stimpson, 1851 (ELLOBIIDAE H. and A. Adams, 1855)  
**J. (KIM/TTH)–Rec.**  
Brackish/Semi-terr.

**First:** Mesauriculastra accelerata (White, 1886), Morrison Formation, Canyon City, Colorado, USA, M. morrisonensis and M. spiralis Yen, 1952, Morrison Formation, USA (Yen, 1952).  
**Extant**

**F. ZAPTYCHIIDAE** Zilch, 1959  
C. (l.)–K. (SEN)  
**FW**

**F. CARYCHIIDAE** Jeffreys, 1830  
**C. (BSH)–Rec.**  
Terr./Semi-aquatic/FW

**First:** Anthracopupa britannica Cox, 1926, Westphalian A, northern England and southern Scotland (Solem and Yochelson, 1979).  
**Extant**

**F. OTINIDAE** H. and A. Adams, 1855  
**J. (KIM/TTH)–Rec.**  
Mar./Semi-terr.

**First:** ?Limnopsis jurassica Yen, 1952, Morrison Formation, Wyoming, USA (Yen, 1952).  
**Extant**

**Comment:** This monotypic genus is based on a dubious internal mould and is unlikely to be connected to this family. There are no intervening occurrences.

**Order** BASOMMATOPHORA Keferstein, 1864

**Superfamily** SIPHONARIOIDEA Gray, 1840

**F. SIPHONARIOIDEA** Gray, 1840  
**J. (OXY)–Rec.**  
Littoral mar./Brackish

**First:** Berlieria ledonica de Loriol, Chatillon-sur-Ain, France (Zilch, 1959).  
**Extant**
Superfamily AMPHIBOLOIDEA H. and A. Adams, 1855

F. AMPHIBOLIDAE H. and A. Adams, 1855
T. (Olig.)—Rec. FW

First: Trimusculus sp. Oligocene, Europe (noted in Zilch, 1959).

Superfamily CHILINOIDEA H. and A. Adams, 1855

F. CHILINIDAE H. and A. Adams, 1855
T. (Pliocene)—Rec. FW


Superfamily LYMNAEOIDEA Rafinesque, 1815

F. LYMNAEIDAE Rafinesque, 1815
J. (KIM/TTH)—Rec. FW


Comment: Acroloxus radiatus Whiteaves, 1886 from the Paskapoo Formation of Alberta, Canada, was referred doubtfully to Ferrissia Walker, 1903 by Henderson (1935).

Superfamily COCHLICOPOIDEA Pilsbry, 1900

F. COCHLICOPIDAE Pilsbry, 1900

First: Azeca Fleming, 1828 is indicated from the Palaeocene of Europe and USA and Cochlicopa Risso, 1826 from Europe by Zilch (1959).

Superfamily PUPILLOIDEA Turton, 1831

The earliest record of the Pupilloidea (family uncertain) is Pupa bigsbei Dawson, 1880, Carboniferous (Westphalian B), Group XV, Cumberland Group, Joggins, Nova Scotia, Canada (Solem and Yochelson, 1979).

First: Gastrocopta? sp. (La Rocque, 1960), Flagstaff Formation, Utah, USA and Albertanella minuta Russell, 1931, Saunders Formation, McLeod River, Alberta, Canada and Flagstaff Formation, central Utah, USA (La Rocque, 1960).

F. VALLONIIDAE Pilsbry, 1900
T. (THA)—Rec. Terr.

First: Acanthinula dumasi (Boissier, 1848), Calcaire de Rilly, Rilly, France (Cossmann and Pissarro, 1913), and Agallospira
multispiralis and Shanghuspira costata Yú, 1977, Palaeocene, South China.

F. VERTIGINIDAE Stimpson, 1851 T. (YPR)–Rec. Terr.

First: Vertigo oviformis Michaud in Deshayes, 1863 and V. interferens (Deshayes, 1863), both Sparnacian, Grauves, France (Cossmann and Pissarro, 1913).

Extant


First: Ocula plateaui (Cossmann, 1889), Sables de Chalons, Chenay (Marne), France (Cossmann and Pissarro, 1913).

Extant

F. PLEURODISCIDAE Wenz, 1923 T. (?CHT/PLI)–Rec. Terr.

First: Pleurodiscus sp. Chattian, Europe (noted by Zilch, 1959).


Extant


Extant


First: Pyramidula Fitzinger, 1833 is indicated from the Eocene of Europe by Zilch (1959).

Extant


First: Abida Turton, 1831 is indicated from the Middle Eocene of Europe by Zilch (1959).

Extant

Superfamily BULIMINOIDEA Clessin, 1879


First: Dendropupa vestuta (Dawson, 1855), group VIII, Cumberland Group, Joggins, Nova Scotia. Canada, and D. grandaeva (Dawson, 1880), D. primaeva (Matthew, 1895), both Fern Ledges beds, Little River Group, St John, New Brunswick, Canada, all Westphalian B.

Extant

Comment: Solem and Yochelson (1979) gave reasons for including Dendropupa in this family, rather than the Cyclophoridae where they were formerly placed.


First: ?Procerastus dautzenbergi (Cossmann, 1907), Sparnacian, Grauves, France (Cossmann and Pissarro, 1913).

Next oldest: Cerastua sp. Lower Miocene. East Africa (noted by Zilch, 1959).

Extant

Comment: The genus Procerastus was included with some doubt in the Anadromidae by Nordsieck (1986).

Superfamily CLAUSILIOIDEA Mörch, 1864

F. CLAUSILIIDAE Mörch, 1864 K. (SAN)–Rec. Terr.

First: Dextrospira minutula Hrubesch, 1965a, Gosau Group, Glanegg near Salzburg, Austria.

Extant

Superfamily PARTULOIDEA Pilsby, 1900

F. PARTULIDAE Pilsby, 1900 Extant Terr.

Superfamily ORTHALICOIDEA Albers-Martens, 1860


Extant


First: ?Conobulimus fuggeri (Tausch) and ?Juavaiva juavensis (Tausch), both Turonian, Algen near Salzburg (Zilch, 1959).

Next oldest: Lychnus sanchezi (Vidal, 1874), Gosau Group, Glanegg near Salzburg, Austria (Hrubesch, 1965).

Last: Lychnus ellipticus Matheron, 1832, Les Baux (Bouches-du-Rhone), southern France, Anadromus proboseudes (Matheron), Peynier (Bouches-du-Rhone), southern France, and Vidalissi darzeri (Vidal), Danian, Selva, Mallorca, Spain (Zilch, 1959).

Extant


First: Hyperaulax americanus (Heilprin, 1887) s.s. (and nine other species/subspecies, Silex Beds, Ballast Point near Tampa, Florida, USA (Dall, 1915; Henderson, 1935).

Extant


First: Grangerella macleodensis (Russell, 1929), upper Saunders Formation, west side of McLeod River, Alberta, Canada (Henderson, 1935).

Extant

F. AMPHIBULIMIDAE Crosse and Fischer, 1873

Extant Terr.


First: Holospora cf. leidyi (Meek, 1872), Flagstaff Formation, central Utah, USA (La Rocque, 1960).

Extant


First: Eostrophia anodonta (Dall, 1890), Silex Beds, Ballast Point nr. Tampa, Florida, USA (Dall, 1915; Henderson, 1935).

Extant

F. MEGASPIRIDAE Pilsby, 1904


?First: Palaeostoa exarata (Michaud), Sables de Chalons, Chalons-sur-Vesle near Reims (Marne), France (Cossmann, 1889).

Extant

Comment: Nordsieck (1987) indicated a late Cretaceous origin for Palaeostoa Andreae, 1884 (removed to the Palaeostoidae H. Nordsieck, 1986) and a Turonian origin for Ptychicula Tausch, which is possibly cofamilial.

Extant

F. COELOCIIDAE H. Nordsieck, 1986

Extant Terr.

Superfamily ACHATINOIDEA Swainson, 1840
Animals: Invertebrates

![Table and Diagram]

Fig. 8.7

F. **FERUSSACIIDAE** Bourguignat, 1883  
T. (PRB)-Rec. Terr.  
**First:** *Coilostele* sp., Upper Eocene, southern Europe (noted by Zilch, 1959).

F. **SUBULINIDAE** Thiele, 1931  
K. (SAN)-Rec. Terr.  
**First:** *Cylindrellina permaxima* Hrubesch, 1965a, Gosau Group, Glanegg near Salzburg, Austria.

F. **ACHATINIDAE** Swainson, 1840  
Q. (PLE)-Rec. Terr.  
**First:** *Achatina (Lissachatina)* sp., PLE, tropical Africa (noted in Zilch, 1959).

F. **COELAXIDAE** Pilsbry, 1907  
**Extant** Terr.

F. **THYROPHORELLIDAE** Thiele, 1926  
**Extant** Terr.

**Superfamily** AILLYOIDEA Baker, 1930  
F. **AILLYIDAE** Baker, 1930  
**Extant** Terr.

**Superfamily** OLEACINOIDEA H. and A. Adams, 1855  
F. **SPIRAXIDAE** Baker, 1939  
**First:** *Spiraxis* sp. (Poinar and Roth, 1991), Upper Eocene/Upper Oligocene, Dominican Republic.
Next oldest: *Spiraxis tampae* Dall, 1915, Silex Beds, Ballast Point near Tampa, Florida, USA (Dall, 1915; Henderson, 1935). Extant

F. OLEACINIDAE H. and A. Adams, 1855 T. (THA)–Rec. Terr. Extant

First: *Palaeoglindana cordieri* (Deshayes, 1863), Thanetian, Crantam, France (Zilch, 1959).

F. TESTACEILLIDAE Gray, in Turton, 1840 T. (LUT)–Rec. Terr. Extant

First: *Parmacellina vitrinaeformis* Sandberger, 1872, Buchsweiler, Unter Elsass, Germany (Zilch, 1959).

Superfamily STREPTAXOIDEA Gray, 1860

F. STREPTAXIDAE Gray, 1806 K. (CON)–Rec. Terr. Extant

First: *Eoplicadomus austriaca* Hrubesch, 1965b, Gosau Group, Windisch Garsten, Austria.

Superfamily STROPHOCHEILOIDEA Thiele, 1926

F. STROPHOCHEILIDAE Thiele, 1926 T. (DANfTHA)–Rec. Terr. Extant

First: *Strophocheilus* Spix, 1827, Patagonia, Brazil (noted by Zilch, 1959).


First: *Dorcasia antiqua* Wenz, 1926, marly sandstone at Chalcedontafelberg, west of the old Lüderitz fields, Namibia (Connolly, 1939).


Superfamily RHYTIDOIDEA Pilsbry, 1895

F. RHYTIDIDAE Pilsbry, 1895 Q. (PLE)–Rec. Terr. Extant

First: *Hebeispira hebeiensis* Youlou, 1978, Lower Tertiary, Bohai, China. Extant

Next oldest: *Cookeconcha subpacificus* (Ladd, 1958), Lower Miocene, Bikini Atoll, Pacific Ocean (Solem, 1977).

F. PUNCTIDAE Morse, 1864 T. (CHT)–Rec. Terr. Extant

First: *Punctum* Morse, 1864, Lower Oligocene, Europe (noted by Zilch, 1959).


First: *Helicodiscus singleyanus* (Pilsbry, 1890), Rexroad Formation, XI Member, Seward County, south-west Kansas, USA (Taylor, 1960).

F. CHAROPIDAE Hutton, 1884 Q. (PLE)–Rec. Terr. Extant

First: The endemic subgenera of *Ptychodon*, *Helenoconcha* Pilsbry 1892 and *Pseudohelenoconcha* Germain, 1932 occur in the Pleistocene of St Helena (Zilch, 1959).

F. OTOCONCHIDAE Cockerell, 1893 K. (MAA)–Rec. Terr. Extant

First: *Oreohelix angulifera*, and *O. obtusata* (Whiteaves, 1885), both St Mary Cretaceous, Pincher Creek and Old Man River, Alberta, Canada (Henderson, 1935).

F. OOPELTIDAE Cockerell, 1891 Extant Terr. Extant

Superfamily SUCCINEOIDEA Beck, 1837

F. SUCCINEIDAE Beck, 1837 T. (THA)–Rec. Terr. Extant

First: *Succinea boissyi* (Deshayes, 1863), Calcarea de Rilly, Rilly, France.

Superfamily ATHORACOPHOROIDAE Fischer, 1883

F. ATHORACOPHORIDAE Fischer, 1883 Extant Terr. Extant

Shell reduced or absent. No fossil record.
Superfamily SAGDIDOIDEA Pilsbry, 1895
F. SAGDIDIDAE Pilsbry, 1895 Extant Terr.
Superfamily GASTRODONTOIDAE Tryon, 1866
F. GASTRODONTIDAE Tryon, 1866 K. (SAN/CMP)--Rec. Terr.
First: Ventridens lens (Gabb, 1864), Chico Formation, Texas Flat, Placer County, California, USA (Henderson, 1935).

Superfamily HELIXARIONOIDAE Godwin-Austen, 1888
F. EUCONULIDAE Baker, 1928
?K (SEN)/T. (Pal.)--Rec. Terr./Semi-aquatic
First: Euconulus Reinhardt, 1883 is indicated by Ziich (1959) from the Middle Palaeocene of Europe and doubtfully from the Upper Cretaceous.

Superfamily ARIOPHANTIDAE Godwin-Austen, 1888
Extant Terr.
F. TROCHOMORPHIDAE Moellendorff, 1890 Extant Terr.
F. UROCYCLIDAE Simroth, 1889 Q. (?PLE) --Rec. Terr.
First: Hamya revoili Bourguignat, 1885, occurs in Neogene deposits in Portugal and East Africa (Ziich, 1959).

Superfamily VITRINOIDEA Fitzinger, 1833
F. VITRINIDAE Fitzinger, 1833 T. (THA)--Rec. Terr.
First: Provitrina rillyensis (Boissy, 1848), Calcaire de Rilly, Rilly near Reims, France (Ziich, 1959).

Next oldest: Grandipatula (Grandipatula) hemisphaerica (Michaud), and G. (Sphaerozonites) oppenheimi (Pfeffer, 1929), both Calcaire de Rilly, Rilly, near Reims, France.

First: Daudebardia sp., Upper Miocene, Europe (noted by Ziich, 1959).
F. HYGROMIIDAE Tryon, 1866
T. (?BRT/CHT)—Rec. Terr.


Next oldest: Pseudoxerotrucha subconspurcata (Sandberger, 1873), and Hemirometonea quadrunvisiosa (O. Boettger, 1897), Upper Oligocene, Hochheim—Floßheim, Hessen (Zilch, 1959).


First: Loganiopharynx rana (Boissy, 1840), Sparnacian, Mont-de-Bernon near Epernay (Marne), France (Zilch, 1959) or Nanhaispersa eversilabia Yu and Zhang, 1982, Palaeocene or Eocene, Sanshui Basin, Guangdong, China.

Intervening: ?BRT, CHT-HOL.


First: Conulota diarti (Cossmann, 1907), Sparnacian, Grauves (Marne), France (Cossmann and Pissarro, 1913; Zilch, 1959).

Extant Terr.


First: Mesoglypterus sagensis Yen, 1952, Mill Creek, Wind River Mountains, Wyoming, USA.

Intervening: DAN—CHT.

F. XANTHONYCHIDAE Strebel and Pfeffer, 1880 Terr.

Superfamily ARIONOIDEA Gray, in Turton, 1840

F. PHILOMYCIDAEB Gray, 1847 Terr.


First: Craterarium pachyostracon Taylor, 1954, Barstow Formation, San Bernardino Co., California, USA and Geomalacus indifferens (O. Boettger, 1911?), Landschneckenmergel, Frankfurt am Main, Germany (Zilch, 1959).

REFERENCES

Omitted references to sources prior to 1941 can be found in Knight (1941) and Knight et al. (1960).


MOLLUSCA: CEPHALOPODA (NAUTILOIDEA)

A. H. King

The term Nautiloidea is used here in a broad sense, incorporating the subclasses Endoceratoidea, Actinoceratoidea, Orthoceratoidea and Nautiloidea as perceived by Teichert (1967). Classification at order level is relatively stable; taxonomic complications arise in recognizing the greater diversity of nautiloids in comparison with ammonoids and reconciling this within a classification at higher level (Holland, 1979, 1987). The scheme adopted below essentially follows Teichert and Moore (in Teichert et al., 1964) to order level, variations from this are noted in the text; the treatment of Cambrian orders follows Chen and Teichert (1983).

The enigmatic genera Salterella (=Volborthella) and Vologdinella have been regarded as taxa 'doubtfully classifiable' within the nautiloids and treated as a separate order Volborthellida (Teichert in Teichert et al., 1964). The present author follows Yochelson (1977, 1981), and assigns these genera to the extinct phylum Agmata.

No detailed cladistic analysis has been carried out on nautiloids; comments concerning the mono- or paraphyletic nature of some orders are mainly the author's own views.

Order PLECTRONOCERIDA Flower, 1964

(see Fig. 9.1)

F. PLECTRONOCERATIDAE Kobayashi, 1935

€. (DOL) Mar.

First: Plectronoceras cambria (Walcott, 1905), Ptychaspis–Tsinania Zone, lower Fengshan Formation, Shandong Province, China; P. liaoningense Kobayashi, 1935 from Liaodong Peninsula and P. huaibeiense Chen and Qi 1979, from Anhui Province, China, are coeval (Chen and Teichert, 1983).


F. BALKOCERATIDAE Flower, 1964

€. (DOL) Mar.

First and Last: Theskeloceras benxiense Chen and Teichert, 1983, T. subrectum Chen and Teichert, 1983, upper Fengshan Formation, Liaoiong Province, China; Balkoceras gracile Flower, 1964, San Saba Limestone, central Texas, USA (Chen and Teichert, 1983).

Order ELLESMEROCERIDA Flower, in Flower and Kummel, 1950

Suborder Ellesmerocerina Flower, 1964

F. ELLESMEROCERATIDAE Kobayashi, 1934

€. (DOL)–O. (CRD) Mar.

First: Eburnoceras pisinum Chen and Qi, 1980, upper Quadraticcephalus Zone, lower Fengshan Formation, Anhui Province, China (Chen and Teichert, 1983).


Intervening: TRE–LLO.

F. ACAROCERATIDAE Chen et al., 1979

€. (DOL) Mar.

First: Acaroceras primordium Chen and Qi, 1982, lower Quadraticcephalus Zone, lower Fengshan Formation, Hanjia, Suxian County, Anhui Province, China (Chen and Teichert, 1983).

Last: Weishanhuceras rarum Chen and Qi, 1979, numerous species assigned to Acaroceras (Chen and Teichert, 1983), upper Fengshan and Sinyangshan formations, Liaoiong, Shandong, Anhui, Shanxi, Zhejiang Provinces and Nei Monggol, China (Chen and Teichert, 1983).

F. HUAIHECERATIDAE Zou and Chen, 1979

€. (DOL) Mar.

First: Huaiheceras ?longicollum Zou and Chen, 1979, upper Quadraticcephalus Zone, lower Fengshan Formation, Suxian County, Anhui Province, China (Chen and Teichert, 1983).

Last: Huaihecerina elegans Chen and Teichert, 1983, Zhuibnanoceras conicum Chen and Qi, 1981, numerous species assigned to Huaiheceras, upper Fengshan and Sinyangshan formations, Liaoiong, Shandong, Anhui and Zhejiang Provinces, China (Chen and Teichert, 1983).
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<th>RHT</th>
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<th>26. Emmonosoceratidae</th>
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<td>INTEJOCERIDA</td>
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<td>50. Paraphragmatidae</td>
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**Fig. 9.1**

F. **XIAOSHANOCERATIDAE** Chen and Teichert, 1983 (DOL) Mar.

First and Last: Xiaoshanoceras jini Chen and Teichert, 1983, X. *subincarulare* Chen and Teichert, 1983, *Acaroceras* Zone, upper Siyangshan Formation, Xiaoshigai, Zhejiang Province, China (Chen and Teichert, 1983).


First: *Microbaltoceras minore* Flower, 1964, Tanyard Formation, Gillespie County, Texas, USA. This species is based on fragmentary material and may be referable to the Ellesmeroceratidae. The next oldest species is *Rioceras expansum* Flower, 1964, Cooks Formation, El Paso Group, Rhodes Canyon, New Mexico, USA (Flower, 1964a).

Last: *Protocycloceras deprati* Reed, 1917, *P. wongi* (Yū, 1930), Shihtzupu Formation, Hunan Province, China (Sheng, 1980).

Intervening: ARG–LLN.


First: *Microbaltoceras minore* Flower, 1964, Tanyard Formation, Gillespie County, Texas, USA. This species is based on fragmentary material and may be referable to the Ellesmeroceratidae. The next oldest species is *Rioceras expansum* Flower, 1964, Cooks Formation, El Paso Group, Rhodes Canyon, New Mexico, USA (Flower, 1964a).

Limestone, New York, USA, C. shideleri Flower, 1964, Carter's Limestone, Tennessee, USA (Flower, 1964a).

Intervening: ARG—LLO.

F. APOCRINOCERATIDAE Flower in Flower and Teichert, 1957 O. (ARG) Mar.

First: Apocrinoceras talbodi Teichert and Glenister, 1954, Emanuel Formation ('horizon 3'), Emanuel Creek, Kimberley Division, Western Australia (Teichert and Glenister, 1954).

Last: Glenisteroceras obscurum Flower in Flower and Teichert, 1957, Fort Cassin Formation, Champlain Valley, New York, USA (Flower, 1964a).


First: Cyclostomiceras cassinense (Whitfield, 1886), C. minimum (Whitfield, 1886), Fort Cassin Formation, Champlain Valley, New York, USA (Flower, 1964a).

Last: Pictetoceras euchalidi (De Verneuil, 1845), Kundan Stage (Aluojan Substage), Ural Mountains and Estonia, former USSR (Mutvei and Stumbur, 1971).


First and Last: Shideleroceras sinuatum Flower, 1946, S. simplex Flower, 1946, lower Whitewater Formation, Cincinnati; S. gracile Flower, 1946, Saluda Formation, Cincinnati, USA, all Richmondian (Flower, 1964a).

Suborder Cyrtocerinina Flower, 1964


First: Eothinoceras americanum Ulrich, F. A. Forster, Miller and Unklesbay, 1944, Rochdale Limestone, New York, USA; E. mutilandicum Teichert and Glenister, 1954, Emanuel Formation, Emanuel Creek, Kimberley Division, Western Australia; E. marchense Balashov, 1960, Chunjiskiy Stage, Siberian Platform, former USSR (Flower, 1964a).


Intervening: LLN.


First: Cyrtocerina sp. Flower, 1952, Lowville Formation, Ottawa, Canada (Flower, 1952a).

Last: Cyrtocerina madisonensis (Miller, 1894), C. patella Flower, 1943, C. modesta Flower, 1943, upper Whitewater Formation, Madison, Indiana, USA; C. ? carinifera Flower, 1946, Saluda Formation, Oxford, Ohio, USA (Flower, 1964a).

Order PROTACTINOCERIDA Chen and Qi, 1979

F. PROTACTINOCERATIDAE Chen and Qi, 1979 C. (DOL) Mar.

First: Piloceras and Biscoeceras (B. corniforme Flower, 1964, Biscoeceras spp. Flower, 1964), Victario Hills Formation (first piloceroid zone), El Paso Group, New Mexico, USA (Flower, 1964a, 1964b); also Piloceras tuvense Balashov, 1968 and Allolopiceras sevierense Ulrich et al. 1943, Maly Karatau Mountains, Kazakhstan, former USSR (Balashov, 1968).

Last: Cассinoceras explanator (Whitfield, 1886), Fort Cassin Formation, Vermont, USA, and St George Group, western Newfoundland (Ulrich and Forste, 1936; Flower, 1978). Other species assigned to Cассinoceras, Piloceras and Allolopiceras are known from western Newfoundland, north-western Australia and northern China (Teichert and Glenister, 1954; Flower, 1978; Sheng, 1980); these are all
of approximate Cassinian age but cannot be separated stratigraphically.


First: Stumbur (1962) reported Endoceras from the basal Arenig Leetse Stage, but provided no illustration or description. Dideroceras leetsense Balashov, 1968, Leztskiy Beds, Estonia, former USSR; is poorly known and Allocotoceras insigne Teichert and Glenister, 1953; upper Canadian, Admasfield, Tasmania, is known only from isolated endosiphuncules (Balashov, 1968; Teichert and Glenister, 1953). The earliest undoubted endoceratid is Dideroceras glauconiticum (Heinrichson, 1935), 'Dikari Beds', lower Volkhovian Stage, Tiskre, Estonia, former USSR (Heinrichson, 1935).

Last: Rossioceras priguense Balashov, 1968, Pirgu Stage, Estonia, former USSR; Foerstellites tiberi (Foerste, 1930), Saluda Formation, Indiana, USA (Kobayashi, 1940; Balashov, 1968).

Intervening: LLN–CRD.


First: Cyrtendoceras carnegiei Teichert and Glenister, 1954, Emanuel Formation, Emanuel Creek, Kimberley Division, Western Australia (Teichert and Glenister, 1954).

Last: Cyrtendoceras hircus (Holm, 1892), Folkeslunda Formation, Lasnamaegian Stage, Oland, Sweden; C. schmidtii (Holm, 1892), Echinophaerites Limestone, Lasnamaegian/Uhakuan Stage, Estonia, former USSR (Holm, 1892); also Cyrtendoceras n. sp. Sweet, 1958, Cephalopod Shale, Nes-Hamar District, Norway (Sweet, 1958).

Intervening: LLN.


First and Last: Chihiloceras nathani Grabau, 1922, C. chinghuautaoense Grabau, 1922, Peiltintze Limestone (=Hunghuayuan Formation), Hubei Province, China (Grabau, 1922).


Genera assigned to the Coreanoceratidae (Chen, 1976; Lai and Xu, 1987) are typically based on incomplete, often recrystallized endosiphuncules. The taxonomic importance of endosiphuncular structures is currently being reassessed (MS in preparation). Consequently, Coreanoceras and allied forms are here provisionally included within the Manchuroceratidae pending further study.

First: Coreanoceroides variabilis Qi, 1980, Chaohuceras contractum Qi, 1980, and numerous species assigned to Manchuroceras and Coreanoceras from the lower Arenig of East Asia (including North China, Nei Monggol, Korea, southern Thailand), Tasmania and Texas, USA (Chen, 1976; Zou, 1981; Stait and Burret, 1984).

concluded that Intejoceras and Bajkaloceras were not related to the endocerids but may be derived from the Baltoceratidae (Ellesmerocerida). Flower (1976b) and Gil (1988) placed Padunoceras, Evenoceras and Rossoceras in the Padunoceratidae and retained them in the Endocerida. Zhuravleva (1978) described the Bajkaloceratidae as comprising the Chunskiy Stage, Angara River Basin, Siberian Platform, former USSR (Balashov, 1960).

The last two families are recognized here as belonging in the Orthocerida and the taxonomic scheme used below follows Balashov (1968) and Crick (1988).


Order ACTINOCERIDA Teichert, 1933
First: Ordosoceras contractum Chen, 1976, lower Chatsun Formation (Zone 3), Mt. Jolmolungma, Himalayas (Sheng, 1980). Several other species assigned to Ordosoceras and Polydesmia occur in Arenig-aged limestones (Santaokan, Chuatyzhan, Pelanchuang, lower Machiakou formations) in Nei Monggol, Hebei and Shandong Provinces, China (Chen and Liu, 1976, Stait and Burrett, 1984), Tha Manao Formation, Kanchanaburi Province, Thailand and G. kongurensis Chen and Wang, 1983, Kuweixi Formation, Mount Kongur, Xinjiang Province, China are approximately coeval (Chen and Wang, 1983; Stait and Burrett, 1984).

First: Ormoceras sp., Santaokan Formation, Nei Monggol, China (Chen, 1976).


First: Armenoceras cf. tani (Grabau, 1922), Chuotzhezhan Limestone, Nei Monggol, China (Sheng, 1980).

First: Hoeloceras yimengshanense Chen and Liu, 1976, Chuotzhezhan Limestone, Shandong Province, China (Chen and Liu, 1976).

First: Wutinoceras sp., Santaoaka Formation, Nei Monggol, China (Sheng, 1980).

First: Metactinoceras boreale Balashov, 1962, Actinoceras sp. nov., Machiakou Limestone (middle beds), Shandong Province, China (Chen, 1976).

First: Georgina duquieri Wade, 1977, upper Nora Formation, Georgina Basin, Australia (Wade, 1977); Georgina sp. (Stait and Burrett, 1984), Tha Manao Formation, Kanchanaburi Province, Thailand and G. kongurensis Chen and Wang, 1983, Kuweixi Formation, Mount Kongur, Xinjiang Province, China are approximately coeval (Chen and Wang, 1983; Stait and Burrett, 1984).

First: Armenoceras cf. tani (Grabau, 1922), Chuotzhezhan Limestone, Nei Monggol, China (Sheng, 1980).

First: Armenoceras pseuidoimbricatum (Barrande, 1874), A. kiaeri Teichert 1934, Hemse Group, Gotland, Sweden (Mutvei, 1964).

First: Hoeloceras yimengshanense Chen and Liu, 1976, Chuotzhezhan Limestone, Shandong Province, China (Chen and Liu, 1976).

First: Wutinoceras sp., Santaoaka Formation, Nei Monggol, China (Sheng, 1980).

First: Armenoceras cf. tani (Grabau, 1922), Chuotzhezhan Limestone, Nei Monggol, China (Sheng, 1980).

First: Armenoceras pseuidoimbricatum (Barrande, 1874), A. kiaeri Teichert 1934, Hemse Group, Gotland, Sweden (Mutvei, 1964).

First: Armenoceras cf. tani (Grabau, 1922), Chuotzhezhan Limestone, Nei Monggol, China (Sheng, 1980).

First: Armenoceras pseuidoimbricatum (Barrande, 1874), A. kiaeri Teichert 1934, Hemse Group, Gotland, Sweden (Mutvei, 1964).
F. HURONIIDAE Foerste and Teichert, 1930

**First:** *Discoactinoceras wuyangshanense* Chen and Liu, 1976, *D. platyventrum* Chen and Liu, 1976, Machiakou Limestone, Shandong Province, China (Chen and Liu, 1976); *D. multiplexum* Kobayashi, 1927, Middle Ordovician, southern Manchuria, is approximately coeval (Kobayashi, 1927); *Climacoceras wuyangshanense* Chen, 1976, Machiakou Limestone, Shandong Province, China, is based on an isolated siphuncle barely referable to the Huroniidae (Chen, 1976).

**Last:** *Huronia bigskyi* Stokes, 1824; *H. paulodiata* Foerste, 1925; *Huroniella inflecta* (Parks, 1915), Niagaran, Michigan, USA; *Huronia vertebralis* Stokes, 1824, Middle Silurian, Drummond Island, Lake Huron, Canada (Foerste, 1925; Shimer and Shrock, 1944). These taxa cannot be separated stratigraphically until revised.

**Intervening:** ASH–LLY.

F. CARBACTINOCERATIDAE Schindewolf, 1943

**First:** *Carbactinoceras torleyi* Schindewolf, 1943, Viséan, Germany (Schindewolf, 1943).

**Last:** *Raymoceras solidiforme* Croneis, 1926, *R. fayetevillensis* Croneis, 1926, *R. bassleri* Foerste and Teichert, 1930, *R. girtyi* Foerste and Teichert, 1930, Fayetteville Formation (and equivalents), Mississippian, of Oklahoma, Arkansas and California, USA (Gordon, 1964); *Raymoceras* is also recorded from the Namurian (E zone) of Scotland (Turner, 1951) and the Moscow Basin, former USSR (Shimanskiy, 1961).

**Order** ORTHOCERIDA Kuhn, 1940

Derived from the Balcoceratidae (Ellesmerocerida) during Arenig (Cassinian) times. Hook and Flower (1976, 1977) regarded the Orthocerida (=Michelinoceratida of Flower, in Flower and Kummel, 1950) as diphyletic; baltoceratids with 'siphonal rods' giving rise to the Troedssonellidae and vacuosiphonate baltoceratids leading to the Michelinoceratidae (sensu Hook and Flower). Many of these early orthocerids are based solely on thin sections of fragmentary conchs.

**Superfamily** ORTHOCERATACEAE M'Coy, 1844

**F. ORTHOCERATIDAE M'Coy, 1844**

O. (ARG)–Tr. (NOR) Mar.

**First:** *Michelinoceras primum* Flower, 1962, Scenic Drive Formation, El Paso, Texas, USA (Flower, 1962b). Several other orthocerids (*Michelinoceras floridanae* Hook and Flower, 1977, *M. melleni* Hook and Flower, 1977, *M. spp*. Hook and Flower, 1977, *Wardoceras orygoformae* Hook and Flower, 1977) have been recorded from the lower Arenig Florida Mountains Formation and Wahwah Formation of Texas and western Utah, USA (Hook and Flower, 1977); all these forms possess relatively broad siphuncles with extensive siphonal deposits. Such features are not known in *Michelinoceras sensu stricto* (Ristedt, 1968; Serpagli and Gnoli, 1977) and assignment to this genus is suspect. Further study may ultimately separate these early American taxa into a new family which probably includes Baltic Volkovian forms described under 'Orthoceras' *nilsoni* (Boll, 1857) and 'O.: *wahlenbergii* (Boll, 1857) by Dzik (1984).

**Last:** *'Orthoceras' spp.*, 'Zone of Trachyceras archaelus', Italian Alps (Mojisivos, 1882), Halorites Limestone, Himalayan Mountains (Mojisivos, 1899) and 'Karnisch-Norishe Trias' (Bulow, 1915).

**Intervening:** LLN–LUD, D. (m.), C. (l.), P.

F. TROEDSSONELLIDAE Kobayashi, 1935

**First:** *Tajacoceras werdae* Hook and Flower, 1976, Wahwah Formation, Ibex area, Utah, USA (Hook and Flower, 1976).

**Last:** *Troedssonella endoceroides* (Troedsson, 1932), Folkeslunda Limestone Formation, Öland, Sweden (Troedsson, 1932); *T. huansen* Lai and Tsi, 1977, and *T. cf. endoceroides* (Troedsson, 1932), Shihtzupu Formation, Hunan Province, China are approximately coeval (Lai and Tsi, 1977).

**F. SACTORTHOCERATIDAE Flower, 1946**

**First:** *Sactorthoceras spp. nov.* (Chen, 1976), upper Namurian (Machiakou Limestone), Shandong Province, China. According to Chen (1976) this occurrence is of late Arenig (*Didymograptus hirundo* Biozone) age. However, associated cephalopods (including *Dideroceus wenneansen* Chen and Liu, 1976, *Discoactinoceras wuyangshanense* Chen and Liu, 1976, *Stolbovoceras boreale* Balashov, 1962), support an early Llanvirn age (Chen, 1976; Chen and Liu, 1976; Sheng, 1980).

**Last:** *Centroonoceras josephianum* (Foerste, 1932), Lourdes Formation, Port au Port Peninsula, western Newfoundland (Stait, 1988).

**Intervening:** LLO.

F. GEISONOCERATIDAE Zhuravleva, 1959

**First:** *Geisonoceras sp.*, erratic boulder of Volkovian age, Rozewie, Poland (Dzik, 1984).

**Last:** *Striacoceras typum* (Saemann, 1854), Cherry Valley Limestone, New York, USA (Flower, 1936); *Temperoceras caucassium* Zhuravleva, 1978, Zhivetskii Stage, Nakhichevan, Armenia, former USSR (Zhuravleva, 1978).

**Intervening:** LLV–EIF.

F. CLINOCERATIDAE Flower, 1946

**First:** *Clinoceras maskei* (Dewitz, 1879), 'Red Orthoceras Limestone of Bii–Ci Stufe' (Kundan–Asieran stages), erratic boulder, DDR (Neben and Krueger, 1971).

**Last:** *Whiteavesites winnipegense* (Whiteaves, 1892), Red River Formation, southern Manitoba, Canada (Foerste, 1929).

**Intervening:** LLO–CRD.

F. DAWSONOCERATIDAE Flower, 1962
S. (LLY?–WEN)–D. (l./m.?–? Mar.

**First:** *Dawsonoceras tenuilinetum* Savage, 1927, Lower Silurian of North America is poorly known (Flower, 1962b); several species of *Dawsonoceras* (including the type *D. annulatum* Sowerby, 1818) are recorded from the Middle Silurian of North America, Europe and Gotland (Flower, 1962b).

**Last:** *Dawsonoceras americanum* Foord, 1888, Lower Devonian, Michigan, USA and Ontario, Canada (Shimer and Shrock, 1944). Arazdajanes mamedovi Zhuravleva, 1978, Middle Devonian, Mt. Arazdayai, former USSR, is
represented only by a small conch fragment which may belong in the Geisonoceratidae (Zhuravleva, 1978).

Intervening: LUD.

F. SPHOOCERATIDAE Flower, 1962

First and Last: Sphooceras truncatum (Barrande, 1868), Middle Silurian, Czechoslovakia (Barrande, 1868). Sphooceras ? sp., Lower Devonian, south-western Sardinia (Gnoli, 1982) is based on an incomplete conch in which the decollation features are imperfectly known, and therefore its generic assignment is tentative. No other records are known.

F. OFFLEYOCERATIDAE Flower, 1962

Flower (1962b) erected the Offleyoceratidae for orthocerids with relatively large siphuncles and holochoanitic septal necks. The present author follows Zhuravleva (1978) in regarding the Folioceratidae as synonymous.

First: Offleyoceras arcticum (Foord, 1888), Middle Silurian (Wenlock?), Kennedy Channel, north-west Greenland (Flower, 1962b).

Intervening: GED.


First: Several species assigned to Paraphragmites, Calocystoceras, Gasparcryctoceras and Lyecoceras, Middle Silurian of Canada, Sweden and Czechoslovakia (Barrande, 1866; Flower, 1943a; Mutvei, 1957).


F. LAMELLORTHOCERATIDAE Teichert, 1961 D. (SIG–EIF) Mar. (see Fig. 9.2)


Last: Lamellorthoceras vermicularis Termier and Termier, 1950, Morocco; Arthrophyllum crassus Roemer, 1843, Harz Mountains, Germany; Gorgonoceras vusliman Zhuravleva, 1961, Sverdlovsk District, former USSR; Coralloceras coralliforme Le Maitre, 1950, North Africa (Zhuravleva, 1978).

Intervening: EMS.


Zhuravleva (1978) distinguished this family from the Offleyoceratidae by the former's shorter septal necks. However, both families contain forms with similar 'septal' deposits and future work may ultimately synonymize all these Middle Silurian–Lower Devonian taxa within the Offleyoceratidae.

First: Jangziceras yinkiangense Lai, 1964, Middle Silurian, Tsingki, Guizhou Province, China (Lai, 1964); Neo­sichuanoceras columnum Chen and Liu, 1974, and numerous species assigned to Sichuanoceras are recorded from the Middle Silurian of Shaanxi, Gansu and Ningxia Provinces, China (Chen and Liu, 1974; Lai, 1982).


Intervening: ASH.

F. BRACHYCYCLOCERATIDAE Furnish et al., 1964 D. (EIF)–P. Mar.


Last: Brachycyclcoceras, Permian, Western Australia (Teichert and Glenister, 1952).

Intervening: SPK–MOS/KAS.

Superfamily PSEUDORTHOCERATACEAE Flower and Caster, 1935


First: Gangshanoceras jurongense Zou, 1988, G. densum Zou, 1988, Dawan Formation, Jurong, Jiangsu Province, China (Zou, 1988).

Last: Cyrtacticoceras rebelle (Barrande, 1866), 'Stage e2', Bubovitz, Czechoslovakia (Barrande, 1866).

Intervening: LLO-ASH.


First: Stereoplasmoceras, lower Machiakou Limestone (Didymograptus hirundo Biozone), Hebei Province, China (Sheng, 1980).

Last: Ningkiangoceras centrale Lai, 1965, Lopjing Formation, Ningkiang, Shaanxi Province, China (Lai, 1965). The siphonal deposits are of uncertain structure in this Middle Silurian species which may equally well be referable to the Pseudorthoceratidae or Proteoceratidae. The youngest taxon assignable to the Stereoplasmoceratidae is Badouceras pyriforme Chen and Liu, 1976, Badou Formation, Shandong Province, China (Chen and Liu, 1976).

Intervening: LLO.


First: Paradnatoceras modestum Chen, 1987, Xainza, northern Xizang Province, China (Chen, 1987).


Intervening: LLO–C. (u.).


Last: Mysterioceras shengi Lai, 1965, Nancheng Shale Formation, Liangshan, Shensi Province, China (Lai, 1965). Siphonal deposits are poorly known in this species and assignment to Mysterioceras is uncertain. The next youngest record is M. australi Teichert and Glenister, 1953, Gordon Group (Cashion's Creek Limestone and equivalents) of Tasmania (Stait and Flower, 1985).

Order ASCOCERIDA Kuhn, 1949

An apparently monophyletic group of nautiloids which exhibit truncation of conch with septal and apertural modification at maturity; derived from the Orthocerida (Clnoceridae) (Flower, 1976c).


Last: Ecdyoceras foerstei Flower, 1962, Arnhem Beds, Labanon, Kentucky, USA (Flower 1962a).
F. ASCOCERATIDAE Kuhn, 1949

First: Redpathoceras clarki Flower, 1963, Leray Limestone, Québec Ridge, Quebec, Canada (Flower, 1963).
Last: Asoceras cf. gradatum Lindström, 1890, Sundre Limestone Formation, Gotland, Sweden (Lindström 1890); Asoceras, Aphragmites and Glossoceras are all recorded from ‘Stage e2’ (Budňanian), Czechoslovakia (Barrande, 1865).

Intervening: ASH, WEN.

First and Last: Unklesbay and Young, 1956, stone', Frogm'lya, Oslo area, Norway (Strand, 1934; Frey, 1982).

Order TARPHYCERIDA Flower, in Flower and Kummel, 1950

Probably a monophyletic order, derived from the Ellesmerocerida via basslerocerid-like forms (Teichert, 1967; Flower, 1976c). The Bassleroceridae retain connecting rings of ellesmerocerid type but lack siphonal diaphragms. Following Flower (1976c), the family is assigned to the Tarphycerida.

F. BASSLEROERIDAE Ulrich et al., 1944

First: Anguloceras ovatum Unklesby and Young, 1956, A. depressum Unklesby and Young, 1956, A. rotundum Unklesby and Young, 1956, Bassleroceras cf. bridgei Ulrich, Foerste, Miller, and Unklesby, 1944, Chepultepec–Stonehenge, Strasburg, Virginia, USA (Unklesby and Young, 1956).
Last: Bassleroceras xintaiense Chen, 1976, Machiakou Limestone, Shandong Province, China (Chen, 1976).

Intervening: ARG.

F. TARPHERCYTIDAE Hyatt, 1894
O. (TRE–ARG2/LLN1, LLO?, ASH?) Mar.

First: Campbelloceras, Victorio Hills Formation (first piloceroid zone), El Paso Group, New Mexico, USA (Flower, 1964a).
Last: Tarphyceras ? morkokense Baalashov, 1962, T ? excentricum Balashov, 1962, Upper Ordovician, Morkoka River, Siberian Platform, former USSR (Baalashov, 1962); Flower (1984) regarded these generic assignments as questionable. He previously (1976c) reported a new undescribed genus from the Chazyan of New York. The youngest undoubted member of the family is Centrotarphyceras sp., Neišiaashanian portion of Shuichuan Formation, Ningxia Province, China (Lai, 1982).

Intervening: ARG.

F. ESTONIACERATIDAE Hyatt in Zittel, 1900

First: Aphtoceras, Victorio Hills Formation (first piloceroid zone), El Paso Group, New Mexico, USA (Flower, 1964a).

Intervening: ARG.

F. TROCHOLITIDAE Chapman, 1857

First: Trocholitoceras walcotti Hyatt, 1894, Beekmanoceras priscum Ruedemann, 1906, Curtoceras euloni (Whitfield, 1886), C. cassinem (Whitfield, 1886), C. internastratum (Whitfield, 1886), Fort Cassin Formation (and equivalents), New York and Vermont, USA (Ruedemann, 1906); several species assigned to Hardmanoceras, Western Australia and East Asia, are approximately coeval (Stait and Burrett, 1984).

Last: Graftonoceras graffonense (Meek and Worthen, 1870), Niagaran Series, Ohio, USA (Foerste, 1925).

Intervening: LLN–ASH.

F. LITUITIDAE Phillips, 1848

Considerable morphological evidence (including form of cameral deposits and ‘muscle scars’) suggests that this family may belong in the Orthocerida. The family is conventionally retained within the Tarphycerida here, pending results from the present author’s revision of Baltoscandian liuittids (MS in preparation).

First: Rhynochoceras aff. becichry (Remelé, 1880), erratic boulder, Volkovian Stage, Opatów, Poland (Dzik, 1984); Pseudanistroceras hubeiense Lai and Xu, 1987, middle Dawan Formation, Hubei Province, China, is approximately coeval (Lai and Xu, 1987).
Last: Tyrioceras warburgae Frey, 1982, Boda Formation, Dalarna, Sweden; T. kjerulfi Strand, 1934, Trinucleus limestone’, Frogneyal, Oslo area, Norway (Strand, 1934; Frey, 1982).

Intervening: LLN–CRD.

F. OPHIDIOERIDAE Hyatt, 1894

First: Ophioceras simplex Barrande, 1865, O. rudens Barrande, 1865, Wenlock, Czechoslovakia (Barrande, 1865); O. reticulatum Angelin (in Angelin and Lindström, 1880), Gotland, Sweden (Angelin and Lindström, 1880).
Last: Ophiceras rute Lindström, 1890, Ludlow, Gotland, Sweden (Lindström, 1890).

Order BARRANEODETERIDAE Flower, in Flower and Kummel, 1950

Originally separated from the Tarphycerida on the basis of their thin, homogeneous connecting rings. Flower (1984) briefly presented new evidence indicating that the Barrandeocerida was polyphyletic and suggested the order should be abolished and forms previously assigned to it be included within the Tarphycerida. The Barrandeocerida is temporarily retained here pending further study.

F. PLECTOCERIDAE Hyatt in Zittel, 1900

First: Plectoceras jason (Billings, 1859), Avilionella multicornatum (Ruedemann, 1906); Chazy Limestone, Champlain Valley, New York, USA and Canada (Ruedemann, 1906; Flower, 1984).
Last: Lauroceras cumingesi Flower, 1943, Laurel Limestone Formation, Indiana, USA (Flower, 1943b).

Intervening: CRD.

F. BARRANEODETERIDAE Foerste, 1925

First: Barrandeoceras natator (Billings, 1859), Chazy Limestone, Champlain Valley, New York, USA, Ontario and Quebec, Canada (Ruedemann, 1906; Flower, 1984).
F. APSIDOCERATIDAE Haytt, 1884

First: Apsidoceras montrealense Flower, 1943, upper Trenton Limestone, Isle Jesus, Quebec, Canada; Fremontoceras jewettii Flower, 1947, Sherman Falls Limestone, New York, USA (Flower, 1943c, 1947).


F. URANOCERATIDAE Haytt, in Zittel, 1900

First and Last: Records of Uranoceras from the Upper Ordovician (Ashgill) of Sweden (Sweet in Teichert et al., 1964) are probably referable to Charactoceras of the Apsidoceratidae (Frey, 1982). Undoubted members of the Uranoceratidae are species assigned to Uranoceras, Cumingsoceras and Jolietoceras from the Middle Silurian of Europe and the USA (Foerste, 1925); without further revision these cannot be separated stratigraphically.


First: Lechrithrochoceras desplainense Hall, 1868, Racine Member, Wisconsin, USA; L. placidum (Barrande, 1865), Butovitz, Czechoslovakia; Trochidictyoceras slocomi Foerste, 1926, Racine Member, Stony Island, Illinois, USA: Leurotrochoceras aeneus (Hall, 1868), Racine Member, Iowa, USA (Foerste, 1926).

Last: Catyrephoceras giganteum (Blake, 1882), early Ludlow, Leintwardine, UK; Peismoceras optatum (Barrande, 1865) and Systrophiceras arietinum (Barrande, 1865), 'Stage e' at Lochkov and Kozorz, Czechoslovakia respectively, may be coeval or slightly younger (Foerste, 1926).

F. NEPHRITICERATIDAE Hyatt, 1894

First: Sphyradoceras cloi (Hall, 1861), Schoharie Formation, New York, USA (Zhravleva, 1974).

Last: Baeopleuroceras incipiens Williams, in Cooper and Williams, 1935, Tully Limestone, New York, USA; Triplooceras is also reported from the Tully Limestone of New York (Flower, 1945).

Order ONCOCERIDA Flower, in Flower and Kummel, 1950

The Oncocerida were thought to have developed from bassleroceratid-like forms via the Graciloceratidae (Flower, 1976c). The discovery of older oncocerids (Phthanoncoceratidae) from Sweden and Spitsbergen (Evans and King, 1990) indicates the order may have arisen from at least two independent elasmoserid lineages and is therefore polyphyletic.


This family possesses primary siphonal diaphragms and thickened connecting rings typical of the Elasmoseroida, but exhibits an exogastric curvature and narrow siphuncle characteristic of the Oncocerida. Evans and King (1990) regarded conch form (combined with stratigraphical arguments) as sufficient evidence for assignment of the Phthanoncoceratidae to the Oncocerida.


First: Leonardoceras parvum Flower, 1968, Antelope Valley Limestone Formation, Nevada, USA (Flower, 1968b).

Last: Ringoceras praecurum Strand, 1934, Lyckholm-Stufe, Norway (Strand, 1934).

Intervening: LLN–CRD.


Last: Kindleoceras reversatum Foerste, 1924, Manitoulinoceras lyssander (Billings, 1865), Ontario, Canada (Foerste, 1924); Augustoceras? molense Stait, 1982, Den Member, Chudleigh Limestone, northern Tasmania (Stait, 1982).

Intervening: LLO–CRD.


First: Oonoceras sp. and undescribed oncoceratids, mid–Kundan Stage, Öland, Sweden (Dzik, 1984); Richardsononoceras tangaense Lai and Xu, 1987, upper Dawan Formation, Hubei Province, China, is approximately equivalent. Flower (1976c) reported undescribed Whiterockian oncoceratids from Newfoundland and Spitsbergen.

Last: Oocerina lentigradium (Barrande, 1866), 'Stage e', Lochkov, Czechoslovakia; O. stygiale (Barrande, 1877), 'Stage e', Dvoretz, Czechoslovakia; O. stragulatum (Barrande, 1877), 'Stage e2', Dvoretz, Czechoslovakia (Foerste, 1926); Paroocerina podolskensis Zhravleva, 1961, Upper Silurian, Podolia, former USSR (Zhravleva, 1961).

Intervening: LLO–WEN.


Some taxa placed within this family exhibit extensive cameral deposits of a type usually associated with the Orthocerida (Flower, 1962b).


Last: Tripteroceras xiphias (Billings, 1857), Richmondian, Anticosti Island, Canada (Foerste, 1926).
Mollusca: Cephalopoda (Nautiloidea)

F. DIESTOCERATIDAE Foerste, 1926
O. (LLN/LLO ?, CRD-ASH)

First: Xainzanoceras xainzaense Chen, 1987, Xunmei Formation, northern Xizang province, China (Chen, 1987).

Chen questioned the familial assignment of this taxon, whose conch form alone indicates placement elsewhere. Earliest undoubted representatives of the Diestoceratidae are Diestoceras latavalense Flower, 1952, D. sinclairi Flower, 1952, Terrebonne Formation, Quebec, Canada; D. sycon Flower, 1952, Black River Limestone, Poland, New York and Danoceras inutilis Flower, 1952, Gull River Formation, Ontario, Canada (Flower, 1952a).

Last: Diestoceras indiense (Miller and Faber, 1894), lower Whitewater Formation, Oxford, Ohio and Saluda Formation, Versailles, Indiana, USA; D. scalaris Foerste, 1921, Richmond Formation, Anticosti Island, Canada (Foerste, 1926), Lyckholmoceras estoniae Teichert, 1930, Lyckholm-Stufe, Estonia and L. graciliforme Lai, 1982, Peikouoshan Formation, Shaanxi Province, China, are approximately coeval (Teichert, 1930; Lai, 1982).

F. GUANGYUANOCERATIDAE Lai and Zhu, 1985
S. (LLY) Mar.


F. CYRTOCERATIDAE Chapman, 1857

First: Blakeoceras llandovery (Blake, 1882), lower Llandovery, Craig-yr-Wyddon, Wales, UK (Foerste, 1926).

Last: Cyrtochonetes depressus (Bronn, 1835), C. lineatus (D’Archaic and De Verneuil, 1842), C. alatus (Holzapfel, 1886), Middel Devonian, Germany (Zhuravleva, 1974).

Intervening: LVD, EIF.

F. KAROCERATIDAE Teichert, 1939

First: Osbornoceras swinnertoni Foerste, 1936, lower Silurian, Ohio, USA (Foerste, 1936).

Last: Geitonoceras lucidum Zhuravleva, 1974, Aktyubinsk Region, Kirgizya Steppe, Kazakhstan, former USSR (Zhuravleva, 1974).


F. TRIPLEUROCERATIDAE Foerste, 1926

First: Tripleuroceras robsoni Whiteaves, 1906, Niagaran, Stonewall, Manitoba, Canada (Foerste, 1926).

Last: Psiaoceras hesperis (Eichwald, 1860), Viséan, Kalouga, former USSR (Shimanskiy, 1957).

Intervening: EMS-GIV.

F. JOVELLANIIDAE Foord, 1888


F. HEMIPHRAGMOCERATIDAE Foerste, 1926

First and Last: Numerous species assigned to Hemiphragmoceras, Conadocerad, Tetraromeroceras and Hexameroceras, Viscocilka, Hinter-Kopanina, Dvoretz, Lockchov, Czechoslovakia (Barrande, 1867).


First: Numerous species assigned to Amphicyrtoceras, Anomelioceras, Aulococeras, Byronoceras, Chadwickoceras, Crateroceras, Eocyrtoceras, Euryziceratoceras, Galtoceras, Herco­cyrtoceras, Perioidanoceras, Rhomboceras, Slocomoceras, Streptoceras, and Worthoceras, Middle Silurian, Illinois, Ohio, New York, USA and Ontario, Quebec, Canada (Foerste, 1924, 1930, 1934).

Last: Acleistoceras olla (Saemann, 1854), A. eximium (Hall, 1888), A. mitra (Hall, 1888), Middle Devonian, Columbus, Ohio, USA (Foerste, 1926), Paracleistoceras devonianum (Barrande, 1865), Poteriocerina lumborum (Barrande, 1877), Gonatocyrtoceras hetero­lytum (Barrande, 1866), G. postscripti (Barrande, 1866), ‘Stage g3’, Middle Devonian, Hlucesoep, Czechoslovakia (Barrande, 1865-77).

F. TRIMEROCERATIDAE Hyatt, in Zittel, 1900 S. (WEN-LUD) Mar.

First and Last: Several species assigned to Trimeroceras, Clathroceras, Eotrikerceras, Inversoceras, Pentameroceras and Stenogomphoceras, Middle Silurian of Europe (Sweden, Czechoslovakia), North America and Canada (Barrande, 1865; Foerste, 1928, 1930).


First: Danaoceras danai (Barrande, 1866), D. insociale (Barrande, 1866), ‘Stage e’, Kozor, Czechoslovakia (Foerste, 1926).

Last: Cyclopites cuclops (Venyukov, 1886), Elnanoceras eulamensis (Nalivkin, 1947), Siberian Platform, former USSR (Zhuravleva, 1972); Codoceras indomitum (Barrande, 1866), ‘Stage e’, Lockchov, Czechoslovakia (Foerste, 1926).

Intervening: EMS-GIV.


First: Cyrtogomphoceras lunatus (Hall, 1879), C. metula (Hall, 1879), upper Helderbergian, New York (Zhuravleva, 1972).

Last: Poterioceras fusiforme (Sowerby, 1829), P. latiseptatum (Foord, 1898), Viséan, Dublin, Republic of Ireland (Foerste, 1926); Welleroceras liratum (Miller and Furnish, 1938), lower Mississippian, Missouri, USA (Miller and Furnish, 1938); Argocheilus ? chinesc Shimanskiy, 1957, Lower Carboniferous, China (Shimanskiy, 1957).

Intervening: D. (m., u.).


First: Lorieroceras lorieri (Barrande, 1874), Lower Devonian, Courtoisieres, Sarthe, France (Foerste, 1926).
Last: *Nothoceras bohemicum* Barrande, 1867, Horizon G₃, Hlubocep, Czechoslovakia (Foerste, 1926); *Oligoceras rusanovi* (Kuzmin, 1965), Eifelian, Novaya Zemlya, former Arctic USSR (Foerste, 1926).

**F. ARCHIACOCRATIDAE** Teichert, 1939


**First and Last:** *Archiacoceras* subventricosus (D’Archaic and De Verneuil, 1842), Givetian, Novaya Zemlya, former Arctic USSR lacks the diagnostic actinosiphonate lamellae and therefore its affinities are uncertain. Sweet (in Teichert et al., 1964) recorded *Cyrtoceratites flexuosus* (Scholethim, 1820) from the Middle Devonian of Germany, but noted *Cyrtoceratites* as possibly being a senior synonym of *Archiacoceras*. Teichert et al. (1979) reported *Cyrtoceratites* to range from the Siegenian to the Givetian.

**F. BOLLOCERATIDAE** Zhuravleva, 1962

D. (EIF) Mar.

**First and Last:** Numerous species assigned to *Bolloceras, Metaphragmoceras* and *Paraconradoceras*, Eifelian, Czechoslovakia and New York, USA (Zhuravleva, 1974).

**F. AKTIJUBOCRATIDAE** Zhuravleva, 1972

D. (FAM) Mar.


**Last:** *Kijoceras clarum* Zhuravleva, 1972, upper Famennian, Aktyubinsk region, former USSR (Zhuravleva, 1972).

**Order** DISCOSORIDA Flower, in Flower and Kummel, 1950

Probably monophyletic; believed to be directly derived from the Electronocerida (Flower and Teichert, 1957; Flower, 1964a) although an origin in the Ellesmerocerida may be equally plausible.

**F. GOULDOCERATIDAE** Stait, 1984


**First:** *Madiganella magna* Teichert and Glenister, 1952, Horn Valley Siltstone, Amadeus Basin, central Australia (Teichert and Glenister, 1952).


**F. RUDEMANNOCERATIDAE** Flower, 1940


**First:** Small doubtfully assigned fragment of *Ruedemannoceras?* sp., Badger Flat Limestone, Inyo County, California, USA (Flower, 1968b); the approximately coeval taxon *Elkanoceras pluto* (Billings, 1865), from the Table Head Limestone, Newfoundland is better known (Flower, 1971).

**Last:** *Taoqupoceras peculare* Lai, 1982, Peikuoshan Formation, Shaanxi Province, China (Lai, 1982).

**Intervening:** LLO–CRD.

**F. WESTONOCERATIDAE** Teichert, 1933


**First:** *Sinclairoceras hauna* Flower, 1952, Chazyan, Ste. Anne de Chicoutimi, Quebec, Canada (Flower, 1952a).

**Last:** *Glyptodendron eatonense* Claypole, 1878, Lower Silurian, Ohio, USA (Flower, in Flower and Teichert, 1957).

**Intervening:** CRD–ASH.

**F. CYRTOGOMPHOCERATIDAE** Flower, 1940


**First:** *Strandoceras strandii* Sweet, 1958, Cephalopod Shale, Helgøya, Norway (Sweet, 1958).

**Last:** *Konglungenoceras norvegicum* Sweet, 1959, middle Stricklandian Series, Konglungen, Oslo, Norway (Sweet, 1959).

**Intervening:** CRD–ASH.


The form of the siphonal deposits in *Greenlandoceras* are poorly known and assignment of the genus to the Orthocerida may be correct.

**First and Last:** *Greenlandoceras striatum* (Troedsson, 1926), *G. lineatum* (Troedsson, 1926), Cape Calhoun Series, Cape Calhoun, north Greenland (Troedsson, 1926).

**F. DISCOSORIDAE** Miller, 1889


**First:** Several species assigned to *Discosorus, Endodiscosorus, Kayoceras,* and *Stokesoceras*, Millerd Silurian, USA (New York, Ohio, Iowa, Michigan), Canada and Europe (Flower and Teichert, 1957).

**Last:** *Alpenoceras? robustum* (Schindewolf, 1944), Kellerwald, Germany, is poorly known from only two specimens but assignment to *Alpenoceras* seems likely (Flower, in Flower and Teichert, 1957).

**Intervening:** LUD, GIV.


**First:** Several species assigned to the genera *Mandaloceras, Cinctoceras, Ovocerina, Pseudogomphoceras, Umbeloceras* and *Vespoceras*, all from the Middle Silurian of North America (Ohio, Illinois, New York), Canada (Quebec), England, UK and Czechoslovakia (Shimer and Shrock, 1944; Flower, in Flower and Teichert, 1957).

**Last:** *Mandaloceras emaciatum* (Barrande, 1866), Czechoslovakia (Zhuravleva, 1972).

**Intervening:** LUD–PRD.

**F. ENTIMOCERATIDAE** Zhuravleva, 1972


**First:** *Gonatocyrtoceras inflatum* Foerste, 1930, Niagaran, Illinois, USA (Foerste, 1930).


**Intervening:** GED?, SIG?, EMS–FRS.

?F. MESOCERATIDAE Hyatt, 1884

S. (WEN/LUD) Mar. (see Fig. 9.3)
Mesoceras is only known from body chambers and recognition of the family is uncertain.

First and Last: Mesoceras bohemicum Barrande, 1877, Middle Silurian, Czechoslovakia (Barrande, 1877).

F. LOWOCERATIDAE Flower, 1940

First and Last: Loxoceras southamptonense Foerste and Savage, 1927, Tuyloceras percurvatum Foerste and Savage, 1927, Hudson Bay, Canada (Foerste and Savage, 1927).

F. PHRAGMOCERATIDAE Miller, 1877

First: Several species assigned to Phragmoceras, Endoplacoceras, Protophragmoceras and Sthenoceras, Czechoslovakia and Gotland, Sweden (Hedstrom, 1917; Zhuravleva, 1972).

Last: Protophragmoceras nonnullum Zhuravleva, 1972, Endoplacoceras podolicum Zhuravleva, 1972, Khudkovtsy, Melbintsy–Podolbski, former USSR; Sthenoceras aduncum (Barrande, 1866), ‘Stage g1’, Czechoslovakia (Zhuravleva, 1972).

Intervening: PRD.

F. NAEDYCERATIDAE Shimanskiy, 1956

First: Oxygonioceras oxynotum (Barrande, 1865), ‘Stage e’, Kozoroz, Czechoslovakia (Foerste, 1926).


Intervening: SIG–FRS.

F. UKHTOCERATIDAE Zhuravleva, 1972


Intervening: GED–FRS.

F. BREVICERATIDAE Flower, 1941

First: Xenoceras oncoceroides Flower, 1951, Helderbergian, New York, USA (Flower, 1951).


Intervening: EIF–FRS.

F. TAXYOCERATIDAE Zhuravleva, 1972


Last: Pachtoceras asiaticum Zhuravleva, 1972, Prolobitovyi Horizon, Karagandinsk region, former USSR (Zhuravleva, 1972).

Intervening: EMS–FRS.

F. MECYNOCERATIDAE Zhuravleva, 1972

First: Laumontoceras laumonti (Barrande, 1866), Lower Devonian, Nehou, Manche, France (Foerste, 1926).

Last: Mecynoceras rex (Pacht, 1856), Pareucynoceras fixum Zhuravleva, 1972, Novaya Zemlya, former Arctic USSR; Laumontoceras improvisum Zhuravleva, 1972, Shushakovsk region, former USSR (Zhuravleva, 1972).

F. DEVONOCHELIDAE Zhuravleva, 1972


Intervening: EIF–FRS.

Order NAUTILIDA Agassiz, 1847

Most, if not all, Devonian to Triassic nautiloids are apparently derived from the Rutoceratidae (Tainoceratae). Early forms have cyrtocoanitic siphuncles with actinosiphonate deposits interpreted as relict features retained from their ancestors in the Oncocerida (Kummel in Teichert et al., 1964).

Superfamily TAINOCERATACEAE Hyatt, 1883

F. RUTOCERATIDAE Hyatt, 1884

First: Ptenoceras alatum (Barrande, 1865), Trochoceras davidsoni Barrande, 1865, ‘Stage β2’, Upper Konéprusy Limestone, Pragian, Czechoslovakia (Foerste, 1926).


Intervening: EMS–FRS, VIS.

F. TETRAGONOCERATIDAE Flower, 1945

First: Nassauceras subtuberculatum (Sandberger and Sandberger, 1852), Orthoceras-Schiefer, Rhineland, Germany; Wellsoaceras columbiense (Whitfield, 1882), Columbus Limestone, Ohio, USA (Zhuravleva, 1974).

Last: Tetragonoceras gracile Whiteaves, 1891, Winnipegosis Dolomite, Manitoba, Canada (Whiteaves, 1891).

F. TAINOCERATIDAE Hyatt, 1883
C. (VIS)–Tr. (NOR) Mar.


Intervening: C. (u.)–P. (u.), SCY–CRN.
### Key for both diagrams

<table>
<thead>
<tr>
<th>QU.</th>
<th>Key for both diagrams</th>
</tr>
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<tbody>
<tr>
<td>HOL</td>
<td>1. Mesoceratidae</td>
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<tr>
<td>PLE</td>
<td>2. Lowoceratidae</td>
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<td>UMI</td>
<td>4. Naedyceratidae</td>
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<td>5. Ukhoceratidae</td>
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<td>7. Taxyceratidae</td>
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<td>11. Tetragonoceratidae</td>
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<td>23. Liroceratidae</td>
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<td>25. Clydonautidae</td>
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<td>26. Siberianautidae</td>
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<td>BER</td>
<td>29. Pseudonautilidae</td>
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### TERTIARY

<table>
<thead>
<tr>
<th>CRUSTACEOUS</th>
<th>30. Paracenoceratidae</th>
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<tbody>
<tr>
<td>31. Cymatoceratidae</td>
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<td>32. Hercoglossidae</td>
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<td>33. Aturidae</td>
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### JURASSIC

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<th>CRETACEOUS</th>
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<td>35. Paracenoceratidae</td>
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<td>36. Cymatoceratidae</td>
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<td>37. Hercoglossidae</td>
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<td>38. Aturidae</td>
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### Fig. 9.3

**F. KONINCKIOCERATIDAE** Hyatt, in Zittel, 1990

<table>
<thead>
<tr>
<th>(VIS)–(ART) Mar.</th>
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<tbody>
<tr>
<td>First: <strong>Millkoninckioceras konincki</strong> (Miller and Kemp, 1947), Viséan, Belgium; <strong>Lophoceras rossicum</strong> Shimanskiy, 1957, <em>L. regulus</em> (Eichwald, 1857), Viséan?, Lower Carboniferous; <strong>L. pentagonum</strong> (Sowerby, 1819), Viséan?, Lower Carboniferous, England, UK; <strong>Planetoceeras retardatum</strong> Hyatt, 1893, Viséan, Belgium; <strong>Subvestinautilus crassimarginatus</strong> (Foord, 1900), Viséan, Republic of Ireland; <strong>Temocheilus coronatus</strong> (M'Coy, 1844), Viséan, Republic of Ireland (Shimanskiy, 1967).</td>
</tr>
<tr>
<td>Last: <strong>Foordiceras goliathum</strong> (Waagen, 1879), Productus Limestone, Lower Permian, Western Australia (Teichert and Glenister, 1952).</td>
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<table>
<thead>
<tr>
<th>(VIS)–(ZEC) Mar.</th>
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<tr>
<td>First: Undescribed species of <strong>Centroceras</strong>, Pine Point Limestone, Lower Permian, Pine Point, Great Slave Lake region, Canada; Columbus Limestone, Ohio and Jeffersonville Limestone, Indiana, USA (Flower, 1952b).</td>
</tr>
<tr>
<td>Last: <strong>Phacoceras</strong>, Lower Permian, Western Australia (Teichert and Glenister, 1952).</td>
</tr>
</tbody>
</table>

**Intervening:** (C. (u.)).

**First and Last:** **Pararhiphaeoacerastastubense** (Krugov, 1928), **Rhphaeaunaiutus curticosatus** Ruzhentsev and Shimanskiy, 1954; **Sholakoceras bisulcatum** Ruzhentsev and Shimanskiy, 1954, Lower Permian, southern Urals, former USSR (Ruzhentsev and Shimanskiy, 1954).

### Superfamily TRIGONOCERATACEAE Hyatt, 1884

**F. CENTROCERATIDAE** Hyatt, in Zittel, 1900

<table>
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<td>First: Undescribed species of <strong>Centroceras</strong>, Pine Point Limestone, Great Slave Lake region, Canada; Columbus Limestone, Ohio and Jeffersonville Limestone, Indiana, USA (Flower, 1952b).</td>
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<tr>
<td>Last: <strong>Phacoceras</strong>, Lower Permian, Western Australia (Teichert and Glenister, 1952).</td>
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**Intervening:** (GIV, FAM, VIS–SPK, MOS).

**F. TRIGONOCERATIDAE** Hyatt, 1884

<table>
<thead>
<tr>
<th>(VIS)–(ZEC) Mar.</th>
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| First: Numerous species assigned to **Trigonoceras**, **Aphelaeceras**, **Chouteauceras**, **Diodoceras**, **Discioceras**, **Epi-**
Fig. 9.3

stroboceras, Leuroceras, Liscoceras, Maccoycoceras, Mesocasmo-
ceras, Pararincoceras, Rinecaris, Stroboceras, Subclymenia, and
Thoroceras, Lower Carboniferous of England, UK, Belgium, Germany, Canada, USA, and Republic of Ireland
(Furnish and Glenister, in Teichert et al., 1964). It is difficult
to relate the age of Viséan, Lower Carboniferous or
Mississippian records.

Last: Apogonoceras remotum Ruzhentsev and Shimanskiy,
1954, Lower Permian, southern Urals, former USSR
(Ruzhentsev and Shimanskiy, 1954).

Intervening: SPK-BSK.

F. GRYPOCERATIDAE Hyatt, in, Zittel, 1990

C. (VIS)–Tr. (NOR) Mar.

First: Epidomatoceras maccyi Turner, 1954, Viséan,
Republic of Ireland; E. aemulum Shimanskiy, 1967, Viséan,
Kazakhstan, former USSR; E. doohylensae (Foord, 1900),
Viséan, Republic of Ireland (Shimanskiy, 1967).

Last: Grypoceras mesoticum (Quenstedt, 1843), Norian, Alps
(Mojsisovics, 1873).

Intervening: SPK–C. (u.), ZEC, SCY.

F. PERMOCERATIDAE Miller and Collinson, 1953


First and Last: Permoceras bitauniensis (Haniel, 1915),
Lower Permian, Timor, Indonesia (Miller and Collinson,
1953).

F. SYRINGONAUTILIDAE Mojsisovics, 1902

Tr. (ANS–NOR)

First: Syringonautilus lilianus Mojsisovics, 1882, Anisian,
Alps (Mojsisovics, 1882); *Syringoceras*, Anisian, Nevada and California, USA (Kummel, 1953).

**Last**: *Claymenonautus ehrlichii* (Mojsisovics, 1873), *Juvavionautilus heterophyllus* (Hauer, 1849), *Oxynautilus acutus* (Hauer, 1846), Norian, Alps (Mojsisovics, 1873, 1902); *Syringoceras*, Norian, Timor, Indonesia (Kummel, 1953).

**Intervening**: CRN.

**Superfamily** AIPOCERATACEAE Hyatt, 1883

**Family** AIPOCERATIDAE Hyatt, 1883 C. (TOU–MOS) Mar.

**First**: *Aipoceras gibberosum* (De Koninck 1880), Tournaisian, Belgium; *A. compressus* (Foord, 1900), Tournaisian, Republic of Ireland; *A. easleynse* Miller and Furnish, 1938, 1938, A. *oweni* Miller and Furnish, 1938, A. *pinhookense* Miller and Furnish, 1938, *Chouteau* Limestone, Kinderhookian, Missouri, USA (Miller and Furnish, 1938); *Asymptoceras crassilabrum* (Foord, 1900), Tournaisian, Republic of Ireland (Foord, 1900).

**Last**: *Libronitschiceras atuberculatus* (Tzwetaev, 1888), Moscow, former USSR (Shimanskiy, 1967).

**Intervening**: VIS–SPK.

**Family** SOLENOCHILIDAE Hyatt, 1893 C. (VIS)–P. (ZEC) Mar.

**First**: *Acanthonautus bispinosus* Foord, 1896, Viséan, Republic of Ireland; *A. sp. Shimanskiy, 1967, Viséan, European former USSR (Shimanskiy, 1967).

**Last**: *Solenochilus kempae* Miller and Youngquist, 1949, lower Lueder’s Formation, Texas, USA (Miller and Youngquist, 1949); *Solenochilus ?auriculus* Chao, 1954, is from the Yangsinian Formation of Tanchiashan, Hunan Province, China (Chao, 1954), but its siphuncular structure is unknown and generic assignment is tentative. If confirmed this would represent a younger record than *S. inexpectans* (Chao, 1954).

**Intervening**: C. (u.).

**Family** SCYPHOCERATIDAE Ruzhentsev and Shimanskiy, 1954 P. (ART) Mar.


**Superfamily** CLYDONAULTACEAE Hyatt, in Zittel, 1900

**Family** LIROCERATIDAE Miller and Youngquist, 1949 D. (FRS)?/C. (VIS)–Tr. (NOR) Mar.

**First**: *Potoceras dwium* Hyatt, 1894; *Hyllia* (1953) suggested an early Carboniferous (Viséan) age. Kummel (1953) noted the specimen was thought probably to have come from the Frasnian Ilberger Kaik of Germany or Viséan of Belgium. If a Viséan age is correct then the taxon becomes inseparable from: *Liroceras fornicateum* Shimanskiy, 1967, Viséan, former European USSR; *L. hyatti* Miller et al., 1933, Viséan, Belgium; *L. praelunense* Shimanskiy, 1967, Viséan, Severnyle Uvaly, former USSR; *Bistrialites bistrialis* Phillips, 1836, Viséan?, England, UK (Shimanskiy, 1967).

**Last**: *Indonautilus krafftii* (Mojsisovics, 1902), Norian, Himalayas; *Paranautilus simonyi* (Hauer, 1849), Norian, Alps (Mojsisovics, 1902).

**Intervening**: SPK–C. (u.), P., ANS–CRN.


**First**: *Ephippioceras bilobatum* (Sowerby, 1840), Lower Carboniferous, Scotland, UK; *E. spirale* Ramsbottom and Moore, 1961, Viséan, Republic of Ireland (Ramsbottom and Moore, 1961).

**Last**: *Ephippioceras hunanense* Chao, 1954, *E. involutum* Chao, 1954, Lower Permian, Hunan Province, China (Chao, 1954); *E. inexpectans* Miller and Youngquist, 1949, Lower Permian, Texas, USA (Miller and Youngquist, 1949).

**Intervening**: SPK–MOS.

**Family** CLYDONAULTIDAE Hyatt, in Zittel, 1900 Tr. (ANS–NOR) Mar.

**First**: *Styrionautus*, Anisian, Nevada, USA (Kummel, 1953).

**Last**: *Clydonautilus noricus* (Mojsisovics, 1873), Norian, Alps (Mojsisovics, 1873); *Callaionautus turgidus* Kieslinger, 1924, *Cosmonautus*, Upper Triassic, Timor, Indonesia, and *Procydonautilus griesbachii* (Mojsisovics, 1896), Upper Triassic, India are probably coeval (Kummel, 1953).

**Family** SIBERIONAULTIDAE Popov, 1951 Tr. (CRN) Mar.

**First and Last**: *Siberionautilus multilobatus* Popov, 1951, Carnian, Siberia, former USSR (Popov, 1951).

**Family** GONIONAULTIDAE Kummel, in Flower and Kummel, 1950 Tr. (NOR) Mar.

**First and Last**: *Gonionautus securis* (Von Dittmar, 1866), Norian, Alps (Mojsisovics, 1902).

**Superfamily** NAUTILACEAE De Blainville, 1825

**Family** NAUTILIDAE De Blainville, 1825 Tr. (CRN)–Rec. Mar.

**First**: *Cenoceras trechmanni* Kummel, 1953, Carnian, Hokonui Hills, New Zealand (Kummel, 1956).


**First**: *Pseudogamides kochi* (Prinz, 1906), Lias of Austria and Hungary (Kummel, 1956).

**Last**: *Pseudonautilus aturoides* (Picket, 1867), lower Valanginian, France (Kummel, 1956).

**Intervening**: BAJ–OXF, TTH, BER.


**First**: *Somalianautus fuscus* (Crick, 1898), England, UK (Kummel, 1956).

**Last**: *Paracenoceras rhodani* (Roux, 1848), Switzerland (Kummel, 1956).

**Intervening**: BTH–TTH.
Mollusca: Cephalopoda (Nautiloidea) 185

F. CYMATOCERATIDAE Spachat, 1897

First: Cymatoceras sturianum (D'Orbigny, 1850), Belfort, France; Procyamatoceras subtruncatum (Morris and Lyckett, 1850), P. baberi (Morris and Lyckett, 1850), Gloucestershire, England, UK (Kummer, 1956).

Last: Cymatoceras tsukushiense (Kobayashi, 1954), Oligocene, northern Kyushu, Japan (Kummer, 1956).

Intervening: CLV–J. (u.), HAU, MAA.

F. HERCOGLOSSIDAE Spachat, 1897

First: Cimomia turcicus (Krumbeck, 1905), upper Jurassic, Libya (Kummer, 1956).

Last: Cimomia blakei (Avnimelech, 1947), Oligocene, Palestine; Deltoidonautilus bakeri Teichert, 1947, Oligocene, Victoria, Australia (Kummer, 1956).

Intervening: K. (u.) DAN–PRB.

F. ATURIIDAE Chapman, 1857

First: Aturia praecizae Oppenheim, 1903, Palaeocene, Thebes, Egypt (Kummer, 1956).

Last: Numerous species assigned to Aturia (including A. aturi (Basterot, 1825), A. augustata Conrad, 1866, A. coxi Miller, 1947), from the Miocene of France, USA, Venezuela, Zanzibar, Angola, Italy and Japan (Kummer, 1956).

Intervening: T. (Eoc.–Oli.).

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MOLLUSCA: CEPHALOPODA
(PRE-JURASSIC AMMONOIDEA)


This chapter was compiled by several authors, each working on a geological period: MRH on the Devonian ammonoids, JK on the Carboniferous, BFG on the Permian, and RAH and WYG on the Triassic. The typical ammonoids of the Jurassic and Cretaceous are treated in the next chapter. The listings for Permian ammonoids are based largely on MSS for the revision of Volume L, Mollusca 4 of the Treatise on Invertebrate Paleontology, prepared by B. F. Glenister, W. M. Furnish and Z.-Z. Zhou. The Triassic ammonoid classification is based on Shevyrev (1986), which should probably be analysed by equating his superfamilies with the cited families of Palaeozoic ammonoids. Some of the Shevyrev families are placed in synonymy and are indicated by upper-case letters in the body of the text.

The subdivision of the Devonian follows recent recommendations by the Subcommission on Devonian stratigraphy (Kirchgasser and House, 1981). The stratigraphical subdivisions of the Permo-Carboniferous follow the standard stage names set out at the beginning of the volume, but several schemes are mixed in order that the most appropriate terms may be used for each case. However, note that the Lower Carboniferous zones cannot be applied for ammonoid zonation (Kullman et al., 1991).

Russian stage names for the Lower Permian (Asselian, Sakmarian, Artinskian) are legitimate time-rock terms that serve effectively for international reference. However, those recommended (e.g. Harland et al., 1982) for the higher Permian (Kungurian, Ufimian, Kazanian, Tatarian) are primarily ecological entities with limited chronological significance. Serviceable post-Artinskian references (Roadian, Wordian and Capitanian = Guadalupian) are available in objective stratigraphical succession in the North American south-west, and are supplemented by the highest Permian sequences in Transcaucasia (Dzhulian, Dorashamian). The present chapter uses the succession Asselian (ASS), Sakmarian (SAK), Artinskian (ART), Roadian (ROD) as Lower Permian, and Guadalupian (GUA) (Wordian (WOR) and Capitanian (CAP)), Dzhulian (DZH) and Dorashamian (DOR) (= Changxingian (CHX)) as Upper Permian. The authors are mindful, however, that Roadian through Capitanian (roughly Kungurian to early Kazanian) will probably be segregated in future as a Middle Permian Series (Glenister et al., in press), and that the presently defined base of the boreal Triassic in Canada (GRI) may well be defined eventually to correspond approximately with the base of the Asian Dorashamian (Sheng et al., 1984).

The Triassic has been divided into 39 zonal units, each of which is composed of no more than two subzones (a, older; b, younger half of zone). They are numbered in chronological order within each of the stages cited in this volume, and their totals per stage are as follows: GRI (4), NML (4), SPA (3), ANS (9), LAD (5), CRN (5), NOR (6), RHT (3). The RHT symbol denotes the upper Norian substage defined by the base of the Cordilleranus Zone (Tozer, 1984). The other zonal units were derived from table 2 of Tozer (1984) by addition of the Mulleri Zone (ANS, 1) of Bucher (1989) and recognition of informal upper (ANS, 5) and lower (ANS, 4) Ismidicum Zones (Fantini Sestini, 1988). The three main Triassic ammonoid extinctions extended through two subzones, and are situated in the Ellesmerian Substage (GRI, 3–4), the Austriacum Zone (CRN, 2), and the final Marschi Zone (RHT, 3).
Subclass **AMMONOIDEA** Zittel, 1984

**Order** ANARCESTIDA Miller and Furnish, 1954

**Suborder** BACTRITINA Miller and Furnish, 1954

It is generally agreed that this group of orthocones with egg-shaped protoconchs and marginal siphuncles is ancestral to the Ammonoidea. But it is possible that similar egg-shaped protoconchs may have arisen several times among orthoconic nautiloids, and deciding which, if any, of the known early forms with this feature is likely to be the ancestor, is a speculative and rather idle occupation. Few of the known early forms with this feature is likely to be the ancestor, a feature which they share with belemnoids and spirulids, bactritids and the earliest coiled ammonoids. Such time as relationships can be established with earlier forms. It seems most reasonable to presume these are the earliest known, until such time as relationships can be established with earlier forms.

F. BACTRITIDAE Hyatt, 1884

D. (EMS)--Tr. (CRN) Mar. (see Fig. 10.1)


Last: Dillerties stahsensis Gordon, 1966, Hosselkus Limestone, Triassic (CRN 4), California, USA.

Intervening: Fair later Devonian, Carboniferous and Permian record.

Comment: This classification groups the cyrtococonic to partly gyroconic genera Metabactrites and Kokenia with the anetoceratids rather than the bactritids as was recommended by Dzik (1984).

F. BOJOBACTRITIDAE Horny, 1956

D. (EMS) Mar.

First and Last: Pseudobactrites bicornatus (=Bojobactrites ammonitans) Horny, 1956, Zilichov Limestone, upper Emsian, Czechoslovakia.

F. PARABACTRITIDAE Shimskiy, 1951


First: Angustobactrites Saundersi Mapes, 1979, Imo Formation, Chester, Mississippian, Arkansas, USA.

Last: Parabactrites rhuzhencevi and other spp., Shimskiy, 1962, Artinskian, Permian, southern Urals, former USSR.

F. SINUOBACTRITIDAE Mapes, 1979


First: Sinuobactrites morrowanensis Mapes, 1979, Gene Autry Formation, Morrowian, Upper Carboniferous, Oklahoma, USA.

Last: Dilatobactrites missouriensis Mapes, 1979, Eudora Shale, upper Missourian, Upper Carboniferous, Kansas, USA.

Suborder **AGONIATITINA** Ruzhentsev, 1957

Superfamily **MIMOSPHINCTIDAE** Steinmann, 1890

F. MIMOSPHINCTIDAE Erben, 1953


Last: Kokenia obliquecostata Holzapfel, 1895, Odershauser Kalk, D. (U. EIF), Bonzel, Germany.

Comment: This classification groups the gyroconic to partly gyroconic genera Metabactrites and Kokenia with the anetoceratids rather than the bactritids as was recommended by Dzik (1984).

F. MIMOSPHINCTIDAE Steinmann, 1890

D. (EMS), Mar.

First: Gyroceratites laevis Chlapáč and Turek, 1980, Daleje Shale, lower Emsian, Czechoslovakia.

Last: Gyroceratites gracilis Chlapáč and Turek, 1980, Trebetov Limestone, upper Emsian, Czechoslovakia.

Superfamily **AGONIATITACEAE** Holzapfel, 1899

F. MINAGONIATIDAE Miller, 1938


This family comprises advolute and convolute agoniatitaceans with perforate first whorls.

First: Minagoniatites fallacis Chlapáč and Turek, 1983, lower Emsian, Germany.


F. PARENTITIDAE Bogoslovskiy, 1980

D. (EMS) Mar.

First and Last: Kimocerites lentiforme and Dillertites sp., Zilichovian, Emsian, former USSR.

F. PINACITIDAE Schindewolf, 1933 (emend.)

D. (EIF) Mar.

First and Last: Pinacites jugleri Chlapáč and Turek, 1980, Eifelian, Czechoslovakia, Morocco, etc.

F. AGONIATITIDAE Holzapfel, 1899


This family comprises involute agoniatitaceans with perforate first whorls.


Last: Agoniatites sp. House, 1963, terebratum Zone, mid-Givetian, Trevose Slates, north Cornwall. Similar records in Germany and Morocco.

Superfamily **AUGURITACEAE** Bogoslovskiy, 1961

F. AUGURITIDAE Bogoslovskiy, 1961

D. (EMS) Mar.

First and Last: Celaeceras praematurum Chlapáč and Turek, 1980, upper Zilichovian or possibly lower Dalejan, Emsian, Czechoslovakia.

Suborder **ANARCESTINA** Steinmann, 1890

Superfamily **ANARCESTACEAE** Steinmann, 1890
### F. ANARCESTIDAE Steinmann, 1890

**First:** *Latanarcestes boreus* Bogoslovskiy, 1972, *regularissimus* Zone, lower Dalejan, Emsian, Novaya Zemlya, former USSR.

**Last:** *Archoceras paeckelmanni* Schindewolf, 1937b, lower Famennian Ill, Nehdenschiefer, Germany.

### Intervening: GIV, FRS.


**First:** *Sobolewia rotella* Petter, 1959, middle Eifelian, Morocco.

**Last:** *Sobolewia nuciformis* Petter, 1959, middle Givetian, *terebratum* Zone, Morocco.
Superfamily PHARCICERATAEAE Hyatt, 1900

F. MAENIOCERATIDAE Bogoslovskiy, 1958
First: Maenioceras molarium House, 1963, molarium Zone, lower Givetian, Wolborough Limestone, Devon, UK.
Last: Maenioceras crassum Bensaid, 1974, tridens Zone, Givetian, Oued Mzerreb, Morocco.

F. PHARCICERATIDAE Hyatt, 1900
First: Pharciceras amplicum House, 1962, Tully Limestone, Mid. tarcus condont Zone, New York State, USA.
Last: Petteroceras feisti House et al., 1985, lowest Frasnian (la), lower asymmetrics condont Zone, Montagne Noire.

F. MAENIOCERATIDAE Hyatt, 1900
First: Tamarites subitus Bogoslovskiy, 1958, upper Givetian, Tarbagatae Mountains, Kazakhstan, former USSR.

F. DEVONONPRONORITIDAE Bogoslovskiy, 1958
First and Last: Devononpronorites ruzhencevi Bogoslovskiy, 1969, Frasnian, Rudnyi Altai, former USSR.

Superfamily GEPHUCERATACEAE Frech, 1897

First: Pseudoprobloceras nebechense Bensaid, 1974, lunulicosta Zone, Givetian (la), Morocco, now late Givetian on redefinition of base of Frasnian.
Last: Crickites holzapfeli Becker et al., 1989, holzappeli Zone, upper Frasnian (Ib), Montagne Noire, France.

F. BELOCERATIDAE Hyatt, 1884
First: Probloceras lutheri House and Kirchgasser, 1993, Cashqua Shale, New York State, USA.
Last: Beloceras tenuistratum Feist et al., 1989, holzappeli Zone, upper Frasnian (Ib), Montagne Noire, France.

Order CLYMENIIDA Wedekind, 1914

These extraordinary dorsal-siphuncled ammonoids are confined to the Famennian. Their diversity will confuse taxon tots. The classification mostly follows one recently proposed by Korn (1992) and acknowledgement is made of the unpublished thesis of Price (1982). The ranges against the detailed Famennian zonation given here is preliminary.

Suborder CLYMENIINA Hyatt, 1884

Superfamily CYRTOCLYMENIACEAE Hyatt, 1884

F. CYRTOCLYMENIIIDAE Hyatt, 1884
D. (FAM) Mar.
First: Cyrtoclymenia involuta Wedekind, 1908, delphinus Zone, Famennian (IIIb), Enkeberg, Germany.
Last: Cyrtoclymenia angustisepata Schindewolf, 1937a, sphaeroides Zone, Famennian (VI), Hönnetal, Germany.

F. CYMACLYMENIIIDAE Hyatt, 1884
D. (FAM) Mar.
First: Gymaclymenia borni Schindewolf, 1923, delphinus Zone, Famennian (IIia), Kirch-Gattendorf, Germany.
Last: Cymaclymenia evoluta (= euryomphala) Schindewolf, 1937a, euryomphala Zone, Famennian (VI), Hönnetal, Germany.

F. RECTOCLYMENIIIDAE Schindewolf, 1923
D. (FAM) Mar.
First: Rectoclymenia roemeri Wedekind, 1908, delphinus Zone, Famennian (IIlb), Enkeberg, Germany.

F. CARINOCLYMENIIIDAE Bogoslovskiy, 1975
D. (FAM) Mar.
First: Carinoclymenia bevelense Lange, 1929, annulata Zone, Famennian (IV), Enkeberg, Germany.
Last: Pachyclymenia inexpectata Bogoslovskiy, 1985, acuticosta Zone, Clymenia Stufe, Famennian (V), Urals, former USSR.

First: Uraloclymenia nodosa Bogoslovskiy in Simakov (ed.), 1985, upper annulata Zone, Famennian (IV), Urals, former USSR.
Last: Pachyclymenia intermedia Bogoslovskiy in Simakov (ed.), 1985, upper Clymenia Stufe, Famennian (V), Urals, former USSR.

F. BILOCYLMENIIIDAE Bogoslovskiy, 1955
D. (FAM) Mar.
First: Borkinia kozlowskii Czarnocki, 1989, upper Platy­clymenia Stufe or Clymenia Stufe, Famennian (VI or V), Holy Cross Mountains, Poland.
Last: Dimero­clymenia semicostata Czarnocki, 1989, paradoxa Zone, Famennian (VI), Holy Cross Mountains, Poland.

Superfamily CLYMENIACEAE Edwards, 1849

F. PLATYCLYMENIIIDAE Wedekind, 1914
D. (FAM) Mar.
First: Platyclymenia brevicosta and others, Wedekind, 1908, delphinus Zone, Famennian (IIIb), Enkeberg, Germany.
Last: Platyclymenia (Spinoclymenia) aculeata Bogoslovskiy, in Simakov et al. 1985, ornata Zone, Famennian (V), Mugodzhar, former USSR.

First: Sulcoclymenia sulcata Schindewolf, 1971, delphinus Zone, Famennian (IIlb), Ebersdorf, Poland (Schindewolf, 1972).
Last: Piriclymenia piriforme Schmidt, 1924, piriforme Zone, Famennian (V), Franken­berg Germany.

First: Gymoclymenia dunkeri Lange, 1929 (see Price, 1982), annulata Zone, Famennian (IV), Gattendorf, Germany.
Last: Kosmoclymenia (Lissoclymenia) wocklumeri Korn and Price, 1987, upper paradoxa Zone, Famennian (VI), Germany.
Mollusca: Cephalopoda (pre-Jurassic Ammonoidea) 193

F. GLATZIELLIDAE Schindewolf, 1928  
D. (FAM) Mar.  
First: Soliclymenia paradoxa Schindewolf, 1937a, subarmata Zone, Famennian (Vβ), Hönnetal, Germany.  
Last: Postglatziella carinata Schindewolf, 1937a, sphaeroides Zone, Famennian (VI), Hönnetal, Germany.  

Superfamily GONIOCLYMENIACEAE Hyatt, 1884  
F. COSTACLYMENIIDAE Schindewolf, 1920  
D. (FAM) Mar.  
First: Costaclymenia multistipata Bogoslovskiy, 1981, annulata Zone, Famennian (Vα), Urals, former USSR.  
Last: Costaclymenia kiliani Wedekind, 1914, acuticostata Zone, Famennian (Vβ), Dasberg, Germany.  

Superfamily GONIOCLYMENIACEAE Hyatt, 1884  
F. GONIOCLYMENIIDAE Hyatt, 1884  
D. (FAM) Mar.  
First: Gonioclymenia (Gonioclymenia) speciosa Price, 1982, Clymenia Stufe, Famennian (V), Germany.  
Last: Gonioclymenia (Finiclymenia) wocklumensis Wedekind, 1914, acuticostata Zone, Famennian (VI), Schübelhammer, Germany.  

F. SELLACLYMENIIDAE Korn, 1992 (T. S. Price, 1982)  
D. (FAM) Mar.  
First: Sellaclymenia torleyi Wedekind, 1914, annulata Zone, Famennian (IV), Hoevel, Germany.  
Last: Sellaclymenia plana Schindewolf, 1923, Wocklumeria Stufe, Famennian (VI), Germany.  

Superfamily WOCKLUMERIACEAE Schindewolf, 1937  
F. PARAWOCKLUMERIIDAE Schindewolf, 1937  
D. (FAM) Mar.  
First: Parawocklumeria paprothae Clausen et al., 1989, lower paraaxa Zone (= endogona Zone, Famennian (VI), Müssenberg, Germany.  
Last: Parawocklumeria paradoxa Schindewolf, 1937a, sphaeroides Zone, Famennian (VI), Hönnetal, Germany.  

F. WOCKLUMERIIDAE Schindewolf, 1937  
D. (FAM) Mar.  
First and Last: Wocklumeria sphaeroides Schindewolf, 1937a, sphaeroides Zone, Famennian (VI), Hönnetal, Germany.  

Order GONIATITIDAE Hyatt, 1884  
Goniatite ranges are based on Bogolovskiy (1971a,b), Wedekind (1917 (1918)), and other sources.  

Suborder TORNOCERATINA Wedekind, 1917  
Superfamily TORNOCERATAEAE Arthaber, 1911  
F. TORNOCERATIDAE Arthaber, 1911  
First: Parodiceras brachystoma Petter, 1959, jugleri Zone, Eifelian, Algeria.  
Last: Lobotornoceras (= Falcitornoceras) sp. Bartzsch and Weyer, 1986, sphaeroides Zone, upper Famennian (VI), Thüringia, Germany.  

Superfamily PRAEGLYPHIOCERATACEAE Ruzhencev, 1957  
F. SPORADOCERATIDAE Miller and Furnish, 1957  
D. (FAM) Mar.  
First: Maeneceras biforum and others, Schindewolf, 1923, Cheiloceras Stufe, Famennian (IIβ), Germany (also Australia, Morocco, etc.).  
Last: Sporadoceras orbiculare Schindewolf, 1937a, sphaeroides Zone, upper Famennian (VI), Germany.  

F. PRAEGLYPHIOCERATIDAE Ruzhentsev, 1957  
D. (FAM) Mar.  
First: Posttornoceratidae Bogoslovskiy, 1962  
D. (FAM) Mar.  
First: Posttornoceras balvei Lange, 1929, annulata Zone, Famennian (IV), Germany.  
Last: Discoclymenia cucullata Schindewolf, 1937a, sphaeroides Zone, upper Famennian (VI), Hönnetal, Germany.  

Superfamily DIMEROCERATAEAE Hyatt, 1884  
F. CHEILOCERATIDAE Frech, 1897  
D. (FAM) Mar.  
First: Cheiloceras verneuili Buggisch and Clausen, 1972, upper Pa. triangularis conodont Zone, upper Famennian (IIa), Erfoud, Morocco.  
Last: Sinotites aktubensis Bogoslovskiy, 1969, Clymenia Stufe, Famennian (III), Khingan, China.  

F. DIMEROCERATIDAE Hyatt, 1884  
D. (FAM) Mar.  
First: Gen. nov. aff. Dimeroceras petterae Becker, 1990, Cheiloceras Stufe, lower Famennian (IIa), Enkeberg, Germany.  
Last: Dimeroceras mammilliferum Wedekind, 1908, delphinus Zone, Famennian (III), Enkeberg, Germany.  

F. PROLOBITIDAE Wedekind, 1913  
D. (FAM) Mar.  
First: Prolobites insulatus Lange, 1929, Cheiloceras Stufe, lower Famennian (IIa), Erfoud, Morocco.  
Last: Renites kiensis Bogoslovskiy, 1969, Clymenia Stufe, Famennian (V), Urals, former USSR.  

F. SINOTITIDAE Chang, 1960  
D. (FAM) Mar.  
First: Sinotites aktubensis Bogoslovskiy, 1971a, Cheiloceras Stufe, Famennian (IIa), Urals, former USSR.  
Last: Sunites suni Chang, 1960, Famennian (?III), Great Khingan, China.  

?F. PHENACOCERATIDAE Frech, 1902  
D. (FAM) Mar.  
First: Clymenoceras insolatum Schindewolf, 1937b, Famennian (IIIb), Enkeberg, Germany.  
Last: Cycloclymenia planorbiforme Schindewolf, 1937a, upper Famennian (IV), Germany.
Superfamily PRIONOCERATACEAE Hyatt, 1884

F. PRIONOCERATIDAE (FAM)—C. (ARN) Mar.

First: Prionoceras dixiunum (Münster, 1832), P. frechi (Wedekind, 1913), Plagyclymenia Zone, Rheinisches Schiefergebirge, Germany (Schindewolf, 1923).


Comment: The family is monotypic, and it is characterized by a bifid ventral lobe that is unique within the Ochelata Group, Missourian, Oklahoma, USA (Frest et al., 1981).

F. MAXIMITIDAE of Ruzhentsev, 1960


First: Maximites alexanderi Nassichuk, 1975, Hare Fiord Formation, Atokan, Ellesmere Island, Arctic Archipelago, Canada.

Last: Maximites cherokeensis (Miller and Owen, 1939), Ochelata Group, Missourian, Oklahoma, USA (Frest et al., 1981).

Comment: The family is monotypic, and it is characterized by a bifid ventral lobe that is unique within the Cheilocerataceae (Frest et al., 1981).

F. PSEUDOHALORITIDAE of Ruzhentsev, 1957


First: Neogaganides graminensis Plummer and Scott, 1937, Missourian, Iowa—Texas, Ohio, USA.

Last: Neogaganides sp. 2 (Frest et al., 1981), Ali Bashi Formation, Kuh-e-Ali Bashi, Iran.

Comment: The family is characterized by the position of the siphuncle at maturity, ranging from subcentral to within the dorsal septal flexure. Three component sub-families are based on the advent and extent of sutural serration, ‘goniatitic’, ‘ceratitic’, or ‘ammonitic’.

Suborder GONIATITIINA Hyatt, 1884

Superfamily KARAGANDOCERATACEAE Librovich, 1957

F. KARAGANDOCERATIDAE Librovich, 1957

C. (TOU) Mar.

First: Voehringenites peracutus (Vöhringer, 1960), Gattendorfia Zone, Rheinisches Schiefergebirge, Germany (Manger, 1971).

Last: Karagandoceras sp., Luton Formation, upper Tournaisian, New South Wales, Australia (Campbell et al., 1983).

Comment: These are the oldest goniatitids with a subdivided ventral lobe; this is an artificial grouping, the relationship is not known.

Superfamily PERICYCLACEAE Hyatt, 1900

F. PERICYCLIDAE Hyatt, 1900


First: Goniocycus blairi (Miller and Gurley, 1896), Caballero Formation, upper Kinderhookian series, New Mexico, USA (Gordon, 1986).

Last: Ammonellipsites kochi (Holzapfel), Erdbracher Kalk, Pericyclus Zone (lower VIS), Rheinisches Schiefergebirge, Germany, and other species of pericyclids.

Comment: The mostly prominently sculptured Pericyclidae were strictly limited to the Pericyclus Zone (upper TOU and lower VIS) and ended rather abruptly.

F. MUNESTROCERATIDAE Librovich, 1957


Last: Ballandites castletonense (Bisat, 1924), Beyrichoceras Zone, England, UK.

Comment: The family comprises forms with smooth shell surface. It is not clear if the first muensteroceratid form is Intoceras osagense (Swallow, 1860), Chouteau Limestone, upper Kinderhookian series, Missouri, USA (see below, Girtyoceratidae). If the peculiar genus Clathoceras Currie belongs in the Muensteroceratidae, the last species would be: Clathoceras truemanii Currie, 1954, Eumorphoceras Zone, Scotland, UK.

Superfamily NOMISMACERATACEAE Librovich, 1957

F. NOMISMACERATIDAE Librovich, 1957

C. (VIS—MRD) Mar. (see Fig. 10.2)

First: Pseudonomismoceras spiratissimum (Holzapfel, 1889), Erdbracher Kalk, Pericyclus Zone (lower VIS), Rheinisches Schiefergebirge, Germany.

Last: Baschikirites vasilkovskiyi (Ruzhentsev and Bogoslovskaya, 1978), upper Reticulocesta Zone, Central Asia.

Comment: This group is characterized at the beginning by a thin-disoidal and vermicular conch form which is smooth and later with simple or divaricate ribs.

Superfamily DIMORPHOCERATACEAE Hyatt, 1884

F. DIMORPHOCERATIDAE Hyatt, 1884

C. (VIS—YEA) Mar.

First: Dimorphoceras gilbertsoni (Phillips, 1836), Goniatites Zone, upper VIS, England, UK.

Last: Metadimorphoceras subdivisum Manger and Quinn, 1972, lower Gastriceras Zone, Arkansas, USA (Manger, 1988).

Comment: This is the first goniatitid group with denticle or subdivided ventral or lateral lobes.

F. BERKHOCEARTIDAE Librovich, 1957


First: Kazakhoceras hatokinsi (Moore, 1930), Goniatites Zone, upper VIS, Republic of Ireland.

Last: Kazakhoceras hatokinsi (Moore, 1930), Eumorphoceras Zone, England, Spain, former USSR.

Comment: Only one genus known, no descendants.

F. ANTHRACOCERATIDAE Librovich, 1957


First: Anthracoceras paucilobum (Phillips, 1836), Eumorphoceras Zone, England, UK (Bisat, 1924).

### Fig. 10.2

**F. GITYOCERATIDAE** Wedekind, 1918  

**First:** *Intoceras osagense* (Swallow, 1860), upper Kinderhookian, Missouri, USA.  
**Last:** *Peytonoceras ornatum* Saunders, 1966, Chesterian Series, Arkansas, USA.  
**Comment:** If the assignment of the subfamily Intoceratinae to Muensteroceratidae is correct, then the first appearance of this family would be: *Winchelloceras allei* (Winchell, 1862), Marshall Sandstone, Osagean Series, Michigan, USA.

**F. EOGONIOLOBOCERATIDAE** Ruzhentsev and Bogoslovskaya, 1978  

**First:** *Eogonioloboceras asiaticum* (Librovich, 1940), *Goniatites* Zone, upper VIS, Kazakhstan, former USSR.

**Last:** *Arcanoceras burmai* (Miller and Downs, 1950), *Eumorphoceras* Zone, southern Urals, former USSR.

**Superfamily GONIATITACEAE** de Haan, 1825

**F. GONIATITIDAE** de Haan, 1825  
C. (VIS) Mar.

**First:** *Goniatites hudsoni* (Bisat, 1934), *Brigantian*, *Goniatites* Zone, upper VIS, England, UK.  
**Last:** *Lusitanoceras granosum* (Portlock, 1843), *Goniatites* Zone, upper VIS, Republic of Ireland.  
**Comment:** Older species of *Goniatites* doubtful.

**F. DELEPINOCERATIDAE** Ruzhentsev, 1957  

**First:** *Platygoniatites molaris* Ruzhentsev, 1956, *Goniatites* Zone, upper VIS, southern Urals, former USSR.
Last: Delipinoceras bressoni Ruzhentsev, 1958, Eumorphoceras Zone, southern Urals, former USSR.

F. AGATHICERATIDAE Arthaber, 1911

First: Dombarites poststriatus (Brüning, 1923), Goniatites Zone, Rheinisches Schiefergebirge, Germany.

Last: Agathiceras suessi Gemmellaro, 1888, Sosio beds, Sicily, Italy.

Comment: Dombarites seems to occur at the same time in many regions. The families Delipinoceratidae and Agathiceratidae show for the first time in the history of the ammonoids an increase of lateral lobes through trifurcation. The latter family persisted until late Permian times without any significant change in shell form.

Superfamily NEOGLYPHIOCERATACEAE
Plummer and Scott, 1937


First: Ophilyloceras tersum Ruzhentsev and Bogoslovskaya, 1971, Goniatites Zone, southern Urals, former USSR.

Last: Rhymoceras gracilentum Ruzhentsev, 1958, Eumorphoceras Zone, Serbia, former Yugoslavia.


First: Neoglaphyloceras spirale (Phillips, 1841), Goniatites Zone, upper VIS, England, UK.

Last: Neoglaphyloceras litvinovici Ruzhentsev and Bogoslovskaya, 1971, Eumorphoceras Zone, Kazahkstan, former USSR.

Comment: Numerous short-lived species of Neoglaphioceratins and related genera became extinct at about the same time.


First: Lyrogoniatites eisenbergi (Ruprecht, 1937), Goniatites Zone, Rheinisches Schiefergebirge, Germany.

Last: Aenigmaticeras rhapaeum Ruzhentsev and Bogoslovskaya, 1978, Reticuloceras Zone, southern Urals, former USSR.

Superfamily NEODIMORPHOCERATACEAE
Furnish and Knapp, 1966


First: Craendmeroceratoides edalensis (Bisat, 1928), Eumorphoceras Zone, England, UK.

Last: Ramosites praesagus (Ruzhentsev and Bogoslovskaya, 1978), Gastrioceras Zone, Middle Asia.


First: Cymoceras miseri McCabe, 1964, Bloyd, upper Morrowan Series, Arkansas, USA.

Last: Neodimorphoceras (Neodimorphoceras) texanum (Smith, 1903), Graham Formation, Virgilian series, Texas, USA.

Comment: Tendency of subdividing ventral portion of suture.

Superfamily GASTRIOCERATACEAE Hyatt, 1884


First: Various species of Glaphyrites and related genera in Europe, Asia and North America.

Last: Neoshumardites triceps (Ruzhentsev, 1936), Aktastinian Stage, southern Urals, former USSR.

Comment: This family is closely linked with the Cravenoceratidae and the Gastrioceratidae.

F. HOMOCERATIDAE Spath, 1934

First: Homoceras subglobosum (Bisat, 1924), Homoceras Zone, England, UK.

Last: Umbetoceras aravanense (Ruzhentsev and Bogoslovskaya, 1978), Middle Asia.


First: Reticuloceras compressum (Bisat and Hudson, 1943), Reticuloceras Zone, England, UK.

Last: Melvilloceras sabinense Nassichuk, 1975, upper Morrowan Series, Melville Island, Arctic Canada.

F. GASTRIOCERATIDAE Hyatt, 1884

First: Gastrioceras sigma Wright, 1926, upper Reticuloceras Zone, England, UK.

Last: Gastrioceras glenisteri Nassichuk, 1975, Ellesmere Island, Arctic Canada.

Comment: The majority of gastrioceratids appeared for the first time in the Yeadonian Stage, with various species of Cancelloceras.

Superfamily THALASSOCERATACEAE Hyatt, 1900


Last: Neoglaphyrites satrus (Maximova, 1940), southern Urals, former USSR (Nassichuk, 1975).


First: Eothalassoceras inexpectans (Miller and Owen, 1937), lower Missourian Series, Oklahoma, USA.

Last: Epithalassoceras ruzenceti Miller and Furnish, 1940, Coahuila, Mexico (Miller and Furnish, 1940).

Comment: Tendency of increasing digitation of the lobes, but no increase of sutural elements.

Superfamily SCHISTOCERATACEAE Schmidt, 1929


First: Phaneroceras compressum (Hyatt, 1891), upper Morrowan Series, Oklahoma, USA (McCaleb, 1968).

Last: Pseudoparalegoceras tzvetaeae Ruzhentsev, 1951, Podolskian Stage, Kazakhstan, former USSR.


First: Branneroceras branneri (Smith, 1896), upper Morrowan Series, Arkansas, USA.
**Schistoceras uralense** Ruzhentsev, 1939, Orenburgian Stage, southern Urals, former USSR.

**Comment:** Additional suture elements in umbilical area.

F. **ORULGANITIDAE** Ruzhentsev, 1965

C. (BSH) Mar.

**First:** Yakutoceras albidicum Popov, 1965, Omolon Massif, eastern Siberia, former USSR.

**Last:** Ruzhentsev and Ganelin, 1971, Omolon Massif, eastern Siberia, former USSR (Ruzhentsev and Ganelin, 1971).

**Comment:** These are triangularly coiled ammonoids, restricted to the upper Bashkirian strata of eastern Siberia. This endemic group is thought to be derived from the Schistoceratidae.

F. **WELLERITIDAE** Plummer and Scott, 1937


**First:** Axinolobus modulus Gordon, 1961, upper Morrowan Series, Arkansas, USA.

**Last:** Wellerites mohri Plummer and Scott, 1937, Desmoinesian Series, Texas, USA.

F. **CHRISTIOCERATIDAE** Nassichuk and Furnish, 1965

C. (MOS) Mar.

**First and Last:** Christioceras trifurcatum Nassichuk and Furnish, 1965, Atokan, Arctic Canada and Texas, USA.

**Comment:** This family is based on Christioceras only, with its distinctive trifurcation of all external lobes, probably a descendant of the Schistoceratidae.

**Superfamily GONIOLOBOCERATACEAE** Spath, 1934

F. **WIEDEYOCERATIDAE** Ruzhentsev and Bogoslovskaya, 1978


**First:** Donetzoceras donetzense (Librovich, 1939), C. (BSH), Donbass, former USSR.

**Last:** Wiedeyoceras sanctijoizanis Wiedey, 1929, C. (MOS), Desmoinesian Series, Iowa, USA (Furnish and Spinosa, 1968).

**Comment:** If the peculiar form Pennoceras seamani Miller and Unklesby, 1942 from the Missourian Series of Pennsylvania, USA belongs here, the range of the family ends later (KAS). This genus differs from the Wiedeyoceratidae in its straight, prominent ribbing.

F. **GONIOLOBOCERATIDAE** Spath, 1934

C. (MOS)–P. (ASS) Mar.

**First:** Gonioloboceratoides curvatus Nassichuk, 1975, Atokan Series, Ellesmere Island, Arctic Canada.

**Last:** Mescalites discoidalis (Böse, 1920), New Mexico, USA (Furnish and Glenister, 1971).

**Comment:** This family comprises only three genera, and is probably an artificial grouping of evolved goniolitids.

F. **PARAGASTRIOCERATIDAE** Ruzhentsev, 1951

P. (ASS)–Tr. (GRI) Mar.

**First:** Stretlandoceras spp., widespread, but documented best from the Urals, former USSR (Ruzhentsev, 1951) and Western Australia (Glenister et al., 1990).

**Last:** Pseudogastrioceras spp., Bed ACT 31 with Metophiceras (GRI, 1–2), Meishan, Zhejiang Province and elsewhere, China (Wang, 1984).

**Comments:** Paragastrioceratids in which growth lines form a ventral salient (Paragastrioceratinae) are restricted to the Lower Permian (ASS–ART, Baigendzhinian Substage), whereas those with a shallow to deep hyponomic sinus (Pseudogastrioceratinae) characterize the Upper Permian (Mikes et al., 1988).

F. **METALEGOCERATIDAE** Plummer and Scott, 1937


**First:** Juresanites spp., locally abundant in the Boreal Realm, but documented best from the Ursals, former USSR (Ruzhentsev, 1952), Western Australia and Timor (Glenister et al., 1973).

**Last:** Clinolobus telleri (Gemmellaro, 1887), Sosio Limestone, Sicily, Italy.

**Comments:** Metalegoceratinae are the most abundant representatives of the family, and characterize the Lower Permian (ASS–ART, Baigendzhinian Substage). Other subfamilies extend through the Lower Permian (ROD). The monotypic Clinolobinae are recognized herein as the youngest Metalegoceratidae, extending as rare elements into the Upper Permian (WOR).

**Superfamily SHUMARDITACEAE** Plummer and Scott, 1937

F. **SHUMARDITIDAE** Plummer and Scott, 1937


**First:** Aktubites trifidus Ruzhentsev, 1955, ?MOS, southern Urals, former USSR.

**Last:** Shumardites spp., abundant in Orenburgian of the Ursals, former USSR (Ruzhentsev, 1950) and Virgilian of Texas, USA (Miller and Downs, 1950).

F. **PERRINITIDAE** Miller and Furnish, 1940


**First:** Properrinites bakeri (Plummer and Scott, 1937), Wolfcampian, Texas, New Mexico, Kansas, USA (Thalasson, 1984).

**Last:** Perrinites vidriensis Böse, 1919, Roadian, Texas, Oklahoma, New Mexico, Arizona, USA; Coahuila, Mexico; Venezuela; Colombia; Afghanistan.

**Comment:** Identity of the shumarditid ancestor of Properrinites is uncertain (Thalasson, 1984). Perrinitidids characterize Tethyan faunas, but are virtually absent from the Boreal Realm.

**Superfamily CYCLOLOBACEAE** Zittel, 1895

This superfamily originated from the marathontacean family Marathonitidae, and diversified in the Permian to range through that system. Their rapid evolution (especially in the late Permian) and general abundance make them one of the biostratigraphically most useful groups of Permian ammonoids.
F. VIDRIOCERATIDAE Plummer and Scott, 1937
   C. (GZE)–P. (DOR) Mar.

First: Vidrioceras spp. (the only Carboniferous representative), Virgilian, Texas and Kansas, USA (Plummer and Scott, 1937); Orenburgian, southern Urals, former USSR (Ruzhentsev, 1950).

Last: Stacheceras spp., widespread in uppermost Permian (DOR).

Comment: Total number of lobes increased during phylogenesis from twenty to more than fifty, but denticulation remained confined to lobe bases.

F. CYCLOLOBIDAE Zittel, 1895

First: The family were derived in ROD from Vidrioceratidae, and diversified rapidly before the late Permian.

Last: Changsingoceras spp., DOR, Zhejiang, China (Zhao et al., 1978).

Comment: The origin of the Marathonitidae in the Atokan is probable, and definite occurrences commence in the overlying Desmoinesian. The family represents a dominant ammonoid stock from the GZE (Missourian) through the WOD.

Superfamily MARATHONITACEAE Ruzhentsev, 1938

F. MARATHONITIDAE Ruzhentsev, 1938


Last: Pseudovidrioceras pygmaeum (Gemmellaro, 1887), Soiso limestone, WOD, Italy (Sicily) (Glenister and Furnish, 1988a).

Comment: During phylogenesis, the prongs of the ventral lobe became strongly expanded, the number of external lobes across the flanks to umbilical shoulders increased from three to 12 pairs, denticulation of lobes extended almost to the crest of saddles, and the sutural traces became strongly arched.

Superfamily PROLECANITACEAE Gehling, 1986

F. PROLECANITIDAE Miller and Furnish, 1957

First: Leeites leei (Glenister and Furnish, 1987), Riepetown Formation, Nevada, USA.

Last: Hyatoceras subgeinitzi Haniel, 1915, Amarassi Beds, Indonesia (Timor). Comparative forms are known from correlative strata, Beihua Mts (Yangtze), southern China (Zhao et al., 1978).

Comment: The origin of the Marathonitidae in the Atokan is probable, and definite occurrences commence in the overlying Desmoinesian. The family represents a dominant ammonoid stock from the GZE (Missourian) through the ART (Lower Permian).

F. HYATTOCERATIDAE Miller and Furnish, 1957

First: Protopopanoceras sublahuseni (Gerassimov, 1937), platform adjacent to southern Urals, former USSR (Ruzhentsev, 1951).

Last: Epitauroceras soewarnoi Glenister and Furnish 1988b, Amarassi Beds, Indonesia (Timor).

Comment: This ancestral family originated in the ASS with one rare, diminutive species. Size, abundance and diversity increased to a maximum in the ‘middle’ Permian (ART through WOD). Thereafter, the group declined to eventual extinction ending with a rare paedomorphic relic in the basal DZH Stage, substantially before the end of the Permian (Glenister and Furnish, 1988b).

F. MONGOLOCERTIDAE Ruzhentsev and Bogoslovskaya, 1978

First: Mongoloceras omanicum Glenister and Furnish, 1988b, base of Hamrat Dura Group, WOD, Ba’ad area, Oman.


Comment: This family is rare; morphology and stratigraphical occurrence are both poorly known. Its early Permian history, after presumed divergence from primitive popanoceratids, is unknown (Glenister and Furnish, 1988b).

Superfamily ADRIANITACEAE Schindewolf, 1931

F. ADRIANITIDAE Schindewolf, 1931

First: Dunbarites n. sp. Chatelain, 1984, Desmoinesian, Wewoka Formation, Oklahoma, USA.

Last: Epadrianites timorensis (Boehm, 1908) and E. involutus (Haniel, 1915), Amarassi Beds, Indonesia (Timor).

Comment: A gradation in conch form, sculpture and sutural complexity exists between virtually all adrianitids, and this major complex constitutes the Adrianitinae (Upper Carboniferous, GZE (Missourian)–Upper Permian (DZH)). Rare monotypic extremes in conch form are recognized as the primitive Dunbaritinae (Upper Carboniferous, MO–GZE (Desmoinesian–Virgilian)) and advanced Hoddmanniinae (Upper Permian, WOR), and rounded lobes with parallel sides characterize the Texoceratinae (Lower Permian, ROD). The family is normally rare, with abundance and diversity greatest in GU (WOR). Suprafamilial homeomorphs exist in some associated taxa, especially Agathiceratidae, but represent a distinctive separate lineage.

Order PROLECANITIDA Miller and Furnish, 1954

Superfamily PROLECANITACEAE Hyatt, 1884

F. PROLECANITIDAE Hyatt, 1884

First: Eocanites nodosus (Schmidt, 1925), Gattendorfia Zone, Rheinisches Schiefergebirge, Germany.

Last: Metacanites chancharensis (Gerassimov, 1937), Amarassi Beds, Indonesia (Timor).

Comment: Tendency of increase of lateral suture elements.

F. PRODROMITIDAE Arthaber, 1911
   C. (TOU) Mar.

First: Eoprodomites kinderhooki Work et al., 1988, Kinderhookian Series, Missouri, USA (Work et al., 1988).

Last: Acrocanites tornacensis Delepine, 1940, Pericyclus Zone, Belgium (Weyer, 1972).

Comment: This family comprises multilobate forms, some of them exhibiting serrate lateral lobes.

F. DARAELITIDAE Tchernov, 1907

First: Pracanaelites culmiensis (Kobold), Goniatites Zone, upper VIS, Rheinisches Schiefergebirge, Germany.
Last: *Daraelites* meeki Gemmelaro, 1888, Sosio Beds, Sicily, Italy.

**Comment:** Digitate lateral suture elements.

**Superfamily** MEDICOTTIACEAE Karpinsky, 1889

F. **PRONORITIDAE** Frech, 1901 C. (VIS)–P. (DZH) Mar. (includes the SHIKHANITIDAE Ruzhentsev, 1951)

**First:** Pronorites cyclolobus (Phillips, 1836), Goniatitidae Zone, upper VIS, England (Kullmann, 1963).

**Last:** gen. and sp. nov., Glenister et al., in prep., Amarassi Beds, Timor, Indonesia. This genus is interpreted as a terminal pronoritid paedomorph, characterized by small size, sutural simplification and low abundance, and conforming to the pattern displayed by many family-level Upper Palaeozoic ammonoid taxa (Glenister and Fumish, 1988a,b).

**Comment:** Ancestral medlicotitaceans characterized by moderately evolute conch and relatively simple sutures.

**F. MEDICOTTIIIDAE** Karpinsky, 1889

C. (KAS)–Tr. (NML) Mar.

**First:** Prouddenites n. sp., Chatelain, 1984, Wewoka Formation, Desmoinesian Series, Oklahoma, USA; next oldest is *Prouddenites primus* Miller, 1930, Missourian Series, Missouri, USA.

**Last:** Episageceras noetlingi Haniel, 1915, with *Anasibirites* (NML, 4), Timor (Shevyrev, 1986); *Latisageceras* Ruzhentsev, 1956 is known from GRI of Pakistan (Salt Range) and possibly Indonesia (Timor), with *Episageceras* spp.

**Comments:** This family comprises advanced medlicottaceans characterized by involute conch and complex sutures. Each suture comprises a total of 13 to approximately 30 lobes. The ventral prong of the broad, primary, lateral lobe was transformed during phylembryogenesis into a progressively more complexly subdivided ventrolateral saddle. The family comprises *Uddenitinae* (MOS–DZH), *Medlicottiinae* (CZE–Vigiljan–DZH), *Sicanitinae* (ASS–WOR), *Propinacoceratinae* (ASS–DZH), and *Episageceratinae* (DZH–NML). An expanded Episageceratidae Ruzhentsev, 1956 (ASS–NML, 4) was recognized as an alternative by Shevyrev (1986).


**First and Last:** This is a monotypic family, with undoubted representatives known only from the Amarassi Beds, Timor, Indonesia.

**Order** CERATITIDA Hyatt, 1884

**Suborder** OTOCERATINA Shevyrev and Ermakova, 1979

The affinities of the Permian 'Ceratitida' were reviewed by *Spinosa* et al. (1975), Zhao et al. (1978), Shevyrev and Ermakova (1978), Shevyrev (1986) and Zakharov (1988). If the base of the Triassic continues to be defined as the base of the *Otoceras woodwardi* ammonoid zone, then the Otoceratina survived the late Permian interval of extinction to extend into the earliest Triassic (GRI).

Fig. 10.3

F. KASHMIRITIDAE Spath, 1930 Tr. (GRI–SPA) Mar.
First: Metopiceras trivale Spath, 1930, Wordie Creek Formation, Concavum Zone (GRI, 1), East Greenland (Trümper, 1969).
Last: Hemilecanites cf. paradiscus Kummel, 1969, Welteri Beds, Prida Formation (SPA, 3b), Star Creek Canyon, Nevada (Bucher, 1989).

First: Tirolites injucundus Krafft and Diener, 1909, Spiti Beds, Nepal (Wang, 1985), T. cassianus (Quenstedt, 1849) is SPA, 1 index (Krystyn, 1974).
Last: Tirolites carniolicus Mojsisovics, 1882 and T. mangyshlakensis Shevyrev, 1968, 20 m below Gutensteinr dolomit, Campill Beds, former Yugoslavia (Krystyn, 1974).

F. DINARITIDAE Mojsisovics, 1882 Tr. (SPA) Mar.
First: Dorikranites bogdanus (Buch, 1831) and D. disoides (Astashkova, 1960), Dorikranites Beds (SPA, 1), Mangyshlak, eastern Caspian Sea. Dorikranites cf. dalmatinus (Hauer, 1865), 20 m up the Campill Beds (SPA, 1), former Yugoslavia (Krystyn, 1974; Dagys et al., 1979).
Last: Stachites concanus Shevyrev, 1968, Stachites Beds (SPA, 37), Mangyshlak. Dorikranites sp., Unit C (SPA, 37), Kialingkiang Group, Weiyuan, Szechwan Province, China (Wang, 1985).

Comment: Shevyrev (1986) separated a monogeneric Dorikranitidae Astachova, 1960, but indicated that it is most closely related to this family. Tozer (1981a) subordinated it to the Tirolitidae.

F. COLUMBITIDAE Spath, 1934 Tr. (SPA) Mar.
First: Columbites parisianus Hyatt and Smith, 1905, middle shale unit, Thaynes Formation (SPA, 1), Utah (Silberling and Tozer, 1968).

First: Kazakhstanites pilatoides Guex, 1978, Bed 6d at Zaluch, Pluriformis Zone (NML, 4), former USSR. Parasibirites granbergi (Popov, 1961), lower Spiniplicatus Zone (SPA, 1), Lena–Anabar region, former USSR (Dagys et al., 1979, p. 38; Guex, 1978).
Last: Kazakhstanites dolnapensis Shevyrev, 1968, Mangyshlak (SPA, 27) and Sibirites eichwaldi (Keyserling, 1845), upper Spiniplicatus Zone (SPA, 2), Lena–Anabar region, former USSR (Dagys et al., 1979, p. 39).

Comment: Shevyrev (1986) accepts that the monogeneric Kazakhstanitidae Shevyrev, 1986 are most closely related to...
this family and restricts the range to his Parisianus and McKelvei Zones (SPA, 2–37).

**Suborder ARCESTINA** Hyatt, 1884, s.l.

**F. PARANANNITIDAE** Spath, 1930

**First:** Dwarf *Melagathiceras crassus* (Tozer, 1961), *Juvenites canadensis* Tozer, 1961 and Paranannites spathi (Frebold, 1930), 0.6-mm-thick *Meokoceras bed of Romunderi Zone* (NML, 3), Blind Fiord Group, Ellesmere Island (Tozer, 1965, 1984).

**Last:** *Isclitoides* sp. A of Bucher (1989), upper *Hauji Zone* (SPA, 3a), Prida Formation, northern Humboldt Range, Nevada, USA.

**Comment:** The dwarf and cosmopolitan Melagathiceratidae Tozer, 1971 are sometimes associated with one of the largest Triassic ammonoids, the 550-mm-diameter *Hedenstroemia*, and has the same limited stratigraphical range (NML, 3). Shevyrev (1986) interprets it as the ancestral form of this family. Actually it has the same first record and may be considered as a minor initial variant of a stock which produced the Arcestina s.s.

**F. PARAPOPANOCERATIDAE** Tozer, 1971

**First:** *Proshpingites czekanowski* Moshovisics, 1886, 8-mm-thick upper *Spiniplicatus Zone* (SPA, 27), Lena–Anabar region, former USSR (Dagys et al., 1979, p. 49; Arkadiev and Vavilov, 1984). A more morphological definition of the family yields a slightly later first record: *Stenopapparoceras karangatiense* (Popov, 1968) and *S. mirabile* Popov, 1961, Last: *Amhippaparoceras dzeginem* (Voinova, 1961), Humboldtensis Zone (SPA, 8), Kolyma Basin, Siberia (Dagys et al., 1979, p. 72).

**F. STURIDAE** Kiparisova, 1958

**First:** *Ziyunites ziyunnensis* Wang, 1978, 0.2-mm-thick *Ziyun limestone* (SPA, 2 or condensed), Guizhou Province, China. *Ziyunites assereti* Fantini Sestini, 1981 and *Stuaria sp.*, Bed T329 Chios, Greece (SPA, 3-ANS, 27); *Polosturia* and *Eosturia* in rocks of similar age elsewhere (Wang, 1985; Shevyrev, 1986; Bucher, 1989).

**Last:** *Sturia karpinskyi* Mojsisovics, 1902; the CRN of Alps record is not verified by modern stratigraphy (Tozer, 1980a, 1981a). *Sturia semiarata* Mojsisovics, 1882, Unit 5 with LAD, 4 *Doloceras* fauna, upper *Laibuxi Formation*, Tulong, Tibet (Wang and He, 1980, upper *Protrachyceras–Joannites bed*).

**F. ISCULITIDAE** Spath, 1951

**First:** *Isclites meeki* (Hyatt and Smith, 1905), *Caurus Zone* (ANS, 2), Prida Formation, Humboldt Range, Nevada, USA (Silberling and Nichols, 1982).

**Last:** *Isclites assereti* Fantini Sestini, 1988, upper *Ismidicun Zone* (ANS, 5), Nodular Limestone of Gebze, Turkey (Fantini Sestini, 1988).

**F. PTYCHITIDAE** Mojsisovics, 1882

**First:** *Mallettophytites kotschetkovi* Popov, 1961, *Decipiens Subzone* (ANS, 5), Lena–Anabar Region, former USSR (Dagys et al., 1979, p. 40).

**Last:** *Aristophytites kolymaensis* (Kiparisova, 1937), Mconnelli Subzone (LAD 4–5), Omulevsk region (Dagys et al., 1979, p. 93).

**F. CLADISCITIDAE** Zittel, 1884

**First:** *Procladiscites simplex* Wang, 1978, 0.2-mm-thick *Ziyun limestone* (SPA, 2 or later), Guizhou Province. *Procladiscites sp.* of *Procladiscites beds* and Bed T329 Chios, Greece (Wang, 1985; Bucher, 1989 imply SPA).

**Last:** *Cladiscites sp.* and *Procladiscites sp.*., middle member, Gabb Formation (RHT 3a), New York Canyon, Nevada (Silberling and Tozer 1968, Tozer, 1980). *Cladiscites sp.*, *Marshii Zone* (RHT 3), Koessen Beds, Austria (Krystyn, 1973).

**F. ARCESTIDAE** Mojsisovics, 1875

**First:** *Proarcestes from Usmani Zone* (ANS, 3) implied by Shevyrev (1986). *Proarcestes braamtel* (Mojsisovics, 1869), upper *Ismidicum Zone* (ANS, 5), Nodular Limestone of Gebze, Turkey (Fantini Sestini, 1988).

**Last:** *Arcestes sp.*., upper member, Gabb Formation (RHT 3b), Nevada. A. *rheticus*, Clark, 1887 and A. *tenus* Pompejek, 1895, Koessen Beds (RHT, 3b?), Austria. *Stenarcestes polysphinctus* (Mojsisovics, 1875), Koessen Beds (RHT, 3a?), Austria (Silberling and Tozer, 1968; Krystyn, 1973; Tozer, 1980).

**F. JOANNITIDAE** Mojsisovics, 1882

**First:** *Arcestes compressus* Wang and He, 1976, Bed JSB 83b, *Rugifer Zone* (ANS, 7), Laibuxi Formation, Tulong, southern Tibet (Wang and He, 1980).

**Last:** *Joannites cymbiformis* Wolfen, 1793, *Austriacum Subzone* (CRN, 2a), Feuerkogel, Austria (Krystyn, 1973) and the *Sirenetes nanseni* Zone of China.

**F. SPHINGITIDAE** Arthur, 1911

**First and Last:** *Sphingites coangustatus* (Hauer, 1860) and spp., Bed 70/78 in lower *Anatropites Bereich*, Feuerkogel (CRN, 5), Austria (Krystyn, 1973). All the typical species of the genus are described as CRN in the old literature and it is not clear why this age was revised to LAD–2CRN by Tozer (1981a) and LAD, 3–CRN, 1 by Shevyrev (1986).

**F. LOBITIDAE** Mojsisovics, 1875


**Last:** *Coroceras cf. suessi* (Mojsisovics, 1875), *Sirenetes nanseni* Zone (CRN, 2), Kupreanof Island, Alaska, USA (Silberling and Tozer, 1968).

**F. MEGAPHYLLITIDAE** Mojsisovics, 1896


**Last:** *Megaphyllites robustus* Wiedmann, 1973, *Zlambach Beds*, Grünbachgraben, Austria. M. *bohmi* Pompejek, 1895 and M. *insectus* Mojsisovics, 1873, Koessen Beds and White Crinoidal Limestone of Steinbergkogel, Austria. Shevyrev
implies that *Megaphyllites* died out later than the index of the *Marshi* Zone (RHT 3b).

**Comment:** Shevyrev (1986) and other authors have regarded this family and the Lobitidae as separate problematic suborders with an affinity with the Acestina. Previous comparisons with *Nathorites* and *Parapopanoceras* are plausibly rejected (Arkadiev and Vavilov, 1984). The derivation of the general morphology of *Megaphyllites* from *Procarinites* (Wang, 1985) is opposed by Shevyrev (1986), who favours an origin in the early Paranannitidae.

The next suborder (*Sageceratina*) was independently derived from the Medlicottiaceae by Zacharov (1988), but is united here with the Ceratitida as suggested by Shevyrev (1986).

**Suborder SAGECERATINA** Shevyrev, 1983 s.l.

F. **OPHICERATIDAE** Arthaber, 1911

**Tr. (GRI–SPA)** Mar.


**Last:** *Nordopheris schmidti* Mojsisovics, 1886 and N. sp., upper *Spiniplicatus* Zone (SPA, 2?), Lena–Anabar region (Dagys et al., 1979, p. 49).

F. **PROPTYCHITIDAE** Waagen, 1895

**Tr. (GRI–SPA)** Mar.

**First:** *Propychites* sp. of Bando (1981), Bed 56 at Guryul, middle *Woodwardi* Zone (GRI, 27), Kashmir. *P. strigatus* Tozer, 1961 and P. *rosenkrantzi* Spath, 1930, 30 m above *Boreale* Zone, Blind Fiord Group (GRI, 4), Griesbach Creek, Axel Heiberg Island (Tozer, 1965).


**Comment:** This family links the Sageceratina *sensu* Shevyrev (1986) with the ancestral Ophioceratidae in his phylogenetic interpretation.

F. **KHVALYNITIDAE** Shevyrev, 1968

**Tr. (SPA–ANS)** Mar.

**First:** *Khvalynites mangyshlakensis* Shevyrev, 1968, *Parisianus Zone* (SPA, 2), Mangyshlak, Transcaspia (Shevyrev, 1986).

**Last:** *Ismidites marmarensis* Arthaber, 1914, upper *Ismidicum* Zone (ANS, 5), Nodular Limestone of Gebze, Turkey (Fantini Sestini, 1988).

F. **LANCEOLITIDAE** Spath, 1934

**Tr. (NML–ANS)** Mar.

**First:** *Lanceolites compactus* Hyatt and Smith, 1905, *Gracilitatus Zone* (NML, 3), California, USA (Silberling and Tozer, 1968).


**Comment:** The septal sutures of *Metadagnoceras* and *Dagnoceras* link them to the more involute and compressed *Lanceolitidae* (NML, 3-SPA, 3) of Shevyrev (1986).

F. **ARCTOCERATIDAE** Arthaber, 1911

**Tr. (NML)** Mar.

**First and Last:** *Arctoceras polare* (Mojsisovics, 1886), Fish Beds, Sassendal (NML, 3), Spitsbergen. *A. mushbachanum* (White, 1879), USA and Siberia, also correlated with *Romunderi Zone* (Dagys et al., 1979).

F. **USSURIIDAE** Spath, 1930

**Tr. (NML–SPA)** Mar.

**First:** *Metussuria waageni* (Hyatt and Smith, 1905), *Gracilitatus Zone* (NML, 3), Idaho and Utah, USA (Silberling and Tozer, 1968).

**Last:** *Parussuria latilobata* Zhao, 1959, *Columbites asymmetricus* Zone (SPA, 1), Linglo, Guangxi Province, China (Wang and He, 1980). Shevyrev (1986) only accepted NML, 3.

F. **SAGECERATIDAE** Hyatt, 1884

**Tr. (NML–CRN)** Mar.

**First:** *Pseudosageceras multilatum* Noetling, 1905, Lower Limestone and Ceratite Marl, Chideru (NML, 17), Salt Range, Pakistan. Modern records are later and include *Sverdrupi Zone* (NML, 2), Blind Fiord Group, Axel Heiberg Island (Tozer, 1965) and Bed 15 at Tulong (NML, 3) in southern Tibet (Wang and He, 1980).

**Last:** *Sageceras haidingeri* (Hauer, 1847), Bed 70/6 at Feuerkogel, *Austriaucum Subzone* (CRN, 2a), Austria (Krysyn, 1973).

F. **NORITIDAE** Karpinsky, 1889

**Tr. (SPA–LAD)** Mar.

**First:** *Metahedenstroemia castriotoe* (Arthaber, 1911) and *Beatties berthoe* Arthaber, 1911, *Subcolumbites Beds* (SPA, 2), Kēira, Albania.

**Last:** *Norites subcarinatus* (Hauer, 1887), *Avisianum Zone* (ANS, 9), Zgorigrad, Bulgaria, and allies ranging up to Bed 162 of *Grenzbiteminenzone* (LAD, 1), Monte San Giorgio, Switzerland (Rieber, 1973; Barnes, 1986). *Neo­clypites desertorum* Johnson, 1941, New Pass, Nevada and Neo­clypites? *perigrinus* Müller, 1973, Grenzdomolit, Reisdorf (CRN, 1), were accepted as isolated records by Shevyrev (1986). They are reinterpreted as a later offshoot of the *Sageceras* here.

F. **BENEKEIIDAE** Waagen, 1895

**Tr. (SPA–ANS)** Mar.


**Last:** *Beneckia levantina* Barnes, 1962, middle Gevanim Formation, Makhlesh Ramon, Israel (ANS, 6–77 of Barnes, 1986).

**Comment:** This rather unsatisfactory monogeneric family could be a polyphyletic group of the *Sageceratidae* in a marginal marine facies.

F. **PROCARNITIDAE** Zhao, 1959

**Tr. (SPA)** Mar.

**First:** *Procarinates oxynostus* Zhao, 1959, *Columbites asymmetricus* Zone (SPA, 1), Linglo, Guangxi Province, China (Wang and He, 1980).

**Last:** *Neopopanoceras haugi* (Hyatt and Smith, 1905), upper *Hauzi* Zone (SPA, 3a), Union Wash and Prida Formations, Nevada (Bucher, 1989).
F. ASPENITIDAE Spath, 1934 Tr. (NML) Mar.

First and Last: Aspenites acutus Hyatt and Smith, 1905, Gracilitatus Zone (NML, 3), Aspen Mountains, Idaho, USA and elsewhere (Silberling and Tozer, 1968).

Comment: The tentative extension of the range to SPA by Shevyrev (1986) was based on Beatites: here transferred to the Noritidae.

F. HEDENSTROEMIIDAE Waagen, 1895 Tr. (NML) Mar.

First: ?Clypeoceras crassum (Krafft, 1909), Bed JSB 10 of Kamshare Formation, Psilograpsus Zone (NML, 1), Tulung, southern Tibet (Wang and He, 1980; Shevyrev, 1986).

Last: Hedenstroemia hedenstroemi (Keyserling, 1845), Hedenstroemi Zone (NML, 3), Verkhoyansk (Dagys et al., 1970, p. 27). Tozer (1981a) plausibly restricted the range of the family.

Suborder PINACOCERATINA Waagen, 1895 s.l.

F. MEEKOCERATIDAE Waagen, 1895 Tr. (NML) Mar.

First: Gyronites plicatilis (Waagen, 1895), Bed 6b, upper Lower Ceratite Limestone, defines base of NML, 1, Nammal, Pakistan (Guex, 1978).


Comment: The Meekoceratidae s.s. (NML, 1–3) appear to continue as the Prionitidae Hyatt, 1900 (NML, 3–4) and closely allied Inyoitidae Spath, 1934 (NML, 3), rather than the stratigraphically isolated Proavites. Shevyrev (1986) derived Inyoites from the Prionitidae, but it could be a variant of the frequently associated Anasibrites.

F. STEPHANITIDAE Arthaber, 1896 Tr. (NML) Mar.


F. FLEMINGITIDAE Hyatt, 1900 Tr. (NML–SPA) Mar.

First: Flemingites rohilla Diener, 1897, Bed JSB10 at Tulung, Kangshare Formation, Psilograpsus Zone (NML, 1), southern Tibet (Wang and He, 1980).

Last: Preflorianites sp. (cf. P. intermedius Tozer, 1965), upper Haugi Zone (SPA, 3a), Prida Formation, Nevada, USA (Bucher, 1989).


F. GYMNITIDAE Waagen, 1895 Tr. (ANS–RHT) Mar.

First: Gymnmites billingsii Bucher, 1989, Mulleri Zone (ANS, 1), Prida Formation, Humboldt Range, Nevada, USA (Bucher, 1989).

Last: Placites sp., middle member, Gabbs Formation (RHT, 3a), Nevada and Sutton Formation, British Columbia, Canada (Silberling and Tozer, 1968; Tozer, 1980).


First: Pompeckites layeri (Hauer, 1847), basal bed 68/58 Feuerkogel, Aon Subzone (CRN, 1a), Austria (Krystyn, 1973). Tozer (1981a) cites LAD–CRN.

Last: Pinacoceras sp., middle member, Gabbs Formation (RHT, 3a), Crickmayi Zone, Nevada (Silberling and Tozer, 1968). P. metternichii (Hauer, 1846), highest bed 68/55 or Rotkalk, Sommeraukogel, Suessi Zone (RHT, 1–2), Austria (Krystyn, 1973; Tozer, 1980).

Suborder CERATITINA Hyatt, 1884

The phylogenetic interpretation of Shevyrev (1986) is modified by the linkage of the Paraceratitinae Silberling, 1962 to Eoprotarchyceras, and changes made by Krystyn (1982) and Krystyn and Wiedmann (1985) to late Triassic systematics. The Phylloceratida and other orders reviewed by Page (this vol.) were derived from the Flemingitidae (above) in Shevyrev (1986) and appear to be allied to the Ceratitina.

Superfamily CLYDONITACEAE Mojsisovics, 1879 s.l.


First: Hyrcanites nodosus Shevyrev, 1968, Mangyshlak, Transcaucasia, former USSR, Harti Zone (SPA, 1) of Shevyrev (1986). Olenikites spiniplicatus (Mojsisovics, 1886), lower Spiniplicatus Zone (SPA, 1), Lena–Anabar region, former USSR (Dagys et al., 1979).

Last: Olenekites sp. indet., upper Haugi Zone (SPA, 3a), Nevada (Bucher, 1989). O. canadenis Tozer, 1961, 72 m up Blind Fjord Group, Subrobustus Zone (SPA, 3a), Ellesmere Island (Tozer, 1965).


Last: Natherstites concentricus (Oeberg, 1877) (=N. gibbosus Stolley, 1911), Tenuis Zone (LAD, 5 or CRN, 1), Spitsbergen and Yana–Kolyma region, Siberia, former USSR (Dagys et al., 1979, p. 81; Tozer, 1981b; Arkadiiev and Vavilov, 1984).

Comment: A combination of ontogenetic and stratigraphical work has produced an arbitrary boundary between this family and the Natherstitidae Spatt, 1951, at the base of strata bearing Indigrites krugi Popov, 1961 (LAD, 3a of Siberia). Since there is no indication of lineage bifurcation, the two so-called families can be combined, although this was not advocated by Arkadiiev and Vavilov (1984, 1989).

First: Karangatites multicameratus (Smith, 1914), upper Haugi Zone (SPA, 3a), Prida Formation, Nevada, USA (Bucher, 1989).

Last: Epiceratites elevatus (Dittmar, 1866), Halstadt Limestone, Austria, CRN, 4–5 according to Tozer (1981a) and Shevyrev (1986).

Comment: The relatively limited and stratigraphically correlated intraspecific variation of Aplococeras species was investigated in a pioneer statistical study by S. Bubnoff (Spath, 1951) and Silberling and Nichols (1982). Thus the family is likely to be a monophyletic group, rather than polyphyletic dwarfs produced by the ecophenotypic starvation of macromorphs.

F. PROTEUSITIDAE Spath, 1951 Tr. (ANS) Mar.

First: Tropigastrites lahontanus Smith, 1914, base of Rotelliformis Zone (ANS, 7), Humboldt Range, Nevada, USA (Silberling and Nichols, 1982). Proteusites kelneri Hauer, 1887, Trinodosus Zone (ANS, 7), Han Bulog, Bosnia, former Yugoslavia (Spath, 1951).

Last: Tozerites polygyratus (Smith, 1914), upper Nevadites Beds, Occidentalis Zone (ANS, 9), Prida Formation, Humboldt Range, Nevada, USA (Silberling and Nichols, 1982).

Comment: The Tropigastrites–Tozerites lineage of Nevada was associated with similar but less regularly modified Aplococeras, and seems unlikely to be conspecific with this potentially ancestral, long-ranging morphology.

F. NANNITIDAE Mojsisovics, 1884 Tr. (CRN) Mar.

First and Last: Nannites spurius (Münster, 1848), Aonoides Zone (CRN, 1), Cassian Formation, Italy (Shevyrev, 1986).

Comment: Spath (1951) suggested that this rare dwarf morphology was derived from the local aplococeratids, while O. H. Schindewolf showed that the goniatitic septal suture was somewhat different to the associated dwarf Lecanitidae (Shevyrev, 1986). Shevyrev indicates a close phylogenetic position to the latter family and the longer-ranging Celtitidae. Tozer (1981a) rejects the Celtitidae, while maintaining the separate status of the three dwarf families from the Cassian Formation.


First: Thanamites ?contractus (Smith, 1914), Nevadites hombolensis Beds, Occidentalis Zone (ANS, 9), Humboldt Range, Nevada, USA (Silberling and Nichols, 1982). Shevyrev (1986) cited no records before the Archelaus Zone (LAD, 47).


Last: Orthocelites buchi (Klipstein, 1843), Cassian Formation, Italy, Aonoides Zone (CRN, 1) of Shevyrev (1986).

F. LECANITIDAE Hyatt, 1900 Tr. (LAD–CRN) Mar.

First: Lecanites glaucus (Münster, 1834), Pachycardienstufe with Macleanoceras (LAD, 4), Seiser Alm, Austria (Urlichs, 1977). Both Tozer (1981a) and Shevyrev (1986), doubt or overlook LAD records.

Last: Lecanites glaucus (Münster, 1834) and Badiotites eryx (Münster, 1834), Aonoides Zone (CRN, 1), Cassian Formation, Italy (Shevyrev, 1986). Lecanites trauhii Johnson, 1941, Desatoyense Zone (CRN, 1), New Pass, Nevada, USA (Spath, 1951; Silberling and Tozer, 1968).

Comment: The contemporaneous and monogenic Badiotitidae Hyatt, 1900 (CRN, 1) was kept separate by Tozer (1981a) and Shevyrev (1986), although Spath (1951) remarked ‘that Lecanites and Badiotites are not separable into two distinct families’.

F. TROPICELITIDAE Spath, 1951 Tr. (CRN–NOR) Mar.

First: Tropiceratites abalinus (Dittmar, 1866), Bed VII Feuerkogel and elsewhere, Subballatus Zone (CRN, 4), Hallstatt Limestone, Austria (Krystyn, 1973). Tozer (1981a) indicates first occurrence in Dilleri Zone (CRN, 3).

Last: Tropicelites columbianus (McLearn, 1940), Kerri Zone (NOR, 1b), Pardonet Hill, British Columbia, Canada (Tozer, 1981a, 1984). Tropicelites rotundus Mojsisovics, 1893, sample B16, Jandianus Zone (NOR, 1), Hallstatt Limestone, Austria (Krystyn, 1973).


First: Thishites dawsoni (McLearn, 1940), Macrolobatus Zone (CRN, 5), Pardonet Formation, Brown Hill, British Columbia, Canada (Tozer 1981a, 1984). Thishites agricolae Mojsisovics, 1893, Bed IV Feuerkogel, Obere Anatropites–Bereich (CRN, 5b), Hallstatt Limestone, Austria (Krystyn, 1973).


First: Clionitites sp., , Sutherlandia/Regoledanus Zones (LAD, 5), Roten Bankkalk, Epaurodis, Greece (Krystyn and Mariolakos, 1975). The occurrence in the Maclearn Zone (LAD, 4) is cited by E. T. Tozer in Darby et al. (1979). Clionitites rarecostatus (Parnes, 1962), Matsoq Nahal Ramon, Sirentiforme Zone (LAD, 5 of Parnes, 1986), Israel. Clionitites barwick (Johnston, 1941), Desatoyense Zone (CRN, 1), New Pass, Nevada (Johnston, 1941).

Last: Steinmannites sp., mixed Suessi Zone fissure fauna with Cladiscites (RHT, 1–2), Millibrunnkogel, Austria (Tozer, 1980) and elsewhere (Krystyn, 1973).

First: Traskites merriami (Hyatt and Smith, 1905), Dilleri Zone (CRN, 3), California, USA (Silberling and Tozer, 1968).

Last: Sandlingites oribasus (Dittmar, 1866) Hallstatt Limestone, Austria. Sandlingites sp., Subbullatites Zone (CRN, 4), Saltzkammergut area (Krystyn, 1973), and a generic range of CRN, 3–5 (Tozer, 1981a) indicates the age of this species.

F. PALICITIDAE Krystyn, 1982 Tr. (NOR) Mar.


F. NORIDISCIDITAE Spath, 1951 Tr. (NOR) Mar.

First and Last: Noridosicites viator (Mojsisovics, 1893) Hallstatt Limestone, Austria. Nairites armenius Kiparisova and Azarian, 1963 and Nairites laevis Kiparisova and Azarian, 1963, Armenia, former USSR. All from Bicrenatus Zone (NOR, 4) according to Shevyrev (1986).

F. CLYDONITIDAE Mojsisovics, 1879 Tr. (NOR–RHT) Mar.

First: Parathisbites baunensis Tatzreiter, 1980, Bed 12, Watsoni Subzone (NOR, 5a), Limestone block A, Baun, Tirol, Austria. Leislingites pseudoorchibaldi Tatzreiter, 1980, Bed 16, base of Macer Zone (NOR, 6a), block A, Baun, and also ?Lower Suessi Zone (RHT, 1), Timor (Tatzreiter, 1980).

Last: Choristoceras marshi Hauer, 1865, middle Suessi (RHT, 1) to upper Marshi Zones (RHT, 3b), Koessen Beds, Austria (Krystyn and Wiedmann, 1986). The last occurrence of the Thetidiidae Tozer, 1971 is Pseudothetidites praemarsi Krystyn and Wiedmann, 1986, of Bed 18, highest Macer Zone (NOR, 6b), block A, Baun, Tirol. The last occurrence of the CLYDONITIDAE s.s. is Leislingites of the lower Suessi Zone (RHT, 1) cited by Tatzreiter (1980) and Shevyrev (1986).

Comment: Tatzreiter (1980) combined this family with the Thetidiidae Tozer, 1971 and Shevyrev (1986) derived the one directly from the other. Krystyn and Wiedmann (1986) have undermined the Choristoceracea H. Hyatt, 1900 (RHT) by deriving Choristoceras from the last Pseudothetidites. They have a similar morphology, but are separated by a small stratigraphical gap (most of RHT, 1). Shevyrev (1986) suggested that Choristoceras and the early heteromorphic members of the Choristoceracea were derived from Helicites (NOR, 6) of the Metasibiritidae. An expanded Clydonitidae is an alternative source of the heteromorphs and appears to be the last of the Ceratitida in both Nevada (Silberling and Tozer, 1968) and elsewhere (Tozer, 1980).

F. METASIBIRITIDAE Spath, 1951 Tr. (NOR–RHT) Mar. (see Fig. 10.4)


Last: Metasibirites cf. spiniscens (Hauer, 1855), Bed 20, block F, Reticulatus Subzone (RHT, 2) Baum, Timor, and beds of equivalent age at Kotel, Bulgaria (Tozer, 1980; Krystyn and Wiedmann 1986).


First and Last: Lissosites canadensis Tozer, 1979, Upper Cordilleranus Zone (RHT 1b), Pardonet Formation, Ne-Parle-Fas Rapids and elsewhere, British Columbia, Canada. 'Tozerites' (junior homonymn) hernsteini Tatzreiter, 1985 and Psamateiceras saxicastelli Tatzreiter, 1985, Grey Hallstatt Limestone, upper Suessi Zone (RHT, 2), Hernstein, Austria. Also Kotel, Bulgaria (Tatzreiter, 1985; Tozer, 1982).

F. Rhabdoceratidae Tozer, 1979 Tr. (RHT) Mar.

First: Rhabdoceras boreale Aftitsky, 1965, Ochotica Zone (RHT, 1), Siberia (Dagys et al., 1979, p. 153). R. suessi Hauer, 1860, lower Cordilleranus Zone (RHT 1a), Mt. Ludington, USA (Silberling and Tozer, 1968).

Last: Rhabdoceras (?) sp., Zlambach Marl, Grunbachgarten, Austria (Wiedmann, 1977). Rhabdoceras suessi Hauer, 1860, lower Marshi Zone (RHT 3a), Koessen Beds and crinoidal limestone of Steinbergkogel, Austria (Krystyn, 1973; Tozer, 1980).

F. Cyclocelititidae Tozer, 1979 Tr. (RHT) Mar.

First and Last: Cyclocelites cornes Kollarova-Andrusov, 1973, Steurzenbaumi Subzone (RHT 3a), Bleskoy Pramen, Czechoslovakia. C. arduini Mojsisovics, 1882, middle member, Gabbs Formation (RHT, 3a), Nevada, and other contemporaneous records (Tozer, 1980).

F. Cochloceratidae Hyatt, 1900 Tr. (RHT) Mar.

First and Last: Cochloceras fisheri Hauer, 1860 and C. canaliculatum Hauer, 1860, Grey Hallstatt Limestone, Reticularis Subzone (RHT, 2), Steinbergkogel, Austria. C. fisheri, Lower member, Gabbs Formation, Amoebum Zone (RHT, 2), Nevada, USA, and other contemporaneous localities (Tozer, 1980).

Comment: This helicoid spiral was derived from the relatively straight Peripleurites (RHT, 1–2) of the Rhabdoceratidae (Shevyrev, 1986), and should perhaps be united with it.

F. Danubitidae Spath, 1951 Tr. (SPA–ANS) Mar.


Comment: This family was given an important position in the superfamilies of Tozer (1981a) and Shevyrev (1986), but has been classified with the Ceratitaceae in the past, and at least some genera might still be placed there (Spacht, 1951).
Fig. 10.4

Superfamily CERATITACEAE Mojsisovics, 1879 s.l.

F. KEYSERLINGITIDAE Zacharov, 1970
Tr. (SPA–ANS) Mar.

First: Olenekoceras middendorffi (Keyserling, 1845), middle Spiniplicatus Zone (SPA, 1 of Wang, 1985), Lena–Anabar region, former USSR (Dagys et al., 1979, p. 30).

Last: Keyserlingites dieneri (Mojsisovics, 1903), Meridianus Subzone (ANS, 1 or 3), Naocanjian guo, Qinghai Province, China (Wang, 1985; Bucher, 1989). Silberlingites mulleri Bucher, 1989 and S. tregoi Bucher, 1989, Mulleri Zone (ANS, 1), Coyote Canyon, northern Humboldt Range, Nevada, USA (Bucher, 1989).


First: Dimorphic Nicomedites osmani Toula, 1896, base of Osmani Zone and Nodular Limestone of Gebze (ANS, 3), Turkey (Fantini Sestini, 1988).

Last: Frechites johnstoni Silberling and Nichols, 1982, Subaspersum Zone (LAD, 1), Humboldt Range, Nevada, USA (Silberling and Nichols, 1982).

Comment: The inclusion of Serpianites antecedens (Beyrich, 1958) in this family (Shevyrev, 1986), might suggest that 'Paraceratites' binodosus (Hauer, 1850) should be transferred here, and not regarded as the ancestral form of the Trachyceratidae (e.g. Silberling and Nichols, 1982; Urlich and Mundlos, 1985; Tozer, 1981b; Fantini Sestini, 1988). However this 'Paraceratites' shows a larger number of saddles than Serpianities, and the Nevada Berichitidae. Shelyrev (1986) interprets this family as a separate and ultimately infertile lineage.

F. BALATONITIDAE Spath, 1951 Tr. (ANS) Mar.

First: Platycuccoceras bonaevistae (Hyatt and Smith, 1905), lower Hyatti Zone (ANS, 3), Prida Formation, Nevada, USA (Silberling and Nichols, 1982).

Last: Balatonites balatonicus Mojsisovics, 1873 and ?Reiflingites eugeniae Arthaber, 1896, 0.15-m-thick Deqen limestone, Trinodosus Zone (ANS, 7), Chaqupu Formation, 67 km NW of Lhasa, Tibet (Wang and He, 1980).

F. ACROCHORDICERATIDAE Arthaber, 1911 Tr. (SPA–ANS) Mar.


Last: Acrochordiceras haueri Arthaber, 1911, Trinodosus Zone (ANS, 7), Nodular Limestone of Gebze, Turkey (Fantini Sestini, 1988).
F. CERATITIDAE Mojsisovics, 1879
Tr. (ANS–CRN) Mar.

First: "Hungarites" yatesi Hyatt and Smith, 1905, Haugi Zone (SPA, 3a), California and Nevada, USA (Spath, 1951; Bucher, 1889).
"Paraceratites" inodorus (Hauer, 1850), Balatonics Zone (ANS, 6), Nodular Limestone of Gebze, Turkey and Dont, Italy (Fanti, Sestini, 1988).
"Paraceratitoides" brotzeni (Avinimeleck, 1956), Lower Saharaon Formation, Har Gavanum, Israel (ANS, 7 of Parnes, 1986).

Last: Alloceratites schmidtii (Zimmerman, 1883), Grenzdolomit (CRN, 17), Sülzenbrucken, Germany (Müller, 1973). "Perrinoceras" novaditus Johnston, 1941, Desatoyense Zone (CRN, 1), South Canyon, Nevada, USA (Johnston, 1941). Discoceratites dorosplanus (Philippi, 1901), upper Ceratite Beds, upper Muschelkalk (LAD), Germany (Parnes, 1986).

Comment: The family and order are defined by the rediscovered holotype of Ceratitis nodosa Bruguière, 1792, which has the morphology of Doloceratites robustus Riedel, 1918 from the Spinusos Zone, lower Ceratite Beds, Upper Muschelkalk (LAD, 27), Germany (Rieber and Tozer, 1986). It is reasonable to define the Ceratitidae s.s. by the success of morphologies in the poorly dated Upper Muschelkalk and the more cosmopolitan occurrences of Progonoceratites noted above. Both the CRN species listed above have more affinity with the Hungaritidae Waagen, 1895 defined by Shevyrev (1986). Thus the Ceratitidae s.s. would be confined to the LAD, and the nebulous and Middle Eastern Hungaritidae would have a longer range (ANS–CRN). Parnes (1986) rejected the reinterpretation of his ANS genera by Tozer (1981a) and Shevyrev (1986), while Silberling and Nichols (1982) demonstrated that the Paraceratitinae and Beyrichitidae lost any resemblance to Progonoceratites by ANS, 8–9. The plausible hypothesis of ceratitization in marginal marine embayments (Urlichs and Mundlos, 1988), therefore must have involved the Hungaritidae and the closely related Rimkinididae if it took place in Germany.

It is proposed that the Ceratitidae and the Hungaritidae be united as a separate and highly variable group, which appeared in the Balatonics Zone (ANS, 6) and persisted in marginal marine facies (Israel, China, Germany), without loss of lobes, until it became widespread in the Poseidon (LAD, 2) and Desatoyense (CRN, 1) Zones. The ancestral form seems likely to have been derived from the early Beyrichitidae.

F. RIMKINIDIDAE Wang and He, 1976 Tr. (LAD) Mar.

First and Last: Rimkinites nitens (Mojsisovics, 1896) and other species, Bed JSB-11, correlated with the Macleurni Zone (LAD, 4), Laibuxi Formation, Tulong, southern Tibet (Wang and He, 1980).

Comment: This family provides an ammonitic link between Hungarites and Carnites, with a range confined to the LAD (Spath, 1951; Shevyrev, 1986).


First: Pseudocarnites arthaberi Simionescu, 1913, Agighol, Romania (LAD, 4–5 of Shevyrev, 1986).

Last: Carnites multilobatus Diener, 1908, Bed JSB 33c, Acutus Zone (CRN, 5), Tulong, southern Tibet (Wang and He, 1980), and contemporaneous Klamathites, California, USA (Silberling and Tozer, 1968).

F. TRACHYCYRATIDAE Haug, 1894 Tr. (ANS–CRN) Mar.

First: Paraceratites burckhardtii (Smith, 1914), base Rotelliformis Zone (ANS, 7), Prida Formation, Nevada, USA. Alternative definitions are favoured by Tozer (1981a): Eoprotrachyceras dunnii (Smith, 1974), base of Subaspersum Zone (LAD, 1), Nevada, USA (Silberling and Nichols, 1982) defines first Arpaditidae Hyatt, 1900; Anolites doleriticum (Mojsisovics, 1869), middle Pachycardienstuffen (LAD, 4), Seiser Alm, Italy (Urzlichs, 1977) defines the first Trachyceratidae s.s.

Last: Trachysagenites herbichi (Mojsisovics, 1893), lower Subbaurus Zone (CRN, 4a), Feuerkogel and elsewhere, Austria (Krystyn, 1973).

Comment: The distinction made by Silberling and Nichols (1982) between Nevadites (supposed Ceratitidae) and Eoprotrachyceras, appears to be an arbitrary stratigraphical convention, which previously confused Rieber (1973). Since there is hardly anything in common between the Arpaditidae Hyatt, 1900 of Tozer (1981a) and that of Shevyrev (1986), it may be wise to unite it with this expanded Trachyceratidae. The origin of both families in the Danubitidae (Shevyrev, 1986) is rejected in favour of a linkage with the Acrochordiceratidae via the Paraceratitinae Silberling, 1962.


First: Diplosirentites raineri (Mojsisovics, 1893), generic-level identification of Krystyn (1973), Bed 70/66, Aonoides Subzone (CRN, 1b), Feuerkogel, Austria. Also the same subzone in Nepal (Krystyn, 1982).

Last: Wangoceras pax (Tozer, 1980), Malayites boccki bed, Dausoni Zone (NOR, 2), Pardonet Formation, Pardonet Hill, British Columbia, Canada (Tozer, 1981a).


First: Heraclites robustus (Hauer, 1855) and Ectolcites pseudoaries (Hauer, 1849): generic identifications by Krystyn (1973), Brecrenatus lager (NOR, 4), Feuerkogel, Austria.

Last: Sagenites reticulatus (Hauer, 1849), Reticulatus Subzone (RHT, 2) Grey Hallstatt Limestone, Steinbergkogel, Austria (Tozer, 1980, 1984).

F. CYRTOPLEURITIDAE Diener, 1925 Tr. (NOR–RHT) Mar.

First: Lipites totiae Jeannet, 1959, Bed 78b upper Thinigaon Formation, upper Jandanus Zone (NOR, 1b), Jomson, Nepal (Krystyn, 1982).

Last: Pseudosirentites sp., Limestone of Aliambata, Cordilleranus Zone (RHT, 1), Timor (Tozer, 1980). Krystyn (1982) limits family to NOR.
F. TIBETITIDAE Hyatt, 1900 Tr. (NOR–RHT) Mar.

First: Nodotibetites nodosus Zhao and Wang, 1973, Bed JSB 34b of Dasalong Formation, Nodosus Zone (NOR 1a), Tulung, S. Tibet (Wang and He, 1980; Krystyn, 1982).

Last: Parabitetites weterlingi (Krumbke, 1913), Cordilleranus Zone (RHT, 1), Fogi Beds, Buru (Tozer, 1980). Parabitetites bertrandii Mojsisovics, 1896, Bed 113 at Jomson and Halorites Limestone at Bambanag, upper Columbusian Zone (NOR, 6), Nepal and India (Krystyn, 1982).

Superfamily TROPITACEAE Mojsisovics, 1875

This superfamily was defined by Krystyn (1982) as a branch of the CRN Trachyceratidae. It is separated here to preserve the nomenclature of the Ceratitaceae Mojsisovics, 1879 and to emphasize that Shevyrev (1986) derived these families from the early Tropiceltitidae.

F. TROPITIDAE Mojsisovics, 1875 Tr. (CRN–NOR) Mar.

First: Gymnotropites dinarus (Diener, 1916), Bed VII Feuerkogel. Dilleri Zone (CRN, 3), Austria (Krystyn, 1973).

Last: Eusiculites heimi (Mojsisovics, 1893) is implied to range up to the Kerri Zone (NOR, 1b) at Feuerkogel, Austria (Krystyn, 1980; Tozer, 1981a). E. bittieri (Gemellaro, 1940) from Tibet (CRN, 5b) is reviewed by Krystyn (1982).

F. PARAGANITIDAE Wang and He MSS Tr. (CRN) Mar.

First and Last: New family for the generally unclassified Paraganites californicus Hyatt and Smith, 1905, California, and similar Chinese new genus. Family ranges through CRN.


First: Projuvavites crasseplicatus (Mojsisovics, 1893), Bed VII Feuerkogel, base of Subbullatus Zone (CRN, 4), Austria (Krystyn, 1980).

Last: Indojuvavites angulatus (Diener, 1908), Bed 106, top of Magnus Zone (NOR, 3b), Tarap Formation, Jomson, Nepal (Krystyn, 1982).

F. DIDYMITIDAE Haug, 1894 Tr. (NOR) Mar.


F. HALORITIDAE Mojsisovics, 1893 Tr. (NOR–RHT) Mar.


Last: Halorites sp., Grey Hallstatt Limestone, Reticulatus Subzone (RHT, 2), Steinbergkogel, Austria (Krystyn, 1973; Tozer, 1980).

F. EPISICULITIDAE Spath, 1951 Tr. (NOR) Mar.

First and Last: Episculus descrenes (Hauer, 1855), Hallstatt Limestone, Austria and other species from British Columbia, Nevada and Timor, all within the Columbusianus Zone (NOR, 5–6) (McLearm, 1960; Silberling and Tozer, 1968; Shevyrev, 1986).

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MOLLUSCA: CEPHALOPODA (AMMONOIDEA: PHYLLOCERATINA, LYTOCERATINA, AMMONITINA AND ANCYLOCERATINA)

K. N. Page

The classification followed here is essentially that of Donovan et al. (1981) and Wright (1981). When known, bio- and chronostratigraphical details are quoted, in a form which follows conventional usage, i.e. for Triassic, Jurassic and early Cretaceous (Berriasian to Barremian) zones, non-italicized specific names of indices are used (e.g. Herveyi Zone); for mid to late Cretaceous (Aptian to Maastrichtian) zones, specific names are italicized (e.g. ultimus Zone).

Only selected examples of early and late records are quoted, and it should be noted that for many, alternative localities and nominal taxa could be cited, frequently in regions widely separated geographically.

Faunal provincialism can create problems of correlation between such regions, and commonly precludes the accurate stratigraphical separation of different records. In addition, the frequent use of the first occurrence of genera to correlate the base of zones can lead to a spurious simultaneity of early occurrences in different provinces.

Continually improving zonal schemes and interregional correlations will eventually resolve some of these problems, and it should be emphasized therefore that no list of first and last ammonite family occurrences can ever be in any way definitive.

Contributions from J. H. Callomon, D. T. Donovan and P. F. Rawson (University College, London), W. J. Kennedy (University of Oxford) and R. A. Hewitt (Leigh-on-Sea) are indicated by [JHC], [DTD], [PFR], [WJK] and [RAH] respectively.

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Order AMMONOIDEA Zittel, 1884

Suborder PHYLLOCERATINA Zittel, 1884

(see Fig. 11.1)

Superfamily PHYLLOCERATACEAE Zittel, 1884

F. USSURITIDAE Hyatt, 1900 Tr. (SCY–RHT) Mar.

First: Burijites skorochodi (Burijzharnikovi); Prinoye, former USSR (Shevyrev, 1986). Upper Nammalian. [RAH]

Last: Eopsiloceras planorboides (Giimbel); Schicht alpha 5, Alps (Wiedmann et al., 1979, p. 138). Marshi Zone, Stuerzenbaumi Subzone (RHT 3a).

F. DISCOPHYLLITIDAE Spath, 1927 Tr. (SCY–RHT) Mar.

First: Rhacophyllites zitteli (Mojsisovics); Lubites Beds, Feuerkogel, Austria (Shevyrev, 1986, Spath, 1934). Aonoides Zone (CRN 1). [RAH]

Last: Rhacophyllites neojurensis (Quenstedt); Kössener Schichten, Austria (Krystyn, 1973). ?Upper Marshi Zone (RHT 3b). [RAH]


First: ?Calliphylloceras psilomorphum (Neumayr); eastern Karwendelgebirge north of Innsbruck, Austria (Lange, 1952). Calliphyllum Zone (Planorbis Zone of sub-boreal zonation).

Last: Phylloceratid indet.; Upper Unit 12 (1 m below Cretaceous–Tertiary boundary, Zumaya, Spain (Wiedmann, 1988, p. 136) [RAH]. Neophylloceras velledaeforme (Schlüter); terminal Maastrichtian hardground, Stevns Klint, Denmark (Birkelund, 1979). Belemnitella casimirovensis Zone.


First: Schistophylloceras aulonotum (Herbich); eastern Karwendelgebirge north of Innsbruck, Austria (Lange, 1952). Calliphyllum Zone (Planorbis Zone). Nevadaphyllites compressus Guex; Bed Z-5, New York Canyon, Gabbs Valley Range, Nevada, USA (Guex, 1980, pp. 129, 135; pl. 1, fig. 7). Planorbis Zone, Planorbis Subzone.

Last: Meneghiniceras lariense (Meneghini); Grey Shales,

**Suborder** **LYTOCERATINA** Hyatt, 1889

**Superfamily** **LYTOCERATACEAE** Neumayr, 1875

**F. PLEUROACANTHITIDAE** Hyatt, 1900

**J. (HET)** Mar.

**First:** *Analytoceras articulatus* (Sowerby); Austria (Wähner, 1894, pl. 3, fig. 3; pl. 7, figs 1–5; pl. 8, fig. 1; pl. 9, figs 1–2; Roman, 1938, p. 31, fig. 3–23). Lower Hettangian.
Last: *Pleurocanthites biformis* (J. de C. Sowerby); Italy (Canavari, 1882), Hettangian.

F. **ECTOCENTRITIDAE** Spath, 1926

First: *Ectocentrites* cf. *petersi* (Hauer); South America (von Hillebrandt, 1981; Riccardi et al., 1990, p. 95). Reissi Zone.


F. **DEROLYTOCRATIDAE** Spath, 1927

First: *Derolytoceras haueri* (Stur); Hierlatz, Austria (Rosenberg, 1909; Roman, 1938, p. 32). ?Sinemurian (according to Roman).

Last: *Derolytoceras tortum* (Quenstedt); Swabia, Germany (Rosenberg, 1909, p. 259, figs 29a–d, 30; Roman, 1938, p. 32, fig. 3–24). Upper Pliensbachian.

F. **LYTOCERATIDAE** Neumayr, 1875

First: *Lytoceras interlineratum* (Buckman); Radstock, Avon, England, UK (Buckman, 1921, pl. 204A, B). Ibex Zone, Valdani Subzone.

Last: *Ammonoceratites ezoense*; Bas Autan, near Digne, Basses-Alpes, SE France (Sturani, 1966, p. 23, pl. 3, fig. 8). Progracilis Zone.

**Superfamily** TETRAGONITACEAE Hyatt, 1900

F. **PROTETRAGONITIDAE** Spath, 1923
J. (K)–(ALB) Mar.

First: *Protetragonitites quadrisulcatum* (d’Orbigny); Djebel Oust, northern Tunisia (Memmi and Salai, 1975). Upper Tithonian, ‘Jacobi Zone’ (lower part, = Microcanith Zone?).


F. **TETRAGONITIDAE** Hyatt, 1900

First: *Jauberticeras jauberti* (d’Orbigny); Lesches-ends-Dios, Drôme, SE France (Moullade, 1966, fig. 16). Lower ‘Gargasien’ (Upper Aptian), guettardi Zone.

Last: *Saghalinites* sp.; terminal Maastrichtian hardground, Stevns Klint, Denmark (Birkelund, 1979). Belemnitella casimirovensis Zone.

F. **GAUDRYCERATIDAE** Spath, 1927

First: *Eogaudryceras numidum* (Coquand) Say; Gargasien, SE France (Jacob, 1908; Casey, 1960, pp. 7–8). Aptian.

Last: *Zelandites varuna* Forbes; terminal Maastrichtian, Lopez de Bertodano Formation, Seymour Island, Antarctica (Macellari, 1986). ultimus Zone.

**Suborder** AMMONITINA Hyatt, 1889

**Superfamily** PSILOCERATACEAE Hyatt, 1867

F. **PSILOCERATIDAE** Hyatt, 1867

?Tr. (RHT)–J. (HET) Mar.

First: *Psiloceras* sp. indet.; Westbury Formation, Penarth Group, Chipping Sodbury, Avon, England, UK (Donovan et al., 1989). This record is significantly earlier than the first occurrence of *Psiloceras* ex grp planorbis (J. de C. Sowerby) in the British succession in the overlying Lower Lias Group. Following Torrens and Getty (in Cope et al., 1980), the Penarth Group is considered to be of Triassic (Rhaetian) age.

Last: *Caloceras leptopyctylum* (Lange); Lower Lias Group, Burton Row Borehole, Somerset, England, UK (Ivimey-Cook and Donovan, in Whitaker and Green, 1983). Liasicus Zone, upper part of Laqueus Subzone.

F. **SCHLOTHEIMIIDAE** Spath, 1923
J. (HET–SIN) Mar.

First: *Waehneroceras* spp. including *W. prometheus* (Reynes); Bed 43, Lower Lias Group, West Somerset coast, England, UK (Ivimey-Cook and Donovan, in Whitaker and Green, 1983). Liasicus Zone, basal Portlocki Subzone.


**Superfamily** ARIETITACEA Hyatt, 1875

F. **ARIETITIDAE** Hyatt, 1875 J. (HET–SIN) Mar.

First: *Alsatites* [Proraitites] *laqueolus* (Schloenbach); Lia, southern Germany (Lange, 1931). ‘Zone des Saxoceras Schroeder’ (alpha 1d), (Liasicus Zone, Portlocki Subzone; Donovan in Dean et al., 1961, p. 446).

Last: *Eparietites denotatus* (Simpson); Lower Lias Group, Robin Hood’s Bay, North Yorkshire, England, UK (Simpson, 1855, p. 76; Buckman, 1912, pl. 67A, B). Obtusum Zone, Denotatus Subzone.

Comment: *Eparietites* evolved directly into *Oxynoticeras* (family Oxynoticeratidae); the disappearance of the Arietitidae is therefore a pseudo-extinction.

F. **ECHIOCERATIDAE** Buckman, 1913
J. (SIN) Mar.

First: *Epophioceras* [‘Caenisites’] *pseudobonnardi* (Spath); Bed 75, Shales-with-Beef, Lyme Regis, Dorset, England, UK (Lang et al., 1923, p. 76). Turneri Zone, Birchi Subzone.


Comments: The Echioceratidae are direct descendants of the Arietitid genus *Epophioceras* (Getty, 1973). Inclusion of *Epiphioceras* in the Echioceratidae is therefore preferable on phylogenetic grounds. Features characteristic of *Epophioceras* occur already in ‘Caenisites’ *pseudobonnardi* (Spath).

F. **OXYNOTICERATIDAE** Hyatt, 1875

First: *Oxynoticeras simpsoni* (Simpson); Lower Lias Group, Robin Hood’s Bay, North Yorkshire, England, UK
(Simpson, 1843, pp. 37, 38; Buckman, 1912, pls 66A, B). Oxynotum Zone, basal Simpsoni Subzone.

**Last:** Fanninoceras disciforme von Hillebrandt; Chile, Argentina, Peru (von Hillebrandt, 1981; 1984). Disciforme Zone (top Pliensbachian). [DTD]

Superfamily CYMBITACEAE Buckman, 1919


**First:** Cymbites laevigatus (J. de C. Sowerby); Lower Lias Group, Burton Row Borehole, Somerset, England, UK (Ivimey-Cook and Donovan, in Whittaker and Green, 1983, p. 127). Bucklandi Zone, Rotiforme Subzone.

**Last:** Cymbites centriglobus (Oppel); Bed 2, Eype Clay, Middle Lias, near Eype, Dorset, England, UK (Howarth, 1957, p. 196, pl. 17, figs 3a–d). Margaritatus Zone, Stokesi Subzone.

**Comment:** A group of dwarf, globose ammonites. Diagnostic features are few and a polyphyletic origin has often been postulated (e.g. in Arkell et al., 1957, p. L240). However, an early sutural ontogeny distinct from contemporary Ammonitina may indicate a single origin (Schindewolf, 1962; Donovan et al., 1981, p. 109).

Superfamily EODEROCERATACEAE Spath, 1929


**First:** Microderoceras sp.; Bed 74g, Shales-with-Beef, Lower Lias Group, Lyme Regis–Charmouth district, Dorset, England, UK (Lang et al., 1923). Turneri Zone, basal Birchi Subzone. A record from the Semicostatum Zone (Walliser, 1956) is considered to be unconfirmed by Donovan et al. (1967, p. 453).

**Last:** Metadroughtoceras mouterei (Frebold); western Canada and USA (Smith et al., 1988, p. 1511). Lowest Kunae Zone, probably equivalent to upper Davoei Zone of European succession.


**First:** Tetraspidoceras aff. birchiae (Rosenberg); Gola del Fiume Bosse, Appennino Marchigiano, Umbria, Italy (Ferretti, 1975, p. 177, pl. 23; Donovan, 1990a, p. 259). Oxynotum Zone, Oxynotum Subzone. [DTD]

**Last:** Coeloceras pettos (Quenstedt); Bed 118b, Belemnite Marls, Lower Lias Group, Charmouth-Seatown district, Dorset coast, England, UK (Lang et al., 1928, p. 192). Jamesoni Zone, Jamesoni Subzone.


**First:** Epideroceras exhaeredatum S. Buckman; Bed 103, Black Ven Marls, Lower Lias Group, Charmouth, Dorset, England, UK (Lang et al., 1926, p. 155). Raricostatum Zone, Raricostatoides Subzone.

**Last:** Phricoderoceras subtylorii (Krumbeck); Arzo, Breggia, etc. Lombardi Alps (Wiedenmayer, 1980, pp. 50–51). Margaritatus Zone, Subnodosus Subzone.


**First:** Leptonotoceras suessi (Hauer); Lower Lias Group, Stowell Park Borehole, Gloucestershire, England, UK (Spath, 1956, p. 149). Raricostatum Zone, ?Densinodulum Subzone.

**Last:** Acanthopleuroceras lepidum Tutcher and Trueman (="aliiense auctt., stahli auct. non Oppel"); Portugal (Dommargues and Mouterde, 1981). Ibex Zone, Luridum Subzone [JHC].


**First:** Vicinonidoceras simplicicosta (Trueman); fine-grained sandstone band in Fabbia Shale, Allt Fearn, Isle of Raasay, Hebrides, Scotland, UK (Donovan, 1990b). Raricostatum Zone, topmost Aplanatum Subzone. [DTD]

**Last:** Liparoceras (Becheiceras) nautiforme (J. Buckman); Thorncomb Sands, Middle Lias, near Eype, Dorset, England, UK (Howarth, 1957, p. 196). Margaritatus Zone, Subnodosus Subzone.


**First:** Amalthus ex grp stokesi (J. Sowerby); Bed 131 Green Ammonite Beds, Lower Lias Group, Seatown district, Dorset, England, UK (Lang, 1936, p. 431). Margaritatus Zone, Stokesi Subzone.

**Last:** Pleuroceras haukerensis (Young and Bird); Bed 25, Kettleness, North Yorkshire, England, UK (Howarth, 1955, pp. 156, 164). Spinatum Zone, Haukerensis Subzone.

**Comment:** Descendants of the Beuniceras–Aegoceras–Oistoceras lineage (Liparoceratidae), originating in the Ibex Zone.


**First:** Reynesococeras praecinctum Dommargues and Mouterde; Peniche, Portugal (Dommargues et al., 1983). Ibex Zone, Luridum Subzone.

**Last:** Catacococeras confectum Buckman, C. duntorii (Mauberge); Cotswolds Sands, Gloucestershire, England, UK (Buckman, 1889). Variabilis Zone.

Superfamily HILDOCERATACEAE Hyatt, 1867


**First:** Protagrammoceras mellahense Dubar; 3 m below Tropidoceras stahli Bed, south-east of Gourama and also west of Ziz, Morocco (Dubar, 1961). Ibex Zone.

**Last:** Vacekia intermedia Imlay [Macroconch]/Astheneroceras deliciatum Imlay [Macroconch]; Oregon and south Alaska, USA (Imlay, 1973). Lower Bajocius, ?Ovalis Zone. [JHC]

**Comment:** A complex multibranching family comprising many separate lineages.


**First:** Phymatoceras ex grp lilli Hauer; Hildoceras bifrons Horizon (D), central-west France (Gabilly in Gabilly et al., 1971, p. 612). Bifrons Zone, ?Fibulatum Subzone.

**Last:** Fissilobieeras fissilobatum (Waagen), Sandford Lane, near Sherborne, Dorset, England, UK (Callomon and Chandler, 1990, p. 97). Laeviuscula Zone, Trigonalis Subzone.


**First:** Ludwigia crassa (Horn); L. haugi Douville; opalinoides Horizon, SE French Jura (Contini, 1969). Murchisonae Zone, Haugi Subzone.

**Last:** Hyperioceras subectum (Buckman); Horizon Bj 3,

Last: Dorsetensia regrediens Haug; Bed 4c, Oborne Road Stone, Inferior Oolite, Oborne, Dorset, England, UK (Parsons, 1976, p. 130). Humphriesianum Zone, Humphriesianum Subzone.

Superfamily SPIROCERATACEAE Hyatt, 1900

First: Spireceras baculatum (Quenstedt); Bed 6d, Cadomensis Beds, Inferior Oolite, Oborne, Dorset, England, UK (Parsons, 1976, pp. 126, 129). Subfurcatum Zone, Baculata Subzone.
Comment: As discussed by Callomon (in Donovan et al., 1981, p. 130), the Spirurocerataeae are stratigraphically isolated from later heteromorphs assigned to the Suborder Ancyloceratina. Important sutural differences may also suggest a separate derivation, with the Spirocerataeae apparently developing from the Hildocerataceae genus Temtoceras (Callomon, loc. cit.).

Superfamily HAPLOCERATACEAE Zittel, 1884

First: Praestrigites praenuntius S. Buckman; Hornpark Ironshot Beds, Inferior Oolite, Beaminster, Dorset, England, UK (Buckman, 1924, pl. 466; Callomon in Donovan et al., 1981, pp. 120, 144). Murchisonae Zone, Bradfordensis Subzone.
Last: Phlycticeras pustulatum (Reinecke); Beds 8c–d, Sengenthal, Franconia, Germany (Callomon et al., 1987). Upper Coronatum Zone.

Last: Binneyites rugosus Cobban; Kelvin Member, southwest of Shelby, Montana, USA (Cobban, 1961). vermiciformis Zone.

Last: Lissoeras (Lissoeratoides) erato (d’Orbigny); Schilli Horizon, France (Enay et al., 1971, p. 640). Transversarium Zone, Parandieri Subzone.

First: Haploceras subclimatum (Fontannes); southern Germany (White Jura E) and Ardèche, France (Bercchemer and Höldecker, 1959, p. 106). Beckeri Zone (Upper Kimmeridgian).
[HJC]
Last: Haploceras (Neolissoceras) grasianum (d’Orbigny); Beds 1–4, Angles, Basses-Alpes, SE France (Busnardo, 1965, p. 105, table 1). Sayni Zone.

Superfamily STEPHANOCERATACEAE Neumayr, 1875

[HJC]
Last: Cadomites altispinosum Dietl and Herold; quenstedti Horizon, Macrocephalen-Oolith, SW Germany (Dietl and Herold, 1986; Callomon et al., 1989). Herveyi Zone, Keppleri Subzone.

[HJC]

Last: Zemistephanus richardsoni (Whiteaves); Queen Charlotte Islands, British Columbia, Canada; southern Alaska, USA (Hall and Westermann, 1980, p. 20). Richardsoni Subzone (=upper Sauzei Zone?). [JHC]

Last: Epimayites subtumidus (Waagen), E. transiens (Waagen), etc.; Kantcote Sandstone, west of Kantcote, Cutch, India (Spath, 1928). Upper Oxfordian.

First: Cranoceratites borealis (Spath); East Greenland (Callomon, 1985, pp. 63, 64). Boreal Bathonian, Borealis Zone (equivalent to upper Bajocien of sub-boreal region).
Last: Amoeboceras (Nannocardioceras) anglicum (Salfeld); Kimmeridge Clay, Dorset, Yorkshire, widespread in the UK (Callomon, 1985, p. 74). Lower Autissiodorens Zone.

Superfamily PERISPHINCTACEAE Steinmann, 1890
F. PERISPINHICTIDAE Steinmann, 1890
J. (BAJ–KIM) Mar.

First: *Leptosphinctes* (L.) *chadonensis* Pavia; Chandon, SE France (Pavia, 1983, p. 163). Humphriesianum Zone, Blagdeni Subzone. [JHC]


Comment: The Perispinctaceae have always created close homeomorphism between stratigraphically and classification problems, largely due to wide intraspecific geographically unrelated forms. An attempt at a primarily 1981, p. 123) ‘revealed a family tree of almost innumerable trunks and branches of all lengths and thicknesses’.

F. MORPHOCERATIDAE Hyatt, 1900


Last: *Asphinctes tenuiplicatus* (Brauns); Swabia, Germany (Hahn, in Buck et al., 1966, p. 34; Torrens, 1971, p. 586). Zigzag Zone, Yeovilensis Subzone (=Tenuiplicatus Subzone of Hahn, 1971).

F. TULITIDAE Buckman, 1921

First: *Bullatimorphites latecentratus* (Quenstedt); Fucus Bank, Swabia, Germany (Hahn, in Torrens, 1971, p. 58). Zigzag Zone, Yeovilensis Subzone.

Last: *Kheriaceras* (Bomburites) *bombur* (Oppel); Swabia, Germany (Callomon et al., 1989, p. 11). Koenigi Zone, Curtiolobus Subzone, subcostarius Horizon. [JHC]

F. REINECKEIIDAE Hyatt, 1900

First: *Neuqueniceras* ex grp *steinmanni* (Stehn); Andean Province, eastern Pacific (Riccardi et al., 1989). Upper Bathonian, Steinmanni Zone. [JHC]


F. PACHYKERATIDAE Buckman, 1918


Last: *Tornquistes liesbergensis* (De Loriol) and *T.* spp.; Swiss and French Jura (Thierry and Charpy, 1982). Plicatilis Zone, Antecedens Subzone.

F. ASPIDOCERATIDAE Zittel, 1895


Last: *Aspidoceras neobürgense* (Oppel) [=A. rogozicense? (Zeuschner)]; southern Spain (Cecca, 1985, p. 111). Jacobi Zone.

F. AULACOSTEPHANIDAE Spath, 1924
J. (OXF–KIM) Mar.


Last: *Aulacostephanus autissiodorensis* (Cotteau); Kimmeridge Clay, Dorset, widespread in England, UK, also occurs in France (Cope, 1968). Autissiodorens Zone. [JHC]

F. SIMOCERATIDAE Spath, 1924
J. (TTH) Mar.

First: *Aulacosphinctes ruberti* (Pervinquière); Betic Cordilleras, southern Spain (Enay and Geyssant, 1975, p. 41). Lower Tithonian, upper part of Hybonotum Zone.

Last: *Cordubiceras guminatum* Oloriz and Tavera [=Simoceratinae gen. et sp. nov.]; Betic Cordilleras, southern Spain (Enay and Geyssant, 1975, p. 45). Upper Tithonian, Microacanthum Zone. [JHC]

F. HIMALAYITIDAE Spath, 1925

First: *Aulacosphinctes ex grp linoptycus* Uhlig, A. ex grp. *spinitesis* Uhlig, A. cf. *rectefurcatus* (Zittel), ‘*Microacanthoceras* pontii’ (Fallto and Termier); Betic Cordilleras, southern Spain (Enay and Geyssant, 1975, p. 44). Middle Tithonian, Ponti Zone.

Last: *Himalayites* (?) *nieri* (Picket); SE France (Le Hégarat, 1971, pp. 144, 145). Roubardi Zone, Pertransiens Subzone.

F. OLCOSTEPHANIDAE Pavlov, 1892


Last: *Olcostephanus* (Jeannoticeras) *jeannoti* (d’Orbigny), O. (*O.*) *variegatus* Paquier; SE France (Bullot, 1990). Base of Nodosoplicatum Zone. [PFR]

F. ATAXIOCERATIDAE Buckman, 1921

First: ‘*Orthospinctes*’ *virgulatus* (Quenstedt) *laufensis* (Siemiradzki); ‘*O.*’ *suevicus* Siemiradzki, SE France (Atrops, 1982, p. 48). Bimammatum Zone.


F. NEOCOMITIDAE Salfeld, 1921
J. (TTH)–K. (HAU) Mar. (see Fig. 11.2)

First: *Berrisella* spp. including *B. subeudichotoma* Nikolov; Titcha Formation, Ticha Gorge, near Preslav, Bulgaria (Nikolov, 1982, pp. 20, 22). Transitorius Zone, Micranthus Subzone.

Last: *Crusiceras* *crusense* (Torcapel); SE France (Thieuloy, 1977, pp. 435–6). Nodosoplicatum Zone. [PFR]

F. OOSTERELIIDAE Breistroffer, 1940

First: *Oosterella culturata* (d’Orbigny); Agadir Basin, Morocco (Wiedmann et al., 1978); ‘Middle’ Valanginian. *O. aff. culturata* (d’Orbigny); Varelheide, northern Germany (Kemper et al., 1981, p. 302). Crassus Zone. [PFR]
### Mollusca: Cephalopoda (Jurassic and Cretaceous Ammonoidea)

#### Superfamily DESMOCERATAEAE Zittel, 1895

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**Fig. 11.2**

**Last:** Oosterella cultrata (d’Orbigny); Kraptchéně, Mikhailovgrad region, Bulgaria (Nikolov, 1965). Lower Hauterivian, Radiatus Zone.

**F. VIRGATITIDAE** Spath, 1923 J. (TTH) Mar.

**First:** Illewaiiska klimovi Ilovaisky and Florensky; Ural River Basin, former USSR (Mikhailov, 1964). Basal Lower Volgian.

**Last:** Epivirgatites nikitini (Mich.), E. bipliciformis (Nikitin); Bed 13 (j.V._nk), middle Volga, near Gorodische, Ulianovks, former USSR (Gerasimov et al., 1971). Volgian, Nikitini Zone.


**First:** Pectinatites (Propectinatites) websteri Cope; Kimmeridge Clay, Dorset, England, UK (Cope, 1968, p. 2). Upper Autissiodorensis Zone.

**Last:** Chetagites sihricus; former USSR (Gerasimov et al., 1971, fig. 2). Ryazanian, Rjasanensis Zone.

**F. CRASPEDITIDAE** Spath, 1924 J. (TTH)–K. (BRM) Mar.

**First:** Kachpurites sp.; former USSR (Gerasimov et al., 1971, p. 351). Volgian, Virgatus Zone, Rosanov Subzone.

**Last:** Simbirsites (Crasedicus) cf. juddi Rawson; lower Division B, Bed 5e (LB5E), Speeton Clay Formation, Speeton, North Yorkshire, England, UK (Rawson and Mutterlöse, 1983). Variabilis Zone.

**F. HOLCODISCIDAE** Spath, 1924 K. (HAU–BRM) Mar.

**First:** Holocodiscus intermedius (d’Orbigny); La Charce, Drôme, SE France (Moullade, 1966, p. 161, fig. 8). Jeannetian–castellanensis Zone.

**Last:** Holocodiscus sp. juv.; Bed 116, Angles, Basse-Alpes, SE France (Busnardo, 1965, p. 106, table 1; Moullade, 1966, fig. 11). Lower Barremian, compressissima Horizon.

**Superfamily DESMOCERATAEAE** Zittel, 1895
F. EODESMOCERATIDAE Wright, 1955

First: Eodesmoceras celestini (Pictet and Campiche); Sainte-Croix, Switzerland. E. haughtoni Spath; Uitenhage, South Africa (Spath, 1930, p. 141; Howarth and Wright, in Donovan et al., 1967, p. 455). Upper Valanginian.


Last: Neosilesites madagascariensis Collignon; west of Ambarimantina, Madagascar (Collignon, 1963). Middle Albian, Lemuroceras spathi and Brancoceras besariet Zone.


First: Psilotissotia cf. favrei (Ooster); Bed 3, Crans, Ardèche, France (Sayn and Roman, 1905, p. 634; Donovan et al., 1967, p. 455). Sayn Zone.


F. DESMOCCERATIDAE Zittel, 1895

First: Abrutusites juliangi Honnorat-Bastide; Rottier, Drôme, SE France (Thieuloy, 1972). Nodosiplotidum Zone. [PRF]

Last: Kitchinites laurae Macellari; Lopez de Bertodano Formation, Seymour Island, Antarctica (Macellari, 1986). Terminal Maastrichtian, ultimus Zone.

F. KOSSMATICERATIDAE Spath, 1922


Last: Maorites densicostatus Kilian and Reboul; Lopez de Bertodano Formation, Seymour Island, Antarctica (Macellari, 1986). Terminal Maastrichtian, ultimus Zone.


First: Eopachydiscus marcianus (Shumard); Duck Creek Limestone, north Texas, USA (Kennedy et al., 1983). marcianus Zone.

Last: Pachydiscus aff. colligatus (von Binkhorst); terminal Maastrichtian hardground, Stevns Klint, Denmark (Birkelund, 1979); Belenmitella casimirovensis Zone. P. ultimus Macellari; Lopez de Bertodano Formation, Seymour Island, Antarctica (Macellari, 1986); terminal Maastrichtian, ultimus Zone.

F. MUNIERICERATIDAE Wright, 1952

First: Tragodesmoceras bassi Morrow, T. socorroense Cobban and Hook; Colorado and New Mexico, USA (Cobban, 1984). nadosoides Zone. [WJK]

Last: Pseudoschloenbachia (Termierella) lenticularis Colignon; Madagascar (Collignon, 1969). Upper Lower Campanian. [WJK]

Superfamily HOPLITACEAE H. Douvillé, 1890


F. SCHLOENBACHIIIDAE Parona and Bonnarelli, 1897 K. (ALB–CEN) Mar.

First: Salteiceras saltieri (Sharpe); Akkup, Tuarkyr, Transcaspia, former USSR (Marinowski, 1983, p. 15). dispar Zone. [WJK]


F. PLACENTICERATIDAE Hyatt, 1900

First: Semenovites iphitus (Spath), S. graciilis (Spath); Upper Greensand, Blackdown, Devon, England, UK (Spath, 1926, p. 183; 1927, p. 187; Casey, 1965, p. 461). inflatum Zone, varicosum Subzone.

Last: Hoplitoplacenticeras lasfresnayanum (d’Orbigny); Calcaire à Baculites, Cotentin Peninsula, Manche, France (Kennedy, 1986a). Upper Maastrichtian.

Comment: Casey (1965, p. 461) considers the genus Semenovites Glasunova, 1960 to be the ‘root stock’ of Albian placenticeratids such as Hengestites Casey, 1960.

F. ENGONOCERATIDAE Hyatt, 1900


Last: Metengonoceras acutum Hyatt, Britton Formation, north-central Texas (Kennedy, 1988, p. 34). Upper Cenomanian, gracile Zone.

Superfamily ACANTHOCERATACEAE Hyatt, 1900


First: Proleymeriella schrammeni (Jacob); northern Germany (Brinkmann, 1937; Casey, 1979, p. 593). Lower Albian, tardefucrata Zone, schrammeni Subzone.


F. BRANCOCCERATIDAE Spath, 1933
Mollusca: Cephalopoda (Jurassic and Cretaceous Ammonoidea)

First: *Uppermost Turonian or Lower Coniacian. [WJK]*

F. MOJISOVICSIIDAE Hyatt, 1903 K. (ALB)
First: *Upper Greensand, Isle of Wight, England, UK; Aube, France (Kennedy and Wright, 1984, p. 96).*
Last: *Last:
First: *Lower Coniacian.*
Last: *Upper Turonian, Zone VI.*

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First: *Graysonites adkinsi Young; Texas, USA (Young, 1958). Lower Cenomanian.*
Last: *Buchiceras bilobatum Hyatt; Otusco, Peru (Brüggen, 1910; Kennedy et al., 1980). Lower Coniacian.*

First: *Vascoceras diatium (d’Orbigny); New Mexico, USA (Cobb et al., 1989, p. 47). masyense Zone.*
Last: *First: *Upper Turonian, Zone VI.*

First: *Cibolaire sp. cf. molencrasti Cobban and Hook; Devon, England, UK; Aube, France (Kennedy et al., 1986, p. 209). juddii Zone.*
Last: *Texanites campaniensis (Grossouvre); Aquitaine, France (Sérénie-Vivien, 1972, pp. 141, 142). Middle Campanian.*

First: *Metatissota nodosa Hyatt; Torsac, Charente, France; M. desmoulini (de Grossouvre) and M.? nanculaii (de Grossouvre); Périgueux, Dordogne, France (Kennedy, 1984). petrocoriensis Zone.*
Last: *Tissotia steinnanni Lissón; Célandin Formation, northern Peru (Benavides-Caceres, 1956, p. 31). balrai Zone.*

First: *Hoploites; Algerian Sahara (Armand et al., 1981). Lower Turonian, Zone VI.*
First: *First: *Upper Turonian, Zone VI.*

First: *First: *Upper Turonian, Zone VI.*

Suborder ANCYLOCERATINA Wiedmann, 1960
Superfamily ANCYLOCERATACEAE Gill, 1871

First: *Protancyloceras sp.; Betic Cordilleras, southern Spain (Enay and Geysant, 1953, p. 43). Lower Turonian, Darwini Zone.*

First: *Crioceratites sp.; Orpierre, Hautes-Alpes, SE France (Moullade, 1966, fig. 4). Upper Valanginian, ‘Lyticoceras sans Crioceratites Zone’.* 

Last: *Ptychoceras closteroid Eetheridge, Point Charles Beds,
Darwin Formation, Point Charles, Northern Territory, Australia (Whitehouse, 1928). Upper Albian.

F. HETEROCERATIDAE Hyatt, 1900
K. (HAU−APT) Mar.
First: Moutoniceras annulare (d'Orbigny); Basses-Alpes, SE France (Thomel, 1964, p. 65). Top of Duvali Zone.
Last: Heteroceras (?Argvetites) vohimaranaensis Collignon; Vohimarana, Madagascar (Collignon, 1962, pl. 221, fig. 962). Upper Aptian, Epichelonicerus ischerisclerchi Zone.

F. HEMIHOPLITIDAE Spath, 1924
K. (HAU−BRM) Mar.

Superfamily DOUVILLEICERATACEAE Parona and Bonarelli, 1897
F. DOUVILLEICERATIDAE Parona and Bonarelli, 1897
K. (HAU−BRM) Mar.
Last: Douvilleiceras clementianum (d'Orbigny); Lower Gault, Aube, Paris Basin, France (Casey, 1962, p. 263). deniatus Zone, benettian Subzone.

F. ASTIERICERATIDAE Breistroffer, 1953
K. (ALB−BRM) Mar.
?First: Astiericeras sp. [= 'Scaphites (Eoscaphtes) nov. sp. of Colleté et al., 1982, pl. 25, fig. 6'; Courcelles, Aube, France (Kennedy, 1986b). deniatus Zone, lyelli Subzone. ?Last: Astiericeras astierianum (d'Orbigny); phosphorite deposits, Escragolles, Gourdon, etc., SE France (Wiedmann, 1965a; Kennedy, 1986b). deniatus Zone, lyelli or spathi Subzone.
Comments: The affinities and age of A. astierianum and the monotypic family Astiericeratidae are discussed by Kennedy (1986b).

F. TROCHLEICERATIDAE Breistroffer, 1952
K. (APT−ALB) Mar.
First: Trochleiceras balearense (Fallot); Sierras of Alicante and Murcia, southern Spain (Wiedmann, 1965a, table V). Aptian.
Last: Trochleiceras magneti (Collignon); Madagascar (Collignon, 1950). Lower Albian.

Superfamily DESHAYESITACEAE Stoyanow, 1949
F. DESHAYESITIDAE Stoyanow, 1949
K. (AP−ALB) Mar.

Last: 'Dufrenoyia' spp.; Apulo anticline, Cundinamarca, Colombia (Bürgl, 1955, p. 13; Casey, 1964, p. 377). Basal Albian?
F. PARAHOPLITIDAE Spath, 1922
K. (APT−ALB) Mar.
First: Paraehoplites weissi (Neumayr and Uhlig); 'Couches de la Carrière à ciment', Cassis, near La Bédoule, Bouches du Rhône, France (Fabre-Taxy et al., 1965, fig. 8, p. 189). Lower Aptian (basal Bédoulian), 'Zone I'.

Superfamily TURRILITACEAE Gill, 1871
F. HAMITIDAE Gill, 1871
K. (ALB−TUR) Mar.

F. ANISOCERATIDAE Hyatt, 1900
K. (APT−CON) Mar.
First: Labeceras crassetuberculatus (Collignon; west of Ambanjabe, Madagascar (Collignon, 1962, pl. 229). Aconiceras nicus and Melchiorites melchiors Zone.
Last: Phyltoceras trinodosus (Geinitz); Craie de Villedieu, La Ribochère, Loir-et-Cher, France (Kennedy, 1984). Upper Coniacian, serrat marginatus Zone.

F. LABECERATIDAE Spath, 1925
K. (ALB−BRM) Mar.
First: Labeceras cressetuberculatus Klinger; Zululand, Africa (Klinger, 1989). Lower Albian V.
Last: Labeceras besairiei Collignon; Zululand, Africa (Klinger, 1989). Upper Albian V.
Comment: Klinger (1989, p. 190) discusses the dimorphic pairing of Labeceras [m] and Myloceras [M]. He suggests that the family Labeceratidae be reduced to a subfamily Labeceratinae containing a single dimorphic genus. Inclusion in the Ancyloloceratidae is a possibility, but stratigraphical confirmation is lacking.

F. TURRILITIDAE Gill, 1871
K. (ALB−MAA) Mar.
Last: Diplomoceras sp., ?Phylloptychoceras sp; terminal Maastrichtian hardground, Stevns Klint, Denmark (Birkelund, 1979); Belemnitella casimivovensis Zone. Diplomoceras lambi Spath; Lopez de Bertodano Formation, Seymour Island, Antarctica. (Macellari, 1986); terminal Maastrichtian, ultimus Zone.

F. BACULITIDAE Meek, 1876
K. (ALB−MAA) Mar.
Last: Baculites vertebralis Lamark, B. valognensis Boehn;
Mollusca: Cephalopoda (Jurassic and Cretaceous Ammonoidea) 223

terminal Maastrichtian hardground, Stevns Klint, Denmark (Birkeland, 1979). Belemnitella casimirovensis Zone.

**Superfamily SCAPHITACEAE Meek, 1876**


Last: *Hoploscaphites constrictus constrictus* (J. Sowerby), *H. constrictus* (Sow.) *crassus* Lopuski; terminal Maastrichtian hardground, Stevns Klint, Denmark (Birkeland, 1979). Belemnitella casimirovensis Zone.

**Superfamily INCERTAE SEDIS**

First: *Macroscaphites yoani* (Puzos); Silesia (Kilian, 1892). Barremian.

Last: *Macroscaphites sp.*; Uchaux, France (Roman and Mazeran, 1913; Roman, 1938, p. 39). Turonian.

Comment: Included in the Lytoceratina by Wright (in Arkell et al., 1957, p. L204), although subsequently only provisionally (Wright, 1981).


First and Last: *Cicatrites abichi* (Anthula); Caucasus, etc. (Anthula, 1899). Lower to Upper Aptian.

Comment: Only one species known, apparently showing affinities to *Costidiscus* (Macroscaphitidae) (Wright in Arkell et al., 1957, p. L205).

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Animals: Invertebrates


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MOLLUSCA: CEPHALOPODA (COLEOIDA)

P. Doyle

The higher classification of the Coleoidea is presently in a state of flux; the scheme used below largely follows Jeletzky (1966), ranking major groups as orders. However, a departure is the separation of the Spirulida from the Sepiida at order level, which largely follows Donovan (1977) and Engeser and Bandel (1988). No attempt has been made to distinguish paraphyletic from monophyletic families, due to the lack of detailed cladistic treatment of the coleoids at family level. The Coleoidea are wholly marine.

Order Status UNCERTAIN

??F. PROTOAULACOCERATIDAE Bandel et al., 1983 D. (EMS) Mar. (see Fig. 12.1)


Comment: This taxon, possibly the earliest of the Aulaco cerida, is a doubtful coleoid, given its subcentral siphunde and late ontogenetic development of the 'rostrum'. Some authorities believe that the 'rostrum' of this taxon could actually be a fish spine (J. Dzik, pers. comm., 1991).

Order AULACOCERIDA Stolley, 1919

F. AULACOCERANADE Mojsisovics, 1882

D. (EIF?)-Tr. (RHT) Mar.

First: Aulacoceras? sp. indet., Couvain, Belgium. This record is based on a very poor specimen figured by de Koninck (1843) and cannot be considered to be reliable. The next oldest forms are Paleoconus bakeri Flower and Gordon, 1959, Hematites barbarae Flower and Gordon, 1959, H. burkakensis Flower and Gordon, 1959, Bactritinum ulrichi Flower and Gordon, 1959 and H. girtyi Flower and Gordon, 1959, Mississippian, Fayetteville Shale, Arkansas and Chainman Shale, Utah, USA (Flower and Gordon, 1959).


Intervening: P. (u.), ANS-NOR.

F. PALAEOBLELEMNOPSISIDAE Chen, 1982


First and Last: Palaeoblemnopsis sinensis Chen, 1982, Upper Permian, Dalong Formation, Hubei and Zhejiang Provinces, China (Chen and Sun, 1982).

F. XIPHOTEUTHIDIDAE Naef, 1922

Tr. (SCY)-J. (OXF?) Mar.


Last: Atractites? argoviense Dreyfuss, 1957, Vis Valley, Hérault, France. This species is based on phragmocones only and cannot be assigned definitely to the Aulacocerida (Dreyfuss, 1957). The next youngest record is Atractites idunense (Meneghini, 1867), A. inflatum (Stoppanini, 1857) and A. stoppanii (Meneghini, 1867), Toarcian, Rosso Amonitico, Lombardy, Italy (Meneghini, 1867).

Intervening: ANS–RHT, SIN–TOA.

F. CHITINOTEUTHIDIDAE Müller-Stoll, 1936

J. (PLB) Mar.

First: Chitinoteuthis? sp. indet., Lower Pliensbachian, Kirchheim, Württemberg, Germany (Müller-Stoll, 1936).


Intervening: P. (u.), ANS–NOR.

F. PHRAGMOTEUTHIDIDAE Jeletzky, 1965


First: Permotuethis groenlandica Rosenkrantz, 1946, Foldvik Creek Formation, Posidonia Shale Member, Clavering Island, East Greenland (Rosenkrantz, 1946).

Last: Phragmoteuthis conocauda (Quenstedt, 1849), Hildoceras bifrons Zone, Posidonienschiefer, Dotternhausen to Aalen, Württemberg, Germany (Riegraf et al., 1984).

Intervening: ANS, CRN, NOR, PLB.

Order BELEMNITIDA Zittel, 1895

The age of the oldest Belemnitida is open to some discussion. Phylogenetically, derivation of the Belemnitida from the Bactritida (Jeletzky, 1966) would support Palaeozoic belemnites, while derivation from the Aulacocerida or Phragmoteuthida (Engeser and Bandel, 1988) would allow only for Mesozoic belemnites. Palaeozoic records are equivocal: Eobelemnites caneyensis Flower is a true belemnite phragmocone, reputed to be from the Caney Shale (Mississippian), Oklahoma, USA (Flower, 1945), and the coleoid Jeletzky douglassae Johnson and Richardson from the middle Pennsylvanian of Illinois is considered by Gordon and Jeletzky (in Gordon, 1971) to be a true belemnite. As the former is represented by a single museum specimen with indifferent provenance, it can be discounted, with the
reidentification of the only other specimen (Flower and Gordon, 1959) as an orthoconic nautiloid (Gordon, 1966). Jeletzkya, although an undoubted Carboniferous coleoid, is perhaps even more problematic. On the basis of associated gladius-like structures, Saunders and Richardson (1979) reaffirmed Johnson and Richardson’s assignment to the Teuthida, but these structures are now known to be fish scales (Riccardi and Sabattini, 1985). Therefore, on the basis of its ten equal arms with paired arm hooks Jeletzkya could be placed tentatively with the Belemnitida. Other alternatives are that it is an aulacocerid, or a phragmoteuthid, both of which are considered to have possessed ten arms, although arm hooks are confirmed only in phragmoteuthids.

**Suborder** Status UNCERTAIN


**First and Last:** Jeletzkya douglassae Johnson and Richardson, 1968, Middle Pennsylvanian (Desmoinesian) Francis Creek Shale, Western Springs, Illinois, USA (Saunders and Richardson, 1979).

**Comments:** Considered by Jeletzky (in Gordon, 1971) to be a belemnite, and by Johnson and Richardson (1968) and Saunders and Richardson (1979) to be a teuthid.

**Suborder** Status UNCERTAIN

F. SINOBELMNITIDAE Zhu and Bian, 1984

Tr. (CRN) Mar.

**First and Last:** Sinobelemnites cornutus Zhu and Bian, 1984, S. typica Zhu and Bian, 1984, S. elongata Zhu and Bian, 1984,

Comments: The belemnoids figured by Zhu and Bian (1984) are, as far as can be ascertained from the illustrations and descriptions, true belemnites. However, they are unusual in being closer in morphology to Middle and Upper Jurassic Belemnopseidae than to the earlier Jurassic Belemnitidae. This poses significant phylogenetic problems, and further clarification of stratigraphical data is necessary.

Suborder BELEMNITINA Zittel, 1895

F. BELEMNITIDAE d’Orhigny, 1845


First: *Schwegleria fujelii* (Schwegler, 1939), *S. praecox* (Schwegler, 1939), *S. psilonoti* (Schwegler, 1939), Psilonotentone, Steinenberg near Nürtlingen, Württemberg, Germany (Riegraf, 1980).


Intervening: SIN–BTH.

F. SALPINGOTEUTHIDIDAE Doyle, 1992


First: *Salpingoteuthis tessoniana* (d’Orbigny, 1842), Toarcian, Amaye-sur-Orne, Calvados, France (Doyle, 1992).

Last: *Salpingoteuthis hartmanni* Lissajous, 1927, Aalenian of Vénède, Lozère, France (Lissajous, 1927).

F. HASTITIDAE Naef, 1922


First: *Hastites clavatus* (Schlotheim, 1820), *Uptonia jamesoni* Zone, Reutlingen, Württemberg, Germany (Riegraf, 1980).

Last: *Rhabdobelus* (Neoclavibelus) *neumarktensis* (Oppel, 1856), Middle Jurassic Alpha, Metzingen, Württemberg, Germany (Riegraf, 1980). All post-Aalenian records of *Hastites* are more properly referred to *Hibolithes* (Belemnopseidae).

Intervening: TOA.
F. BELEMNOTHEUTIDIDAE Zittel, 1885


Intervening: CLV, KIM.

F. CYLINDROTEUTHIDIDAE Stolley, 1919
J. (BTH)–K. (BRM) Mar.


Last: Actinotethis (Boreotethis) spp. Aklavik Range, northern Richardson Mountains, North-West Territories, Canada (Dobey and Kelly, 1988).

Intervening: CLV–HAU.

F. OXYTEUTHIDIDAE Stolley, 1919

First: Praeoxteuthis jaksofianna (Lahusen, 1874), Bed VIIa, Speeton Clay, Speeton, North Yorkshire, England, UK (Mutterlose, 1983).


Intervening: BRM.

Suborder BELEMNOPSEINAE Jeletzky, 1965

F. BELEMNOPSEIDAE Naef, 1922

First: Belennopis canaliculata (Schlotheim, 1820), Stephanoceras humphriesianum Zone, Gammelshausen, Wurttemberg, Germany (Riegraf, 1980). Earlier Belennopis possibly occur in the Ludwigia murchisonae Zone (Aalenian) of Normandy, France (Riegraf, 1980, p. 172).

Last: Neohtibolites ultimus (d’Orbigny, 1845), Mantelliceras mantelli Zone, Glaucolithic Marl and Lower Chalk, south-east England, UK (Donovan and Hancock, 1967).

Intervening: BTH–APT.

F. DICOELITIDAE Saks and Na’nyaeva, 1967


Intervening: TOA, BAJ–OXF.

F. PSEUDODICOELITIDAE Saks and Na’nyaeva, 1967


Last: Pseudodicoelites sp., Arctocephalites elegans Zone, Bathonian, Siberia (Saks and Na’nyaeva, 1975).

Intervening: AAL, BAJ.

F. DUVALIIDAE Pavlov, 1914

First: Rhopalocteuthis gillieroni (Mayer, 1866), Couches de Klaus, Fribourg, Switzerland; Trzebionka, Poland (Malecki, 1984).


Intervening: CLV, OXF, TTH–HAU, APT.

F. BELEMNITELLIDAE Pavlov, 1914

First: Actinocamax (Praeactinocamax) primus Arkhangelsky, 1912, Mantelliceras mantelli Zone, Russian Platform, former USSR; Glauconite Sands, Antrim, Northern Ireland, UK (Chrisansen, 1974).


Intervening: TUR–CMP.

F. DIMITOBELIDAE Whitehouse, 1924


Last: Dimitobelus (Dimitocamax) hectori Stevens, 1965, Haumurian (Maastrichtian), Amuri Bluff, New Zealand (Stevens, 1965).

Intervening: ALB–CMP.

Suborder DIPLOBELINA Jeletzky, 1965

F. DIPLOBELIDAE Naef, 1926

First: Diplobelus belemnoides (Zittel, 1868), Tithonian, Stromberg, Czechoslovakia (Jeletzky, 1981); Quiricobelus italicus Combecorell and Mariotti, 1986, Tithonian, Aptychus Limestones, Serra San Quirico, Ancona Province, Italy (Combecorell and Mariotti), 1986).

Last: Unnamed, Maastrichtian of the Pacific Coast of Canada (Jeletzky, 1981). The next youngest species is Conoteuthis syriacea (Roger, 1944) from the Cenomanian of the Lebanon (Jeletzky, 1981).

Intervening: BER–ALB.

Order Status UNCERTAIN


Comments: This taxon is claimed by the authors to be an ‘intermediate form’ between belemnoids and sepiids. Although it possesses a rostrum which is somewhat similar to that of Spirulirostra (Sepiida), it is clearly a belemnoid, further work is needed to clarify its position.

Order Status UNCERTAIN
Comments: The true nature of Bayonoteuthis is yet to be determined, with its phylogenetic and taxonomic position unclear. Riegraf (1991), following earlier authors (e.g. Branco, 1885), considers that this form is actually a pentatulacean coral.

Order BOLETZKYIDA Bandel et al., 1983


Order TEUTHIDA Naef, 1922

The more familiar nominal order Teuthida Naef, 1922, is employed here in place of Vampyromorpha Robson, 1930, used for these fossils by Engeser and Bandel (1988) and Engeser (1988b), based on a variety of evidence discussed by Bandel and Leich (1986). Although the gladius of the living genus Vampyroteuthis resembles those of fossil genera Loligosepia and Teudopsis (Loligospidae), other forms included in the Vampyromorpha by these authors (such as Plesioteuthis) have gladii which are closer to those of modern teuthids (Donovan and Toll, 1988). Clearly, further work is needed to clarify the position of these fossils. Engeser (1988b) has exhaustively reviewed all fossil teuthids.

Suborder Status UNCERTAIN

??F. GLOCHINOMORPHIDAE Gordon, 1971

First and Last: Glochinomorpha stifeli Gordon, 1971, Meade Peak Phosphatic Shale Member, Phosphoria Formation, Box Elder County, Utah, USA (Gordon, 1971).

Comments: This taxon has doubtful status within the Teuthida, and requires much further study.

Suborder LOLIGOSEPIINA Jeletzky, 1965

F. LOLIGOSEPIIDAE Regteren Altena, 1949


Last: Neololigosepia vinarensis (Fritsch, 1910), Weissenberger Schichten, Vinar near Hohenmauth, Czechoslovakia.

Intervening: SIN, TOA, TTH, BRM.

F. GEOPELTIDIDAE Regteren Altena, 1949

First: Geopeltis simplex (Voltz, 1830), Posidonienschiefer, Ohmden, Württemberg, Germany.

Last: Geopeltis sp., Fish Beds, Sahel-Alma, Lebanon.

Intervening: TTH.

F. MASTIGOPHORIDAE Engeser and Reitner, 1985


Last: Mastigophora stuehmeri Engeser and Reitner, 1985, Lower Aptian of Heligoland, Schleswig-Holstein, Germany.

Intervening: TTH.

F. LEPTOTHEUThIDIDAE Naef, 1921

First: Leptotheuthis gigas Meyer, 1834, Solnhofen Limestone, Solnhofen, Bavaria, Germany.

F. LIOTEUThIDIDAE Naef, 1922

First: Lioteuthis problematica Naef, 1922, Posidonienschiefer, Ohmden, Württemberg, Germany.

Suborder PROTOTEUThIDINA Naef, 1921

F. PLESIOTEUThIDIDAE Naef, 1921

First: Plesioteuthis hastata (Münster, 1843); P. sagitata (Münster, 1843), Posidonienschiefer, Holzmaden, Württemberg, Germany.

Last: Mioiteuthis maestrichtensis (Binkhorst van den Binkhorst, 1862), Maastrichtian of Fauquemont, Limbourg, Holland.

Intervening: CLV, TTH, BRM, APT, SAN, CMP.

Suborder MESOTHEUThIDINA Naef, 1921

F. PALAEOLOLIGINIDAE Naef, 1922

First: Palaeoalalloceras simplex (Voltz, 1830), Posidonienschiefer, Ohmden, Württemberg, Germany.

Last: Parateudopsis libanotica (Naef, 1922), Fish Beds, Sahel-Alma, Lebanon.

Intervening: TOA, CLV, TTH.

F. TRACHYTEUThIDIDAE Naef, 1922

First: Trachyteuthis palmeri (Schevill, 1950), Oxfordian of Jagua Vieja, Vináles Region, Cuba.

Last: Actinosepia canadensis Whiteaves, 1897, Bearpaw Shale, mouth of Swift Current Creek, southern Saskatchewan, Canada.

Intervening: KIM, TTH, APT, CEN, TUR, SAN.

Suborder KELAENINA Starobogatov, 1983

F. MUIENSTERELLIDAE Roger, 1952

First: Muensterella scutellaris (Münster, 1843), Calaenoteuthis incerta Naef, 1922, Solnhofen Limestone, Solnhofen, Bavaria, Germany.

Last: Tuteuthis longa Logan, 1898, upper Smoky Hill Member, Niobrara Formation, Logan County, Kansas, USA (Nicholls and Isaak, 1987).

Intervening: CON, SAN.
Order OCTOPODA Leach, 1818

F. PALAEOCTOPODIDAE Dollo, 1912


First: Proteroctopus ribeti Fischer and Riou, 1982, Bositra buchi and Ophiopinna elegans beds, Boissine, Voult-sur-Rhône, Ardeche, France (Fischer and Riou, 1982). Engeser (1988a) considers that this record is not a true octopus, with Palaeoctopus the sole representative of the family.

Last: Palaeoctopus newboldi (Woodward, 1896), Fish Beds of Sahel-Alma, Lebanon (Roger, 1944).

F. ARGONAUTIDAE Naef, 1912


First: Obinaultus pulchra Kobayashi, 1954, Oligocene, Nichinan Formation, between Obi and Aburatsu, Province of Hokkaido, between Obi and Aburatsu, Province of Hokkaido, Japan (Kobayashi, 1954). Originally described as a nautiloid (Noda et al., 1986).

Intervening: T. (MMI, PU).

Extant

Order SPIRULIDAE Stolley, 1919

Separation of Spirulida from Sepiida follows Donovan (1977) and Engeser and Bandel (1988).

F. GROENLANDIBELIIDAE Jeletzky, 1966


First: Naefia neogaea Wetzel, 1930, Upper Yezo Group (SAN-CMP), Sakasa-gawa, Haboro area, Hokkaido, Japan (Wetzel, 1930); Ariyalur Group (CMP-MAA), Pondicherry, southern India (Doyle, 1986).

Intervening: ?LUT.

Extant

F. VASSEURIIDAE Naef, 1921 T. (LUT) Mar.

First and Last: Vasseuria occidentalis Munier-Chalmas, 1880, Lutetian, Bois-Gouet, Loire-Inferieure, France (Munier-Chalmas, 1880; Curry, 1987). Please note that purely taxonomic references are not included.

Intervening: ?RUP.

Extant

References

Please note that purely taxonomic references are not included.


Lissajous, M. (1927) Description of quelques nouvelles espèces de bénédemites jurassiques. Travaux de Laboratoire de Géologie de la Faculté des Sciences de Université de Lyon, 7 (Supplément), 1–43.


MOLLUSCA: ROSTROCONCHIA, SCAPHOPODA AND BIVALVIA

P. W. Skelton and M. J. Benton

Three molluscan classes, the extinct Rostroconchia and the extant Scaphopoda and Bivalvia were united by Runnegar and Pojeta (1974) in the Subphylum Diasoma ('through-body'), characterized by a primitively bilobate shell associated with a relatively straight gut running from near the anterior arch to the posterior arch of the shell aperture. The rostroconchs are regarded as having evolved as a shallow-burrowing offshoot of early monoplacophorans, in turn giving rise to both the scaphopods and the bivalves. However, Peel (1991) expressed an opposing view, that the Diasoma is a diphyletic group, since he considers that the exogastric and endogastric molluscs had separate origins. Hence, the Bivalvia and Rostroconchia would be entirely separate.

In the rostroconchs, the two lateral lobes of the shell are separated ventrally by a narrow gape, which became occluded in some advanced forms, leaving only anterior and posterior gapes. Continuous fracturing and repair along the dorsal midline of the shell accompanied the forcing apart of the opposing shell lobes as they grew ventrally, although, in certain advanced forms, the midline seems to have become flexible. In early forms, the two lobes are joined internally by a transverse dorsal ridge (pegma). Most rostroconchs are believed to have been deposit feeders, though a few may have been suspension feeders. The systematics of the class is comprehensively reviewed by Pojeta and Runnegar (1976) and Pojeta (1985), from whom the data given here are derived. Rostroconchs were of moderate diversity in shallow Palaeozoic seas, but declined in the Permian, becoming extinct by its close.

The adult shell of scaphopods is fused ventrally, so forming a conical tube, open at both ends, and extended by growth mainly at the posterior end. They are sluggish shallow burrowers in marine sediments, capturing microscopic prey with anterior feeding tentacles. Their diversity has never been high. See Pojeta (1985) and Palmer (1974) for discussion.

The bivalves are diasome molluscs in which the shell consists of two matching lateral valves, united by a dorsal horny ligament, and which can be drawn together by a pair of adductor muscles (reduced to one in some) against the opening counter-force of the ligament. Primitively, this arrangement has permitted active penetration of sediments, aided by the blade-shaped foot, associated with deposit- and suspension-feeding. Subsequent adaptations have included attachment to surfaces either by means of an organic byssus or by cementation of one of the valves, boring, swimming and the adoption of miniaturized, commensal habits, and, in a few genera, predation. Today, bivalves are among the most common of benthic invertebrates, especially on marine shelves, although there are also many species in fresh water and in abyssal (including rift-vent) habitats.

The fossil record of the class is world-wide and spans the Phanerozoic. In spite of the abundance of bivalve fossils (only a handful of living families are unrepresented), and an extensive literature on their lower-level taxonomy, much uncertainty remains over their higher-level relationships. The relatively small number of taxonomically useful shell characters (e.g. form and arrangement of the teeth on the valve hinges, type of ligament insertion, disposition of muscle scars and the general shape of the shell) are mostly of a simple nature, and frequently show convergence. Cladistic analysis is therefore difficult and has been conducted on only a limited scale to date; the monophyletic versus paraphyletic status of many families is unknown. Also, the taxonomic diversity of families is very uneven: several monogeneric families exist, but most have from a few up to a couple of dozen genera, while two families (Unionidae and Veneridae) have around a hundred genera each.

The precision of stratigraphical information available for bivalve taxa often leaves much to be desired. With a few notable exceptions (e.g. Coal Measures forms, inoceramids, buchiids), the
bivalves themselves are little used for correlation, and many records are from strata which are difficult to date in any case. In most instances, stage-level resolution is all that can be established.

The indispensable sources for taxonomic and stratigraphical information are the three 'Treatise' volumes (Cox et al., 1969, 1971). These formed the basis for the compilation of marine families given by Sepkoski (1982). A full systematic and bibliographic (although not stratigraphical) catalogue of genera is given by Vokes (1980). Photographic illustrations of a number of representative taxa, with guidance on identification, may be found in Skelton (1985a). Several papers in Yonge and Thompson (1978) make important revisions of taxonomic groupings and of ranges across the class, while Pojeta and Runnegar (1985) and Pojeta (1985) provide updated information concerning its early Palaeozoic record. Carter (1990) provides updated coverage of three of the subclasses (Palaeotaxodonta, Pteriomorphia and Isofilibranchia), although a number of the ranges given have not been revised from the 'Treatise' and are thus inconsistent with other data included in his discussions of the taxa. In the list which follows, we have used these sources, together with a number of more specialized works.


EDITOR'S NOTE

This chapter was compiled in several stages. PWS provided the outline classification and stratigraphical range information, as well as more detailed documentation of bivalve families from Palaeotaxodonta to Ostreoida inclusive plus Hippuritoida. MJF filled the gaps, providing documentation of rostroconchs and scaphopods, and other bivalve families from Lucinoida to the end of the listing, and are taken from Pojeta and Runnegar (1976), except where otherwise indicated. The oldest rostroconch is Pseudotechnophorus typicalis Kobayashi, 1933 and Eoischyria billingsi Kobayashi, 1933, both Wanwankou Dolomite, Wanwanian, Fengshanian, southern Manchuria.

Order ISCHYRINIOIDA Pojeta and Runnegar, 1976

F. ISCHYRINIIDAE Kobayashi, 1933

F. BRANSONIIDAE Pojeta and Runnegar, 1976

Order CONOCARDIOIDA Neumayr, 1891

F. EOPTERIIDAE Miller, 1889

F. CONOCARDIOIDA Miller, 1889


Last: Eopteria conocardiformis Pojeta and Runnegar, 1976, Little Oak Limestone, Porterfieldian, Pelham, Alabama, USA and High Bridge Group, Wildermessian, Highbridge, Kentucky, USA.

Comments: A possible eopterid is noted from the ASH of Queensland, Australia (Shergold, 1976).

F. CONOCARDIOIDA Miller, 1889


First: Conocardium attenuatum (Conrad, 1842), Schoharie Formation, New York State, USA.

Last: Arceodomus langenheimii (Wilson, 1970), McCloud Limestone, Shasta County, California, USA.

F. BRANSONIIDAE Pojeta and Runnegar, 1976

The classification is taken from Palmer (1974), and the taxonomic ranges from Ludbrook (1960), except where otherwise noted.

**Class SCAPHOPODA** Bronn, 1862

The classification is taken from Palmer (1974), and the taxonomic ranges from Ludbrook (1960), except where otherwise stated.

**Order DENTALIOIDA** Palmer, 1974
- **F. LAEVIDENTALIIDAE** Palmer 1974
    - **First:** Prodentalium martini (Whitfield, 1882), upper Helderberg Limestone, Dublin, Ohio, USA. **Extant**
      - **Comments:** The Family Dentaliidae was redefined by Palmer (1974) to include only ‘Dentalium sensu lato’ and Prodentalium. Other dentalioids were assigned by him to the Laevidentaliidae.

  - **Order SIPHONODENTALIOIDA** Palmer, 1974
    - **F. CADULIDAE** Grant and Gale, 1931
        - **First:** Calstevenus arcturus Yancey, 1973, Riepetown Formation, Arcturus Group, White Pine County, Nevada, USA (Yancey, 1973). **Extant**

- **F. SIPHONODENTALIIDAE** Simroth, 1894
  - **First:** Ezoconula mactraeformis Nagao, 1938, Japan (Carter, 1990).

**Class BIVALVIA** Linné, 1758

Details of taxa are taken from Cox et al. (1969, 1971) unless otherwise noted.

**Subclass PALAEOTAXODONTA** Korobkov, 1954
- **Order NUCULOIDA**, Dall, 1889
    - **First and Last:** Thoralia longitude (Thoral, 1935), lower ARG, Languedoc, southern France (Morris, 1980).
Fig. 13.1

First: *Tindaria arata* Bellardi, 1875, lower PLI, Piemonte and Liguria, Italy.

**Extant**

Comments: The fossil record of these deep-water forms is very poor (N. J. Morris, pers. comm., 1992). See also Allen (1978).

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**Order** SOLEYMIOIDA Dall, 1889

**F. SOLEYMYIDAE** Adams and Adams, 1857 (1840)


First: *Psiloconcha senecta* (Sardeson, 1896), St Peter Sandstone, St Paul, Minnesota, USA; *Dystactella ordovicicus* (Pojeta and Runnegar, 1985) and *D. aedilis* (Eichwald, 1856), Kukruse Stage, Estonia, former USSR (Pojeta, 1988). **Extant**

Comments: The Nucinellidae is included in the Manzanellidae by many authors (e.g. Beu and Maxwell, 1990). Placement of the family in the Limopsacea Dall, 1895, in Cox et al. (1969) is rejected (see Pojeta, 1988).
**Fig. 13.1**

*Subclass* ISOFILIBRANCHIA Iredale, 1939

*Order* MODIOMORPHOIDA Newell, 1969

**F. FORDILLIDAE** Pojeta, 1975

*E. (TOM)—O. (CRD) Mar.*

**First:** Fordilla sp., TOM, Khara-Ulakh, Lena River, Siberia, Russia (Jermak, 1986 in Rozanov and Zhoravlev, 1992). The next oldest fossil is *Fordilla troyensis* (Barrande, 1881), Hyolithes Limestone (lower ATB), Leicestershire, England, as well as Siberia, former USSR and New York, USA (Brasier, 1984).

**Last:** *Neofordilla elegans* Krasilova, 1977, middle Dolborian Beds, Cherlechine River, Siberia, former USSR (Pojeta and Runnegar, 1985).

**Comments:** *Fordilla* was tentatively assigned to the Isofilibranchia by Pojeta (1975) on the basis of similarity in its external morphology to later forms. It is not clear whether the feeding gill had evolved before the Ordovician (J. C. W. Cope, pers. comm., 1992).

**F. MODIOMORPHIDAE** Miller, 1877

(*= Modiolopsidae Fischer, 1887)*

*O. (ARG)—P. (ROT) Mar.*

**First:** *Modiolopsis?* sp., Couches du Foulon, Croix de Roquebrun, Montagne Noire, France (Babin, 1982a).

**Last:** *Goniophora, Goniophorina*, Lower Permian, southwestern USA.

**Comments:** *Glyptarca primaeva* Hicks, 1873, Ogof Hên


**F. ORTHONOTIDAE** Miller, 1877  O. (ARG)–P. (ZEC) Mar.

*First:* ?Cymatonota sp., Couches du Foulon, Croix de Roquebrun, Montagne Noire, France (Babin, 1982a).

*Last:* Solenomorpha minor (M’Coy, 1844), (Runnegar, 1974).


*First:* Rimmyjimima arcula Chronic, 1952, Kaibab Formation, Walnut Canyon, Arizona, USA.


*Order* MYTILOIDA Ferussac, 1822
Mollusca: Rostroconchia, Scaphopoda and Bivalvia

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**Key for both diagrams**

1. Inoceramidae
2. Aaloconchidae
3. Eurydesmidae
4. Pergamidiidae
5. Monopteriidae
6. Pterineidae
7. Umburridae
8. Kochiidae
9. Pteridae
10. Bakevelliidae
11. Lithioidae
20. Myodacryotidae
21. Limidae
22. Plicatulidae
23. Dimyidae
24. Ostreidae
25. Gryphaeidae
26. Eligmidae
27. Picatostylidae
28. Leiopectinidae
29. Pterinopectinidae
30. Aviculopectinidae
31. Deltopectinidae
32. Euchondriidae
33. Monotidae
34. Aesoellidae
35. Buchiidae
36. Oxytomidae
37. Pseudomonotidae
38. Terquemiidae
39. Permanomiidae
40. Anomidiidae
41. Chaenocardidae
42. Propcamussiidae
43. Entolidae
44. Syncycloneidae
45. Pectinidae
46. Spondylidae
47. Cycloconchidae
48. Lyrodesmatidae
49. Redoniidae
50. Caryidiidae
51. Eoschizodiidae
52. Schizodiidae

**Fig. 13.2**

**F. MYTILIDAE** Rafinesque, 1815


First: ?Myitilops precedens (Hall, 1870), Chemung Group, New York State, USA.

Extant

**F. MYSIDIALLIDAE** Cox, 1964

Tr. (SCY–RHT) Mar.

First: Protopis triptycha Kittl, 1904, Werfen Beds, Austrian Alps.

Last: Mysidella orientalis (Bittner, 1891), Anatolia; M. cordillerana Newton, 1987, NOR, Wallowa Terrane, Oregon, USA (Carter, 1990); M. aequilateralis (Stoppani, 1865), Zlambach Beds, Austria (Hallam, 1981).

**Subclass** PTERIOMORPHIA Beurlen, 1944

**Order** TUARANGIOIDA MacKinnon, 1982


Last: Tuarangia sp., Miedzyzdroye, Poland (Berg-Madsen, 1987).

**Order** PRAECARDIOIDA Newell, 1965


First: Praecardium primulum Barrande, 1881, E2, Middle Silurian, Bohemia, Czechoslovakia.

Last: Dexiobia whitei Winchell, 1863, Kinderhookian, Iowa, USA.

**Comments:** Eopteria Billings, 1865, included in the family by Cox et al. (1969), is a rostroconch.

**F. ANTIPELURIDAE** Neumayr, 1891


First: Shanina viastoides Reed, 1915, upper Naugkangyi Beds, North Shan States, India.

Last: Hercynella beyrichi Kayser, 1878, Harz Mountains, Germany.


First and Last: Butovicella migrans (Barrande, 1881), Motol Formation, C. lundgreni Zone, Bohemia, Czechoslovakia.
### Animals: Invertebrates

#### F. LUNULACARDIIDAE Fischer, 1887

**First:** *Patrocardia* sp., WEN, Carnic Alps, Austria (J. Kríž, pers. comm., 1992).

**Last:** *Lunulacardium (Lunulacardium) semistriatum* Münster, 1840, Europe, North America.

**Comments:** All the early taxa are poorly understood, and the bivalve status of some is even questionable. *Euchasma* Billings, 1865, included here by Cox et al. (1969), is a rostroconch (Pojeta and Runnegar, 1976). In addition, *Maminka* has been reassigned to the Antipleuridae (Carter, 1990, p. 204).

**Order ARCOIDA Stoliczka, 1871**

F. CARDIOLIDAE Fischer, 1886

**First:** *Cardiobeleba lavina* Kríž, 1979, lower WEN, Carnic Alps, Austria.

**Last:** *Cardiolinka concubina* Kríž, 1979, uppermost PRD, Bohemia, Czechoslovakia.

**Comments:** Devonian and Carboniferous records, noted in Cox et al. (1969, p. N245) are not accepted by J. Kríž (pers. comm., 1992).


**First:** *Slava semirugata* (Portlock, 1843), Pomeroy, Co. Tyrone, Northern Ireland.

**Last:** *Slavinka oforâta* (Barrande, 1881), LUD, Bohemia, Czechoslovakia.

**F. CYRTOCONIDAE Ulrich, 1894**

**O. (ARG?)—D. (GIV) Mar.**

**First:** *Cyrtoconulida hadzeli* Pojeta and Gilbert-Tomlinson,

**Last:** *Ptychodesma knappianum* Hall and Whitfield, 1872, Hamilton Group, New York State, USA; *Pycinodesma* Kirk, 1927, Alaska, USA (Pojeta and Runnegar, 1985).

**Comments:** *Pharcidoconcha parallelus* (Hsu, 1948) has been noted from the ?TRE of China, but these beds are probably ARG in age (J. C. W. Cope, pers. comm., 1992). Devonian *'Macrodus'* from the Rhine Devonian may belong here.

**F. ARCIDAE** Lamarck, 1809  J. (AAL)—Rec. Mar.

**First:** *Arca (Eonavicula) minuta* J. de C. Sowerby, 1824, various formations, England, UK, France, Germany (Hallam, 1976). Extant

**F. PARALLELODONTIDAE** Dall, 1898  P. (KUN)—Rec.? Mar.

**First:** *Parallelodon capillatus* Waterhouse, 1987, Brae Formation, Bowen Basin, Queensland, Australia (Waterhouse, 1987). Extant?

**Comments:** Pojeta (1971) regards the poorly known *'Parallelodon' antiquus* Barrois, 1891, from the Gres Armoricain, France (ARG), as misplaced in this family; likewise the *Glyptarca* Hicks, 1873, cited by Cox et al. (1969, p. N256). Devonian *'Macrodus'* from the Rhine Devonian may belong here.

**F. CUCULLAEIDAE** Stewart, 1930  J. (HET)—Rec. Mar.

**First:** *Cucullaea (Idonearca) mabuchii* Hayami, 1958, *Alsatites* Bed, Shizukawa Group, NE Japan (Damborenea, 1987). Extant

**F. NOETIIDAE** Stewart, 1930  K. (APT)—Rec. Mar.

**First:** *Noetia (Incanopsis) palestina* (Whitfield, 1891), Lebanon. Extant

**F. GLYCIMERIDIDAENewton, 1922**  J. (?BTH)—Rec. Mar.

**First:** *'Limopsis' minima* (J. de C. Sowerby, 1825), BTH, England, UK (Hallam, 1976). Extant

**Comment:** This taxon has been transferred from the Limopsidae (Oliver, 1981).
Fig. 13.4

Comments: Hoferia Bittner, 1894 and Pitchleria Bittner, 1894 are rejected from the family (Oliver, 1981); their affinities are unknown. Likewise, Jurassic species previously assigned to Limopsis Sassi, 1827, are now considered to be glycymeridids (see Carter, 1990, p. 194).


First: Isoarca subspirata (Münster, 1837), Germany (Hallam, 1976).  Last: Isoarca sp. The latest BMNH specimens are CEN, but there may be a MAA record (N. J. Morris, pers. comm., 1992).
Comments: The family has been transferred to the Arcoida from the Palaeotaxodonta: Keen's assertion (in Cox et al., 1969, p. N241) that the shell is nacreous (implying placement of the family with palaeotaxodonts) is not borne out by inspection of specimens of type species in the British Museum (Natural History), London (N. J. Morris, pers. comm., 1992).

F. PITCHLERIDAE Scarlato and Starobogatov, 1979  Tr. (CRN)—Mar.
First and Last: Pitchleria auingeri (Laube, 1865) and Hoferia
**Mollusca: Rostroconchia, Scaphopoda and Bivalvia**

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<th>Genus</th>
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**Order PTERIOIDA Newell, 1965**

**F. AMBONYCHIIDAE** Miller, 1877

**First:** *Cleionychia lamellosa* (Whitefield, 1882), Chazy Formation, New York State, USA; *Pteronychia haupti* Pojeta and Gilbert-Tomlinson, 1977, Stairway Sandstone (LL/LLO), Amadeus Basin, southern Northern Territory, Australia (Pojeta and Runnegar, 1985).

**Last:** *Mytilarca chemungensis* (Conrad, 1842), Chemung Group (FRS), New York State, USA. Comments: *Mytilarca* has been noted doubtfully from the lower Mississippian of Europe and North America.

**F. MYALINIDAE** Frech, 1891

**First:** *Myalina (Myalina) goldfussiana* De Koninck, 1842, Cementstone Group, Calciferous Sandstone Series, Berwickshire, Scotland, UK, and other species (Gray, 1988).

**Last:** *Promyalina groenlandica* (Newell, 1955) and *Myalinella meeki* (Dunbar, 1924), both SCY, East Greenland.

**Comments:** Two Jurassic taxa, *Pachymytilus* Zittel, 1881 and *Pseudopachymytilus* Krumbeck, 1923, and one Devonian form, *Boiomytilus* Richard and Prantl, 1961, were assigned to the Myalinidae by Cox et al. (1969, pp. N289–N295), but these are all disregarded here.

**F. ATOMODESMIDAE** Waterhouse, 1976

**First:** *Aphanaia tivertonensis* Waterhouse, 1979, Tiverton Formation, Bowen Basin, Queensland, Australia (Waterhouse, 1979a).

**Last:** *Atomodesma variabile* Wanner, 1922, Timor; Panjang Formation, Nepal (possibly derived, J. B. Waterhouse, pers. comm., 1992).

**F. INOCERAMIDAE** Zittel, 1881

**First:** *Inoceramus* (Inoceramus) deformis De Koninck, 1842, Cementstone Group, Calciferous Sandstone Series, Berwickshire, Scotland, UK, and other species (Gray, 1988).

**Last:** *Promyalina groenlandica* (Newell, 1955) and *Myalinella meeki* (Dunbar, 1924), both SCY, East Greenland.

**Comments:** Two Jurassic taxa, *Pachymytilus* Zittel, 1881 and *Pseudopachymytilus* Krumbeck, 1923, and one Devonian form, *Boiomytilus* Richard and Prantl, 1961, were assigned to the Myalinidae by Cox et al. (1969, pp. N289–N295), but these are all disregarded here.

**Fig. 13.4**

duplicata (Münster, 1838), both Cassian Formation, Italian Alps (Carter, 1990, p. 196).

**Order PTERIOIDA Newell, 1965**

**F. AMBONYCHIIDAE** Miller, 1877

**O. (LLO)–D. (FRS) Mar.**

**First:** *Cleionychia lamellosa* (Whitefield, 1882), Chazy Formation, New York State, USA; *Pteronychia haupti* Pojeta and Gilbert-Tomlinson, 1977, Stairway Sandstone (LL/LLO), Amadeus Basin, southern Northern Territory, Australia (Pojeta and Runnegar, 1985).

**Last:** *Mytilarca chemungensis* (Conrad, 1842), Chemung Group (FRS), New York State, USA. Comments: *Mytilarca* has been noted doubtfully from the lower Mississippian of Europe and North America.

**F. MYALINIDAE** Frech, 1891

**C. (TOU)–Tr. (SCY) Mar./Brackish**

**First:** *Myalina (Myalina) goldfussiana* De Koninck, 1842, Cementstone Group, Calciferous Sandstone Series, Berwickshire, Scotland, UK, and other species (Gray, 1988).

**Last:** *Promyalina groenlandica* (Newell, 1955) and *Myalinella meeki* (Dunbar, 1924), both SCY, East Greenland.

**Comments:** Two Jurassic taxa, *Pachymytilus* Zittel, 1881 and *Pseudopachymytilus* Krumbeck, 1923, and one Devonian form, *Boiomytilus* Richard and Prantl, 1961, were assigned to the Myalinidae by Cox et al. (1969, pp. N289–N295), but these are all disregarded here.

**F. ATOMODESMIDAE** Waterhouse, 1976

**P. (SAK)–Tr. (SCY) Mar.**

**First:** *Aphanaia tivertonensis* Waterhouse, 1979, Tiverton Formation, Bowen Basin, Queensland, Australia (Waterhouse, 1979a).

**Last:** *Atomodesma variabile* Wanner, 1922, Timor; Panjang Formation, Nepal (possibly derived, J. B. Waterhouse, pers. comm., 1992).

**F. INOCERAMIDAE** Zittel, 1881

**P. (SAK)–K. (MAA) Mar.**
**Animals: Invertebrates**

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**Fig. 13.5**


**Last:** *Tenuipteria argentea* (Conrad, 1858), Owl Creek Formation, Montana, USA; uppermost MAA, Middle Vistula Valley, Poland (Abdel-Gawad, 1986); and upper MAA, Sint Pietersberg, The Netherlands.

**Comments:** It is not clear whether *Tenuipteria* is a true inoceramid; it occurs in the MAA after the extinction of *Inoceramus* species. See Ward et al. (1991) and Dhondt (1992).

**F. ALATOCONCHIDAE** Termier et al., 1973

**First:** *Shikamaia (Tanchintongia) perakensis* (Runnegar and Gobbett, 1975) and *Saikraconcha (Dereconcha) kamparensis* Yancey and Boyd, 1983, both *Pseudofusulina ambigua* Zone, Malaysia.

**Last:** *Shikamaia (Alatoconcha) vampyra* (Termier et al., 1973), Afghanistan, *Saikraconcha ogulineci* (Kochansky-Devidé, 1978), former Yugoslavia, and *S. tunisiensis* Yancey and Boyd, 1983, Tunisia; all in the *Neoschwagerina* Assemblage Zone (Yancey and Boyd, 1983).

**F. EURYDESMIDAE** Reed, 1932


F. PERGAMIDIIDAE Cox, 1969
Tr. (CRN)–J. (SIN) Mar.
First: Oretia coxi Marwick, 1953, Oretian, North and South Islands, New Zealand; Manticula problematica (Zittel, 1864), Otamitan, North and South Islands, New Zealand and upper CRN, Baie de Saint-Vincent, New Caledonia (Waterhouse, 1979b).
Last: Semuridia dorsetensis (Cox, 1926), Lias, Dorset, England, UK (Hallam, 1987).
Comment: A possible later pergamidiid, Manticula sp., is known from the Cretaceous (BER) of South Shetland Island, Antarctica (J. A. Crame, pers. comm., 1992).

F. MONOPTERIIDAE Newell, 1969
First: Monopteria longispina Meek and Worthen, 1866, Desmoinesian, Appalachian Basin, USA.

Last: Monopteria sp., Virgilian, Jacksboro, Texas, USA.
Comment: Cox et al. (1969, p. N297) note 'L. Perm.' material from the USA, but this has not been substantiated.

F. PTERINEIDAE Miller, 1877
First: Denticelox turtuosa (Tate, 1896), Stairway Sandstone, Amadeus Basin, southern Northern Territory, Australia (Pojeta and Gilbert-Tomlinson, 1977).
Last: Leptodesma sp., Tenjinnoki Formation, Miyagi, Japan (Nakazawa and Newell, 1968).


F. KOCHIIDAE Maillieux, 1931
First: Kochia capuliformis (Koch, 1881), Siegener Grauwacke, Rheinland, Germany.
**Last:** Kochia capuliformis (Koch, 1881) and K. alata Maurer, 1902, Grès de Mormont, Ardennes, Belgium.

F. PTERIIDAE Gray, 1847 Tr. (LAD)—Rec. Mar. 
**First:** Arcavicula cassiana (Bittner, 1895), ?Pachycardiuntuffe, Cassian Formation, eastern Alps. **Extant**

**First:** Bakevellia sp., Buckhorn Asphalt, Desmoinesian Stage, south-central Oklahoma, USA (T. Yancey, pers. comm., 1992).

**Ativiculoperna aviculina** (Deshayes, 1864), Paris Basin, France. 
**Comment:** The next oldest well-known record is *Bakevellia binneyi* (Brown, 1841), Lower Magnesian Limestone (UFI), north-east England, UK.

F. LITHIOTIDAE Reis, 1903 J. (PLB) Mar. 
**First and Last:** Lithiota problematica Gumbel, 1874, widespread in lower Lias on southern Tethyan platforms, and Cochlearites loppianus (Tausch, 1890), upper Calcarei Grigi, Verona, north Italy (Chinzei, 1982).

**Comment:** Could be included in *Plicatystylidae* (S. Damborenea, pers. comm., 1992).

**First:** Cassianella crassispinosus Chronic, 1949, Copacabana Group, Peru.

**Last:** Cassianellid (N. J. Morris, pers. comm., 1992).

**Comments:** If the Permian records are not accepted, the oldest cassianellid would be *Septihorbesia johannisaustriae* (Klipstein, 1845), south Tyrol, eastern Alps; *S. subglobosa* (Credner), Muschelkalk, Germany (both LAD).

F. DATTIDAE Healey 1908 Tr. (NOR) Mar. 
**First and Last:** Datta oscillaris Healey, 1908, ?NOR (N. J. Morris, pers. comm., 1992), Burma.

**Comments:** This family is of dubious status, being based on a single internal mould of a left valve (Cox et al., 1969, p. N314). The age is given as RHT by the latter authors.

**First:** Retroceramus subtilis, *P. macklniokzi* Zone, lower AAL, Priokhotye, Siberia, former USSR; *R. levis Koskelkina*, 1969, ?TOA and AAL, and four other AAL species, former USSR (Damborenea, 1990).

**Last:** Retroceramus everesti (Oppel, 1865), lower Fossil Bluff Formation, Callisto Cliffs and Tombaugh Cliffs, Alexander Island, Antarctica (Crame, 1982); *R. foliiformis* Pokhialainen, 1969, BER, Anadyr-Koryak, Far East of former USSR.

**First:** Waagenoperna (Pernoperna) hayamii Nakazawa and Newell, 1968, Tenjinnoki Formation, NE Japan. **Extant**

**Comment:** Waagenoperna laterelatana (Waagen, 1907), supposedly from the SAK of Japan, is an Upper Triassic species (I. Hayami, pers. comm., 1992).

**First:** Pulvinites (Hypotrema) laevis Damborenea, 1987, Fanninoceras Zone, upper PLB, southern Mendoza and Neuquén Provinces, Argentina (Damborenea, 1987). **Extant**

**First:** Vusella sp., THA, France. **Extant**

**Comments:** Waller (1978) removed several of the genera cited by Cox et al. (1969, pp. 326–32) from this family, leaving *Vusella* as the earliest genus, of which the earliest undoubted record is Upper Palaeocene (N. J. Morris, pers. comm., 1992). A confirmed record is *V. angusta* Deshayes, 1858, Auverian (PRB), France.

**First:** Pinna costata Phillips, 1848, Visé, Belgium, *Pinna spatula* M’Coy, 1853, Visé, Belgium, Central France, Harz Mountains, Germany. **Extant**

**Comments:** The family is allied with the Pteriacea (Pojeta, 1978).

**First:** Posidonia becheri Bronn, 1828, Lower Carboniferous, Germany.

**Last:** Didymotis variabilis Gerhardt, 1897, lower CON, Colombia. 
**Comments:** Affinities of the family are reviewed by Carter (1990, p. 211). Inclusion of *Didymotis* in the family is questionable (N. J. Morris, pers. comm., 1992); the next youngest taxon is *Pseudodidymotis lamberti* Gillet, 1924, NEO, France.

**Order** LIMOIDA Rafinesque, 1815 
**First and Last:** Myodakryotus deigny Tunnicliff, 1987, Alt-Tair-fynyon Beds, Llanfyllin, Powys, and Celli Grin Formation, Bala, Cwm Eigiau Formation, Roman Bridge, and specimens from North America (Tunnicliff, 1987). **Extant**

**First:** Palacolima simplex (Phillips, 1836), Harz Mountains, Germany, eastern Alps, Austria, Yorkshire, England, UK, and other species. **Extant**

**Comments:** Ordovician material from North America referred to *Prolabella* by Pojeta and Runnegar (1985) is referred to *Myodakryotidae* by Tunnicliff (1987).

**Order** OSTREOIDA Féruissac, 1822 (Waller, 1978) 
**First:** Plicatula (Eoplicatula) imago Bittner, 1895 and *P. (E.) filifera* Bittner, 1895, north Italy (Yin, 1985; Carter, 1990, pp. 221–6). **Extant**

F. DIMYIDAE Fischer, 1886 Tr. (ANS)—Rec. Mar. 
**First:** Dimyodon sp. (Yin, 1985); *Proostrea* sp., China (N. J. Morris, pers. comm., 1992). **Extant**

**Comments:** The next oldest dimyids are *Atreta intestinalia* (Emmerich, 1853), early RHT of Europe, and *Dimyodon schlumbergeri* Munier-Chalmas, in Fischer, 1886, BTH, France.
F. OSTREIDAE Rafinesque, 1815
Tr. (CRN)–Rec. Mar./Brackish
Comments: Older material of 'Lopha' has been reported from the Upper Permian of Japan (Nakazawa and Newell, 1968), so the range may be greater.

F. GRYPHAEIDAE Vialov, 1936 Tr. (CRN)–Rec. Mar.

First: Eligmus rollandi (Douville, 1907), East Africa (Hallam, 1977).
Last: Euphenax jamaicensis (Trechmann, 1923), LUT, Jamaica, North Africa, Pakistan; Nyadina (Exputens) llajesensis Clark, 1934, LUT, California, USA, Jamaica; Pseudoheligmus morgani Douville, 1904, LUT, France.
Comments: Eligmus was included in the Malleidae by Cox et al. (1969, p. N329), but this was rejected by Weller (1978), and the family is recognized as distinct, with the inclusion of the 'Chondrodontidae' (N. J. Morris, pers. comm., 1992).

First and Last: Plicatostylus gregarius Lupher and Packard, 1930, Robertson Formation, Oregon, USA; also Peru and Chile.

First: Rhombopteria mira (Barrande, 1881), stage e2, lower LUD, Bohemia, Czechoslovakia.
Last: Leiopecten rectangularis Khalfin, 1940, Pribalkhash, Siberia, former USSR.

First: Pterinopecten (Pterinopecten) undosus Hall, 1883, LUD, cosmopolitan.
Last: Claraia griesbachi (Bittner, 1900), SPA, northern Pacific, Timor; Periclaraia sp., China (Yin, 1985).
Comments: Carter (1990, pp. 239–40), following other authors, includes Claraia Bittner, 1901 and Pseod Claraia here. If these are not pterinopectinids, the youngest form is Pterinopectinella welleri Newell, 1938, Leonardian, Kansas, USA.

F. AVICULOPECTINIDAE Meek and Hayden, 1864 C. (TOU)–Tr. (CRN) Mar.
First: Aviculopecten ? affinis de Koninck, 1885, Tournai, Belgium; A. grandocostatus White, 1862, Kinderhookian, Iowa and Missouri, USA, and other species.

Last: Eumorphotis telleri (Bittner, 1898), CRN, western Tethys, Arctic (Hallam, 1981).
Comments: Otapiria Marwick, 1935 (TTH) has been transferred to the Monotidae, and Claraia Bittner, 1901 may belong to the Pterinopectinidae (q.v.).

Last: Corrugopecten altoprimus Waterhouse, 1982, Mangarewa Formation, South Island, New Zealand and Flat Top Formation, Bowen Basin, Queensland, Australia (both KAZ); Corrugopecten sp., upper Dorashamian-Chaxingxian of Pig Valley Formation, Nelson, New Zealand (Waterhouse, 1982b).

First: Crenipexchus crenulatus Hall, 1883, New York State, USA.
Last: Euchondria, Upper Permian, North America, Europe, Japan.

F. MONOTIDAE Fischer, 1887 Tr. (CRN)–J. (TTH) Mar.
First: Otapiria dubia (Ichikawa, 1954), Kochigatani Group, Tokushima Prefecture, Shikoku, Japan (Damborenea, 1987).
Last: Otapiria masoni Marwick, 1953, Puaraoan, TTH, Port Waikato, North Island, New Zealand.
Comments: Otapiria has been transferred to this family from the Aviculopectinidae (Carter, 1990, pp. 245–8). The KIM and TTH records of Otapiria is doubtful (J. A. Crame, pers. comm., 1992). Monotis bores Oberg, 1877, SCY, Dickson Land, Spitsbergen is only doubtfully regarded as a member of this family (S. Damborenea, pers. comm., 1992).

Last: Asoella confertoradiata (Tokuyama, 1959) and A. laevigata (Tokuyama, 1959), both Atsu and Mine Series, west Japan.
Comment: Asoella was placed in the Aviculopectinidae by Cox et al. (1969, p. N337). It was transferred to the Buchiacea (= Monotoidea) by Weller (1978), and linked with Etalia in a new family by Begg and Campbell (1985). The latter authors very tentatively include Chlamys kotakiensis Takai and Hayami, 1957 from the Lisas of Japan and China in the family (a pectinid, I. Hayami, pers. comm., 1992).

First: Praebuchia anabarensis Zakharov, 1981, Cadoceras emelianzevi Zone, Siberia, former USSR.
Comments: The range of this family is given as CRN to
CEN by Cox et al. (1969, pp. N374–N377), while Carter (1990, pp. 248–9) indicates possible earlier members from the mid Permian (Glendella dickinsi Runnegar, 1970) and Middle Triassic (Sichuania marwicki Waterhouse, 1980). These, as well as other late Triassic, and early to middle Jurassic taxa are not accepted as buchiids by J. A. Crame or S. R. A. Kelly (pers. comm., 1992).

F. OXYTOMIDAE Ichikawa, 1958
**First:** Cyrtorosta limitans Waterhouse, 1987, Elvinia Formation, Bowen Basin, Queensland, Australia (Waterhouse, 1987).
**Last:** Hypoxytoma sp., MAA or ?DAN, Ocean Point, north Alaska, USA (J. A. Crame, pers. comm., 1992, based on the work of L. Marincovich).

F. PSEUDOMONOTIDAE Newell, 1938
**First:** Pachypteria nobilissima de Konincck, 1851, Visé Limestone, visé, Belgium, Derbyshire and Yorkshire, England, UK (?Iowa, USA (Newell and Boyd, 1970).
**Last:** Pseudomonotis (Pseudomonotis) speluncaria (von Schlotheim, 1816), Zechstein, Germany.
**Comments:** If Claraia Bittner, 1901 is included (Newell and Boyd, 1970), the range is extended to SCY, but this genus is placed in the Pterinopectinidae here.

F. TERQUEMIIDAE Cox, 1964
P. (SAK)–J. (KIM) Mar.
**First:** Palaeowaagia cooperi Newell and Boyd, 1970, Neal Ranch Formation, Glass Mountains, west Texas, USA (Newell and Boyd, 1970).
**Last:** Terqueinia ostreiformis (d’Orbigny), Jura, France.

F. PERMANOMIIDAE Carter, 1990
P. (ART) Mar.
**First and Last:** Permanomia texana, 1970, Leonardian, west Texas, USA (Newell and Boyd, 1970).
**Comments:** Carter (1990, p. 253) erected the family Permanomiidae since Permanomia has a duplicivincular liga­ment, and thus could no longer be regarded as an anomiid.

F. ANOMIIDAE Rafinesque, 1815
J. (BTH)–Rec. Mar.
**First:** Eonomia timida Fürsich and Palmer, 1982, Oppelia (Oxyceritae) sp. (Oxyceridaceae) discus Zones, upper BTH, Normandy, France and Bradford Clay, Wiltshire, England, UK (Fürsich and Palmer, 1982).
**Extant Comments:** E. M. Harper (pers. comm., 1992) notes that Eonomia was not cemented, as first thought, so Permanomia is not precluded as the earliest anomiid (pace Carter, 1990).

F. CHAENOCARDIIDAE Miller, 1889
(= Streblochondriidae Newell, 1938)
C. (L.)–P. (LGT) Mar.
**First:** Streblochondria sp., Mississippian, USA (Newell and Boyd, 1985).
**Last:** Guizhouspecten wangi Chen, 1962, Wujiaping Stage, Ziyun, Guizhou, China.
**Comments:** Streblochondria sculptilis (Miller, 1891) is noted from the upper Pennsylvanian to Lower Permian by Newell and Boyd (1985), who also state that the genus is known from the Lower Carboniferous. Guizhouspecten was transferred from the Aviculopectinidae to this family by Newell and Boyd (1985).

F. PROPEAMUSIIIDAE Tucker Abbott, 1954
**First:** Pernopecten limaformis (White and Whitfield, 1862), Burlington Beds, Osagean, Burlington, Iowa, USA.
**Extant Comments:** Waller (1978, p. 362) notes the oldest de­finite representatives of this family as SCY, but regards Pernopecten as an ancetral propeamussiid. Pernopecten was placed in the polyphyletic family ‘Entoliidae’ by Cox et al. (1969, p. N347), and in the family Pernopectinidae Neveskayat al., 1971 by Carter (1990, p. 259).

F. ENTOLIIDAE von Teppner, 1922
Tr. (ANS)–K. (MAA) Mar.
**First:** Entolium żelleri (Kitti, 1903), Buloger-Kalk, Haliluci, near Sarajevo, Bosnia former Yugoslavia; E. discites (von Schlotheim, 1820), Muschelkalk, Germany (Johnson, 1984).
**Comments:** The family ranges back to the Triassic, with the exclusion of Pernopecten and its assignment to the Propeamussiidae (q.v.). Allasiniz (1972) noted Entolium discites from the SCY, but provides no supporting evidence (A. L. A. Johnson, pers. comm., 1992). Yin (1985) gives the range of Entolium back to LGT, or even GUA, but this is not accepted here.

F. SYNCYCLONEMIDAE Waller, 1978
**First:** Syncyclonema simplicia (Conrad, 1860) and S. halli (Gabb, 1891), both from various localities and formations in North America, such as Ripley Formation, Alabama and Coon Creek Formation, Tennessee, USA.
**Extant**
F. PECTINIDAE Rafinesque, 1815
**First:** Hunanpecten extis Zhang, 1977 and H. qiujiangensis Zhang, 1977, both Dalong Formation, South China (Yin, 1985).
**Extant**
F. NEITHEIDAE Sobetzky, 1960
**First:** Wegyla (Lyuca) unca (Philippi, 1899), several localities in central Chile and western Argentina (Damborenea, 1987).
**Last:** Neithsea alpina (d’Orbigny, 1847), N. regularis (Schlotheim, 1813), and many other species, MAA, cosmo­politan (Dhonid, 1973).

F. SPONDYLIDAE Gray, 1826
J. (BAJ)–Rec. Mar.

Subclass LUCINOIDA Dall, 1889
Order LUCINATA Pojeta, 1978
F. BABINKIDAE Horny, 1960
First: Babinka prima Barrande, 1881, Schistes de Saint-Chinian inférieur, Fédou, Minervois occidental, France (Babin, 1982a).

Last: Babinka prima Barrande, 1881, various formations, Spain; Sárka Beds, Bohemia, Czechoslovakia (Babin and Gutiérrez-Marco, 1991).


First: Illinia canadensis Billings, 1875, Canada; I. prisca (Hisinger, 1837), Sweden. Extant


Comments: The Middle Triassic form, Storthodon liscaviensis J. Morris, pers. comm., 1992). First:

Comments: The Carboniferous species de RyckhoJt, 1871, included in this family by Cox 1909), Charmouthian, France, England, UK. Extant

Comments: Palaeozoic taxa included in this family by Cox 1909), Charmouthian, France, England, UK. Extant

Comments: The Carboniferous species de RyckhoJt, 1871, included in this family by Cox 1909), Charmouthian, France, England, UK. Extant

Comments: The Carboniferous species de RyckhoJt, 1871, included in this family by Cox 1909), Charmouthian, France, England, UK. Extant

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Comments: The Carboniferous species de RyckhoJt, 1871, included in this family by Cox 1909), Charmouthian, France, England, UK. Extant


First: Mactromyopsis (Mactromyella) inflata (Thévenin, 1909), Charmouthian, France, England, UK. Extant

First: Schaфаeutlia ovatum (Schaфаeutl, 1871) and S. mellingi (Hauer, 1857), Europe, South America and Sakawa, Japan. Extant

Comments: The Carboniferous species Scaldia lambotteana de Ryckholt, 1871, included in this family by Cox et al. (1969, pp. N511–N513), such as Montanaria devonicus (Beushausen, 1884) from the Devonian of Europe, Para­cyclus elliptica Hall, 1843 from the Devonian of North America and Europe, Palaeolucina carbonaria Chao, 1927 from the Carboniferous of China, and Plesiocypriniella carinata Holdhaus, 1918 from the Permian of South America, are excluded here.

F. FIMBRIDAE Nicol, 1950 Tr. (CRN)–Rec. Mar.

First: Brachymeris alta Conrad, 1875, North Carolina, USA; Felaniella (Zemysia) sp. Extant


First: Ercyna (Ercyna) pellucida Lamarck, 1805 and Semiercyna (Erycynopsis) semipuncta (Cossman, 1887), both Palaeocene, France. Extant


First: Rhexomyax undulatus (Gabb, 1864), Ten Mile Member, Chucó Formation, lower CMP, California, USA. Extant


First: Lepton (Lepton) sp. Extant


First: Montacuta herberti Aldrich, 1921, Bashí Member, Hatchetigbee Formation, Upper Wilcox Group, Clarke County, Alabama, USA; Mysella minuta (Aldrich, 1921), Bells Landing Member, Tuscaloosa Formation, Middle Wilcox Group, Monroe County, Alabama, USA (Palmer and Brann, 1965). Extant

Comments: Slightly younger forms are Lasoneutra radiata (Deshayes, 1824), Laubrieirea emarginata (Deshayes, 1860), and Namnetia discoides Cossmann, 1905, all LUT, Paris Basin, France.


First: Scintilla clarkeana Aldrich, 1897, Bashí Member, Hatchetigbee Formation, Upper Wilcox Group, Clarke County, Alabama, USA (Palmer and Brann, 1965).

Extant Comments: These two taxa are indicated as uncertain by Cox et al. (1969, p. N536), Passya since it may not be a galeommatid, and Scintilla since the Eocene record is uncertain.

F. CHLAMYDOCONCHIDAE Dall, 1899 Extant Mar.


First: Dirranodesma calvertensis (Glenn, in Dall, 1900), LAN, Calvert Cliffs, Maryland, USA. Extant


First: Turtonia sp. Extant


First: Sportella (Sportella) dubia (Deshayes, 1824), Anisodonta complanatum Deshayes, 1858, and Hindsiella arcuata (Lamarck, 1807), all Palaeocene, France; Cerulina sp.; S. subaequilateralis Cossmann, 1908, and other species, Calcaire de Mons (THA), Mons, Belgium (Glibert and Van de Poel, 1973).

Extant Comments: Cox et al. (1969, p. N541) include Vokesella inopinata Chavan, 1952, from the Jurassic of France, in this family, but it is excluded here.


First: Goodalliospus terminalis (Deshayes, 1858), LUT, Paris Basin, France (Glibert and Van de Poel, 1967). Extant

Comments: If this record is not confirmed, the next oldest are a Duntroonian (CHT) occurrence of Neoleton in New Zealand, and Puyseguria crenulifera Maxwell, 1969, Waitakian (LMI), New Zealand (Beu and Maxwell, 1990).

Subclass HETEROCONCHIA Hertwig, 1895

Order ACTINODONTOIDA Douvillé, 1912

F. CYCLOCONCHIDAE Ulrich, 1894 O. (ARG)–S. (LUD) Mar./FW

First: Copidens browni Pojeta and Gilbert-Tomlinson, 1977, Nora Formation (ARG/LLN), Toko Range, western Queensland, Australia; Actinodonta ramseyensis (Hicks, 1873), Ogo Hên Formation, Pembroke, Wales, UK (Carter, 1971); Actinodonta sp., Armorican Sandstone, Brittany, France (Pojeta, 1971).
First: Costatoria costata (Zenker, 1833), Dzhulfian, Japan.
Comments: Cox et al. (1969, p. N473) note Triassic examples of Costatoria, from the Muschelkalk of Germany and the Upper Triassic of the southern Tyrol, but these are excluded here.

F. MYOPHORIIDAE Bronn, 1849
P. (KUN)–Tr. (RHT) Mar.
First: Paraschizodus elongatus Newell and Boyd, 1975, Grandeur Member, Park City Formation and lower Goose Egg Formation (both upper LEN), Wyoming, USA (Newell and Boyd, 1975).
Last: Lyrionymphoria elongata (Moore, 1861), Penarth Group, England, UK, Myophoria inflata (Emmerich), Zlambach and Kössen Beds, Austria (Hallam, 1981), and species of Neoschizodus.
Comments: Cox et al. (1969, pp. N472–N476) give a much wider interpretation to this family, including in it members of the Costatoriidae, Eoschizoidae, and Schizoidae, all of which were excluded by Newell and Boyd (1975). Other taxa included in the family by Cox et al. (1969) extended its range from Devonian to (?) Lower Jurassic, but these genera (Cytherodon, Hefteria, Liotrigonia, Rhenania, Toechomya) are also omitted from the Myophoriiidae here. Newell and Boyd (1975) indicate a range to Upper Cretaceous with Nipponotrigonia.

F. PACHYCARDIIDAE Cox, 1961
Tr. (LAD)–J. (?PLB) Mar./Brackish
First: Pachycardia rugosa Hauer, 1857, Muschelkalk, Germany; Trigonodus sandbergeri (Stoliczka, 1871), Lettenkohle, Germany.
Last: Cardinioides varius Hayami, 1957, Kuruma Group, central Japan.
Comments: This family is problematic, being indicated with a '?' by Cox et al. (1969, p. N467), and being synonymized with Trigonodidae by Vokes (1980, p. 95). The Permian record of Kádödia noted by Cox et al. (1969, pp. N467–N468) is not accepted here. If the Jurassic records are not accepted, latest forms are CRN and NOR of the Alpine region and Oregon, USA.

First: Lyrodesmus orbicularis Newell and Boyd, 1975, Cathedral Mountain and Road Canyon formations, upper LEN, Texas, USA (Newell and Boyd, 1975).
Extant Comments: Cox et al. (1969, pp. N476–N488) give the oldest as Middle Triassic (ANS): Trigonia (Trigonia) sulcata (Hermann, 1781). Some authors (e.g. Cooper, 1991) split this large family into several, each smaller family, corresponding to one of the subfamilies assumed here.
Mollusca: Rostroconchia, Scaphopoda and Bivalvia

F. TRIGONIOIDIDAE Cox, 1952


Last: Trigonoides kobayashi (Hoffet, 1937), SEN, LAOS.

F. MAGNARITIFERIDAE Haas, 1940

Tr. (RHT)—Rec. FW

First: Magnaritifera sp., RHT, central Iran (Gray, 1988, p. 51).

Extant

F. UNIONIDAE Fleming, 1828

Tr. (CRN)—Rec. FW

First: Unio subplanatus Simpson, 1896, and six other species; Diplodon gregori Reeside, 1927, D. haroldi Reeside, 1927, Antediplodon dockumensis (Simpson, 1896), and two other species, Chiloe Formation and Dockum Group of SW United States, and Pekin Formation, Tuckahoe Formation, Stockton Formation, Lockatong Formation, Wolfville Formation, Newark Super Group of eastern North America (Good, 1989).

Extant

F. MUTELIDAE Swainson, 1840

Tr. (CRN)—Rec. FW

First: Mycetopoda dilicula PILSBRY, 1921, Newark Super Group, York County, Pennsylvania, USA (Good, 1989).

Extant

F. ETHTERIIDAE Swainson, 1840

T. (Pli)—Rec. FW

First: Etheria semilunata Lamarck, 1807, Africa/Indian Ocean.

F. ACTINODONTOPHORIDAE Newell, 1969

P. (Kaz)—Tr. (RHT) FW

First: Actinodontophora katsurenensis Ichikawa, 1951, Katsura Formation, Shikoku, Japan.


Order VENEROIDA Adams and Adams, 1856

F. ASTARTIDAE d’Orbigny, 1844


First: Eodon aff. bicostula (Krantz, 1857), Eifel, Germany; Prosocleaule (Prosocleaule) priscus (Roemer, 1843) and P. (Trileo) pesanseris Zeil and Wirtgen, 1981, both Spireiferansandstein, NW Harz, Germany (Morris, 1978, p. 264).

Extant

Comments: Cox et al. (1969, p. N554) include the latest Silurian (Downtonian) Carditomantea spinata Quenstedt, 1929 in this family, but it is excluded here.

F. CARDITIDAE Fleming, 1828


Extant

Comments: Cox et al. (1969, p. N554) include the latest Silurian (Downtonian) Carditomantea spinata Quenstedt, 1929 in this family, but it is excluded here.

F. CHAMIDAE Blainville, 1825


First: Chama haueri Zittel, 1865 and C. detrta Zittel, 1865, Gosau Beds, Austria (Kennedy et al. 1970).

Extant

F. CONDYLOCARDIIDAE Bernard, 1897


First: Condylocardia atomus (Deshayes, 1858), LUT, Paris Basin, France (Glifert and Van de Poel, 1970).

Extant

Comment: There are abundant condylocardiids in the BRT of France, North America, and New Zealand: Micromeris (Micromeris) minutissima (Lea, 1833), Cuna monoenesis (Meyer, 1887), and C. parva (Lea, 1833), all Gospert Sand, uppermost Claiborne Group, Monroe County, Alabama, USA (Palmer and Brann, 1965); Condylocardina subaequilateralis (Maxwell, 1966), Kaitan, New Zealand (Beu and Maxwell, 1990).

Extant

F. CRASSATELLIDAE Férussac, 1822


Extant

Comments: Cox et al. (1969, pp. N573—N578) include the Devonian to Carboniferous Cypricardella Hall, 1858 in this family, but it is excluded here.

F. CARDINIIDAE Zittel, 1881

Tr. (LAD)—J. (TOA) Mar.


Last: Cardinia concinna (Sowerby, 1817), C. attenuata Stutchbury, 1842, and Nidicrassa slatteri (Wilson and Crick, 1889), all Domerian, lower TOA, Yorkshire, England, UK.

Comments: Cox et al. (1969, pp. N578—N580) give the range of this family as Ordovician to Recent, by including Cypricardina Hall, 1859 (Ordovician—Permian) and Tellidorella Berry, 1963 (Miocene—Recent), both of which are excluded here. Cox et al. (1969, p. N579) also note doubtful BA material of Cardinia.

F. MYOPHORICARDIIDAE Chavan, in Vokes, 1967

Tr. (SCY—NOR) Mar.

First: Pseudocorbula gregaria (Münster, 1837).

Last: Myophoriopsis sp.

F. CORBULIDAE Lamarck, 1818

J. (TOA)—Rec. Mar./FW


Extant


F. ERODONIDAE Winckworth, 1932


First: Potamomya plana (J. Sowerby, 1814), Headon Beds, Hampshire and Isle of Wight, England, UK (Glifert and Van de Poel, 1966b).

Extant

F. CARDIIDAE Lamarck, 1809

Tr. (NOR)—Rec. Mar.

First: Protocardia sp., NOR, Tethys; Septocardia typica Hall and Whitfield, 1877, NOR, North and South America (Hallam, 1981).

Extant

F. LAHILLIDAE Finlay and Marwick, 1937


First: Lahillia n. sp. aff. L. angulata (Philippi, 1887), Piripauan, Haumuri Bluff, New Zealand (Beu and Maxwell, 1990); L. larsi Sharman and Newton, 1897, upper CMP
Mollusca: Rostroconchia, Scaphopoda and Bivalvia

256

to lower MAA, James Ross Basin, western Antarctica (Zinsmeister and Macellari, 1988).

Extant

Comment: Ages of early records are uncertain. Also L. larsoni (Sharman and Newton, 1897), López de Bertodano Formation (MAA), Seymour Island, Antarctica (Zinsmeister and Macellari, 1988).

F. LYMNOCARDIIDAE Stoliczka, 1870

T. (LMI) – Rec. Brackish

First: Eoprosodacna (Eoprosodacna) kartlicum Davidschvilli, 1934 and E. (Sucuridacna) goriense (Davidschvilli, 1934), both south Caucasus, Georgia, former USSR. Extant


First: Avicularium aviculare (Lamarck, 1805), YPR, Paris Basin, France (Gilbert and Van de Poel, 1970). Extant

Comments: A doubtful Late Cretaceous record of T. (Chametrachea) crocea (Lamarck, 1819), noted for this family by Cox et al. (1969, p. 5954) is not included here.


First: Nellia elliptica (Whitfield, 1891), APT, Olive Mountain, Syria. Extant


First: Amotopus arbolensis (Woods, 1922), Middle Eocene, Peru. Last: Raetomya schweinfurthi (Mayer-Eymar, 1887), PRB, Nigeria. Extant

F. ANATELLIDAE Gray, 1853 Extant Mar.

First: Nellia elliptica (Whitfield, 1891), APT, Olive Mountain, Syria. Extant


First: Hemicyclonesta michelini Deshayes, 1850, Middle Eocene, France. Extant


First: Mesodesmatidae. Extant


First: Siluida? sp., Mexia Member, Wills Point Formation, Upper Midway Group, Williamson County, Texas, USA (Palmer and Brann, 1965). Extant

Comments: Oldest records in Cox et al., 1969, pp. N610–N611 are Lower Eocene (Solen (Plectosolen)).


First: Leptosolen bipticata (Conrad, 1858), North America/eastern Europe. Extant


Comments: This family is not listed in Cox et al. (1969), being included in their Solecurtidae (pp. N637–639). The oldest pharid noted here might be a solecurtid (S. R. A. Kelly, pers. comm., 1992).


Comments: The Upper Triassic Rhaetidia zittellii Bittner, 1895 was included doubtfully in this family by Cox et al. (1969, p. N639), but is excluded here (see also Jablonski and Bottjer, 1990, pp. 58–9).

F. TANCREDIIDAE Meek, 1864 Tr. (CRN) – Rec. Mar.


Extant


First: Quenstedtia laevigata (Phillips, 1848), Cephalopod Bed, CRN, lower Kohigatani Group, Tosa Province, Kochi Prefecture, Shikoku Island, Japan (Jablonski and Bottjer, 1990).

Last: Quenstedtid. Extant


Last: Unicardiopsis ace (d’Orbigny, 1850), Sequanian, France.

Extant


First: Linearia subhercynica Maas, 1895, Hilskonglomerat, Hannover, Germany; L. subconcentrica (d’Orbigny), Calcaire à Spatangues, Paris Basin, France, both lower HAU (Jablonski and Bottjer, 1990).

Extant


Comments: The youngest Icanotiid in Cox et al. (1969, pp. N634–N635) is MAA: Icanotia. Extant


F. SOLECURTIDAE d’Orbigny, 1846

**First:** ProtageIus albertinus (d’Orbigny, 1846), Silakkudi Formation, Ariyular Group, lower CMP, Tamil Nadu State, India (Jablonski and Bottier, 1990).

**Extant**

**Comments:** The family might extend back to the TTH, if specimens of Senis, assigned to the Pharidae (q.v.) here, are misidentified.


**First:** Gari (Gobraeus) debilis (Deshayes, 1855), Unnamed unit, Luzankova, northern Ukraine, former USSR; Sochozew Beds, Bochotnica, central Poland; Echinanthus carinatus Zone, eastern flank of Caspian Sea; Adansonella duponti (Cossmann, 1886), Calcaire grossier de Mons, NP2–NP3 (THA), Mons, Belgium (Jablonski and Bottier, 1990).

**Extant**

**Comments:** Cox et al. (1969, p. N633) include the Upper Cretaceous Rhetomaxx undulata (Gabb, 1864) in this family, but it is excluded here.


**First:** Scrobiculabra condamini (Morris, 1854), Woolwich Shell Beds, upper THA (NP9), Thames Valley, England, UK (Jablonski and Bottier, 1990).

**Extant**


**First:** SemeIe langdoniana Aldrich, 1921, Bells Landing Member, Tuscaloosa Formation, upper THA (NP9), Bells Landing, Alabama, USA (Jablonski and Bottier, 1990).

**Extant**

F. DREISSENIDAE Gray, 1840 T. (Eoc.)—Rec.

**FW/Brackish**

**First:** Dreissena (Dreissena) polymorpha (Pallas, 1771), Paratethys.

**Extant**


**First:** Gaimardiid.

**Extant**

**Comments:** The oldest form in Cox et al. (1969, p. N644) is Miocene: Kidderia.

F. ARCTICIDAE Newton, 1891 Tr. (RHT)—Rec.

**Mar.**


**First:** Isocyprina (Eotrapezium) alpinus (Winkler), Kössen and Zlambach Beds, Austria; I. (E.) eawalid (Bomemann), Penarth Group, England, UK, Pleisocyprina gaudryi Fischer, 1887, RHT, Europe (Hallam, 1981).

**Extant**

F. BERNARDINIDAE Keen, 1963 **Extant** Mar.


**First and Last:** Euloxa (Euloxa) corneum (Conrad, 1840), UMI, Virginia, USA: Cabralista schmitzi (Böhm, 1899), UMI, Salvages Island, East Atlantic.

**Extant**


**Extant**

F. NEOMIODONTIDAE Casey, 1955 J. (HET)—K. (CEN) FW/Brackish

**First:** Eomiodon lunulatus (Yokoyama, 1904), Niranohama Formation, Shizukawa Group, NE Japan.

**Last:** Eomiodon matusbasensis Tamura, 1977, Mifune Group, Kyushu, western Japan.


**First:** Pollex obesus Stephenson, 1953, Woodbine Formation, Texas, USA.

**Last:** Neritra polliciformis Stephenson, 1954, ?CMP, ?New Jersey, USA.


**First:** Corbiculopsis birdi Whitfield, 1891, ?APT, Syria.

**Extant**

**Comments:** The hinge of Corbiculopsis is imperfectly known (Cox et al., 1969, pp. N655–N656). If it is not a trapezid, the next oldest record is Pseudopleurophorus rochi Chavan, 1954 from the Upper Cretaceous of Chad.


**First:** Glossid (N. J. Morris, pers. comm., 1992).

**Extant**

**Comments:** The oldest record in Cox et al., 1969, pp. N657–N658 is Palaeocene: Glossus (Meiocardia).

F. DICEROCARDIIDAE Kutassky, 1934 Tr. (NOR)—K. (MAA) Mar.

**First:** Dicercocardium jani Stoliczka, 1871, NOR, northern Italy; D. curionii Stoppani, 1865, NOR, Sicily, Italy; D. dolomiticum (Loretz), NOR, northern Italy (Hallam, 1981).

**Last:** Agelasina plenodonta Riedel, 1932, MAA, West Africa.

**Comment:** Probably a polyphyletic assemblage.


**First:** ?Corbiculid, lacustrine beds, Durham, North Carolina, USA (Olsen et al., 1989, pp. 30, 32).

**Extant**

F. MISIDIDAE Gray, 1840 J. (MLM)—Rec.

**FW**

**First:** Hubertshencksia exoensis (Yokoyama, 1890), Hokkaido, Japan; Pleurophopsis unioiides Palmer, 1919, CHT, West Indies, Central America, NW South America.

**Extant**

**Comments:** Cox et al. (1969, pp. N669-N670) note another doubtful late Jurassic record of Sphaerium (Sphaerium) corneum (Linnaeus, 1758).


**First:** Venus' vendoperana (Leymerie, 1842), VLG, eastern France, Switzerland (Dhondt and Dieni, 1988).

**Extant**


**First:** Petricola ? novaegyptica Whitfield, 1885, Manasquan Formation, Ocean County, New Jersey, USA (Palmer and Brann, 1965).

**Extant**

First: Lajonkaria rupestris (Brocchi, 1814), AQT, Lariey, Bordelais, France (Gilbert and Van de Poel, 1966a). Extant F. GLAUCONOMIDAE Gray, 1853 Extant Mar.


First and Last: Megycodon carinatus (Goldfuss, 1837) and M. oblongus (Goldfuss, 1837), Stringocephalus Limestone, Germany and Onondagan, North America.


First: Megalodonts, Canadian Arctic (Freitas et al., in press). Last: Pachyrisma grande (Goldfuss, 1859), Middle Tethys (Philip and Airaud-Crumiere, 1991). Comments: Cox et al. (1969, pp. N743–N749) give an extended range for this family, by including Middle Silurian (WEN) Megalamoidea canadensis (Hall, 1852), regarded here as a modiomorphid (N. J. Morris, pers. comm., 1992), and Pachysismissella and Pterocardia (OXF), which are transferred to the Cardiidae (N. J. Morris, pers. comm., 1992).


First: Eodicthyoptchus arnaudi Skelton and El-Asa'ad, 1992, upper Khansir Limestone Member, Aruma Formation, central Saudi Arabia (Skelton and El-Asa'ad, 1992). Last: Dicytyopthchus morani (Douville, 1904), Loftusia persica Beds, Bakhtiari Mountains, Iran.


Subclass ANOMALODESMATA Dall, 1889


First: Sanguinolites kaniyassensis Nakazawa and Newell, 1968, Shegejizawa Member, lower Kanokura Formation, Xiangzhou County, Guangxi, China (Pojeta and Zhang, 1984). Last: S. concava Clarke, 1913, Sao Domingos Formation, upper TAT, Kyoto, Japan (Nakazawa and Newell, 1968).

Comments: Cox et al. (1969, pp. N839–N841) doubtfully include early Jurassic records of Burmesia, but these are not accepted here (I. Hayami, pers. comm., 1992).

F. BURMESIIDAE Healey, 1908 Tr. (CRN)–RHT) Mar.

First: Burmesia latouchii Healey, 1908, Asia (Jordan–Burma–Indonesia–Japan). Last: Burmesia latouchii Healey, 1908 and Prolaria sollasi Healey, 1908, both Burma, Indonesia, and P. armencia Robinson, Armenia, former USSR. Comments: Cox et al. (1969, p. N838) include early Jurassic records of Burmesia, but these are not accepted here.

F. CERATOMYIDAE Arkell, 1934 Tr. (RHT)–J. (TTH) Mar.

First: Pteryomya croucombea Moore, 1861, lower Penarth Group, England, UK; Kössen Beds, Austria. Last: Ceratomya excentrica (Roemer, 1836), Dakacha Limestones, Melka Dakacha, NE Kenya (Cox, 1965). Comments: Cox et al. (1969, p. N546) doubtfully include the Miocene Ceromyella miotaurina Sacco, 1901 in this family, but this is not accepted here.


First: Ceratomyopsis sp., Europe. Last: Ceratomyopsis helvetica (de Lorio, 1875), TTH, France.


F. PLEUROMYIDAE Dall, 1900 Tr. (CRN)–K. (ALB) Mar.


First: Pandora dilatata Deshayes, 1858, YPR, Paris Basin, France (Glibert and Van de Poe!, 1966a). Extant


First: Cleidothaerus albidus (Lamarck, 1819), Waitakian, Chatton Formation, Brydon, New Zealand (Beu and Maxwell, 1990) and Fossil Bluff, Wynyard, Tasmania, Australia. Extant
F. LATERNULIDAE Hedley, 1918  Tr. (RHT)—Rec. Mar.
First:  Cercomya (Cercomya) praeceptor (Quenstedt), Penarth Group, England, UK (Hallam, 1981). Extant

First:  Myadora lamellata, Browns Creek Clay, Johanna, Victoria and Blanche Point Marl, Aldinga, South Australia (Darragh, 1985).

F. PERIPLOMATIDAE Dall, 1895  J. (TTH)—Rec. Mar.
F. CUSPIDARIIDAE Dall, 1886  Tr. (LAD)—Rec. Mar.
First:  Cuspidaria triassica (Stoppani, 1865), Austria (Morris, 1967, p. 475).


First:  Clavigella cenomanensis d’Orbigny, 1850, CEN, Le Mans, France.

Order MYOIDA Stoliczka, 1870
First:  Spheinia leptomorpha Cossmann, 1891, THA, Paris Basin, France (Gilbert and Van de Poel, 1966a). Extant
First:  Pleurodesma moulinisi (Potiez and Michaud, 1844), BUR, Bordeaux, France (Gilbert and Van de Poel, 1966a). Last:  Pleurodesma mayeri Hornes, 1859 and P. moulinisi (Potiez and Michaud, 1844), Tortoni, Vienna Basin, Austria (Gilbert and Van de Poel, 1966a).

First:  Sphenopsis scalaris (Braun, 1851), Europe. Extant
First:  Gastrochaena moreaau Buvignier, Europe (Hallam, 1976).
First:  HIATELLIDAE Gray, 1824  Tr. (ANS/LAD)—Rec. Mar.
First:  Panopea (Panopea) glycinemis (Born, 1778), Europe. Extant Comments: Cox et al. (1969, pp. N700–N702) include the Permian Roxoa intrigua Mendes, 1944) in this family, but this species is excluded here.
First:  Martesia (Particoma) australis Moore, 1870, Western Australia (Kelly, 1988). Extant Comments: Cox et al. (1969, pp. N711–N712) note a doubtful Martesia from the Carboniferous, but this is excluded from the family, following Kelly (1988). The ichnogenus Teredolites, probably formed by wood-boring bivalves, is known from the PLB.

Subclass and Order UNCERTAIN
F. ARCHANODONTIDAE Weir, 1969  D. (FAM)—P. (ROT) FW
First:  Archanodon jukes (Forbes, 1853), Kiltoran Formation, Upper Old Red Sandstone, Kilkenny, Republic of Ireland.
Last:  Neamnigenia beljanini Khalfin, 1950 and N. longa Betekhtina, 1966, Siberia, former USSR.
F. ANTHRACOSIIDAE Amalitsky, 1892  C. (VIS)—P. (KAZ) FW
First:  Anthracosia ovalis (Dawson, 1860) and Carbonicola bradorica (Dawson, 1868), Nova Scotia, Canada, and Naiadites fragilis (Meek and Worthen, 1866), Keokuk, Osagean, Illinois, USA.
Last:  Palaeonodonta castor (Eichwald, 1856) and others, Oka-Volga Basin, former USSR, Beaufort Series, South Africa, East Africa, Burma, Norway.
F. PRILUKIELLIDAE Starobogatov, 1970 (= Microdontidae) P. (ROT—ZEC) FW
Last:  Microdonta problematica Lebedev, 1944, Kolchugino Series, Kuznetsk Basin, Siberia, former USSR.
F. PALAEOMUTELIDAE Weir, in Vokes, 1967
C. (u.) – P. (ZEC) FW
First: Angarodon kumssassiensis Ragozin, 1935, western Siberia, former USSR.
Last: Palaeomutela (Palaeomutela) verneuilli Amalitsky, 1892, P. (P.) keyserlingi, P. (Oligodon) geinitzi Amalitsky, 1892, and P. (O.) zittelii, all ZEC, former USSR.

F. FERGANOCONCHIDAE Martinson, 1956
J. (l.–u) FW
First: Ferganoconcha sibirica Chernyshev, 1937, Siberia, former USSR.
Last: Ferganoconcha sibirica Chernyshev, 1937, Siberia, former USSR.

F. PSEUDOCARDINIIDAE Martinson, 1961
J. (l.–u) FW
First: Tutuella chachlovii Ragozin, 1938 and Utschamiella tungussica Ragozin, 1938, both Lias, Tungusska Basin, Siberia, former USSR.

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Waterhouse, J. B. (1979a) New members of the Atomodesmatidae (Bivalvia) from the Permian of Australia and New Zealand. Papers of the Department of Geology, University of Queensland, 9, 1–22.


This chapter contains a number of groups possessing molluscan characteristics, but which cannot be assigned to the phylum with certainty, either because they exhibit additional characteristics outside the accepted molluscan scope, or because they also show affinities with some other group, most frequently the annelids.

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Class TENTACULITOIDEA Ljashenko, 1957
(= CRICONARIDA Fisher, 1962)
Tentaculitoids are best known from the Palaeozoic. They are first recorded in the Lower Ordovician, although they remain fairly uncommon until the Devonian. Maximum diversity is attained in the Middle Devonian, but the class becomes less prominent by the end of this period. Weeden (1990, 1991) considers that certain vermiform ‘gastropods’ should be included within the Tentaculitoidea, establishing the order ‘Microconchida’ to accommodate them. This extends the record of the class up into the Lower Triassic. Additionally, he erects another new order for the enigmatic Devonian genus Trypanopora. Members of the class are united by the possession of gradually tapering, narrow shells, with transverse rings, ringlets and striae.

Order TENTACULITIDA Ljashenko, 1955
(see Fig. 14.1)
Tentaculites all possess minute, conical, calcareous shells with a circular cross-section. These may be composed of a number of layers, and are occasionally divided by septa. The group is most often assigned to the Mollusca, although affinities are also perceived with the annelids. Tentaculitids probably lived as nektobenthos and plankton in shallow seas, and their shells are often a significant constituent of Ordovician and Devonian limestones world-wide. The classification is taken mainly from Larsson (1979).

F. VOLYNITIDAE Ljashenko, 1959
First: Volynites muldiensis Larsson, 1979, and Volynites scalpratus Larsson, 1979, Mulde Beds, Mulde region of Gotland, Sweden.

F. TENTACULITIDAE Walcott, 1886
First: Tentaculites lowdoni Fisher and Young, 1955, Chepultepec Limestone, lowermost Ordovician, Virginia, USA.


Intervening: LUD.

F. GOTLANDELLITIDAE Larsson, 1979
First: Gotlandellites visbyensis Larsson, 1979, lower Visby Beds, Gotland, Sweden.
Last: Gotlandellites areolatus Larsson, 1979, upper Visby Beds, Gotland, Sweden.

F. ROSSIITIDAE Ljashenko, 1959
Last: Dicricococonus sp., FRS of Russia. Dicricococonus mesoconicus (Ljashenko, 1954), Middle Devonian, former USSR (Larsson, 1979).

Order HOMOCTENIDA Bouček, 1964
F. HOMOCTENIDAE Ljashenko, 1959

Order DACRYCONARIDA Fisher, 1962
These are small criconarids, with a pronounced, tear-drop-shaped embryonal bulb at the apex of the shell. The shell broadens faster towards the aperture than in the tentaculitids, and the wall may be appreciably thicker, although none have internal septa. Their greatest abundance is achieved in the Upper Silurian and Lower Devonian of
Australia, and Upper Devonian of North America. Their classification is taken mainly from Bouček (1964).

F. NOWAKIIDAE Bouček and Prantl, 1960


Comment: The position of this stratigraphical interval is in doubt, owing to debate over the position of the Silurian–Devonian boundary in continental Europe.

F. STRIATOSTYLIOLINIDAE Bouček, 1964


F. STYLIOLINIDAE Grabau, 1912

First: Stylolina cf. laevis Richter, 1854, Monograptus riccartonensis Zone, Zebingyi Beds, near Maymyo, Burma
Order MICROCONCHIDA Weedon, 1991

These are forms with helically coiled, attached shells, three-layered in the larva.

F. UNNAMED D. (GIV)—Tr. (GRI) Mar.

First: Vermiform 'gastropods' from the Middle Devonian of northern France (Weedon, 1990).

Last: Vermiform 'gastropods' from the Lower Triassic (Weedon, 1990).

Order TRYPANOPORIDA Weedon, 1991

Small, helically coiled shells with the initial whorls attached, and later whorls regularly or irregularly uncoiled. Larval shell calcitic with simple microlamellar microstructure. Septa branched and anastomosing.


**Class HYOLITHA Marek, 1963**

(= CALYPTOMATIDA Fisher, 1962)

Hyoliths originated in the Lower Cambrian, were very abundant up to the Ordovician and are last represented in the Permian. All are bilaterally symmetrical, mollusclike, marine animals, with thin, conical, calcareous shells, sometimes internally divided into chambers at the apex. The ventral surface is flattened, and projected anteriorly into a tongue. The aperture of the shell is covered by an oval, curved operculum, with sculpture on its inner side which may have supported the soft parts. Long, recurved, tubular appendages lead back along the shell from the oral region in some forms. The system of classification adopted here primarily follows Missarzhevsky (1969), with some additional families.


F. ALLATHECIDA Missarzhevsky, 1969

*E. (TOM) Mar.*


Last: *Majathea tumefacta* Missarzhevsky, 1969, upper part of Tommotian, *D. lenicus—M. tumefacta* Zone, Churgan Village, middle reaches of River Lena, former USSR.

F. CERATOTHECIDAES Fischer, 1962

*S. (LUD)—D. (LOK) Mar.*

First: *Ceratotheca abundica* (Barrande, 1867), Czechoslovakia and England, UK.

Last: *Ceratotheca abundica* (Barrande, 1867), England, UK.

F. CIRCOTHECIDA Missarzhevsky, 1969

*V. (N—DA)—O. (CRD) Mar.*

First: *Circotheca longiconica* Qian, 1978, lower Meischuchunian *Anabarites—Circotheca—Protolherzina* Zone, eastern Yunnan, China (Brazier, 1989).


F. ISITITHECIDA Sysoiev, 1968

*€. (TOM—LEN) Mar.*


F. ORTHOTHECIDA Missarzhevsky, 1958

*€. (TOM)—D. (EIF/GIV) Mar.*

First: *Trapezotheca bicostata* Missarzhevsky, 1969, *D. regularis* and *D. lenicus—M. tumefacta* Zones, Siberian Platform, former USSR.

Last: *Orthotheca intermedia* Novak, 1886, Middle Devonian of Czechoslovakia.

F. TETRATHECIDA Sysoiev, 1968

*€. (TOM)—O. (TRE/ARG) Mar.*

First: *Tetraheca hexagona* Sysoiev, 1968, Tommotian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

Last: Unnamed species, Lower Ordovician (Sepkoski, 1982).

**Intervening:** ATB, LEN.

F. EXILITHECIDA Sysoiev, 1968

*€. (TOM—LEN) Mar.*


Other late spp.: *Lenatheca dolosa* Sysoiev, 1972, *L. pyramidata* (Sysoiev, 1968), and *L. triconcava* (Sysoiev, 1968), Lower Cambrian, Atabdanian and Botomian Stages, Siberian Platform; *L. groenlandica* (Poulson, 1932), Lower Cambrian, Atabdanian and Botomian Stages, Siberian...
Platform (Sokolov and Zhuravleva, 1983). *Holmitheca ulterior* (Sysoiev, 1968), Lower Cambrian, Atdabanian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**F. GRACILITHECIDAE** Sysoiev, 1968  \( \in \) (LEN) Mar.

**First and Last:** *Gracilitheca terna Sysoiev*, 1968, *B. micmacciformis–Erbiella* Zone, Lower Cambrian, Botomian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**F. NOVITATIDAE** Sysoiev, 1968  \( \in \) (ATB–LEN) Mar.

**First:** *Novitatus oblongus* (Meshkova, 1974), *R. zegebarti* and *P. pinus* Zones, Atdabanian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**Last:** *Novitatus lermontovae* and *N. tarynicus Sysoiev*, 1968, *N. incompletus* (Meshkova, 1974), *B. micmacciformis* Zone, Lower Cambrian, Botomian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**F. OBLIQUATHECIDAE** Sysoiev, 1968  \( \in \) (TOM–LEN) Mar.

**First:** *Obliquatheca bicornata* (Missarzhevsky, 1969), and *O. aldani*ca (Sysoiev, 1960), Lower Cambrian, Tommotian and Atdabanian Stages, Siberian Platform (Sokolov and Zhuravleva, 1983).


**F. SPINULITHECIDAE** Sysoiev, 1968  \( \in \) (TOM) Mar.

**First:** *Spinulithexa billingsi* (Sysoiev, 1962) and *S. kuteinikovi* (Missarzhevsky, 1969), *A. sunnaginicus* Zone, Lower Cambrian, lower Tommotian Stage, Siberian Platform. *Ladatheca annae* (Sysoiev, 1959), *A. sunnaginicus* Zone, Lower Cambrian, lower Tommotian Stage, Siberian Platform, former USSR and *M. Karatau*, Mongolia (Sokolov and Zhuravleva, 1983).

**Last:** *Ladatheca sysoevi* (Meshkova, 1974), *D. regularis* Zone, Tommotian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**F. TCHURANITHECIDAE** Sysoiev, 1968  \( \in \) (TOM–ATB) Mar.


**Last:** *Uniformitheca jasmiri* (Sysoiev, 1959), *D. leniacus–T. primigenius* and *R. zegebarti* Zones, Lower Cambrian, Tommotian and Atdabanian Stages, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**Order HYOLITHIDA** Matthew, 1889

These are bilaterally symmetrical, pyramidal shells, with a conical embryonic chamber not separated from the rest of the shell. The operculum has one or two pairs of bilaterally symmetrical muscle scars.

**F. AIMITIDAE** Sysoiev, 1968  \( \in \) (TOM–ATB) Mar.

**First and Last:** *Oxytus sagittalis Sysoiev*, 1968, *D. leniacus–T. primigenius* Zone, upper Tommotian Stage, to *R. zegebarti* Zone, Atdabanian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**F. ALTAICORNIDAE** Sysoiev, 1970  \( \in \) (LEN) Mar.

**First and Last:** *Erraticornus debilis, E. cordeae, Insignicornus rectus, Nitoricornus pictus, N. subtilis* and *N. tegetus Sysoiev*, 1973, *B. asiaticus* Zone, Botomian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**F. AMYDAICORNIDAE** Sysoiev, 1975  \( \in \) (ATB–STD) Mar.


**F. ANGUSTICORNIDAE** Sysoiev, 1968  \( \in \) (ATB–SOL) Mar.


**Next oldest:** *A. reflectus Sysoiev*, 1968, *B. micmacciformis–Erbiella* Zone, Botomian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).


**F. CRESTJAHITIDAE** Sysoiev, 1968  \( \in \) (TOM–LEN) Mar.


F. DORSOJUGATIDAE Sysoiev, 1968  
**First:** Dorsojugatus sedecostatus (Sysoiev, 1962), D. regularis and D. lenicus—T. primigenius Zones, Tommotian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).  
**Last:** Dorsojugatus multicoeostatus (Sysoiev, 1968), R. zegeharti Zone, Atadabanian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

F. GALICORNIDAE Valkov, 1975  
**First:** Galicornus anaburus Valkov, 1975, Atadabanian Stage, Siberian Platform, former USSR.  
**Last:** Galicornus lenicus Valkov, 1975, B. micmacciformis–Erbiella Zone, Botomian Stage, Siberian Platform, former USSR.

F. HYolithidae Nicholson, 1872  
C. (TOM)–P. (KAZ)  Mar.  
**First:** Hyolithes bilabiatius Missarzhevsky, 1969, D. regularis Zone (L. tortuosa Subzone), Tommotian Stage, northwestern slope of Anabar Massif (Fomich River), middle reaches of River Lena, Chekurovka Village, Siberian Platform, former USSR.  
**Last:** Hyolithes kirkbyi (as Theca? kirkbyi Howse, 1857), ‘Magnesian Limestone Series’, Durham, England, UK. Also Permian, upper Guadalupian, Timorites Zone (Downie et al., 1967).

F. NELEGEROCORNIDAE Meshkova, 1974  
C. (TOM)  Mar.  
**First and Last:** Jacoutolitus fusiformis and Microcornus simus Missarzhevsky, 1974, D. regularis Zone, Tommotian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

F. NOTABILITIDAE Sysoiev, 1968  
**First:** Notabilitus costatus and Oblisicornus tetracanovus Sysoiev, 1968, D. regularis Zone, Tommotian Stage. N. orientalis, N. simplex, Oblisicornus compositus and O. duplicanovus Sysoiev, 1968, D. regularis and D. lenicus—T. primigenius Zone, Tommotian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).  
**Last:** Doliutus brevis Meshkova, 1974, B. micmacciformis–Erbiella Zone, Botomian Stage, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

F. PAUXILLITIDAE Marek, 1967 emended  
C. (CRF)–D.  Mar.  
**First:** Neopauxilites zlatarskii Malinky, 1989, Lower Cambrian of Newfoundland, Canada.  
**Last:** Recilitis sp. Marek, 1967, Devonian of south central Europe (Malinky, 1989).

F. PTERYGOTHECIDAE Sysoiev, 1958  
O. (CND/DFD)–D.  Mar.  
**First:** Virgulaxonaria elegans Yin, 1937, Lower Ordovician, China (Fisher, 1962).  
**Last:** Pterygotheca barrandei Novak, 1891, Devonian of Czechoslovakia.

F. SULCavitidae Sysoiev, 1957  
**First:** Yacoutolitus fusiformis Missarzhevsky, 1974, and Microcornus simus Missarzhevsky, 1974, Dokiodacithus regularis Zone, Tommotian Stage, Siberian Platform, former USSR; Linevitus distortus Sysoiev, 1962, Tommotian Stage, Aldan River, Siberia, former USSR (Brais, 1983).  
**Last:** ?Linevitus sp., Silurian, Norway, Sweden, former USSR (Fisher, 1962).  
**Intervening:** ATB, O.

F. TRAPEZOVITIDAE Valkov, 1975,  
**First:** Tuoidachites figuratus Missarzhevsky, 1969, T. costulatus Missarzhevsky, 1969, D. regularis Zone, Tommotian Stage, Siberian Platform, former USSR (Valkov, 1975).  
**Last:** Trapezovites latus Valkov, 1975, Botomian Stage, Siberian Platform; T. sinscus Sysoiev, 1958, Atadabanian and Botomian Stages, Siberian Platform, former USSR (Sokolov and Zhuravleva, 1983).

**Order** GLOBORILIDA Sysoiev, 1957  
These are bilaterally symmetrical, curved shells, with curvature increasing towards the apex, and a globular embryonic chamber. The cross-section of the main shell is circular to subtriangular. A very low, conical operculum is subcircular to subquadrate in outline. No external ornamentation is visible.

F. GLOBORILIDAE Sysoiev, 1958  
**First:** Wyattia reedensis Taylor, 1966, Nemakit–Dalbyn Horizon, Reed Dolomite, White–Inyo Mountain Area, Inyo County, California, USA.  
**Last:** Globorilus globiger (Saito, 1936) Korea. Globeringa ?mantoensis Walcott, ?1905, lower Fouchouan or Hsuchuan Stage at Yenchuang, Shantung, Kwangho Basin, South Korea (Kobayashi, 1956).  
**Comment:** The assignment of Wyattia to the globorilids by Taylor (1966) is questionable.

**Order** CAMEROTHECIDA Sysoiev, 1957  
These shells are bilaterally symmetrical, with an oval cross-section. The embryonic stage is tubular and parallel walled. Small chambers are separated by imperforate partitions in this portion. The angle of divergence increases in adult stages, although the sides become almost parallel near the aperture. An operculum is unknown.

F. CAMEROTHECIDA Sysoiev, 1958  
C. (LEN)  Mar.  
**First and Last:** Camerotheca gracilis Matthew, 1885, North America (Fisher, 1962).

F. DIPLOTHECIDAE Sysoiev, 1958  
C. (LEN)  Mar.  
**First and Last:** Diplotheca acadia Matthew, 1885, Canada (Fisher, 1962).

**Order** TOXEUMORPHORIDA Shimansky, 1962  
F. TOXEUMORPHORIDA Shimansky, 1962  


**REFERENCES**


ANNELIDA

M. A. Wills

The soft-bodied annelids would not be expected to leave an extensive or reliable fossil record. Very few specimens have been preserved intact, most remains being chaetae, scolecodonts, tubes, burrows and castings. Some secreted tubes are very characteristic and can be used reliably to identify the organism that produced them. The calcareous tubes of serpulids, for example, are unmistakable, and known from Palaeozoic and younger rocks. Most burrows and casts, however, are of little value in this respect.

Scolecodonts are thought to be chitinized jaw apparatuses, similar to those found in a number of extant errant polychaetes. They are common in sedimentary rocks of all ages from the Ordovician to the Recent. Their classification is confused, since many eunicids, to which at least some of the fossils have been referred, have five or more jaw pairs. Only in a limited number of cases have complete jaw sets been found, the relationships of dissociated scolecodonts being inferred from these (Clark, 1969). Much elegant work has been conducted by Kozlowski (1956), Kielan-Jaworowska (1962, 1966), and Szaniawski (1968, 1974), on Ordovician and Silurian erratic material from eastern Europe.

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Phylum ANNELIDA Lamarck, 1809
Class POLYCHAETA Grube, 1850 (see Fig. 15.1)

Polychaetes can be assigned to about 87 families without difficulty, but apart from grouping some of them together in what may loosely be regarded as orders, it has not proved possible to devise an entirely satisfactory hierarchical classification (Clarke, 1978). The classification adopted here is modified from Clark (1969), with additions of extinct families from Kielan-Jaworowska (1966). Approximately 44 extant families with no known fossil records are not listed. (*Indicates possible relationship to an unlisted living family.)

Order AMPHINOMORPHA
F. AMPHINOMIDAE Savigny, 1818

First: Raphidiophorus hystix Thompson, 1979, Pennsylvanian Essex fauna, Francis Creek Shale, Mazon Creek, northern Illinois, USA.

Extant

Order EUNICEMORPHA

First and Last: Archaeopforion quadricristatus Mierzejewski and Mierzejewska, 1975, erratic calcareous pebble, Amorphognathus superbus Zone, near Orzechowo, Koszalin Province, Poland.


Last: Atraktoprion anatinus Zawidzka, 1975, lower Muschelkalk, southern Poland.

Intervening: FRS, ZEC.


First: Ophryotrocha lukowensis Szaniawski, 1974, Poland.

Extant


Comment: Kielan-Jaworowska (1966) considers Eunicites to be a bona fide kalloprionid.

F. KIELANOPRIONIDAE Szaniawski, 1968
D. (FRS)-Tr. (LAD) Mar.

First: Kielanoprin elleri Szaniawski and Wrona, 1973, Frasnian Limestone, Opole Lubelskie Borehole, right bank of Vistula River, south of Lublin, south-east Poland.


Intervening: D.

F. LUMBRINEREIDAE Malmgren, 1867

First: Phiops aciculorum Schram, 1979, uppermost Mississippian, Bear Gulch Limestone, Central Montana, USA.

F. MOCHTYELLIDAE Kielan-Jaworowska, 1966

First: Mochtyella cristata Kielan-Jaworowska, 1966, Kukruse or Idavere Stage of Estonian sequence, Mochty Province of Warsaw, Poland.

Last: Oxyprion compressus Szaniawski, 1968, Zechstein, second cyclothem, main dolomite horizon, Pomerania, Poland.
**F. PAULINITIDAE** Lange, 1947  O. (CRD)—C. Mar.

**First:** *Nereidavus angulostus* Eller, 1945, Trenton Series, Ontario, Canada. *Elmhurstia nododontata* Potter, Middle Ordovician (Liberty Formation), Cincinnati, USA (Kielan-Jaworowska, 1966).

**Last:** *Paulinites* spp., Silurian through Carboniferous of North America, South America and Europe (Kielan-Jaworowska, 1966).

**Next youngest:** *Paulinites paranaensis* Lange, 1947, Ponta Grossa Formation, Middle Devonian, Brazil (Howell, 1962; Kielan-Jaworowska, 1966).

**Comment:** Both the genus *Nereidavus* and the species *Elmhurstia nododontata* are placed within the Paulinitidae by Kielan-Jaworowska (1966). She also indicates that the family may possibly be recorded as recently as the Permian.


**First and Last:** *Poluchaetaspis* hydei and *Poluchaetaspis* sp. a. Szaniawski and Wrona, 1973, FRS, Opole Lubelskie Borehole, SE Poland.

**Intervening:** Throughout S.
and *Polychaetura* sp. a, Kielan-Jaworowska, 1966, Kukruse or Idavere Stage of the Estonian sequence, Mochty Province of Warsaw, Poland (Kielan-Jaworowska, 1966).

**Comment:** Specimens assigned to *Polychaetura gracilis* are thought to belong to three or four separate species.


- **First:** *Ramphophrion elongatus*, R. urbaneki and *Ramphophrion* sp. b Kielan-Jaworowska, 1966, Middle Ordovician; *Ramphophrion* sp. a, R. sp. c, and R. sp. d Kielan-Jaworowska, 1966, Kukruse Stage of the Estonian sequence, Mochty Province of Warsaw, Poland.

- **Last:** *Ramphophrion* sp. Gries, 1944, basal Liberty Formation, Ohio, USA (Kielan-Jaworowska, 1966).


- **First:** *Rhytiophrion magnum* Kielan-Jaworowska, 1966, Ordovician, Mochty Province of Warsaw, Poland.

- **Last:** *Rhytiophrion* sp. uncertain, Kielan-Jaworowska, 1966, Silurian of the Baltic region, Poland.


- **First:** *Skalenoprion alatus* Kielan-Jaworowska, 1962, and *Skalenoprion* spp. a, b and c Kielan-Jaworowska, 1966, Ashgillian erratic boulder, Baltic region, Poland (Kielan-Jaworowska, 1966).

- **Last:** *Arabellites hamiltonensis* Stauffer, 1939, lower Mississippian, Lake Erie district, USA (Kielan-Jaworowska, 1962).

**Intervening:** D.

**Comment:** The family may possibly occur as recently as the Permian (Kielan-Jaworowska, 1966).


- **First:** *Symmetrophrion reduplicatus* Kielan-Jaworowska, 1966, Wenlockian erratic boulder, Mochty Province of Warsaw, Poland; *Symmetrophrion* sp. a Kielan-Jaworowska, 1966, ?Wenlockian erratic boulder, Debina, near Ustka, Baltic coast, Poland.

- **Last:** *Symmetrophrion reduplicatus* Kielan-Jaworowska, 1966, lower Ludlow erratic boulder, Mochty Province of Warsaw, Poland.

**Intervening:**


**Intervening:** *Tetraprion* sp. Szaniawski, 1970, Silurian erratic boulders throughout Poland (Szaniawski and Wrona, 1973).


- **First:** *Xianiphrion borealis* Kielan-Jaworowska, 1962, erratic boulder, Kukruse or Idavere Stage of Estonian sequence, Mochty Province of Warsaw, Poland.

- **Last:** *Xianiphrion walliseri* and *Processophrion longiprocessus* Szaniawski and Wrona, 1973, upper FRS, Opole Lubelskie Borehole, SE Poland.

**F. UNNAMED** O. (CRD) Mar.

**First and Last:** *Trentonia shegiriana* Pickrell and Forbes, 1978, Trenton Limestone of Quebec City area, Canada.

**Order PHYLLODOCOCEROMORPHA**


- **First:** *Protoynympha salicifolia* Clarke, 1903, Upper Devonian, Portage Group, New York, USA.

**Extant**


- **First and Last:** *Fossundecima konicerium* Thompson, 1979, Pennsylvanian Essex fauna, Francis Creek Shale, Mazon Creek, northern Illinois, USA.

**Extant**


- **First:** *Glycerites sulcatus* Hinde, 1879, Upper Ordovician, Cincinnati, North America (Howell, 1962).

**Extant**

F. **HESIONIDAE** Malmgren, 1867 C. (MOS)–Rec. Mar.

- **First:** *Rutellifrons wolfforum* Thompson, 1979, Pennsylvanian Essex fauna, Francis Creek Shale, Mazon Creek, northern Illinois, USA.

**Extant**

F. **GONIADIDAE** Kinberg, 1858 C. (SPK)–Rec. Mar.

- **First:** *Carbossosoros megaliphagon* Schram, 1979, uppermost Mississippian, Bear Gulch Limestone, Central Montana, USA. Genus and species unknown, Mazon Creek, northern Illinois, USA.

**Extant**


- **First:** *Astreptoscolex anasillusos* Thompson, 1979, uppermost Mississippian, Bear Gulch Limestone, central Montana, USA (Schram, 1979).

**Extant**

F. **NEREIDEIDAE** Savigny, 1820 O. (CRD)–Rec. Mar.

- **First:** *Proeretes primus* Stauffer, 1933, Middle Ordovician, upper Glenwood Beds, Washington Avenue Bridge, Minnesota, USA; *Dinoscolites mirabilis* Stauffer, 1933, Middle Ordovician, basal Platteville Limestone, Johnson St. Quarry, Minnesota, USA; *Ungulites tridentatus* Stauffer, 1933, Middle Ordovician, basal Platteville Limestone, Johnson St. Quarry, Minnesota; *Ungulites tridentatus* Stauffer, 1933, basal Decorah Shale, Guttenberg and Fillmore, Iowa; *Paleonereites cervicornis* Stauffer, 1933, Middle Ordovician, lower Decorah Shale, University of Minnesota; *Ungulites bicipidatus* Stauffer, 1933, Middle Ordovician, Decorah Shale, Minnesota, USA.

**Extant**

F. **PALMYRIDAE** Kinberg, 1858 C. (MOS)–Rec. Mar.

- **First:** Unnamed species, Pennsylvanian Essex Fauna, Francis Creek Shale, Mazon Creek, northern Illinois, USA (Thompson, 1979).

**Extant**

F. **PHYLLODOCIDAE** Grube, 1850 and Williams, 1851 S.–Rec. Mar.
Annelida

First: *Palaeochaeta devonica* Clarke, 1903, North America and Europe (Czechoslovakia), (Howell, 1962). Extant
Intervening: MOS.

First: *Thalenessites lobatus* Stauffer, 1933, Middle Ordovician, Decorah Shale, Minnesota, USA (Howell, 1962). Extant

Comments: Glaessner (1976) somewhat controversially places *Spriggina floundersi* within the Tomopteridae, which would extend the record of the family back into the Tommotian (see ‘Sprigginidae’ in Chapter 28 on ‘Problematica’, this volume, section 1).

Order SPIOMORPHA Carus, 1863
F. CIRRATULIDAE Carus, 1863 Tr. (Mio).–Rec. Mar.
First: *Dodecaceria concharum* Orsted, 1843, cosmopolitan (Howell, 1962). Extant

F. KEILORITIDAE Allan, 1927 O. (CRD)–S. Mar.
Last: *Keilorites squamosa* (Phillips, 1848), Silurian (Yeringian) strata, junction of the Woori Yallock and Yarra, Victoria, Australia (Allan, 1910); *Keilorites crassituba* (Chapman, 1910), Silurian (Melbournian) strata, Yarra Improvement Works, South Yarra, Victoria, Australia (in Allan, 1927). Extant

Comments: Produces tubes of sand which typically occur in clusters on the ocean floor.

F. SPIONIDAE Grube, 1850, cosmopolitan genus (Howell, 1962). Extant
First: Undescribed sp., Pennsylvanian Essex Fauna, Francis Creek Shale, Mazon Creek, northern Illinois, USA (Thompson, 1979). Extant

Order TEREBELOMORPHA
F. PECTINARIIDAE Quatrefages, 1865 = ?AMPHICTENIDAE Malmgren, 1867
First: *Crininaequus hanyensis* Ettensohn, 1981, Newman Limestone, Haney Member, Chesterian, north of Stanton, east-central Kentucky, USA. Extant

First: *Terebellites franklini* Howell, 1943, Clouds Rapids Formation, Middle Cambrian, Newfoundland, Canada (Howell, 1962).
Extant

Order FLABELLIGERIMORPHA
First: Genus and sp. uncertain, Emu Bay Shale, Lower Cambrian of Kangaroo Island, South Australia (Glaessner, 1976). Extant

Order SERPULIMORPHA
F. SABELLIDAE Malmgren, 1867 T. (DAN)–Rec. Mar. (see Fig. 15.2)
F. SERPULIDAE Burmeister, 1837 O. (LLN)–Rec. most Mar., some FW Extant
First: *Serpularia crenata* Munster, 1840, Orthoceratite Limestone, southern Germany (Howell, 1962). Extant
Intervening: C.

Order INCERTAE SEDIS
First and Last: *Burgessochaeta setigera* (Walcott, 1911), Phyllopod bed, Walcott Quarry, Middle Cambrian Burgess Shale, British Columbia, Canada (Conway Morris, 1979). Extant
First and Last: *Canadia spinosa* Walcott, 1911, Phyllopod Bed, Walcott Quarry, Middle Cambrian Burgess Shale, British Columbia, Canada (Conway Morris, 1979). Extant
First and Last: *Insilicorypha psygma* Conway Morris, 1979, Middle Cambrian Burgess Shale, British Columbia, Canada (Conway Morris, 1979). Extant
First and Last: *Peronochaeta dubia* (Walcott, 1911), Middle Cambrian Burgess Shale, British Columbia, Canada (Conway Morris, 1979). Extant
First and Last: *Stephenoscolex argutus* Conway Morris, 1979, Middle Cambrian Burgess Shale, British Columbia, Canada (Conway Morris, 1979). Extant
First and Last: *Eopolychaetus albaniensis* Ruedmann, 1901,
Hudson River Beds near Albany, New York, USA (Fisher, 1962).


**First and Last:** Pontobdellopsis cometa Ruedemann, 1901, Hudson River Beds near Albany, New York, USA (Fisher, 1962).


**First and Last:** Ramesses magnus Schram, 1979, uppermost Mississippian, Bear Gulch Limestone, central Montana, USA.


**First and Last:** Soris labiosus Schram, 1979, uppermost Mississippian, Bear Gulch Limestone, central Montana, USA.

**Class MYZOSTOMARIA**

The Myzostomaria may be closely related to the polychaetes. They are parasitic on echinoderms, particularly crinoids, often forming gall-like cysts. There are seven extant families, of which only one has a fossil record.


**First:** Myzostomites clarkei Clarke, 1921, a cosmopolitan species from the Ordovician.
Annelida

Class CLITELLATA

Subclass OLIGOCHAETA Grube, 1850

Fossil oligochaetes are rare and disputed. Protoscoleces, sometimes referred to this subclass, is known from marine deposits from the Upper Ordovician to the Upper Silurian. P. batheri from the Silurian of New York (Lockport) inhabited shallow lagoons which may have been brackish. The genus is also referred to the Miskoa (Polychaeta), (Roger, 1959).

Order PLESIOTHECA Michaelsen, 1930

F. PALAEOSCOLECIDA Whittard, 1953

C. (ATB)–S. (u) Mar.

First: Palaeoscoleca sinensis Hou and Sun, 1988, Chiung-chussu Formation, Yunnan Province, China.


Order PROSOTHECA Michaelsen, 1930

F. ENCHYTRAIDAE Vejdovsky, 1879

T. (RUP)–Rec. Terr.

First: Enchytraeus sepultus Menge, 1866, Oligocene Baltic amber (Conway Morris et al., 1982). Extant

Order INCERTAE SEDIS

F. INCERTAE SEDIS Q. (PLE)–Rec. FW

First: Dendrodrilus rubidus Schwert, 1979, Quaternary
lacustrine sequence in Kitchener, southern Ontario, Canada (Schwert, 1979).

Subclass HIRUDINEA d’Orbigny and Lafresnaye, 1837

There are three families of leeches, of which one has a fossil record.


Extant

Class INCERTAE SEDIS


REFERENCES


ARTHROPODA (TRILOBITA)


The classification of the Trilobita above family level has always been contentious. Since the 1959 Treatise, there have been several attempts to review classification (Bergström, 1973; Fortey, 1990), and new high-level taxa have been introduced, such as the Order Proetida Fortey and Owens, 1975. Some of the new concepts have passed into general use, but the classification is not stable, or fully resolved phylogenetically. In this work, the classification mostly follows Fortey (1990, 1991), and should be similar to that which will be used in the revision of the Treatise on Invertebrate Paleontology, Part O, currently in progress.

Class TRILOBITA Walch, 1771

Order REDLICHIDA Richter, 1933 (See Fig. 16.1)

Comments: Redlichiids and olenellids are treated as separate orders in some classifications. Here they are combined in the Redlichiida, as a paraphyletic group including most of the primitive families having more than two or three thoracic segments in the holaspis.

Suborder OLENNELINA Walcott, 1890

Superfamily OLENNELLOIDEA Walcott, 1890

F. OLENNELLIDAE Walcott, 1890 Č (CRF) Mar.
First: Olenellus truncatus Walcott, 1913, Sekwi Formation (Botomian), north-western Canada (Fritz, 1972).
Last: Olenellus gilberti Meek, 1974, and at least four other olenellids, Pioche and Carrara Formations (Toyonian), south-western USA (Palmer and Halley, 1979).

F. HOLMIIDAE Hupé, 1953 Č. (CRF) Mar.
First: Schmidtiellus mickwitzi (Schmidt, 1888), Lukati Formation (Botomian), Estonia, former USSR (Mens et al., 1990).
Last: Elliptocephala asaphoides Emmons, 1844, West Castleton Formation (?Botomian), USA (Theokritoff, 1984). Intercontinental correlation of later Early Cambrian beds is very uncertain. This species seems to be the youngest holmiid with reasonably good stratigraphical control.

Superfamily FALLOTASPOIDEA

F. FALLOTASPIDAE Hupé, 1953 Č. (CRF) Mar.
Last: Parafalotaspis grata Fritz, 1972, Sekwi Formation (Atabdanian), north-western Canada (Fritz, 1972)

F. ARCHAEASPIDAE Repina, 1979 Č. (CRF) Mar.
Last: Bradyfallotaspis patula Fritz, 1972, Sekwi Formation (Atabdanian), north-western Canada (Fritz, 1972). Based on correlations suggested by Repina in Spizharski et al. (1986), this species seems to be younger than any Siberian archaeaspid.

F. DAGUINASPIDAE Hupé, 1953 Č. (CRF) Mar.
First: Choubertella spinosa Hupé, 1953, Amouslek Formation (Atabdanian), Morocco (Hupé, 1953).
Last: Daguinaspis ambroggi Hupé and Abadie, 1950, Amouslek Formation (Atabdanian), Morocco (Hupé, 1953).

Superfamily NEVADIOIDEA Hupé, 1953

F. NEVADIIDAE Hupé, 1953 Č. (CRF) Mar.
Last: Nevadella (Nevadella) perfecta (Walcott, 1913), Mural Formation (Botomian), south-western Canada (Fritz, 1992).

F. JUDOMIIDAE Repina, 1979 Č. (CRF) Mar.
First: Judomia mattajensis Lazarenko, 1962, Tyuser Formation (Atabdanian), north-eastern Siberian Platform, former USSR (Repina et al., 1974).
Comments: In addition to the references cited above, considerable information on olenellid distribution on the Siberian Platform, former USSR is provided by Astashkin et al. (1991).

Suborder REDLICHIINA Harrington, 1959

Superfamily EMUELLOIDEA Pocock, 1970
Fig. 16.1


**Superfamily REDLICHOIDEA** Poulsen, 1927

First:  *Wutingaspis tingi* Kobayashi, 1935, lower Chingchussuan Stage, eastern Yunnan, south-western China (Chang et al., 1980).
Last:  *Redlichia nobilis* Walcott, 1913, top of the Manto Formation, Shandong, North China (Walcott, 1913). The *Redlichia* faunas of northern Australia, including *Redlichia chinensis* Walcott, are of early middle Cambrian age (Ordian Stage) (Opik, 1958, p. 11).

First:  *Dolerolenus zoppii* (Meneghini), Punta Manna Formation, Sardinia, Italy; *Dolerolenus (Malungia) laevigata* Lu, 1975, upper Chingchussuan Stage, eastern Yunnan, SW China (Chang et al., 1980; Pillola, 1989).
Last:  *Paramalungia lubrica* Chang, upper Tsanglangpuan Stage, eastern Yunnan, SW China (Chang et al., 1980).

First:  *Yinites typicalis* Lu, 1975, Minghsingssu Formation, northern Guizhou, SW China (Chang et al., 1980).
Last:  *Drepanuroides latilimbatus* Chang, 1966, *Drepanuroides Zone*, eastern Yunnan, SW China (Chang et al., 1980).

First and Last:  *Mayiella tuberculata* Chang, 1966, upper Tsanglangpuan Stage, eastern Yunnan, SW China (Chang et al., 1980).


First and Last:  *Saukianda andalusiae* Richter and Richter, 1940, Spain and Morocco (Richter and Richter, 1940; Hupé, 1953).

First:  *Metadoxides torosus* Meneghini, lower Punta Manna Formation, Sardinia, Italy (Rasetti, 1972; Pillola, 1989).
Last:  *Onaraspis somniurna* Opik, 1967, Ordian Stage, Northern Territory, Australia (Opik, 1967).
F. ABADIELLIDAE Hupé, 1953
\( s.l. \) (early CRF) Mar.

**First:** *Parabadiella huoi* Chang, lower Chiungchussuan Stage, southern Shaanxi and eastern Yunnan, SW China (Chang et al., 1980).

**Last:** *Guangyuanspis modaoyensis* Chang and Qian, upper Chiungchussuan Stage, northern Sichuan, SW China (Chang et al., 1980).

F. KUEICHOWIIDAE Lu, 1965 \( s.l. \) (CRF) Mar.

**First and Last:** *Kueichouia liui* Lu, 1965, Tsanglangpuan Stage, northern Guizhou, SW China (Chang et al., 1980).

F. MENNERASPIDAE Pokrovskya, 1959 \( s.l. \) (CRF) Mar.

**First and Last:** *Menneraspis striatus* Pokrovskya, 1959, Tojohnian Stage, Tuva, former USSR.

F. REDLICHINIDAE Chang and Lin, 1980 \( s.l. \) (CRF) Mar.

**First and Last:** *Redlichina vologdini* Lermontova, Tojohnian Stage, Sayan-Altai, former USSR.

F. CHENGKOUASPIDAE Chang and Lin, 1980 \( s.l. \) (CRF) Mar.

**First:** *Pseudoesserops oculatus* Repina, 1965, Atabdanian Stage, Siberia, former USSR.

**Last:** *Chengkouaspis longioculus* Chang and Lin, 1980, Yingzuiyan Formation (upper Tsanglangpuan Stage), northern Guizhou, SW China (Chang et al., 1980).

F. NEOREDLICHIIDAE Hupé 1953 \( s.l. \) (CRF) Mar.

**Last:** *Yunnanocephalus*, SW China.

**Superfamily** PARADOXIDOIDEA Hawle and Corda, 1847

F. PARADOXIDIDAE Hawle and Corda, 1847 \( s.l. \) (CRF–STD) Mar.

**First:** *Anabaracops, Anabaraspis*, Toyonian Stage, former USSR (Yakutia). *Paradoxides s.l.* (including *Acadoparadoxides*) appears in the early Middle Cambrian in Europe, North Africa and Scandinavia, where a discordance is often present at the Lower/Middle Cambrian boundary. According to Geyer (1990) the first occurrence of *Paradoxides* (s.l.) in Morocco is older than in Scandinavia.

**Last:** *Paradoxides forchhammeri* Angelin, 1854, upper Middle Cambrian, *Lejopvge laevigata* Zone, Scandinavia.

F. CENTROPLEURIDAE Angelin, 1854 \( s.l. \) (middle–late STD) Mar.

**First:** *Clarella, P. hicksi* Zone, eastern Canada.

**Last:** *Centropleura, P. forchhammeri* ‘Stage’, Scandinavia, China and Australia.

F. XYSTRIDIRIDAE Whitehouse, 1939 \( s.l. \) (early STD) Mar.

**First and Last:** *Xystridura* (including subgenera), Australia and SW China (Hainan).

?F. HICKSIIDAE Hupé, 1953 \( s.l. \) (CRF) Mar.

**First and Last:** *Hicksia*, Portugal and Spain.

F. LERMONTOVIDAE Suvorora, 1956 \( s.l. \) (CRF) Mar.

**Order** AGNOSTIDIA Salter, 1864

Eodiscina and Agnostina are regarded as belonging to separate clades by some authorities (e.g. Shergold, 1991). The peculiarities of Agnostina are taken to indicate that they are derived ‘separately’ from the rest of the trilobites, and the several similarities to Eodiscina are considered to be a result of convergence. Fortey (1990) enumerated a number of characters shared between Agnostina and Eodiscina, and observed that many of the characters of Eodiscina were plesiomorphic. For this reason, Eodiscina and Agnostina are included as a clade here.

**Suborder** AGNOSTINA

**Comments:** Classification of Agnostida: from Shergold et al. 1990; genera incertae familiae omitted.

**Superfamily** AGNOSTOIDEA M'Coy, 1849

F. AGNOSTIDAE M'Coy, 1849 \( s.l. \) (STD)–O. (ARG) Mar.

**First:** *Ammagnostus (Ammagnostus) pisiformis* Bronnhiart, *L. laevigata* Zone, Sweden (Westergård, 1946).

**Last:** *Micragnostus serus* Fortey, 1980, *D. bifidus* Zone, Spitsbergen (Fortey, 1980).

**Comments:** Includes Agnostinae M'Coy, 1849; Ammagnostinae Opik, 1967; Glyptagnostinae Whitehouse, 1936.


**First:** *Pentagnostus praecurrens* (Westergård, 1946), *Paradoxides pinus* Zone, Sweden (Westergård, 1946).

**Last:** *Lejopvge laevigata* (Dalman), *Acmarhachis quasivespa* Zone (= *U. Cedaria* Zone), Queensland, Tasmania (Laurie, 1989).

**Comments:** Occurrence depends on correlation between the pre-Glyptagnostus stolidotus Zones of Kazakhstan (former USSR) and Australia: if *Kormagnostus simplex* post-dates *Acmarhachis quasivespa*, then *Lejopvge armata* (Linnarsson, 1969) is the youngest taxon.

F. PERONOPSIDAE Westergård, 1936 \( s.l. \) (STD) Mar.

**First:** *Peronopsis cuneifera* (Barrande), *E. pusillus* Zone (Upper *P. oelandicus* Zone), Bohemia, Czechoslovakia (Snedr, 1983).

**Last:** *Diplorrhina quadrata* (Tullberg), *Jincella brachymetopa* Zone (*Paradoxides forchhammeri* Zone), Sweden (Westergård, 1946).

**Comments:** First occurrence depends on correlation of *Paradoxides* faunas across Europe.

F. SPINAGNOSTIDAE Howell, 1935a \( s.l. \) (CRF–MER) Mar. (= QUADRAGNOSTIDAE

Arthropoda (Trilobita)
Howell, 1935a sensu Ópik, 1961;
= CYCLOPAGNOSTIDAE Howell, 1937

First: Eoaagnostus roddyi Resser and Howell, 1938, Upper Olenezus Zone, Pennsylvania (Resser and Howell, 1938).
Last: Peralagnostus sp. cf. P. nobilis Ópik, 1961, Rhaagnostus aphis/Wentsuia iota Zone, Queensland (Lower Conaspis Zone), (Schergold, 1980).
Comments: Includes Spingagnostinae Whitehouse, 1936; Cyclopagnostinae Howell (1937); Hypagnostinae Ivshin (1953); Euagnostinae Ópik (1979); Doryagnostinae Schergold et al. (1990).

F. DIPLAGNOSTIDAE Whitehouse, 1936
Ō. (STD)–O. (TRE) Mar.
Comments: Includes Diplagnostinae Whitehouse, 1936; Oialagnostinae Ópik, 1967; Pseudagnostinae Whitehouse, 1936.

F. CLAVAGNOSTIDAE Howell, 1937
Ō. (STD–MER) Mar. (= ACANTHAGNOSTIDAE Qian, 1982)
First: Clavignostus repandus (Westergård, 1946), Jincella brachymetopa Zone (Paradoxides forchhammeri Zone), Sweden (Westergård, 1946).
Comments: Includes Clavignostinae Howell, 1937; Aspidadagnostinae Pokrovskaya, 1960.

= GERAGNOSTIDAE Howell, 1935b;
= ARTHORHACHIDAE Raymond, 1913
First: Angliagnostus? iacuenensis (Capéra et al., 1978), lower Tremadoc, Montagne Noire, France (Capéra et al., 1978).
Last: Arthorhachis tarda (Barrande), upper Ashgill, Dalmanittina Beds, Poland (Kielan, 1959).
Comments: Species of Corrugagnostus, Dividadagnostus and Geragnostus are also reported from the Ashgill.

Superfamilies incertae sedis

F. PHALACHROMIDAE Hawle and Corda, 1847
Ō. (STD) Mar. (= PLATAGNOSTIDAE Howell, 1935b)
First: Phalacroma bibullatum (Barrande), E. pusillus Zone (upper P. oeladicus Zone), Bohemia, Czechoslovakia (Snejdr, 1958).
Last: Phalacroma caudus Pokrovskaya, upper P. davidis Zone (= P. punctuosus Zone), southern Siberia, former USSR (Rozova in Lisogor et al., 1988).
Comments: This family also contains Dignagnostus Hairullina, 1975 and Lisogogognust Rozova, 1988.

F. SPHAERAGNOSTIDAE Kobayashi, 1939
Ō. (TRE–ASH) Mar.
Last: Sphaeragnostus cingulatus (Olin), Staurocephalus clavifrons Zone, Middle Ashgill, Poland, Skåne, Bornholm (Ahlberg, 1989).
Comments: Sphaeragnostus in the Tremadoc of Kazakhstan cannot be definitely confirmed. The next youngest species, of Llandeilo age, is S. similis (Barrande) from Czechoslovakia. Ashgillian species occurring in Scandinavia and Bornholm have been synonymized by Ahlberg (1989). S. gassperi Cooper and Kindle (1936) occurs in the Ashgillian of Quebec, and is also reported from the Rawtheyan (middle Ashgill), D. ances Zone of Wales (Thomas et al., 1984).

Superfamily CONDYLOPYGOIDEA Raymond, 1913

F. CONDYLOPYGIDAE Raymond, 1913
Ō. (CRF–STD) Mar.
Comments: Condylyopyge spinigera Westergård, 1944 is also reported from the Ptychagnostus punctuosus Zone at Andrarum, Sweden.

Suborder EODISCINA

Superfamily EODISCOIDEA Raymond, 1913
Families from Jell (1975).

F. EODISCIDAE Raymond, 1913
Ō. (CRF–basal MER?) Mar.
First: Tsunyidiscus liangshanensis Chang, 1988, Chingchuussu Formation, NW Yangtze Platform, China, or Hupeidiscus orientalis (Chang, 1988), Chingchuussuan Stage, Juimenchong Formation, Hunan, and Hsuijingtuo Formation, Hubei, China (Chang, 1988).
Last: Opsidiscus spp., Lejopyge laevigata Zone, including O. depolitus Romanenko, Middle–Upper Cambrian passage beds (Jago, 1972).
Intervening: Most of the Lower, all of the Middle Cambrian, cosmopolitan.

F. WEYMOUTHIIDAE (sensu Jell, 1975)
Ō. (CRF–low STD) Mar.
First: Serrodiscus bellimarginatus Shaler and Foerste, Callavia broeggeri Zone, Branchian Series, North Atlantic Province (Massachusetts, USA, Newfoundland; England, UK), (Rushton, 1966).
Intervening: Almost exclusively Lower Cambrian.

Order NARAOIIDAE Ė. (CRF)–O. (ASH) Mar.
Naraoiida are an uncalcified sister group to the rest of the Trilobita, with which they may be formally included.
First: Naraoia sp. from Chins (R. A. Fortey, pers. comm.).
Last: Undescribed species cf. Tarricoyia, Soom Shale, South Africa (R. A. Fortey, pers. comm.).

Order CORYNEXOCHIDA Kobayashi, 1935

Suborder CORYNEXOCHINA
Families from Suvorova (1964) and Zhang et al. (1980).
F. CORYNEXOCHIDAE Angelin, 1854
Č. (CRF–low MER) Mar.
Last: Corynexochus plumula Whitehouse, Idamean, Australia, Kazakhstan, former USSR (Öpik, 1967).

F. CHEIRUROIDIDAE Chang, 1963
Č. (CRF–low STD) Mar.
First: Hunanocephalus ovalis Lee, Shuijingtuo Formation (lower Tsanglangpuian), SW China (Chang, 1988).

F. CHENGHUIIDAE in Zhang et al., 1980
Č. (middle CRF) Mar.
First and Last: Chengkouia and Xuigelia spp., Bianmaching Formation (middle Tsanglangpuian), SW China (Zhang et al., 1980).

F. DORYPYGIDAE Kobayashi, 1935 (including OGYGOPSIDAE Rasetti, 1951)
Č. (CRF–early MER) Mar.
First: Kootenia sp., black shale below Balang Formation (early or mid-Tsanglangpuian), Hunan, China (Chang, 1988).
Last: Olenoidestrumans Öpik (1967, p. 174), Mindyallan, Australia; or Dorypyge sp., Mila Formation (basal MER), Iran (Fortey and Rushton, 1976).

F. DOLICHOMETOPIDAE Walcott, 1916
Č. (late CRF–early MER) Mar.
First: Hoffetella spp., Lungwangmiao Formation, SW China (Zhang et al., 1980).
Last: Hemirhodon spp., Dresbachian, Vermont (Raymond, 1937).

F. EDELSTEINASPIDIDAE Hupé, 1953
Č. (CRF) Mar.

F. JAKUTIDAE Suvaroova, 1959 Č. (CRF) Mar.

F. LONGDUIIDAE Zhang and Qian, in Zhang et al., 1980 Č. (mid CRF) Mar.
First and Last: Longduia spp., Tsanglangpu Formation (middle Tsanglangpuian), SW China (Zhang et al., 1980), and Punta Manna Formation (mid CRF), Sardinia (Pillola, 1990).

First: Arthricocephalus chauveauxi Bergeron, Balang Formation, upper Tsanglangpuian, Hunan, China (Chang, 1988).
Last: Tonkinella kobayashi Resser, Machari Formation (high STD, Tonkinella Zone), Neietsu, Korea (Chang, 1988).

First: species of Zacanthopsis, Zacanthopsina and Stephanaspis, upper Olenellus Zone, Nevada, USA (Palmer, 1964) or Chuchiaspis spp., Shilungtung Formation (Lunwangmiaoaan), SW China (Chang, 1988).
Last: Zacanthoides sp., Marjum Formation (Bolaspidella Zone, contracta Subzone), House Range, Utah, USA (Robison, 1964).

First: Ogygopsis batis (Walcott, 1889), upper Olenellus Zone, Nevada, USA (Palmer, 1964).
Last: Ogygopsis, USA.

F. DINESIDAE Lermontova, 1940 Č. (CRF–STD) Mar.
No additional information since Treatise O (1959).

Suborder SCUTELLUINA Hupé, 1953
(See Fig. 16.2)
First: Reymondaspis limbata (Angelin), Scandinavia.
Last: Scutellum, Scabriscutellum, Germany, Czechoslovakia.

Comments: Range taken from Lane and Thomas (1983).

Last: Phillipsinella parabola s.l. Barrande, 1846, Hirnantian, Côte de la Surprise Member, Percé, Quebec (Lespérance, 1988).

F. TSINANIIDAE Kobayashi, 1933 Č. (MER) Mar.
First and Last: Tsiania (T.) spp. and Tsiania (Dictyites) spp., Chaumitien Limestone, Shantung, China (Kobayashi, 1933) and Chatsworth Limestone, Western Queensland, Australia (Shergold, 1975). Australian records of later late Cambrian age; T. (T.) cf. nomas Shergold of ‘latest late Cambrian’ age in Thailand.

Suborder LEIOSTEGIINA Bradley, 1925
F. LEIOSTEGIIDAE Bradley, 1925 Č. (STD)–O. (?CRF) Mar.
Comments: Fortey and Shergold (1984) extended the concept of this family to include Ordovician genera which had previously been referred to other families. These authors also regarded the Eucalemynidae (Lu, 1975) as synonymous.


### F. CHEILOCEPHALIDAE


*Metopolichas? klouceki* (Ruzicka, 1926), Czechoslovakia.

**First:**

**Last:**
- *Radiolichas aranea* (Holzapfel, 1895), Massenkalk Limestone, Germany.

**Comments:**  
A. T. Thomas reported: In the first edition of *The Fossil Record*, Tripp listed *Craspedarges wilcanniae* as the last record. The (lost) type material of that species was collected from erratic boulders of the Amphitheatre Group of New South Wales, Australia. So far as I can gather, the Amphitheatre Group is of D1, Pragian age.' (See also Thomas and Holloway, 1988.)

### F. ILLAENURIDAE

Vogdes, 1890 C. (MER) Mar.

**First:**

**Last:**

**Order** Lichida Moore, 1959

**Superfamily** Lichoidea (sensu Fortey, 1991)

F. Lichidae Hawle and Corda, 1847


**First:**

**Last:**
- *Radiolichas aranea* (Holzapfel, 1895), Massenkalk Limestone, Germany.

**Comments:**  
A. T. Thomas reported: In the first edition of *The Fossil Record*, Tripp listed *Craspedarges wilcanniae* as the last record. The (lost) type material of that species was collected from erratic boulders of the Amphitheatre Group of New South Wales, Australia. So far as I can gather, the Amphitheatre Group is of D1, Pragian age.' (See also Thomas and Holloway, 1988.)

### F. LICHAKEPHALIDAE


**First:**

**Last:**

**Superfamily** Odonotopleuroidea (sensu Fortey, 1991)

F. Odonotopleuridae Burmeister, 1843


**First:**
- *Acidaspides praecurrens* Lermontova, 1951, Kazakhstan, former USSR.

**Last:**
- *Radiaspis radiata* (Goldfuss), Germany.

**Comments:** Bruton (1983a) assigned *Belovia calva* of late middle Cambrian age (eastern Siberia) to the...
Eoca dispididae of the Odontopleuroidea. This species has subsequently been assigned tentatively to Eocatapis of Lichakephalidae (Thomas and Holloway, 1988).

**Superfamily** DAMESELOIDEA Kobayashi, 1935

F. DAMESELLIDAE Kobayashi, 1935


F. KAOLISHANIIDAE Kobayashi, 1935

C. (MER) Mar.

Order PHACOPIDA Salter, 1864

Suborder CALYMPENINA Swinnerton, 1915

F. CALYMPENIDAE Milne Edwards, 1840


**Intervening:** ARG – EIF

**Comments:** All the above *Pharostomina* species occur in strata of known early Tremadoc age. The genus also occurs in the upper Tremadoc of Argentina, and it may occur in the lower Tremadoc of Czechoslovakia. Other, unnamed calymenid species occur in ‘Middle’ Devonian (?GIV) strata.

F. HOMALONOTIDAE Chapman, 1890


First: *Bavarilla hofensis* (Barrande), Germany (Sdzuy, 1955).

Last: *Dipleura dekayi* Green, North and South America (Kozlowski, 1923).

Suborder PHACOPINA Struve, in Moore, 1959

Within the Phacopina, GDE recognizes a Superfamily Acastacea Delo, 1935 comprising a plesion ‘Kloucekinae’ Destombes, 1972 (O. (LLN – ASH)), F. Calmoniidae Delo, 1935 (S. (PRD) – D. (?FAM?)) and F. Acastidae Delo, 1935 (S. (LLY) – D. (FRS)). The plesion is regarded as a paraphyletic grade of Acastacea s.l., within which Baniaspis Destombes, 1972 is most closely related to the Calmoniidae and Acastidae. The classification adopted by DJH follows more closely that used in the first edition of *The Fossil Record*, and five families are recognized (Phacopidae, Calmoniidae, Dalmanitidae, Pterygometopidae, Synphoriidae). Pending the publication of the new edition of the Treatise, the DJH classification is followed.

F. PHACOPIDAE Hawle and Corda, 1847


First: *Morgatia primitiva* Hammann, 1972, Postolonne Formation, France (Henry, 1980, p. 166). This species may belong to *Kloucekia* (Calmoniidae) rather than to *Morgatia*. The next oldest species are *Morgatia zuidensis* (Destombes, 1972), Morocco (LLN/LLO) and *M. hupei* (Nion and Henry, 1966), France, Portugal and Spain (LLO), (Henry, 1980, p. 167–8).

Last: Several species of *Phacops* s.l., *Phacops* (Omegops), *Dianops* and *Cryptops*, England, UK, France, Morocco, Belgium, Germany, Poland, former USSR (Hahn and Hahn, 1975, pp. 21–6; Struve, 1976; Thomas et al., 1984, pp. 62–3).

**Intervening:** ASH – FRS.

F. CALMONIIDAE Delo, 1935


First: *Kloucekia drevermanni drevermanni* Hammann, 1972, Spain (Hammann, 1974, p. 79).

Last: Several species of *Neocalmonia* (*Neocalmonia*), *N. (Bradocryphaeus)*, *N. (Heliopyge)* and *N. (Quadratispina)* are known from the FRS of Spain, England, UK, France, Belgium, Germany and Afghanistan (Hahn and Hahn, 1975, pp. 27–8; Morris, 1988, p. 37). Of these, *N. (Bradocryphaeus) occidentalis* (Whidborne, 1897) occurs in the Morte Slates, England, UK, which may range into the lower FAM (Morris, 1988).

**Intervening:** LLO – GIV.

**Comments:** The family Calmoniidae is here considered to comprise Calmoniini, Acastinae, ‘Acastinae’ and Asteropyginae of *Treatise* O usage, the last two being transferred from the Dalmanitidae. This is consistent with the views of Eldredge and Brania (1980, p. 191) who regarded Acastinae, Acastinae and Asteropyginae as the sister group of the Malvinokaffric calmoniids.

F. DALMANITIDAE Vogdes, 1935


First: *Ormathops borni* (Dean, 1966), *D. extensus* Biozone, from the Couches du Landeyran, Montagne Noire, France.

Last: *Dalmanites patacamayaensis* Kozlowski, 1923, Sicasica Formation?, Bolivia (EIF, precise horizon and age uncertain; Wolfart, 1968, p. 70); *Odontochile aff. carrinata* Maximova (1968, p. 108), Kazakh Horizon (lower EIF), Kazakhstan; *Odontochile (Reussia) kailensis* Maximova (in Modzalevskaya, 1969, p. 148), Imatchinskaya Suite (lower EIF), eastern Siberia, former USSR.

**Intervening:** LLN – EMS.

F. PTERYGOMETOPIDAE Reed, 1905


First: *Pterygometopus scleros* (Dalman, 1827), *Expansus* Limestone, Sweden (Whittington, 1950, p. 538); *P. borni* (Dean, 1966), Couches du Landeyran, Montagne Noire, France, and strata of similar age in Morocco (Destombes, 1972, p. 27) (this species possibly belongs in *Ormathops* – see *Dalmanitidae* above); *P. bredensis* Weber, 1948, Brady Horizon, southern Urals, former USSR (Ancigin, 1970, p. 14).


**Intervening:** LLN – ASH.

F. SYNPHORIIDAE Delo, 1935


Last: Trypaulites calypos (Hall, 1861), Grand Tower Limestone, Illinois and Dundee Limestone, Michigan, USA (Lespérance, 1975, p. 113); Coronula marylandicus (Prosser and Kindle, 1913), Romney Formation, Maryland, USA (Lespérance and Bourque, 1971, fig. 2).

Intervening: LUD, GED–EIF.

F. PROSOPISCIIDAE Forney and Shergold, 1984

First: Prosopiscus praecox Forney and Shergold, 1983, lower part of Nora Formation, central Australia, mid–late Arenig age. Prosopiscus sp. A also occurs with P. praecox. P. latus is known from the upper Arenig of SW China.

Last: Prosopiscus spp., Asia.

Intervening: LLN.

Comments: Prosopiscus is the only genus of the family, and had previously been placed within the F. Cheiruridae or F. Encrinuridae.

Suborder CHEIRURINA Harrington and Leanza, 1957

F. DIAPHANOMETOPIDAE Jaanusson, 1959

First: Gyrometopus lineatus (Angelín, 1854), Megistaspis planilimbata Zone, Västergotland, Oltorp, Sweden.

Last: Diaphanometopus volborthi Schmidt, 1881, Baltoscandia.

Comments: Jaanusson (1975) upgraded Diaphanometopus to a new genus, Gyrometopus, which he regarded as an immediate ancestor of the Phacopina. Diaphanometopus (a monotypic genus) is poorly known, but the family was considered by Jaanusson (1975, p. 215) as most likely to belong to the Cheiruroidea.

F. CHEIRURIDAE Salter, 1864

First: Eocheirurus spp., former USSR.

Last: Crotalocephalus sternbergi (Boeck), Czechoslovakia.

F. PLIOMERIDAE Raymond, 1913

First: Parapilekia anxia Sdzuy, 1955, Leimitz-Schiefer, Germany.

Last: Placoparia (Hawleia) prantli Kielan, 1959, S. claforfons Zone, Poland.

F. ENCRINURIDAE Angelín, 1854

First: Cybelurus sokolensis Bursky, 1970, top Sokolíy Horizont, Pai-Khoya, southern Novaya Zemlya, former USSR (see Fortey, 1980, p. 100). Lyrapype dubius Forney, 1980 from the middle Olenidsletta Member of the Valhallfonna Formation (I. gibberulus Zone), Ny Friesland, Spitsbergen, may be the next oldest.


Intervening: ARG2–PRD.

F. STAurocephalidae Pantl and Pribil, 1948

First: Staurocephalus pilafons Owen and Bruton, 1980, Onnian Stage, upper Solvarg Formation, central Oslo Region, Norway.


Intervening: PUS–HIRM, SHE–HOM.

Order PTYCHOPARIDA Swinnerton, 1915

This group is difficult to define, and is here understood as a paraphyletic group including those families in which the hypostome is not attached to the doublure (nate 1 condition).

Suborder PTYCHOPARINA Richter, 1933

Superfamily ELLIPSOCEPHALOIDEA Matthew, 1887

F. Ellipsocephalidae Matthew, 1887

First: Genera include Ellipsocephalus, Antatlasia, Lusatiops and Strenuessa from Europe, North Africa (Geyer, 1990b, Bani-Stufe, Antatlasia hollardi Zone), Middle East, eastern Canada and Australia.

Last: 'Manchurocephalus, L. laevigata Zone/A. pisiformis Zone, NE China.

F. PROTOLENIDAE R. and E. Richter, 1948

First: Several genera and subgenera, including H. (Hamatolenus), Protolenus and Pseudolenus, Europe, North Africa and eastern Canada.

Last: H. (Hamatolenus), H. (Lotzeia) and H. (Myopsolenus), North Africa and Spain.

Comments: The above ages are based on the conventional view that the Protolenid–Strenuellid Zone of England and Wales, UK (Cowie et al., 1972; Bassett et al., 1976), and the Protolenus Zone of eastern Newfoundland (Hutchinson, 1962) are of late early Cambrian age. On the basis of more recent work in Morocco, Geyer (1990a,b) considered these units to be of early middle Cambrian age as they correspond with strata in which Paradoxides (s.l.) occurs.

F. AGRAULIDAE Raymond, 1913

Superfamily PTYCHOPARIOIDEA Matthew, 1887

F. PTYCHOPARIDAE Matthew, 1887


Last: Irvingella nuneatonensis (Sharman, 1886), top of the Olenus cataractes Zone, Nuneaton, central England, UK; I. major Ulrich and Resser, in Walcott, 1924, Eltionia Zone, USA, also Ishinagnostus ishinity Zone, Kazakhstan, former USSR (Rushton, 1983, p. 113).

F. Marjumiidae Kobayashi, 1935

Comments: The above ages are based on the conventional view that the Protolenid–Strenuellid Zone of England and Wales, UK (Cowie et al., 1972; Bassett et al., 1976), and the Protolenus Zone of eastern Newfoundland (Hutchinson, 1962) are of late early Cambrian age. On the basis of more recent work in Morocco, Geyer (1990a,b) considered these units to be of early middle Cambrian age as they correspond with strata in which Paradoxides (s.l.) occurs.

F. AGRAULIDAE Raymond, 1913

Superfamily PTYCHOPARIOIDEA Matthew, 1887

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Last: Irvingella nuneatonensis (Sharman, 1886), top of the Olenus cataractes Zone, Nuneaton, central England, UK; I. major Ulrich and Resser, in Walcott, 1924, Eltionia Zone, USA, also Ishinagnostus ishinity Zone, Kazakhstan, former USSR (Rushton, 1983, p. 113).

F. Marjumiidae Kobayashi, 1935

Comments: The above ages are based on the conventional view that the Protolenid–Strenuellid Zone of England and Wales, UK (Cowie et al., 1972; Bassett et al., 1976), and the Protolenus Zone of eastern Newfoundland (Hutchinson, 1962) are of late early Cambrian age. On the basis of more recent work in Morocco, Geyer (1990a,b) considered these units to be of early middle Cambrian age as they correspond with strata in which Paradoxides (s.l.) occurs.
Arthropoda (Trilobita)

F. SOLENOPLUSURIDAE Angelin, 1854

F. CONOCORYPHIDAE Angelin, 1854

F. DOKIMOCEPHALIDAE Kobayashi, 1935
€. (MER) Mar.

F. ONCHONOTSPIDAE Rasetti, 1946

F. NEPEIIDAE Whitehouse, 1939

F. CREPICEPHALIDAE Kobayashi, 1935

F. LONCHOCEPHALIDAE Hupe, 1953

F. KINGSTONIIDAE Kobayashi, 1933

F. ASAPHISCIDAE Raymond, 1924


F. NORWOODIIDAE Walcott, 1916

F. MENOMONIIDAE Walcott, 1916


F. PAPYRIASPIDIDAE Whitehouse, 1939

F. EMMPICHILLIDAE Kobayashi, 1935

F. DICERATOCEPHALIDAE Lu, 1954
€. (MER) Mar.


Comments: East Asia and western Canada.


Comments: upper Middle Cambrian to lower Upper Cambrian, China.


Comments: lower Middle Cambrian to lower Upper Cambrian, East Asia.


Comments: Hsuchuangan Stage, NE China.


Comments: Hsuchuangan Stage, China.


Comments: Hsuchuangan and Changhian Stages, Asia.


Comments: Hsuchuangan and lower Changhian Stages of North and NE China.


Comments: lower Middle Cambrian, Hsuchuangan Formation, North China.


Comments: Changhsia Formation, Changhian Stage; North and southern NE China, Australia.

Suborder OLENIINA Burmeister, 1843

F. OLENIDAE Burmeister, 1843
€. (MER)–O. (ASH) Mar.


Last: Triarthrus spp. listed by Ludvigsen and Tuffnell (1983), eastern USA, Scandinavia, SW China. Ludvigsen and Tuffnell cite (1983) a Triarthrus sp. from the Whitby Formation of southern Ontario, Canada, as the last olenid.

Suborder HARPINA Whittington, 1959

F. HARPETIDAE Hawle and Corda, 1847

First: Scotoharpes lauriei Jell and Stait, 1985, Florentine Valley, Tasmania, Australia.


F. HARPIDIDAE Whittington, 1950
€. (MER)–O. (LLN) Mar. (see Fig. 16.3)

First: Harpidoides explicatus Apollonov, Batyrbay Section, Kazakhstan, former USSR.

Last: Harpides atlanticus Billings, Table Head, Newfoundland, Canada (Whittington, 1965).

F. ENTOMASPIDIDAE Ulrich, in Bridge, 1930

First: Entomaspis radiatus Ulrich, in Bridge, 1930, USA.

Last: Hypothetica rawi Ross, 1951, USA.

Order ASAPHIDA Salter, 1864 emend. Fortey, 1991

Superfamily ANOMOCAROIDEA Fortey, 1991

F. ANOMOCARIDAE Poulsen, 1927


Comments: This classification follows that of Fortey and Chatterton (1988) who downgraded the Housiidae to include it within the Pterocephaliidae. The family ranges from the Aphelaspis Zone to the Elvina Zone.


Comments: Conaspis Zone to Ptychaspis–Prosaukia Zone.

Animals: Invertebrates

**Fig. 16.3**

First: *Nomadinis pristinus* Öpik, 1967, Mindyallan, Queensland, Australia.


**Superfamily ASAPHOIDEA** Burmeister, 1843

F. **ASAPHIDAE** Burmeister, 1843

First: *Griphasaphus grifhis* Öpik, 1967, Mindyallan, Queensland, Australia.

Last: *Ectenaspis beckeri* (Slocum), USA. Owen (1986, p. 237) lists four genera from the Hirnantian Stage.

F. **CERATOPYGIDAE** Linnarsson, 1869

C. (STD)–O. (TRE) Mar., includes **MACROPYGIDAE** Kobayashi, 1953

First: *Proceratopyge* spp. (Westergård, 1948), Sweden, Australia.

Last: *Ceratopyge forficula* Sars, *Ceratopyge* Limestone, Scandinavia.

**Superfamily DIKELOCEPHALOIDEA** Miller, 1889

emend. Ludvigsen and Westrop, 1983

F. **DIKELOCEPHALIDAE** Miller, 1889

C. (MER) Mar.
In the Arenig of Argentina.

Recent: Conaspis Zone to Saukia Zone in USA and East Asia.

Comments: Ptychaspis–Prosaukia Zone to Saukia Zone.

F. SAUKIIDAE Ulrich and Resser, 1930
C. (MER) Mar.

Comments: Lower Upper Cambrian in SW China, Ptychaspis–Prosaukia Zone to Saukia Zone in USA.

F. PTYCHASPIDIDAE Raymond, 1924
C. (MER) Mar.

Comments: Conaspis Zone to Saukia Zone in USA and East Asia.

F. EUREKIIDAE Hupé, 1953
C. (MER) Mar.

Comments: Ptychaspis–Prosaukia Zone, and Saukia Zone, USA.

F. LOGANELLIDAE Rasetti, 1959
C. (MER) Mar.

Superfamily REMOPLEURIDOIDEA Hawle and Corda, 1847

F. REMOPLEURIDAE Hawle and Corda, 1847

First: Richardsonella megalops (Billings, 1860), Canada.


F. KAINELLIDAE Ulrich and Resser, 1930

F. OPIPEUTERIDAE Fortey, 1974

First: Opipetre inconnivus Fortey, 1974, Olenidsetta Member, Valhallfonna Formation, Spitsbergen.


F. BOHEMILLIDAE Barrande, 1872

First: Bohemilla (Fennitops) sabulon Fortey and Owens, 1987, Bergama rishtoni Zone, Ponyfenni Formation, upper Arenig, South Wales, UK. An older, upper Tremadoc form is reported by Fortey and Owens (1987, p. 128).

Last: Bohemilla scotica scotica, Mill Formation, Whitehouse Subgroup, Girvan of Pusgillian age (J. K. Ingham, pers. comm.); also recorded from Co. Clare, Republic of Ireland (Whittard, 1952). Bohemilla is present in the Kráľův Dvůr Formation of Czechoslovakia.

F. AURITAMIIDAE Řípík, 1967
C. (MER) Mar.

F. IDAHOIIDAE Lochman, 1956
C. (MER) Mar.

Comments: Elvinia Zone to Saukia Zone, USA.

F. HUNGAIIDAE Raymond, 1924
C. (MER) Mar.

Superfamily CYCLOPYGOIDEA Raymond, 1925

F. CYCLOPYGIDAE Raymond, 1925

First: Prospectatrix genatenta (Stubblefield, 1927), Shumardia pusilla Zone, Shinoten Shales, Shropshire, England, UK.

Last: Cyclopyge, Hirnantian Stage, Pomeroy, North Ireland. Several other genera from Europe, including Ellipsotaphrus, Microparia s.s., M. (Degamella), Psilocella and Symphysops (Marek, 1961; Whittard, 1952), are of Ashgill age.

F. NILEIDAE Angelin, 1854

First: Platypeltoides wimani Troedsson, 1931, ?uppermost Upper Cambrian, Batyrbai Section, Shabakty Formation, Kazakhstan, former USSR.

Last: Elongatinites convexus Ji, Pagoda Formation, China.

F. TAIHUNGSHANIIDAE Sun, 1931


Last: Omeipsis huangi (Sun, 1931), Meitan Formation, China (Kobayashi, 1951, p. 16; Lu, 1975, p. 346) or Taihungshania multisegmentata Sheng, 1958, upper Meitan Formation, China.

Superfamily TRINUCLEIOIDEA Hawle and Corda, 1847

F. TRINUCLEIDAE Hawle and Corda, 1847


Last: Cryptolithus portageensis Lespérance, 1988, Hirnantian, Côte de la Surprise Member, White Head Formation, near Percé, Quebec, Canada. Undetermined trinucleids are also recorded from the Hirnantian of the Anglo-Welsh area (Lespérance, 1988, p. 369).

Intervening: LLN–CRD.

F. OROMETOPIDAE Hupé, 1955

(sensu Fortey and Owens 1991 non Fortey and Shergold 1984; Fortey and Chatterton, 1988)


Intervening: TRE.

F. DIONIDIDAE Gurich, 1908


Intervening: LLN–CRD.

F. RAPHIOPHORIDAE Angelin, 1854

(sensu Fortey, 1975, = Endymionidae Raymond, 1930)

First: Ampyx cf. pater Holm, 1882 of Tjernvik (1956), Megistaspis armata Zone (lower Hunneberg Stage), Sjurberg, Dalarna, Sweden.

Last: Raphiophorus parvulus (Forbes, 1848), Gorstonian
Animals: Invertebrates

First: *Species of Calycinoidia* Lu and Chien, 1978 and *Hermosella* Lu and Chien, 1978 from the Upper Cambrian of Guizhou, China were tentatively assigned to the Alsataspididae by Fortey and Owens (1991, p. 453). Most members of the family are Tremadoc and Arenig in age, including species of *Falanaspis*, *Haplopleura*, *Nambeetella*, and *Seleneceme* from the Anglo-Welsh area, Scandinavia, China, South America, and Australia.

Last: *Seleneceme acuticaudata* (Hicks, 1875), lower LLN, Wales and Welsh borderlands, UK; *Seleneceme* spp., probable lower LLN, Texas and the Appalachians, USA (see Whittard, 1960, pp. 117–18). If *Yumenaspis* Chang and Fan, 1960 is correctly ascribed to the Alsataspididae, the range of the family extends to the Upper Caradoc with *Yumenaspis* sp. of Owen et al. (1986) from the Raheen Formation of Co. Waterford, Republic of Ireland.

Intervening: ARC–ASH, LLY.

**F. ALSATASPIDIDAE** Turner, 1940


First: Species of Calycinoidia Lu and Chien, 1978 and *Hermosella* Lu and Chien, 1978 from the Upper Cambrian of Guizhou, China were tentatively assigned to the Alsataspididae by Fortey and Owens (1991, p. 453). Most members of the family are Tremadoc and Arenig in age, including species of *Falanaspis*, *Haplopleura*, *Nambeetella* and *Seleneceme* from the Anglo-Welsh area, Scandinavia, China, South America, and Australia.

Last: *Seleneceme acuticaudata* (Hicks, 1875), lower LLN, Wales and Welsh borderlands, UK; *Seleneceme* spp., probable lower LLN, Texas and the Appalachians, USA (see Whittard, 1960, pp. 117–18). If *Yumenaspis* Chang and Fan, 1960 is correctly ascribed to the Alsataspididae, the range of the family extends to the Upper Caradoc with *Yumenaspis* sp. of Owen et al. (1986) from the Raheen Formation of Co. Waterford, Republic of Ireland.

Intervening: ARC–ASH, LLY.

**F. LIOSTRACINIDAE** Raymond, 1937

€. (?STD–MER) Mar. (see Fig. 16.4)

**F. RHYSOMETOPIDAE**

**F. MONKASPIDIDAE**

(? = CHELIDONOCEPHALIDAE)

Suborder: UNCERTAIN


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**Fig. 16.4**

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<td>24. Burlingiidae</td>
<td>25. Rasettaspididae</td>
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1. Liostracinidae
2. Ityophoridae
3. Proetidae
4. Phillipsiidae
5. Tropidocoryphidae
6. Aulacopleuridae
7. Brachymetopidae
8. Rorringtoniidae
9. Bathyuridae
10. Lecanopygidia
11. Dimeropygidia
12. Celmidae
13. Glaphuridae
14. Holotrachelidae
15. Telephinidae
16. Catillicephalidae
17. Raymondinidae
18. Avoninidae
19. Pletbopeltidae
20. Batbynotidae
21. Bestjubellidae
22. Burlingiidae
23. Rasettaspididae
24. Catillicephalidae
25. Raymondinidae
Order PROETIDA Fortey and Owens, 1975

Superfamily PROETOIDEA Salter, 1864


Last: Neogriffithides siculus (Gemmellaro, 1892), Sosio, Sicily; Kathkorhosa capitorosa Grant, 1966, upper Guadalupian–Lower Dzhulfian, Middle Beulensis Tourmakeady Limestone, Mayo, Republic of Ireland (Fortey, 1983).

Intervening: Carboniferous–Permian (KAZ)

F. PHILLIPSIIDAE Oehlert, 1886


First: Include Waribole dunnhevidensis (Thomas, 1909), FAM, Launceston district, Cornwall, England, UK; W. beulensis (Richter and Richter, 1926), FAM Rheinisches Schiefergebirge, Germany; W. familiaris (Alberti, 1975), FAM, Morocco. (Cyrtosymbole spp. such as C. escoti (von Koenen, 1886), FAM, southern France and C. (Franconicathole) dillensis (Drevermann, 1901), FAM Rheinisches Schiefergebirge, Germany appear earlier, but may be proetids, not phillipsiids), (Osmolska, 1962).

Last: Include Acropyge weggeni Hahn and Hahn, 1981, uppermost Upper Permian, Iran; Ditomopyge fatmil Hahn and Hahn, 1981, upper Guadalupian–lower Dzhulfian, Middle Productus Limestone, Salt Range, Pakistan, if this is a proetid and not a phillipsiid (Owens, 1983).

Intervening: Westphalian, Art.

F. TROPIDOCORYPHIDAE Pbivy, 1946


Intervening: Silurian–Devonian (FRS).

Superfamily AULACOPLEUROIDEA Angelin, 1854

F. AULACOPLEURIDAE Angelin, 1854


First: Otarion (Aulacopleura) szchuanica Lu, 1975, Panho Formation, Sichuan, China (Thomas and Owens, 1978).

Last: Namurophyge sinica Hahn et al., 1989, Westphalian A, Dala Formation, Guangxi, China (Hahn et al., 1989).

Intervening: ARG–FRS, C. (l.)

F. BRACHYMETOPIDAE Prantl and Pbivy, 1950


Last: Cheirropyge himalayensis Diener, 1897, Chitchuon Limestone, Himalayas, NE India (Owens, 1983).

Intervening: CRD–ASH, WEN, LOK–KAZ.

F. RORRINGTONIIDAE Owens, 1990


Intervening: LLN–ASH, WEN, PRA–EIF.

Superfamily BATHYUROIDEA Walcott, 1886

F. BATHYURIDAE Walcott, 1886


First: Peltantella, Garden City Formation, Utah, USA (Whittington and Ross, in Whittington, 1953), Nevada, USA, and Greenland (Fortey and Peel, 1990).

Last: Bathyurus, Raymondites, eastern USA (Whittington, 1953).

F. LECANOPYGIDAE Lochman, 1953


First: Lecanopyge, Platydiamesus, Resseraspis, especially in eastern USA (Lochman, 1953).

Last: Benthamaspis, western Newfoundland, Canada (Fortey, 1979).

F. DIMEROPYGIDAE Hupé, 1953

O. (?ARG–ASH) Mar.

First: Dimeropygiella spp., Pogonip Group, western USA (Hintze, 1953).

Last: Dimeropyge recorded from the Hirnantian of Mackenzie Mountains, NW Canada (Chatterton and Ludvigsen, 1983; Owen, 1986). Toernquistia nicholsoni Reed, 1896, Keisley Limestone, England, UK; Dimeropyge and Toernquistia nicholsoni, Chair of Kildare Limestone, Republic of Ireland.

F. CELMIDAE Jaanusson, 1956


First and Last: Celma granulatus Angelin, 1854, Lysaker Member (Asaphus Shale), upper ARG (Fennian), Oslo, Norway. The species also occurs in Sweden (Jaanusson, 1956; Bruton, 1983b).

F. GLAPHURIDAE Hupé, 1953


Last: Glaphurella harknessii (Reed, 1896), Keisley Limestone, Westmorland, England, UK; Chair of Kildare Limestone, Republic of Ireland (Dean, 1971, p. 44). Other Ashgill occurrences are known.

F. HOLOTRECHELIDAE Warburg, 1925

O. (ASH) Mar.

First and Last: Holotrehelus is widely distributed in Britain, Scandinavia, eastern USA and the former USSR. H. cf. punctillosus (Törnquist, 1884) is recorded from the lower
Sorbakken Formation, Ringerike, Norway, of Cautleyan age; *Holotrichaeus* is known from the Hirnantian of Siberia (Owen, 1981, 1986; Chugaeva, 1983) and the Kildare Limestone of Eire (Dean, 1971) (middle Cautleyan to Hirnantian; 292 (Owen, 1981, 1986; Chugaeva, 1983) and the Kildare Limestone, Republic of Ireland (Dean, 1971, p. 46) of middle Cautleyan to lower Hirnantian age. *Telephina* spp., Europe.

**POLYPHYLETIC GROUPS IN NEED OF FURTHER ANALYSIS**

**F. CATILLICEPHALIDAE** Raymond, 1938 
* (MER) Mar.

**F. RAYMONDINIDAE** Clark, 1924 
* (MER) Mar.

**F. AVONINIDAE** Lochman, 1936 
* (STD-MER) Mar.

**F. PLETHOPELTIDAE** Raymond, 1925 
* (MER) Mar.

**Order INCERTAE ORDINIS**

**F. BATHYNOTIDAE** Hupé, 1953 
* (CRF-STD) Mar.

**First**: *Bathynotus holopyga* (Hall), Parker Shale (Olenellus Zone), Vermont, USA (Whittington, 1988).

**Last**: *Bathynotinus kielcensis* (Bednarczyk, 1970), lower Middle Cambrian (Paradoxides oelandicus Zone), Holy Cross Mountains, Poland (jakutus kielcensis Bednarczyk is here transferred to *Bathynotinus*).

**Comments**: Of unknown origin (Fortey, 1991); eastern USA, Arctic Eurasia.

**F. BESTJUBELLIDAE** Ivshin, 1983 
* (MER) Mar.

**First and Last**: *Bestjubella munificus* Ivshin, 1983, Kuyandianian Stage, Seletinian Horizon with *Irvingella*, Seleta River Basin District, Kazakhstan, former USSR.

**F. BURLINGIIDEA** Walcott, 1908 
* (STD-MER) Mar.

**First**: *Burlingia laevis* Westergård, 1936, *Paradoxides pinus* Zone, Sweden.

**Last**: *Schmalensea amphionura* Moberg, 1903, *Agnostus pisiformis* Zone, Sweden (Westergård, 1947).

**F. RASSETTASPIDIDAE** Ivshin, 1983 
* (MER) Mar.

**First and Last**: *Rassetaspis francoi* Ivshin, 1983, Kuyandianian Stage, upper Seletinian Horizon, Seleta River Right Bank Basin District, central Kazakhstan, former USSR.

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ARTHROPODA (AGLASPIDIDA, PYCNOGONIDA AND CHELICERATA)

P. A. Selden

Class AGLASPIDIDA Walcott, 1911 (see Fig. 17.1)

Aglaspidida were removed from Chelicerata by Briggs et al. (1979).


Comments: This animal was described in detail by Størmer (1956), in a paper communicated to the Kunglige Svenska Akademien in 1955 but not published until 5 December 1956; meanwhile, Størmer had included the new family, genus and species in the Treatise, published in 1955, so the latter publication included the first description of the new taxa. Bergström (1971) has expressed doubts that this family belongs in the Aglaspidida.


First: Beckwithia typa Resser, 1931, probably upper Weeks Formation, Weeks Canyon, Utah, USA. This form was reviewed by Hesselbo (1989), who removed it from (thereby suppressing) the monotypic family Beckwithiidae.

Last: Aglaspis spinifer Raasch, 1939, A. simplex Raasch, 1939, AglaspeUa granulifera Raasch, 1939, A. eatoni Whitfield, 1880, Glypharthrus thomasi (Walter, 1924), Aglaspoides sculptilis Raasch, 1939, Llarthus instabilis Raasch, 1939, Cyclopites vulgaris (Raasch, 1939), Craspedops modesta Raasch, 1939, Setaspis spinulosa Raasch, 1939, Lodi Shale, St Lawrence Formation, Point Jude, Richland County, Wisconsin, USA.


First: Strabops thacheri Beecher, 1901, Potosi Dolomite, St Lawrence Formation, St François County, Missouri, USA.

Last: Neostrabops martini Caster and Macke, 1952, Maysville Formation, Ohio, USA.

Comment: Bergström (1971) doubted that this family belonged in the Aglaspidida.


First and Last (monotypic family): Sinaglaspis xiashanensis Hong and Niu, 1981, lower Shanxi Formation, Gancaoshan, Xiangning County, Shanxi Province, China.

Class PYCNOGONIDA Latreille, 1810

The classification of Bergström et al. (1980) is used here.

First?: A larval form (D), more comparable with pycnogonids than any other arthropod group, was described by Müller and Walossek (1986) from Upper Cambrian Orsten of Sweden, C. (MNT).

Order PALAEOSISOPODA Bergström et al., 1980


First and Last (monotypic family and order): Palaeoisopus problematicus Broili, 1928, Hunsrückschiefer, Bundenbach, Germany.

Order PALAEOPANTOPODA Broili, 1930


First and Last (monotypic family and order): Palaeopantopus maucheri Broili, 1929, Hunsrückschiefer, Bundenbach, Germany.

Order PANTOPODA Gerstaecker, 1863


First: Palaeothea devonica Bergström et al., 1980, Hunsrückschiefer, Bundenbach, Germany. Extant

Comment: Bergström et al. (1980) declined to place this form in a family; it has incertae sedis status as the only known fossil in the order Pantopoda.

Phylum CHELICERATA Heymons, 1901


First: Sanctacaris uncata Briggs and Collins, 1988, Burgess Shale, British Columbia, Canada. Plesion: plesiomorphic sister taxon to all other Chelicerata.

Comment: The traditional division of the Chelicerata into primarily marine Merostomata and primarily terrestrial Arachnida is untenable. Most authors consider Xiphosura to be a sister group to all other Chelicerata (except Sanctacaris) and not to Eurypterida alone. Many authors place Scorpionida as a sister group to Eurypterida, while others consider Eurypterida to be the sister group of all other chelicerates except Xiphosura and Sanctacaris (i.e. Arachnida). Recently, a novel phylogeny was put forward by Shultz (1990). See Selden (1990) for a discussion.

A particular problem with the terrestrial arachnid groups, such as pseudoscorpions, spiders and mites, is that the majority of fossils are known from Tertiary ambers, the dating of which is insecure. Apart from the difficulty of dating the amber pieces, many specimens which come to be
Fig. 17.1

described have an unspecified provenance, thus rendering their dating by fossils in associated sediments impossible. Dominican amber occurs at numerous sites, spanning an interval of possibly 25–40 Ma BP (Lambert et al., 1985), but probably the majority are at the younger end of that range. There is no consensus regarding the relative ages among Tertiary ambers, and correlation is understandably difficult. For the purposes of this work, Baltic amber is taken to be T. (RUP) in age, and Dominican, Mexican and most other Tertiary ambers with arachnids are placed as T. (CHT) in age.

**Class XIPHOSURA** Latreille, 1802

Recent ideas on the phylogeny and classification of the class Xiphosura were discussed by Selden and Siveter (1987), and their classification is followed here.

**F. EOLIMULIDAE** Bergström, 1968

€. (LEN) Mar.

**First and Last** (monotypic family): *Eolimulus alatus* (Moberg, 1892), Ekerum, Öland, Sweden (Bergström, 1968).

**Comment:** The carapace only is known, so the xiphosuran identity of this animal is uncertain; if confirmed, this would be the oldest known xiphosuran.

**Order** CHASMATASPIDIDA Caster and Brooks, 1956

A large arthropod from the Devonian (GIV/FRS?) of
Vietnam was referred to as Chasmataspididae gen. et sp. indet. by Janvier et al. (1989). Study of the fossil by P. A. Selden (unpublished) suggests that it is a carnososomatid eurypterid.

**F. CHASMATASPIDAE** Caster and Brooks, 1956  
**O. (ARG/LLN1)** Mar.

**First and Last** (monotypic family): *Chasmataspis laurencii* Caster and Brooks, 1956, Douglas Dam, Tennessee, USA.

**F. DIPLOASPIDIDAE** Störmer, 1972  
**D. (EMS)** Mar. ?FW

**First and Last** (monotypic family): *Diploaspis casteri* Störmer, 1972, Alken-an-der-Mosel, Germany.

**F. HETEROASPIDIDAE** Störmer, 1972  
**D. (EMS)** Mar. ?FW

**First and Last** (monotypic family): *Heteroaspis novojilovi* Störmer, 1972, Alken-an-der-Mosel, Germany.

**Order** XIPHOSURIDA Latreille, 1802

**Suborder** SYNZIPHOSURINA Packard, 1886

A possible synziphosurine (unnamed), from the Brandon Bridge Formation, Waukesha County, Wisconsin, S. (TEL), was described briefly by Mikulic et al. (1985).

**F. WEINBERGINIDAE** Richter and Richter, 1929  

**First**: *Legrandella lombardii* Eldredge, 1974, Ruminicorral, Cochabamba Province, Bolivia.

**Last**: *Weinbergina opitzi* Richter and Richter, 1929, Hunsrückschiefer, Bundenbach, Germany.

**F. BUNODIDAE** Packard, 1886  
**S. (GOR–LDF)** Mar.

**First**: *Bunodes lunula* Eichwald, 1854, *Eurypterus* Dolomite, Saaremaa, Estonia, former USSR.


**Suborder** LIMULINA Richter and Richter, 1929

**Infraorder** PSEUDONISCINA Eldredge, 1974

**Superfamily** PSEUDONISCOIDEA Packard, 1886
Intervening: GOR
Intervening: GOR
Infraorder LIMULICINA Richter and Richter, 1929
Superfamily BELLINUROIDEA Zittel and Eastman, 1913
Most authors (e.g. Eldredge, 1974; Fisher, 1982; Raymond, 1944, Selden and Siveter, 1987) agree that this group is the paraphyletic stem group which gave rise to the Euproopoidea and the Limuloidea. Eldredge (1974) put the ‘primitive’ bellinuroids (e.g. Bellinuroopsis rossicus Chernyshev, 1933, Bellinurus bellulus König, 1851) in an unnamed family within the Pseudoniscoidea, but later work, shown in the phylogenetic diagrams of Fisher (1982, fig. 1; 1984, fig. 2) and Selden and Siveter (1987, fig. 2) depict their relationships more clearly.
Intervening (species not included in families below): D. (??FRS, Bellinuroopsis rossicus Chernyshev, 1933, top horizons of Devonian section, right bank of River Don, near Lebedian, former USSR ?FAM, ‘Paleolimulus?’ randalli (Beecher, 1902), Chemung Sandstone, Pennsylvania, USA.

F. ELLERIIDAE Raymond, 1944
D. (??FAM) Mar. /FW
First and Last (monotypic family): Elleria morani (Eller, 1938), Salamanca Sandstone, North Warren, Pennsylvania, USA.
Comment: Elleriidae was placed in Bellinuroidea by Bergström (1975) and Fisher (1982), but Siveter and Selden (1987) considered this placement unsupportable on the basis of the morphological evidence.

F. BELLINUROIDEA Zittel and Eastman, 1913 D. (??GIV) – C. (KSK) Mar./FW
First: Bellinurus carteri Eller, 1940, lower Cattaraugus Beds, Bradford, Pennsylvania, USA.
Last: Bellinurus trechmanni Zittel and Eastman, 1913 D. (?FRS) Mar. – ?FW
First and Last: Fric, 1899, Nyrany, Czechoslovakia.
Superfamily LIMULOIDEA Zittel, 1885
F. ROLFEIIDAE Selden and Siveter, 1987
C. (IVO) Mar.
First and Last (monotypic family): Rolfeia fouldeni Waterston, 1985, Poulen, Berwickshire, Scotland, UK.
F. MORAVURIDAE Pribyl, 1967
C. (PND) Mar.

F. PALEOLIMULIDAE Raymond, 1944
C. (ALP) – J. (HET) Mar. /FW
First: Paleolimulus? longispinus Schram, 1979, Bear Gulch Limestone, Fergus County, Montana, USA.
Last: Limulitella cf. bronni Schimper, 1850, Helmstedt, Germany.
Intervening: KRE – NOG, MYA, ASS, SAK, ART, GRI, SPA, ANS, NOR, RHT.
F. AUSTROLIMULIDAE Riek, 1968
Tr. (LAD) FW
First and Last (monotypic family): Austrolimulus fletcheri Riek, 1955, Hawkesbury Sandstone, Brookvale, New South Wales, Australia.
F. HETEROLIMULIDAE Via Boada and Villalta, 1966
Tr. (LAD) Mar.
First and Last (monotypic family): Heterolimulus gesae Via Boada and Villalta, 1966, Canteras de Monral-Alcover, Tarragona Province, Spain.

F. LIMULIDAE Zittel, 1885
Tr. (SPA) – Rec. Mar./FW
First: Psammolimulus gottinensis Lange, 1922, Göttingen, Germany.
Intervening: LAD, HET – TOA, OXF/KIM, TTH, APT, CEN, CMP, MAA, BUR.

Class EURYPTERIDA Burmeister, 1843
The classification of Tollerton (1989) is used here. A number of genera were excluded from the Order Eurypterida by Tollerton, but their removal has no overall effect on the ranges given below. Tollerton (1989) also excluded the hibbertopteroids, which had been returned to the Order Eurypterida by Waterston et al. (1985); here, they are included in the Order Cyrtoctenida, a taxon originally proposed by Stürmer and Waterston (1968) for these unusual forms. Eurypterids occur mainly in marginal marine facies, lacking good marine, stratigraphically useful, fossils; therefore, the dating of many of the horizons is under constant review.

Order EURYPTERIDA Burmeister, 1843
Suborder EURYPTERINA Burmeister, 1843
Superfamily SLIMONIOIDEA Novojilov, 1962
F. SLIMONIIDAE Novojilov, 1962
S. (TEL ~ PRD) Mar. /FW
First: Slimonia dubia Laurie, 1899, Reservoir Formation, microconodonts.
Gutterford Burn, Pentland Hills, Scotland, UK; *Slimonia acuminata* (Salter, 1856), Patrick Burn and Kip Burn Formations, Lesmahagow, Scotland, UK.

**Last:** *Salteropterus abbreviatus* (Kjellesvig-Waering, 1951), Temeside Shale Formation, Perton, Herefordshire, England, UK.

**Intervening:** LDF

**Comment:** A probable carcinosomatid, referred to under *Simpsonopterus?* (Clarke, 1907), Tuscarora Formation, Dickinson County, Kansas, and Red Rock, Oklahoma, USA.

**Superfamily HUGHMILLERIOIDEA**

*Kjellesvig-Waering, 1951*

**F. HUGHMILLERIIDAE** Kjellesvig-Waering, 1951


**First:** *Waeringopterus? prisca* (Ruedemann, 1942) Deepkill Formation, Mt. Merino, Hudson, New York, USA.

**Last:** *Grossopterus? inexpectans* (Ruedemann, 1919), Oneonta Formation, Gilboa, New York, USA.

**Intervening:** COS—ONN, GED, SIG.

**F. CARCINOSOMATIDAE** Størmer, 1934

O. (ARG)—D. (EMS, possibly GIV/FRS?) Mar.

**First:** *Eocarcinosoma ruedemannii* (Flower, 1945), Deepkill Formation, Rensselaer County, New York, USA.

**Last:** *Carcinosoma* sp., Alken-an-der-Mosel, Germany (Størmer, 1974).

**Intervening:** COS—ONN, HIR, RUH—GLE, FRO, TEL, SHE, GLE, GOR, LDF, PRD, GED.

**Comment:** A probable carcosomatid, referred to under *Chasmataspidida* above, was reported by Janvier et al. (1989) from the Grey Devonian of Do Son, Hai'phong, Vietnam, which these authors considered may be D. (GIV/FRS).

**F. ADELOPHTHALMIDAE** Tollerton, 1989

S. (RHU/FRO)—P. (ART) Mar./FW

**First:** *Parahughmilleria maria* (Clarke, 1907), Tuscarora Formation, Swatara Gap, Pennsylvania, USA.

**Last:** *Adelophilthmus sellardsi* (Dunbar, 1924) Wellington Formation, Dickinson County, Kansas, and Red Rock, Oklahoma, USA.

**Intervening:** TEL, SHE, LDF, PRD, LOK, PRA, EMS, FAM, HLK, MRD, CHE, MEL, VRK, KSX, POD, MYA, NOG, ASS, SAK.

**Superfamily MIXOPTEROIDEA** Caster and Kjellesvig-Waering, 1955

**F. MIXOPTERIDAE** Caster and Kjellesvig-Waering, 1955


**First:** *Mixopterus?* sp., Lower Sintan Formation, Hsin Tan, Hubei, China (Chang, 1957).

**Last:** *Mixopterus multispinosus* (Clarke and Ruedemann, 1912), Vernon Shales, New York, USA; *M. kiaeri* Størmer, 1934, Sundvølle Formation, Ringereike, Norway; *M. sp.*, Perton, Herefordshire, England, UK (Kjellesvig-Waering, 1951).

**Intervening:** LDF.

**F. LANARKOPTERIDAE** Tollerton, 1989

S. (GLE/GOR) Mar.

**First and Last** (monotypic family): *Lanarkopterus dolichoschelus* Ritchie, 1968, Fish Beds of Hagshaw Hills and Lesmahagow, Scotland, UK.

**Superfamily MEGALOGRAPTOIDEA** Caster and Kjellesvig-Waering, 1955

**F. MEGALOGRAPTIDAE** Caster and Kjellesvig-Waering, 1955


**First:** *Echinognathus clevelandi* Walcott, 1882, Utica Shales, Oneida County, New York, USA; *Megalograptus alveolatus* Caster and Kjellesvig-Waering, 1964, Martinsburg Formation, Walker Mountain, Virginia, USA.

**Last:** *Megalograptus ohioensis* Caster and Kjellesvig-Waering, 1964, Elkhorn Formation, Manchester, Ohio, USA.

**Intervening:** CAU, RAW.

**Superfamily EURYPTEROIDEA** Burmeister, 1843

**F. EURYPTERIDAE** Burmeister, 1843

O. (LLO)—D. (FRS) Mar./FW

**First:** *Eurypterus? decipiens* Ruedemann, 1942, Normanskill Grit, Albany County, New York, USA.

**Last:** *Eurypterus?* sp. Bergisch Gladbach, Germany (Jux, 1967).

**Intervening:** COS—ONN, TEL, SHE, WHI, GLE, GOR, LDF, PRD, LOK, EMS.

**F. DOLICHOPTERIDAE** Kjellesvig-Waering and Størmer, 1952


**First:** *Dolichopterus antiquus* Ruedemann, 1942, Deepkill Formation, Merino, Hudson, New York, USA.

**Last:** *Strobilopterus princetonii* Ruedemann, 1935, Beartooth Butte, Wyoming, USA.

**Intervening:** COS—ONN, FRO—LDF, SHE, GOR, PRD, LOK.

**F. ERIEOPTERIDAE** Tollerton, 1989

O. (LLO)—D. (SIG) Mar./FW

**First:** *Erieopterus chadwicki* Clarke and Ruedemann, 1912, Normanskill Slate, Catskill, New York, USA.

**Last:** *Erieopterus statzii* Størmer, 1936, upper Siegener Sandstone, Wahnbachtal, Siegburg, Germany; *Erieopterus latus* Ruedemann, 1935, Beartooth Butte, Wyoming, USA.

**Intervening:** MRB, RUH, GOR, PRD, LOK.

**Superfamily STYLONUROIDEA** Diener, 1924

(=DREPANOPTEROIDEA Kjellesvig-Waering, 1966)

**F. STYLONURIDAE** Diener, 1924

O. (LLO)—D. (FAM) Mar./?FW

**First:** *Stylonurella? modestus* (Clarke and Ruedemann, 1912), Normanskill Slate, Catskill, New York, USA.


**Intervening:** TEL, SHE, WHI, GLE, GOR, LDF, LOK, EMS, ?EIF.

**F. DREPANOPTERIDAE** Kjellesvig-Waering, 1966

O. (COS/ONN)—D. (FAM) Mar./?FW

**First:** *Drepopterus? ruedemannii* (O'Connell, 1916), Schenectady Formation, Schenectady, New York, USA.

**Last:** *Drepopterus abonensis* Simpson, 1951, Portishead, Somerset, England, UK.
Intervening: TEL, PRD, GED, EMS.

F. PARASTYLONURIDAE Waterston, 1979
O. (HAR)–D. (?FAM) Mar./?FW
First: Brachyopterus stubblefieldi Størmer, 1951, Bausley House Shales, Abberley, Montgomeryshire, Wales, UK.
Intervening: COS–ONN, TEL, GOR, LDF, PRD.

F. LAURIEOPTERIDAE Kjeslevig-Waering, 1966
First: Laurieopterus e/egans (Laurie, 1899), Reservoir Formation, Gutterford Burn, Pentland Hills, Scotland, UK.
Last: Mazonipterus cyclophthalmus Kjeslevig-Waering, 1963, Francis Creek Shale, Mazon Creek, Illinois, USA.
Intervening: FRO–LDF, GED, LOK/PRA, FRS, FRS/FAM.

Superfamily KOKOMOPTEROIDEA Kjeslevig-Waering, 1966
F. KOKOMOPTERIDAE Kjeslevig-Waering, 1966
First: Lamontopterus knoxae (La mont, 1955), Reservoir Formation, Gutterford Burn, Pentland Hills, Scotland, UK.
Last: Kokomopterus longicaudatus (Clarke and Ruedemann, 1912), Kokomo Formation, Kokomo, Indiana, USA.

F. HARDIEOPTERIDAE Tollerton, 1989
First: Hardieopterus myops (Clarke, 1907), Tuscarora Formation, Swatara Gap, Pennsylvania; Shawangunk Formation, Delaware Water Gap, Pennsylvania, USA.
Last: Hardieopterus megalops (Salter, 1859), Downton Castle Sandstone Formation, Ludlow, Shropshire, England, UK.
Intervening: RHU–GLE, TEL, FRO–LDF.

Superfamily BRACHYOPTERELLOIDEA Tollerton, 1989
F. BRACHYOPTERELLIDAE Tollerton, 1989
First: Brachyopterella? magna (Clarke and Ruedemann, 1912), Schenectady Formation, Schenectady, New York, USA.
Last: Brachyoptere/la pentagonalis (Stommer, 1934), Sundvoll Formation, Ringerike, Norway.
Intervening: GOR.

Superfamily RHENOPTEROIDEA Størmer, 1951
F. RHENOPTERIDAE Størmer, 1951
D. (SIG–FRS) Mar./FW
First: Rhenopterus tuberculatus Størmer, 1936, Overath, Eifel, Germany.
Last: Rhenopterus? sp., Gogo Formation, Kimberley, Australia (Rolfe, 1966).
Intervening: EMS, GIV.

Superfamily MYCTEROPOIDEA Cope, 1886
F. MYCTEROPIDAE Cope, 1886
C. (PND–MYA) FW
Last: Mycterops fragments, Francis Creek Shale, Mazon Creek, Illinois, USA (Kjeslevig-Waering, 1963).
Intervening: MEL.

F. WOODWARDOPTERIDAE Kjeslevig-Waering, 1959
D. (FAM)/C. (HAS)–C. (MEL/ MYA) FW
First: Woodwardopterus sabrosus (Woodward, 1887), Kiltoran, Republic of Ireland.
Last: Vernonopterus minutiscapus (Peach, 1907), Coal Measures of Airdrie, Scotland, UK.

Suborder PTERYGOTINA Caster and Kjeslevig-Waering, 1964

Superfamily PTERYGOTOIDEA Clarke and Ruedemann, 1912
F. PTERYGOTIDAE Clarke and Ruedemann, 1912
First: Pterygotus? deepkillensis Ruedemann, 1934, Deepkill Formation, Deepkill, New York, USA.
Last: Pterygotus (Pterygotus) montanensis Ruedemann, 1935b, Three Forks Shale, Montana, USA.

F. JAEKELOPTERIDAE Størmer, 1974
First: JaekeLOPTERUS rhenaniae (Jaekel, 1914), Overath, Eifel, Germany.
Last: JaekeLOPTERUS rhenaniae (Jaekel, 1914), Alken-an-der-Mosel, Germany.

Order CYRTOCTENIDA Størmer and Waterston, 1968
Although highly specialized forms, cyrtoctenids may be derived from primitive eurypterids (Waterston et al., 1985).

Superfamily HIBBERTOPTEROIDEA Kjeslevig-Waering, 1959
F. HIBBERTOPTERIDAE Kjeslevig-Waering, 1959
D. (FAM)–P. (?KAZ) Mar./FW
First: Hibbertopterus? sewardi (Strand, 1928), Wagon Drift Formation, Witteberg Group, Grahamstown, South Africa.
Last: Campylocephalus oculatus (Kutorga, 1838), Copper-bearing Sandstones, Dourassoff, Urals, former USSR; Hibbertopterus permianus Ponomarenko, 1985, Intinskaya Suite, Inta, Komi, former USSR.
Intervening: FAM/HAS, ASB, BRI, PND–MEL, ARN, MEL, UFI–TAT.

F. CYRTOCTENIDAE Waterston et al., 1985
D. (FAM)–P. (?KAZ) Mar./FW
First: Dunsopterus? wrightianus (Dawson, 1881), Portage Sandstone, Italy, Yates County, New York, USA.
Last: Hastimima whitei White, 1908, Rio Bonito Formation, Minas, Santa Catarina, Brazil, and Tatui Formation, Sao Paolo, Brazil.
Intervening: FAM, IVO, HLK, ASB, BRI, ARN.

Class SCORPIONIDA Latreille, 1810
A major new classification of Scorpionida was proposed by Kjeslevig–Waering (1986), but this posthumous publica-
A number of fossil scorpions cannot be assigned to categories of lower rank within the Scorpionida, and most of these were listed as Scorpionida incertae sedis by Stockwell (1989). In addition, Hubescorpius gracilitarsis Walssek et al., 1990, from the Devonian of China is added to the list, and Tiphoscorpius hueberi Kjeslevig-Waering, 1986 is removed from Scorpionida (Selden and Shear, 1992). They range through the following stages: S. (PRD), D. (FRS), C. (HLK, York, USA.)

**Intervening**

* EMS.

---

**Order** PROTOSCORPIONES Petrunkevich, 1949

_S. (TEL)- D. (PRA)

First: Dolichophonus loudenensis (Laurie, 1899), Reservoir Formation, Gutterford Burn, Pentland Hills, Scotland, UK.

Last: Palaeoscorpius devonicus Lehmann, 1944, Hunsrückschiefer, Bundenbach, Germany.

**Intervening**

* SHE, GOR/LDF.

---

**Order** PALAEOSCORPIONES Stockwell, 1989

**Superfamily** PROSCORPIOIDEA Scudder, 1885

_S. (PRD) - C. (ALP/CHE)


Last: Labiriscorpius alliedensis Leary, 1980, Milan, Illinois, USA.

**Intervening**

* EMS.

---

**Superfamily** ARCHAEOSTERONIOIDEA


First and Last: Archaeoctonus glaber (Peach, 1883), Pseudochaeroctonus denticulatus (Kjeslevig-Waering, 1986), Loboarchaeoctonus squamosus (Kjesllevig-Waering, 1986), Glencartholm Volcanic Beds, Langholm, Scotland, UK.

**Order** SCORPIONES Hemprich and Ehrenberg, 1829

_Praearcturus_ D. (PRA) Terr.

First: Praearcturus gigas Woodward, 1871, Rowlestone, Herefordshire, England, UK (placed as Scorpiones incertae sedis by Stockwell (1989)).

**Intervening**

* many fossil scorpions cannot be assigned to categories of lower rank within the Scorpiones, and were listed as Scorpionida incertae sedis by Stockwell (1989). They range through the following stages: PRA, HLK, BRI, ALP, CHE, KSK, MEL, MYA, KLA, ANS, TOA.

**Suborder** MESOSCORPIONINA Stockwell, 1989

_C. (HLK) - J. (MET/TOA) Terr.


Last: Mesophonus maculatus Brauer et al., 1889, Ust-Balei, Irkutsk, Siberia, former USSR.

**Intervening**

* CHE, MEL, VRK, KSK, MYA, KLA, ANS.

**Suborder** NEOSCORPIONINA Thorell and Lindström, 1885

**Infraorder** PALEOSTERNI Stockwell, 1989

_C. (MEL - DOR) Terr.

First: Allolobuthiscorpius major (Wills, 1960), Killburn Coal, Trowell Colliery, Nottinghamshire, England, UK.


**Intervening**

* VRK, KSK.

---

**Infraorder** ORTHOSTERNI Pocock, 1911

(see Fig. 17.2) _C. (MEL) - Rec. Terr.

First: Compsoscorpius elegans Petrunkevich, 1949, Coseley, Staffordshire, England, UK. _Extant_

**Intervening**

* MYA, and others assigned to families below.

**Superfamily** BUTHOIDEA Simon, 1880

_F. BUTHIDAE Simon, 1880  Terr.

First: Araripescorpio ligabuei Campos, 1986, Santana Formation K. (APT), Chapado de Araripe, Brazil.

F. SCORPIONIDAE Peters, 1861

_T. (RUP) - Rec. Terr.

First: Tytius eogenus Menge, 1854, Baltic amber. _Extant_

**Intervening**

* CHT.

**Superfamily** SCORPIONOIDEA Peters, 1861

_Araripescorpio

First: Araripescorpio ligabuei Campos, 1986, Santana Formation K. (APT), Chapado de Araripe, Brazil.

_F. CHTHONIIDAE Hansen, 1894  Terr.

First: Chthonius mengei Beier, 1937, Baltic amber. _Extant_

**Intervening**

* CHT.

**Class** PSEUDOSCORPIONES Latreille, 1817

**Intervening**

* undescribed pseudoscorpions were reported from Lebanese amber, K. (BER - APT), by Whalley (1980).

_F. DITHIDAE Chamberlin, 1931  Terr.

First: Dracochela deprehendor Schawaller, 1991 (protonymph and tritonymph), Gilboa Mudstones, New York, USA (Shear et al., 1989; Schawaller et al., 1991).

Comment: Only protonymph and tritonymph are known, which, although modern in many aspects, cannot be assigned with confidence to extant taxa because both diagnostic characters in the fossils and cladistic assessment of extant forms are lacking (Shear et al., 1989; Schawaller et al., 1991).

**Suborder** CHTHONIINA Beier, 1932

**Superfamily** CHTHONIOIDEA Beier, 1932

_F. CHTHONIIDAE Hansen, 1894  Terr.

First: Chthonius mengei Beier, 1937, Baltic amber. _Extant_

**Intervening**

* CHT.


First: Chelignathus kochii (Menge, 1854), Baltic amber. _Extant_
**Suborder** NEOBISIINA Beier, 1932

**Superfamily** NEOBISIOIDEA Beier, 1932


*First:* Neobisium rathkii (Koch and Berendt, 1854), *N. extinctum* Beier, 1937, *Roncus succineus* Beier, 1955, Baltic amber. *Extant*

*Intervening:* CHT, AQT.

**Superfamily** GARYPOIDEA Beier, 1932


**Superfamily** FEAELOIDEA Beier, 1932


*First:* Pseudogarypus hemprichii Beier, 1937, *P. extensus* Beier, 1937, Baltic amber. *Extant*
Suborder **CHELIFERIINA** Hagen, 1879

Superfamily **CHEIRIDIOIDEA** Chamberlin, 1931

F. **CHEIRIDIIDAE** Chamberlin, 1924  
T. (RUP)–Rec.  Terr.  
**First:** *Progonatemnus succineus* Beier, 1955, Baltic amber.  
**Extant**

Intervening:  CHT.

Superfamily **CHELIFEROIDEA** Chamberlin, 1931

F. **CHERNETIDAE** Menge, 1854b  
K. (CMP)–Rec.  Terr.  
**First:** Unnamed deutonymph, Manitoban amber, Canada (Schawaller, 1991).  
**Extant**

Intervening:  RUP, CHT.

F. **ATEMNIDAE** Chamberlin, 1931  
T. (RUP)–Rec.  Terr.  
**First:** *Progonatemnus succineus* Beier, 1955, Baltic amber.  
**Extant**

Intervening:  RUP, CHT.

Class **SOLIFUGAE** Sundevall, 1833

C. (MYA)–Rec.  Terr.  
**First:** *Protosolpuga carbonaria* Petrunkevitch, 1949, Francis Creek Shale, Mazon Creek, Illinois, USA.  
**Extant**

Intervening:  CHT.

Class **OPILIONES** Sundevall, 1833

**First:** *Protosolpuga carbonaria* Petrunkevitch, 1949, Francis Creek Shale, Mazon Creek, Illinois, USA.  
**Extant**

Intervening:  CHT.
First: Unnamed specimen, East Kirkton Limestone, near Bathgate, Scotland, UK (Wood et al., 1985).

Intervening: Unnamed opilionid Koonwarra Fossil Bed, Lower Gippsland, Victoria, Australia (BRM/APT) (Jell and Duncan, 1986).

**F. KUSTARACHNIDAE** Petrunkevitch, 1913
C. (MYA) Terr.

**First and Last** (monotypic family): *Kustarachne tenuipes* Scudder, 1890, *K. conica* Petrunkevitch, 1913, *K. extincta* (Melander, 1903), Francis Creek Shale, Mazon Creek, Illinois, USA.

**Comment:** The order Kustarachnida was erected by Petrunkevitch (1913) for *Kustarachne*. The specimens have been reassessed by Beall (1986) who considered them to belong to Opiliones, an assignment with which other arachnologists who have seen the specimens (P. A. Selden, W. A. Shear) concur.

**Suborder** PALPATORES Thorell, 1876

**Superfamily** TROGULOIDEA Sundevall, 1833

**F. EOTROGULIDAE** Petrunkevitch, 1955
C. (KLA/NOG) Terr.

**First and Last** (monotypic family): *Eotrogulus fayoli* Thévenin, 1901, Commentry, France.

**F. NEMASTOMATIDAE** Simon, 1879
T. (RUP)–Rec. Terr.

**First:** *Nemastoma denticulatum* Koch and Berendt, 1854, *N. tuberculosis* Koch and Berendt, 1854, *N. claiverum* Menge, 1854, *N. succinctum* Röwer, 1939, Baltic amber. Extant

**F. NEMASTOMOIDIDAE** Petrunkevitch, 1955
C. (MYA)–(KLA/NOG) Terr.

**First:** *Nemastomoides longipes* (Petrunkevitch, 1913) and *N. depressus* (Petrunkevitch, 1913), Francis Creek Shale, Mazon Creek, Illinois, USA.

**Last:** *Nemastomoides elaveris* Thévenin, 1901, Commentry, France.

**F. ISCHYROPSALIDAE** Simon, 1879
T. (RUP)–Rec. Terr.

**First:** *Sabacon bachofeni* Röwer, 1939, Baltic amber. Extant

**Superfamily** PHALANGIOIDEA Thorell, 1876

**F. PHALANGIIDAE** Thorell, 1876
T. (RUP)–Rec. Terr.

**First:** *Caddo dentipalpus* (Koch and Berendt, 1854), *Cheiromachus coriaceus* Menge, 1854, *Dicanthropalus ramiger* (Koch and Berendt, 1854). D. coriniger Menge, 1854, *D. palmonckens Röwer, 1939, Lioebunum sarapum* Menge, 1854, L. inclusum Röwer, 1939, *Opilio ovalis* Koch and Berendt, 1854, Baltic amber. Extant

**Intervening:** CHT.

**Suborder** LANIATORES Thorell, 1876

**F. GONYLEPTIDAE** Sundevall, 1833
T. (RUP)–Rec. Terr.

**First:** *Gonyleptes nemastomoides* Koch and Berendt, 1854, Baltic amber. Extant

**Class** PHALANGIOTARBITA Petrunkevitch, 1949

Kjellesvig-Waering left a posthumous monograph on this group in which he drastically reduced in number the genera and species erected by Petrunkevitch (1913–1949). This work was being readied for publication but has yet to appear in print. Thus, the classification used is that of Petrunkevitch (1955).

**F. ARCHITARBITA** Karsch 1882
C. (MEL–MYA) Terr.


**Last:** *Orthotarbus myranensis* Petrunkevitch, 1953, Nýřany, Czechoslovakia. *Gerotarbus bohemicus* Petrunkevitch, 1953 may also come from this horizon in the Coal Measures of Nýřany.

**Intervening:** VRK.

**F. OPILIOTARBITA** Petrunkevitch, 1945
C. (MYA) Terr.

**First and Last** (monotypic family): *Opiliotarbus elongatus* (Scudder, 1890), Francis Creek Shale, Mazon Creek, Illinois, USA.

**Comment:** Petrunkevitch (1953) considered that *Opiliotarbus kliveri* Waterlot, 1934, C. (KSK/POD), did not belong in this family.

**F. HETEROTARBITA** Petrunkevitch, 1913
C. (MYA) Terr.

**First and Last** (monotypic family): *Heterotarbus ovatus* Petrunkevitch, 1913, Francis Creek Shale, Mazon Creek, Illinois, USA.

**Class** RICINULEI Thorell, 1892

**Suborder** NEORICINULEI Selden, 1992

**Comment:** No fossil record. Extant

**Suborder** PALAEORICINULEI Selden, 1992

**F. CURCULIOIDIDAE** Cockerell, 1916
C. (MRD–MYA) Terr.

**First:** *Curculioidea adompha* Brauckmann, 1987, Hagen-Vorballe, Ruhr, Germany.

**Last:** *Curculioidea scaber* (Scudder, 1890), *Amarixys sulcata* (Melander, 1903), A. gracilis (Petrunkevitch, 1945a). Francis Creek Shale, Mazon Creek, Illinois, USA.

**Intervening:** MEL.

**F. POLIOCHERIDAE** Scudder, 1884
C. (MEL–MYA) Terr.

**First:** *Terpsicerotus alticeps* (Pocock, 1911), Coseley, Dudley, England, UK.

**Last:** *Podochera punctulata* Scudder, 1884, *P. glabra* Petrunkevitch, 1913, Francis Creek Shale, Mazon Creek, Illinois, USA.
Class ACARI Latreille, 1802

A review of the classification of the mites in relation to the fossil record was given by Bernini (1986). Acari are divided fundamentally into two major divisions: Actinotrichida and Anactinotrichida, which some authors (e.g. van der Hammen, 1989) considered to be separate arachnid lineages whose common features (small size, modes of life) are due to convergence. For convenience, they are treated as a whole here: the classification of Lindquist (1984) is followed, with the alternative names used by van der Hammen and others in parentheses.

Intervening: Undescribed mites were reported from Lebanese amber, K. (BER–APT), by Whalley (1980).

Order ACTINOTRICHIDA Oudemans, 1931 (ACARIFORMES Zachvatkin, 1952)

Suborder ACTINEDIDIDA van der Hammen, 1968 (PROSTIGMATA Kramer, 1877)

F. NANORCHESTIDAE Grandjean, 1937

First: Protospeleorchestes pseudoprotacarus Dubinin, 1962, Rhynie Chert, Aberdeenshire, Scotland, UK. Extant

F. PACHYGNATHIDAE Kramer, 1877


Comment: These mites were scattered across three families by Dubinin (1962), but Kethley (in Kethley et al., 1989 and Norton et al., 1989) suggested the need for restudy of this material, and considered them all to belong in the Pachygnathidae.

F. ALICORHAGIIDAE Grandjean, 1939

First: Archaeacarus dubinini Kethley and Norton, 1989, Gilboa mudstones, Gilboa, New York, USA. Extant

F. TYDEIDAE Kramer, 1877

First: Possible tydeid larva, amber of Taimyr Peninsula, former USSR (Bulanova-Zakhvatkina, 1974). Extant

F. BDELLIDAE Dugès, 1834

First: Bdella vetusta Ewing, 1937, Manitoban amber, Canada. Extant

Intervening: RUP.

F. ERYTHRÆIDAE Oudemans, 1902

First: Erythraeus foveolatus Koch and Berendt, 1854, E. longipes Koch and Berendt, 1854, E. illustris Koch and Berendt, 1854, E. incertus Koch and Berendt, 1854, E. hirsutissimus Koch and Berendt, 1854, E. raripilus Koch and Berendt, 1854, E. lagopus Koch and Berendt, 1854, E. pravus Koch and Berendt, 1854, Arthysena troguloides Menge, 1854, Baltic amber. Extant

F. TROMBIDIIDAE Leach, 1815

First: Trombidium clavipes Koch and Berendt, 1854. T. serratum Koch and Berendt, 1854, T. scrobiculatum Menge, 1854, T. heterotrichum Menge, 1854, T. crassipes Menge, 1854, T. granulatum Menge, 1854, Baltic amber. Extant

F. ANYSTIDAE Oudemans, 1902

First: Anystis venustula Koch and Berendt, 1854, Baltic amber. Extant

F. CHEYLETIDAE Leach, 1815

First: Cheyletus burmiticus (Cockerell, 1917), Burmese amber. Extant

F. TETRANYCHIDAE Donnadieu, 1875

First: Tetranychus gibbus Koch and Berendt, 1854, Baltic amber. Extant

F. ERIOPHYIDAE Nalepa, 1898

First: Eriophyes daphnogene Ambrus and Hably, 1979, Hungary. Extant

Suborder ACARIDIDA Latreille, 1802 (ASTIGMATA Canestrini, 1891)

F. ACARIDAE Ewing and Nesbitt, 1942

First: Acarus rhombeus Koch and Berendt, 1854, Baltic amber. Extant

Intervening: CHT, TOR.

F. LISTROPHORIDAE Canestrini, 1892

First: unnamed listrophorid, Dominican amber (Poinar, 1988). Extant

Suborder ORIBATIDA Michael, 1884 (CRYPTOSTIGMATA Canestrini, 1891)

The vast majority of known fossil mites belong to this suborder. These animals are characterized by a hard cuticle which allows their preservation, often in large numbers, in certain sedimentary environments. Many are known from Quaternary deposits (especially freshwater forms), but for the most part these have not been included here; the families to which they belong generally have a pre-Quaternary history.

Division ENARTHRONOTA Grandjean, 1947

F. DEVONACARIDAE Norton, 1988

First and Last (monotypic family): Devonacarus sellnicki Norton, 1988, Gilboa mudstones, New York, USA.

F. PROTOCHTHONIIDAE Norton, 1988

First and Last (monotypic family): Protochthonius gigantus Norton, 1988, Gilboa mudstones, New York, USA.

Division MIXONOMATA Grandjean, 1969

Superfamily PHTHIRACAROIDEA Perty, 1841

F. PHTHIRACARIDAE Perty, 1841

First: (RUP)–Rec. Terr.
First: Hoplodera multipunctatum Sellnick, 1918, Baltic amber.

Superfamily EUPHTHIRACAROIDEA Jacot, 1930

F. ORIBOTRITIIDAE Grandjean, 1954
T. (RUP)—Rec. Terr.

First: Oribotritia translucida Sellnick, 1931, O. pyropus (Sellnick, 1918), Baltic amber. Extant

Division DESMONOMATA Woolley, 1973

Superfamily CROTOARIOIDEA Thorell, 1876

F. NOTHRIDAE Berlese, 1896
T. (RUP)—Rec. Terr.

First: Nothrus illautus Sellnick, 1918, Baltic amber. Extant

F. CAMISIIDAE Oudemans, 1900
K. (CON/SAN)—Rec. Terr.

First: Eocamisia sukatshevae Bulanova-Zakhvatkina, 1974, amber of Taimyr Peninsula, former USSR. Extant

Intervening: RUP, PLE/HOL.

Superfamily HERMANNIOIDEA Sellnick, 1928

F. HERMANNIIDAE Sellnick, 1928
Q. (PLE)—Rec. Terr.

First: Hermanniella gigantea Sitnikova, 1975, Anabar River, Siberia, former USSR. Extant

Intervening: RUP, PLE/HOL.

Division BRACHYPYLINA Hull, 1918

Superfamily HERMANNIELLOIDEA Grandjean, 1934

F. HERMANNIELLIDAЕ Grandjean, 1934
T. (RUP)—Rec. Terr.

First: Hermanniella concamerata Sellnick, 1931, H. tuberculata Sellnick, 1918, Baltic amber. Extant

Superfamily LIOODOIDEA Grandjean, 1934

F. LIOIDÆ Grandjean, 1934
T. (RUP)—Rec. Terr.

First: Lioedes quadriscutatus Sellnick, 1918, Platyliodes ensigerus (Sellnick, 1918), Embolocarus pergrratus Sellnick, 1918, Baltic amber. Extant

Superfamily PLATEREMAEIDEOIDEA Trägårdh, 1931

F. GYMNODAMAEIDE Grandjean, 1954

First: Unnamed gymnodamaeid, Canadian amber (McAlpine and Martin, 1963). Extant

Intervening: RUP.

F. PLATEREMAEIDEOIDEA Trägårdh, 1931
K. (CON/SAN)—Rec. Terr.

First: Rasnitsynella punctulata Bulanova-Zachvatina, 1974, Taimyr Peninsula, former USSR. Extant

First: Damaeus? genadensis Sellnick, 1931, Baltic amber. Extant

Intervening: CHT, TOR, ?PLE/HOL.

Superfamily CEPHEOIDEA Berlese, 1896

F. CEPHEIDÆ Berlese, 1896
T. (RUP)—Rec. Terr. (see Fig. 17.3)

First: Cepheus implica tus (Sellnick, 1918), Baltic amber. Extant

Superfamily EREMEOIDEA Sellnick, 1928

F. EREMAEIDE Sellnick, 1928
T. (RUP)—Rec. Terr.

First: Eremaeus oblongus C. L. Koch, 1836, Baltic amber. Extant

Intervening: CHT. ?PLE/HOL.

Superfamily GUSTAVIOIDEA Oudemans, 1900

F. XENILLIDAЕ Woolley and Higgins, 1966
T. (RUP)—Rec. Terr.

First: Xenillus tegeocraniformis (Sellnick, 1918), Baltic amber. Extant

F. ASTEGISTIDÆ Balogh, 1961
J. (OXF—TTH)—Rec. Terr.

First: Cultoribula jurassica Krivolutsky and Ryabinin, 1976, Burea River, Far East of former USSR. Extant

Intervening: RUP.

F. METRIOPPIIDÆ Balogh, 1943
T. (RUP)—Rec. Terr.

First: Ceratoppia bipilis (Hermann, 1804), Baltic amber. Extant

Intervening: PIA, PLE, HOL.

Superfamily CARABODOIDEA C. L. Koch, 1837

F. CARABODIDÆ C. L. Koch, 1837
T. (RUP)—Rec. Terr.

First: Carabodes gerberi Sellnick, 1931, C. dissonus Sellnick, 1931, C. coriaceus C. L. Koch, 1836, C. labyrinthicus (Michael, 1879), Plategeocranus sulcatus (Karsch, 1884), Scutoribates perornatus Sellnick, 1918, Odontocepheus? sp., Baltic amber. Extant

Intervening: TOR.

F. OTOCEPHEIDEA Balogh, 1961
T. (RUP)—Rec. Terr.

First: Otocepheus niger Sellnick, 1931, O. praesignis Sellnick, 1931, Baltic amber. Extant

Superfamily TECTOCEPHEOIDEA Grandjean, 1954

F. TECTOCEPHEIDÆ Grandjean, 1954
T. (RUP)—Rec. Terr.

First: Tectocepheus similis Sellnick, 1931, Baltic amber. Extant

Superfamily OPPIOIDEA Grandjean, 1951
T. (RUP)—Rec. Terr.
### Arthropoda (Aglaspida, Pycnogonida and Chelicerata)

Fig. 17.3

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3. Xenillidae 15. Licneremaeidae 27. Oribatellidae
8. Tectocepheidae 20. Parakalumnidae 32. Digamasellidae
10. Suctobelbidae 22. Euzeyidae 33. Steramarthronidae
11. Hydrozetidae 23. Ceratozetidae 34. Eukoeneniidae

**Superfamily** HYDROZETOIDEA Grandjean, 1954

F. HYDROZETIDAE Grandjean, 1954
J. (SIN)–Rec. Terr. (FW)

**Superfamily** CYMBAEREMAEOIDA Sellnick, 1928

F. CYMBAEREMAEIDAE Sellnick, 1928
J. (OXF–TTH)–Rec. Terr.
Animals: Invertebrates

**First:** Jureremus foveolatus Krivolutsky and Ryabinin, 1976, Burea River, Far East of former USSR. Extant

**Intervening:** RUP, CHT.

F. MICREREMIDAE Grandjean, 1954
T. (RUP)–Rec. Terr.

**First:** Micreremus scrobiculatus Sellnick, 1931, *M. reticulatus* Sellnick, 1931, Baltic amber. Extant

**Superfamily** LICNEREMAEOIDEA Grandjean, 1931

F. LICNEREMAEIDAE Grandjean, 1931
T. (RUP)–Rec. Terr.

**First:** Licneremaeus fritschi Sellnick, 1931, Baltic amber. Extant

**Superfamily** ORIPODOIDEA Jacot, 1925

F. ORIPODIDAE Jacot, 1925
T. (RUP)–Rec. Terr.

**First:** Oripoda baltica Sellnick, 1931, Baltic amber. Extant

**Intervening:** CHT.

**F. SCHELORIBATIDAE** Grandjean, 1933
T. (RUP)–Rec. Terr.

**First:** Scheloribates areatus Sellnick, 1931, *S. setatus* Sellnick, 1931, Baltic amber. Extant

**F. ORIBATULIDAE** Thor, 1929
K. (CMP)–Rec. Terr.

**First:** Unnamed oribatulid, Manitoban amber, Canada (McAlpine and Martin, 1963). Extant

**Intervening:** YPR–PRB, RUP, CHT, PLE.

**F. HAPLOZETIDAE** Grandjean, 1936
T. (RUP)–Rec. Terr.

**First:** Protoribates longipilis Sellnick, 1931, Baltic amber. Extant

F. PARAKALUMNIDAE Grandjean, 1936
T. (RUP)–Rec. Terr.

**First:** Neoribates borussicus Sellnick, 1931, Baltic amber. Extant

**Superfamily** CERATOZETOIDEA Jacot, 1925

F. CHAMOBATIDAE Grandjean, 1954
T. (RUP)–Rec. Terr.

**First:** Chamobates difficilis Sellnick, 1931, Baltic amber. Extant

F. EUZETIDAE Grandjean, 1954
T. (RUP)–Rec. Terr.

**First:** Euzetes convexulus (Koch and Berendt, 1854), Baltic amber. Extant

**F. CERATOZETIDAE** Jacot, 1925
T. (RUP)–Rec. Terr.

**First:** Melanozetes foderatus Sellnick, 1931, *M. mollicomus* (C. L. Koch, 1839). Sphaerozetes convexulus (Koch and Berendt, 1854), *S. primus* Sellnick, 1931, Baltic amber. Extant

**Intervening:** PLE, HOL.

**F. MYCOBATIDAE** Grandjean, 1954
Q. (PLE)–Rec. Terr.

**First:** Mycobates sp., Anabar River, former USSR (Golosova et al., 1985). Extant

**Intervening:** HOL.

**Superfamily** PHENOPELOPOIDEA Petrunkevitch, 1955

F. PHENOPELOPIDAE Petrunkevitch, 1955
T. (RUP)–Rec. Terr.

**First:** Phenopelops punctulatus (Sellnick, 1931), Notaspis sp., Baltic amber. Extant

F. UNDULORIBATIDAE Kunst, 1971
Q. (PLE)–Rec. Terr.

**First:** Scutozetes lanceolatus (Hammer, 1952), Anabar River, Siberia, former USSR. Extant

**Superfamily** ORIBATELLOIDEA Jacot, 1925

F. ORIBATELLIDAE Jacot, 1925
T. (RUP)–Rec. Terr.

**First:** Oribatella mirabilis Sellnick, 1931, *Tectoribates parous* Sellnick, 1931, Baltic amber. Extant

**Superfamily** ACHIPTERIOIDEA Thor, 1929

F. ACHIPTERIIDAE Thor, 1929
J. (OXF–TTH)–Rec. Terr.

**First:** Achipteria? obscura Krivolutsky and Ryabinin, 1976, Far East of former USSR. Extant

**Superfamily** GALUMNOIDEA Jacot, 1925

F. GALUMNIDAE Jacot, 1925
T. (RUP)–Rec. Terr.

**First:** Galumna clavata Sellnick, 1931, *Galumna diversa* Sellnick, 1931, Baltic amber. Extant

**Order** ANACTINOTRICHIDA Oudemans, 1931

**Suborder** OPILIOACARIDA With, 1902
(NOSTOSTIGMATA With, 1904) Terr.

No fossil record.

**Suborder** HOLOTHYRIDA Reuter, 1909
(TETRASTIGMATA Evans et al., 1961) Terr.

No fossil record.

**Suborder** IXODIDA Leach, 1815 (METASTIGMATA Canestrini, 1891)

F. IXODIDAE Leach, 1815
T. (YPR–LUT)–Rec. Terr. (ectoparasites)

**First:** Ixodes tertiarius Scudder, 1890, Green River Formation, Wyoming, USA. Extant

**Suborder** GAMASIDA Leach, 1815
(MESOSTIGMATA Canestrini, 1891)

F. PHYTOSEIIDAE Berlese, 1916
T. (RUP)–Rec. Terr.

**First:** Seius bdelloides Koch and Berendt, 1854, Baltic amber. Extant
F. DIGAMASELLIDAE Evans, 1956
T. (CHT)—Rec. Terr.

First: Dendrolaelaps fossilis Hirschmann, 1971, Chiapas amber, Mexico.

Class PALPIGRADI Thorell, 1888

F. STERNARTHRONIDAE Haase, 1890
T. (JTH) Terr.

First and Last (monotypic family): Sternarthron zitteli Haase, 1890, Lithographic Limestone, Solnhofen, Germany.

Comment: These fossils require restudy to check their identification as palpigrades (Rowland and Sissom, 1980).

Intervening: MEL, VRK, KSK, POD, MYA, DOR.

Last: England, UK.
First: Rochdale, England, UK.

F. EUKOENENIIDAE Petrunkevitch, 1955

First: Paleokoenenia mordax Rowland and Sissom, 1980, 'Onyx Marble', Bonner Quarry, Ashfork, Arizona, USA.

Extant

Class HAPTOPODIDAE Pocock, 1911 (see Fig. 17.4)

F. PLESIOSIRONIDAE Pocock, 1911
C. (CHE)—(MEL) Terr.

First: Plesiosiro madeleyi Pocock, 1911, Sparth Bottoms, Rochdale, England, UK.

Class ANTHRACOMARTIDA Karsch, 1882

F. ANTHRACOMARTIDAE Haase, 1890
C. (CHE—KLA/NOG) Terr.


Last: Pleomartus palatinus (Ammon, 1901), Breitenbach-Schichten, Grube Steinbach bei Brücken, Pfalz, Germany.

Intervening: MEL, VRK, KSK, POD, MYA, DOR.

Class PULMONATA Firstman, 1973

Intervening: Ecchosis pulchribothrium Selden and Shear, 1991, D. (GIV), was placed as Pulmonata incertae sedis.

Order TRIGONOTARBIDA Petrunkevitch, 1949
S. (PRD)—C. (DOR) Terr.

First: Unnamed trigonotarbid from Ludlow Bone Bed Member, Ludlow Lane, Ludlow, Shropshire, England, UK (Jeram et al., 1990).

Intervening: D. (EMS), Alkenia mirabilis Stürmer, 1970, Alken-an-der-Mosel, Germany. This was removed from Palaeocharinidae by Shear et al. (1987).

F. PALAEOCHARINIDAE Hirst, 1923
D. (PRA—GIV) Terr.


Last: Gilboarchae griersoni Shear et al., 1987, Gelaisotarbus reticulatus Shear et al., 1987, G. bonamoe Shear, et al., 1987, G. bifidus Shear et al., 1987, G. heptops Shear et al., 1987, Aculat.tarbus depressus Shear et al., 1987, Gilboa Mudstones, Gilboa, New York, USA.

F. ANTHRACOSIRONIDAE Pocock, 1903b
C. (MEL—KSK) Terr.


Last: Anthracosiro woodwardi Pocock, 1903, Crawcrook, Ryton-on-Tyne, England, UK.

Intervening: VRK.

F. EOPHYRNIDAE Karsch, 1882
C. (HAS—MYA) Terr.

First: Poconia whitiei (Ewing, 1930), lower part of Pocono Formation, Allegheny, Virginia, USA.

Last: Hemiphrynus longipes Frič, 1901, H. hofmanni Frič, 1901, Nýťany, Czechoslovakia; Gondwanaarachne argentinensis Pinto and Hünicken, 1980, Bajo de Véliz Formation, San Luis Province, Argentina.

Intervening: PND, ARN, YEA, CHE, MEL, VRK, KSK, POD.

F. TRIGONOTARBIDA Petrunkevitch, 1949
D. (EMS)—C. (MEL) Terr.


Last: Trigonotarbus johnsoni Pocock, 1911, Coseley, Dudley, England, UK.

Intervening: MRD.

F. APHANTOMARTIDAE Petrunkevitch, 1945
C. (PND/ALP—KRE) Terr.


Last: Aphantomartus areolatus Pocock, 1911, Prado Formation, borehole, Cerezal, Léon Province, Spain.

Intervening: CHE, MEL, VRK, KSK, POD, MYA.

Order ARANEAE Clerck, 1757

The classification used here is essentially the consensus scheme given in Shear (1986). The vast majority of families are first known from Baltic amber; many of the original specimens described by Koch and Berendt (1854) and Menge (in Koch and Berendt, 1854) have been lost or were poorly described so that available specimens cannot be matched to the descriptions (Petrunkevitch, 1958). Consequently, only those early specimens which were studied by Petrunkevitch have been included in the already lengthy lists of ‘firsts’. It should be noted, too, that Petrunkevitch’s work itself is in need of review, in the light of new ideas on classification, and the realization that some supposed Baltic amber is now thought to be pieces of comparatively Recent copal.

Attercopus D. (PRA) Terr./FW

First: Attercopus fimbrianguis (Shear, et al., 1987), Gilboa Mudstones, New York, USA. Plesion: plesiomorphic sister taxon of all other spiders.

Intervening: Undescribed spiders were reported from Lebanese amber, K. (BER—APT), by Whalley (1980).

Suborder LIPHISTIOMORPHAE Pocock, 1892

F. ARTHROLYCOSIDAE Frič, 1904
C. (MEL—MYA) Terr.

Table: Animal Distribution

<table>
<thead>
<tr>
<th>Era</th>
<th>Range</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jurassic</td>
<td>ANS</td>
<td>Rosamygale grauvogeli 1992, France. Extant</td>
</tr>
<tr>
<td>Triassic</td>
<td>ANS</td>
<td>Megarachne servinei 1980, Transbaikalia, former</td>
</tr>
</tbody>
</table>

The monotypic family Megarachnidae was erected for the giant Carboniferous fossil Megarachne servinei Hünicken, 1980, but there is doubt about the araneid (or even arachnid) nature of the fossil (Eskov and Zonshtein, 1990), which has no preserved spinnerets.

F. ARTHROMYGALIDAE Petrunkevitch, 1923
C. (MEL-KRE) Terr.
Last: Protolycosa cebennensis Laurentiaux-Vieira and Laurentiaux, 1963, couche Le Pin, La Grand’Combe, Cevennes, France. Extant
Intervening: POD, MYA.

Suborder OPISTHotHELAE Pocock, 1892
Infraorder MYGALOMORPHAE Pocock, 1892

Fig. 17.4

Last: Arthrolycosa antiqua Harger, 1874, A. danielsi Petrunkevitch, 1913, Francis Creek Shale, Mazon Creek, Illinois, USA.
Intervening: C. (POD).

F. HEXATHELIDAE Simon, 1892
Tr. (ANS)-Rec. Terr.
First: Rosamygale grauvogeli Selden and Gall, 1992, Grès à Voltzia, Vosges, France.
Extant

F. MECICOBOTHRIIDAE Holmberg, 1882
K. (7ALB)-Rec. Terr.
First: Cretohexura coylei Eskov and Zonshtein, 1990, Semyon Creek, Elizovo, near Chita, Transbaikalia, former
### Arthropoda (Aglaspida, Pycnogonida and Chelicerata)

#### Key for both diagrams

<table>
<thead>
<tr>
<th>Infraorder</th>
<th>Superfamily</th>
<th>Family</th>
<th>Genus</th>
<th>Extant</th>
<th>First</th>
<th>Intervening</th>
<th>Rec. Terr.</th>
<th>Extant</th>
</tr>
</thead>
<tbody>
<tr>
<td>Araneomorphae</td>
<td>Haptopopida</td>
<td>15. Nemesiidae</td>
<td>Nemesis</td>
<td>Extant</td>
<td>1988</td>
<td>Dominican amber</td>
<td></td>
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<tr>
<td></td>
<td>16. Barylchelidae</td>
<td>Barylchelus</td>
<td>Extant</td>
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<td>Dominican amber</td>
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<td>17. Theropsopidae</td>
<td>Theropsopus</td>
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<td>Ctenius</td>
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<td>21. Pholcidae</td>
<td>Pholcus</td>
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<td>22. Scytididae</td>
<td>Scytodes</td>
<td>Extant</td>
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<td>23. Tetrablemmidae</td>
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<td>24. Clubionidae</td>
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<td>25. Gnaphosidae</td>
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<td>Arthrodictyum</td>
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<td>27. Selenopidae</td>
<td>Selenopsis</td>
<td>Extant</td>
<td>1988</td>
<td>Dominican amber</td>
<td></td>
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<td>28. Eresidae</td>
<td>Eresus</td>
<td>Extant</td>
<td>1988</td>
<td>Dominican amber</td>
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**Fig. 17.4**

USSR; *Cretomegahexura platnicki* Eskov and Zonshtein, 1990, Bon-Tsagan Lake, central Mongolia.

F. DIPLURIDAE Simon, 1889
T. (RUP)–Rec. Terr.
First: *Clostes priscus* Menge, 1869, Baltic amber.
Intervening: CHT.

F. NEMESIIDAE Simon, 1889
T. (CHT)–Rec. Terr.
First: Unnamed pycnotheline, Dominican amber (Schawaller, 1981).

F. BARYCHELIDAE Simon, 1889
T. (CHT)–Rec. Terr.
First: *Plasistops hispaniolensis* Wunderlich, 1988, Dominican amber.

F. THERAPHOSIDAE Thorell, 1869
T. (CHT)–Rec. Terr.
First: *Ischnocolopsis acutus* Wunderlich, 1988, Dominican amber.

F. CTENIZIDAE Thorell, 1887
T. (CHT)–Rec. Terr.
First: *Bolostromus destructus* Wunderlich, 1988, Dominican amber.

F. ANTRODIAETIDAE Gertsch, 1940
K. (?ALB)–Rec. Terr.

F. ATYPIDAE Thorell, 1870 K. (?ALB)–Rec. Terr.
Intervening: RUP.

**Infraorder ARANEOMORPHAEE Smith, 1902**

The records of araneomorph spiders from Palaeozoic strata do not hold up under close scrutiny (Shear et al., 1989; Selden et al., 1991). These are: *Archaeometa devonica* Starmer, 1976, D. (EMS); *Archaeometa nephi/ina* Pocock, 1911,
Arachnometra tuberculata Petrunkevitch, 1949, C. (KSK); and Eopholcus pedatus Frič, 1904, C. (POD).

Superfamily PHOLCIOIDEA Simon, 1874

F. PHOLCIDAE Simon, 1874
T. (RUP)–Rec. Terr. Extant
First: Microphoncus heteropus Petrunkevitch, 1942, Baltic amber. Intervening: CHT.

F. SCYTODIDAE Blackwall, 1864
T. (CHT)–Rec. Terr. Extant
First: Scytodes piliformis Wunderlich, 1988, S. striulans Wunderlich, 1988, S. planithorax Wunderlich, 1988, Dominican amber. Intervening: CHT.

F. TETRABLEMMIDAE O. Pickard-Cambridge, 1873
T. (CHT)–Rec. Terr. Extant
First: Monolemma (?) spinosum Wunderlich, 1988, Dominican amber. Intervening: CHT.

F. OCHYROCERATIDAE Fage, 1912
T. (CHT)–Rec. Terr. Extant
First: Arachnolithus pygmaeus Wunderlich, 1988, Dominican amber. Intervening: CHT.

F. CAPONIDAE Simon, 1887
T. (CHT)–Rec. Terr. Extant
First: Nops lobatus Wunderlich, 1988, N. segmentatus Wunderlich, 1988, Dominican amber. Intervening: CHT.

F. LOXOSCELIDAE Gertsch, 1949
T. (CHT)–Rec. Terr. Extant
First: Loxosceles deformis Wunderlich, 1988, L. defecta Wunderlich, 1988, Dominican amber. Superfamily HERSILOIDEA Thorell, 1869

F. HERSILIIDAE Thorell, 1869
T. (RUP)–Rec. Terr. Extant
First: Hersilia miranda Koch and Berendt, 1854, Geridia myura Menge, 1854, Baltic amber. Intervening: CHT.

F. UROCTEIDAE Simon, 1875
T. (RUP)–Rec. Terr. Extant
First: Paruroctea blauvelti Petrunkevitch, 1942, Baltic amber. F. OECOBIIDAE Blackwall, 1862
T. (CHT)–Rec. Terr. Extant
First: Unnamed oecobiid, Dominican amber (Schawaller, 1983). Intervening: CRD.

Superfamily DYSDEROIDEA C. L. Koch, 1837

F. SEGESTRIIDAE Petrunkevitch, 1933
T. (RUP)–Rec. Terr. Extant
First: Segestria succinea Berland, 1939, S. cylindrica Koch and Berendt, 1854, S. cristata Menge, 1854, S. elongata Koch and Berendt, 1854, S. exarata Menge, 1854, S. nana Koch and Berendt, 1854, S. pusilla Menge, 1854, S. undulata Menge, 1854; S. tomentosa Koch and Berendt, 1854, S. elongata Koch and Berendt, 1854, S. picata Petrunkevitch, 1950, Baltic amber. Intervening: CHT.

F. DYSDERIDAE C. L. Koch, 1837
T. (RUP)–Rec. Terr.

F. OONOPIDAE Simon, 1892
T. (RUP)–Rec. Terr. Extant
First: Orchestina baltica Petrunkevitch, 1942, Baltic amber. Intervening: CHT.

Superfamily PALPIMANOIDEA Forster and Platnick, 1984

F. PALPIMANIDAE Thorell, 1870
T. (YPR)–Rec. Terr. Extant
First: Protocheres spinosus Gourret, 1886, Aix-en-Provence, France. Intervening: CHT.

F. ZODARIIDAE Simon, 1892
T. (RUP)–Rec. Terr. Extant
First: Anniculus balticus Petrunkevitch, 1942, Eocydrelle mortua Petrunkevitch, 1958, Baltic amber. Intervening: CHT, ZANIPIA.

F. SPATIATORIDAE Petrunkevitch, 1942
T. (RUP) Terr. Extant
First and Last: Spatiator praecps Petrunkevitch, 1942, Adorator brevipes Petrunkevitch, 1942, A. samlandicus Petrunkevitch, 1942, Baltic amber. Extant

F. ARCHAIDAE Koch and Berendt, 1854
CLV–KIM–Rec. Terr. Extant
First: Jurarchaea zherikhini Eskov, 1987, Karatau Mountains, Kazakhstan, former USSR. Intervening: RUP.

F. ARTHRODICYNIDAE Petrunkevitch, 1942
T. (RUP) Terr. Extant
First and Last (monotypic family): Arthrodictyna segmentata Petrunkevitch, 1942, Baltic amber. Extant

F. MIMETIDAE Simon, 1895
T. (RUP)–Rec. Terr. Extant

F. CLUBIONOIDEA Simon, 1895
T. (RUP)–Rec. Terr. Extant

Intervening: CHT, MES.
F. GNAPHOSIDAE Pocock, 1898
T. (RUP)—Rec. Terr.  
First: Eomactator mactatus Petrunkevitch, 1958, Captrix lineata Koch and Berendt, 1854, Baltic amber. Extant  
Intervening: CHT.  
F. INCEPTORIDAE Petrunkevitch, 1942  
T. (RUP) Terr.  
First and Last (monogeneric family): Inceptor aculeatus Petrunkevitch, 1942, I. dubius Petrunkevitch, 1942, Baltic amber.  
F. PARATIIDAE Petrunkevitch, 1922  
T. (RUP) Terr.  
First and Last (monogeneric family): Parattus evocatus Scudder, 1890, P. latitatus Scudder, 1890, P. occlusus Scudder, 1890, P. resurrectus Scudder, 1890, Florissant Shales, Colorado.  

Superfamily PHILODROMOIDEA Thorell, 1970  
F. PHILODROMIDAE Thorell, 1970  
T. (RUP)—Rec. Terr.  
First: Syphax asper Petrunkevitch, 1942, S. crassipes Petrunkevitch, 1942, S. fuliginosus Koch and Berendt, 1854, S. gracilis Koch and Berendt, 1854, S. hirtus Menge, 1854, S. megacephalus Koch and Berendt, 1854, Eothenatus diritatis Petrunkevitch, 1942, Baltic amber. Extant  
Intervening: CHT.  
F. HETEROPOLIDAE Thorell, 1873  
T. (RUP)—Rec. Terr.  
Intervening: CHT.  
F. SELENOPIDAE Simon, 1897  
T. (CHT)—Rec. Terr.  
First: Selenops beynai Schawaller, 1984, Dominican amber. Extant  
Superfamily EREISOIDEA C. L. Koch, 1837  
F. ERESIDAE C. L. Koch, 1837  
T. (RUP)—Rec. Terr.  
First: Eresus curtipes Koch and Berendt, 1854, E. monachus Koch and Berendt, 1854, Baltic amber. Extant  
Superfamily DICTYNOIDEA Simon, 1874  
F. DICTYNIDAE Simon, 1874  
T. (YPR)—Rec. Terr. (see Fig. 17.5)  
First: Sinodictyna fushunensis Hong, 1982, Guchengzi Formation, Fushun Coalfield, Liaoning Province, China. Extant  
Intervening: RUP.  
F. ARGYRONETIDAE Menge, 1869b  
T. (BUR)—Rec. (FW)  
First: Elvina antiqua (von Heyden, 1859) Brown Coal of Siebengebirge, Germany; Argyroneta longipes Heer, 1865, Switzerland. Extant  
Comment: von Heyden placed Elvina antiqua in the Argyronetididae on the basis of the freshwater nature of the enclosing sediment; Petrunkevitch (1946) doubted this family assignment.  
F. ANYPHAENIDAE Bertkau, 1878  
T. (RUP)—Rec. Terr.  
First: Anyphaena fuscata Koch and Berendt, 1854, Baltic amber. Extant  
Intervening: CHT.  
F. HAHNIIDAE Bertkau, 1878  
T. (RUP)—Rec. Terr.  
First: Eohahnia succini Petrunkevitch, 1958, Baltic amber. Extant  
Superfamily AGELENOIDEA Simon, 1898  
F. AGELENIDAE Simon, 1898  
T. (RUP)—Rec. Terr.  
First: Amaurobius succini Petrunkevitch, 1942, Auximus succini Petrunkevitch, 1942, A. fossilis Petrunkevitch, 1942, Baltic amber. Extant  
Intervening: CHT.  
F. INSECUTORIDAE Petrunkevitch, 1942  
T. (RUP) Terr.  
First and Last (monogeneric family): Insecutor aculeatus Petrunkevitch, 1942, I. mandibulatus Petrunkevitch, 1942, I. rufus Petrunkevitch, 1942, Baltic amber.  
Superfamily LYCOSOIDEA Sundevall, 1833  
F. LYCOSIDAE Sundevall, 1833  
T. (RUP)—Rec. Terr.  
First: Lycosa florissanti Petrunkevitch, 1922, Florissant Shales, Colorado, USA. Extant  
Intervening: TOR/MES.  
F. PSECHRIDAE Simon, 1892  
T. (RUP)—Rec. Terr.  
First: Lycosinae florissanti Petrunkevitch, 1922, Florissant Shales, Colorado, USA. Extant  
Intervening: TOR/MES.  
F. CTENIDAE T. (CHT)—Rec. Terr.  
First: Nanoctenus longipes Wunderlich, 1988, Dominican amber. Extant  
F. OXYOPIDAE Thorell, 1870  
T. (RUP)—Rec. Terr.  
First: Oxyopes succini Petrunkevitch, 1958, Baltic amber. Extant  
Intervening: CHT.
Fig. 17.5

F. ZOROPSIDAE Simon, 1892
T. (RUP)—Rec. Terr.
First: Adamator succineus Petrunkevitch, 1942, Baltic amber.
Extant: CHT, MES, ZAN/PIA, HOL.
Intervening: CHT, MES, ZAN/PIA, HOL.

Superfamily SALTICOIDEA F. Pickard-Cambridge, 1900
F. SALTICIDAE F. Pickard-Cambridge, 1900
T. (YPR)—Rec. Terr.
First: Attoides eresiformis Brongniart, 1877, Aix-en-Provence, France.
Extant: RUP, CHT, TOR/MES.
**Fig. 17.5**

**Arthropoda (Agaspidida, Pycnogonida and Chelicerata)**

<table>
<thead>
<tr>
<th>TRIASSIC</th>
<th>PERMIAN</th>
<th>CARBONIFEROUS</th>
<th>DEVONIAN</th>
<th>SILURIAN</th>
<th>ORDOVICIAN</th>
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**Superfamily DEINOPOIDEA C. L. Koch, 1851**

*Palaeouloborus* K. (BER/VAL) Terr.

**First:** *Palaeouloborus lacasae* Selden, 1990, lithographic limestone, Sierra de Montsech, Lérida Province, Spain.

**Comment:** Although not assigned to a family, this fossil bears a greater similarity to the Uloboridae than to any other extant spider family.

**F. ULOBORIDAE** Simon, 1892

**First:** *Miagrammopetes* sp., Dominican amber (Schawaller, 1982; Wunderlich, 1988). Extant

**Superfamily ARANEOIDEA** Latreille, 1806

**Intervening:** *Cretaraneus vilaltae* Selden, 1990a, K. (BER/VAL), lithographic limestone, Sierra de Montsech, Lérida Province, Spain, was referred to Araneoidea but without a family assignment; it probably belongs in Theridiidae or Linyphiidae.

**F. ARANEIDAE** Leach, 1819 T. (LUT)–Rec. Terr.

**First:** unnamed Araneidae, oil shales, Grube Messel, Darmstadt, Germany (Wunderlich, 1986).

**Intervening:** RUP, CHT, TOR/MES, MES, ZAN/PIA.

**Extant**

**F. LINYPHIIDAE** Dahl, 1913 T. (RUP)–Rec. Terr.

**First:** *Impulsor neglectus* Petrunkevitch, 1942, *I. mutilus*

Intervening: CHT, MES.

F. METIDAE Simon, 1892 T. (RUP)–Rec. Terr.


Intervening: CHT, MES.

F. ACROMETIDAE Wunderlich, 1979 T. (RUP) Terr.


F. TETRAGNATHIDAE Menge, 1866 K. (BER/VAL)–Rec. Terr.

First: *Macryphantes coudeni* Selden, 1990a, lithographic limestone, Sierra de Montsech, Lérida Province, Spain. Extant

Intervening: CHT.


First: *Cyclososoma succini* Petrunkevich, 1958, Baltic amber. Extant

Intervening: CHT.


First: Unnamed symphytognathid, Dominican amber (Schawaller, 1981). Extant

F. ANAPIDAE T. (CHT)–Rec. Terr.

First: *Palaeonapis nana* Wunderlich, 1988, Dominican amber. Extant


First and Last (monotypic family): *Juraranus ras nityi* Eskov, 1984, Mukhor-Shibir, near Novospasskoye, Buryat, Siberia, former USSR. Extant


Intervening: CHT, MES.


Intervening: CHT.


Order UROPYGI Thorell, 1882

F. THELYPHONIDAE Lucas, 1835 C. (MRD)–Rec. Terr.

First: *Prothelyphonus naufragus* Brauckmann and Koch, 1983, Hagen-Vorhalle, Ruhr, Germany. Extant

Intervening: CHE, MEL, KSK, MYA, ?ZAN/PIA.

Order SCHIZOMIDA Petrunkevich, 1945

F. CALCITRONIDAE Petrunkevich, 1945 T. (?ZAN/PIA) Terr.


First: *Calcoschizomus latis ternalis* Pierce, 1951, ‘Onyx Marble’, Bonner Quarry, Ashfork, Arizona, USA. Extant

Order AMBLYPYGI Thorell, 1882

Suborder APULVILLATA Quintero, 1986


First: *Phrynos resinae* Schawaller, 1979, Dominican amber. Extant
**Suborder PULVILLATA Quintero, 1986**

F. ELECTROPHRYNIDAE Petrunkevitch, 1971

**First and Last (monotypic family): Electrophrynus mirus**

Petrunkevitch, 1971, Chiapas amber, Mexico.

**REFERENCES**


Transactions of the Connecticut Academy of Arts and Sciences, 41, 97–400.


ARTHROPODA (CRUSTACEA EXCLUDING OSTRACODA)

D. E. G. Briggs, M. J. Weedon and M. A. Whyte

This chapter includes all crustaceans except the ostracodes, which are treated in Chapter 19.


STEM LINEAGE CRUSTACEANS

This category (Walossek and Muller, 1990) accommodates those Upper Cambrian arthropods from the Orsten of Sweden which are interpreted as descendants of early offshoots from the stem-lineage of Crustacea. The most primitive of these stem lineage crustaceans is Henningsmoenia scutula Walossek and Muller, 1990; the most advanced is Martinssonia elongata Müller and Walossek, 1986 (Walossek and Müller, 1990). Only two of the stem lineage crustaceans have been grouped in a higher taxon, currently of unspecified rank.

Taxon CAMBROPACHYCOPIDAE Walossek and Muller, 1990 - C. (MNT) Mar. (see Fig. 18.1)

First and Last: Cambropachycopera clarksoni Walossek and Muller, 1990 and Goticaris longispinosa Walossek and Muller, 1990, Agnostus pisiformis Zone, Alum Shale Formation, Vastergotland, Sweden.

Subphylum CRUSTACEA Pennant, 1777 (excluding Ostracoda)

The classification used here follows that of Schram (1986), with minor additions and modifications. This does not necessarily imply agreement with all his taxonomic conclusions. Families without a fossil record are not included.

Class UNNAMED

Order SKARACARIDA

F. SKARAIIDAE C. (MNT) Mar.


Class REMIPEDIA Yager, 1981

The classification used here follows that of Schram (1986), with minor additions and modifications. This does not necessarily imply agreement with all his taxonomic conclusions. Families without a fossil record are not included.

Class REMIPEDIA Yager, 1981

Order SKARACARIDA

F. SKARAIIDAE C. (MNT) Mar.


Class REMIPEDIA Yager, 1981

Order SKARACARIDA

F. SKARAIIDAE C. (MNT) Mar.


Class REMIPEDIA Yager, 1981

Order SKARACARIDA

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Class REMIPEDIA Yager, 1981

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Order SKARACARIDA

F. SKARAIIDAE C. (MNT) Mar.


Class REMIPEDIA Yager, 1981

Order SKARACARIDA

F. SKARAIIDAE C. (MNT) Mar.
respectively, to *Perimecturus*. Schram and Homer (1978) described *Bairdops beargulchensis* from the Bear Gulch Limestone, but Factor and Feldmann (1985) synonymized the material with *Tyrannophontes theridion*. Schram (pers. comm.) disagrees.

**Order** STOMATOPODA Latreille, 1817

**Suborder** ARCHAEOSTOMATOPODEA Schram, 1969

F. **TYRANNOPHONTIDAE** Schram, 1969


First: *'Perimecturus' pattoni* Peach, 1908, Top Hosie Limestone, East Kilbride, Scotland, UK.

**Last:** *Gorgonophontes peleron* Schram, 1984b, Dennis Formation, Nebraska, USA.

**Comment:** Although unsure about its identity, Schram (1979a) considered the specimen of *'Perimecturus' pattoni* likely to be a tyrannophontid. Other early occurrences of the family were reviewed by Schram (1984b).

**Suborder** UNIPELTA Latreille, 1825

**Superfamily** BATHYSQUILLOIDEA Manning, 1967

F. BATHYSQUILLIDAE Manning, 1967


**Extant**
**Arthropoda (Crustacea excluding Ostracoda)**

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**ORDEREDICIAN**  
**SUPERCLASS** EUMALACOSTRACA  
**SUBCLASS** Syncarida  
**SUPERORDER** Anaspidacea  

**Key for both diagrams**

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**Fig. 18.1**

**F. SCULIDAE** Dames, 1866  
**J. (TTH)−K. (CEN)**  
**Mar.**  
**First:** *Sculda pennata* Münster, 1840, Solnhofen Limestone, Bavaria, Germany.  
**Last:** *Sculda syriaca* Dames, 1886; *Pseudosculda laevis* Schlüter, 1872, Lebanon (see Roger, 1946).  
**Comment:** Schram (1968, p. 1299) considered that this may be the earliest gonodactylid. Otherwise this family ranges from the Upper Miocene.

**Superfamily** LYSIOSQUILLOIDEA Giesbrecht, 1910  
**F. LYSIOSQUILLOIDEA** Giesbrecht, 1910  
**K. (Maa)−Rec. Mar.**

**First:** *Lysiosquilla nkporoensis* Förster, 1982, Nkporo Shale, Nigeria.  
**Extant**

**Superfamily** GONODACTYLOIDEA Giesbrecht, 1910  
**F. GONODACTYLOIDEA** Giesbrecht, 1910  
**(7K. (Gal)) T. (Umi)−Rec. Mar.**

**First:** *Paleosquilla brevicoxa* Schram, 1968, Albian–Cenomanian, Simiti Formation, Antioquia, Columbia.  
**Extant**

**Order** Syncarida Packard, 1885  
**Suborder** Anaspidacea Calman, 1904
Schram (1986) was inconsistent in his spelling of this taxon giving both Anaspidacea (p. 542) and Anaspidinea (p. 85).

F. ANASPIDIDAE Thompson, 1893  
Tr. (ANS)–Rec. FW  
First: *Anaspidites antiquus* (Chilton, 1929) Triassic, Hawkesbury Sandstone, New South Wales, Australia. Extant

**Order** PALAEOCARIDACEA Brooks, 1962  
F. MINICARIDIDAE Schram, 1984  
C. (VIS)–P. (ASS/SAK) FW–?Mar.  
Last: *Erythrogaulos carrizoensis* Schram, 1984a, Red Tanks Member, Madera Formation, Lower Permian, USA.  
Comment: *Minicaris* was first described (*Minicaris brandi* Schram, 1979) from below the Pumpherston Shell Bed, Lower Oil Shale Group, VIS (?Asbian), England, UK.

F. ACANTHOTELSONIDAE Meek and Worthen, 1865  
C. (SPK)–P. (ROT) FW  
First: *Palaeosyncaris dakotensis* Brooks, 1962, Heath Shale, Madera Formation, USA.  
Last: *Uronectes fimbriatus* (Jordan, 1947), Rotliegendes, Saarbrücken, Germany.

F. PALAEOCARIDIDAE Meek and Worthen, 1865  
C. (MOS–KAS) FW  

F. SQUILLITIDAE Schram and Schram, 1974  
C. (SPK)–P. (ROT) FW  
First: *Squillites spinosa* Scott, 1938, Heath Shale, Big Snowy Group, Montana, USA.  
Last: *Nectotelson kreibii* (Fritsch, 1875), Rotliegendes, near Autun, France (Schram, 1984a).  
Comment: Schram (1984a) attributed the Gaskohle of the Humboldt Mine at Nyrany, Bohemia, Czechoslovakia, where *N. kreibii* also occurs, to the Lower Permian, although it is Moscovian (Westphalian D) in age (Gray, 1988).

**Order** BELOTELSONIDA Schram, 1981  
F. BELOTELSONIDAE Schram, 1974  
First: *Belotelson trauquiri* (Peach, 1882), ?Hastarian, Cementstone Group, Berwickshire, Scotland, UK (Locality 9 of Schram, 1979a; the Foulden locality, Briggs and Clarkson, 1985, is similar in age).  
Last: *Belotelson magister* (Packard, 1886), Francis Creek Shale, Mazon Creek, NE Illinois, USA. Extant

**Order** EUHAPSIDA Dana, 1852  
F. UDORELLIDAE Van Straelen, 1924  
J. (TTH)–Rec. Mar.  
First and Last: *Udorella agassizi* Oppel, 1862, Tithonian, Solnhofen Limestone, Bavaria, Germany.  

Suborder EUZYGIDA Burkenroad, 1981  
Infra-order UNCINIDEA Beurlen, 1930  
F. UNICINIDAE, Beurlen, 1928  
J. (TOA) Mar.
First and Last: Uncinia posidoniae, Liassic, lower Toarcian, Holzmaden, Baden-Württemberg, Germany. 

Comment: Schram (1986, p. 284) did not recognize this family, but states that ‘Uncinia bears some sister-group relationship to the living stenopodiids’.

**Suborder** REPTANTIA Boas, 1880


First: Palaeopalaeamon newberryi Whitfield, 1980, Ohio, New York and Iowa, USA (Schram et al., 1978).

Last: ?Palaeopalaeamon newberryi Whitfield, 1880, New Providence Formation, Boyle County, Kentucky, USA (Schram et al., 1978, p. 1376, express some doubt regarding the identity of the specimen upon which this record is based).

**Infra-order** ASTACIDEA Latreille, 1803


Last: Enoploclytis sp. Beikirch and Feldmann, 1980, Austin Formation, Travis County, Texas, USA.

Comment: Protoclytiopsis antiqua Birshtein, 1958, uppermost Permian, Siberia, was placed in the Erymidae by Schram (1980), but he subsequently (1986) declared that it ‘seems to be a glypheid’. Otherwise the earliest records are of Enoploclytis (Glaessner, 1969).

F. NEPHROPIDAE Dana, 1852 J. (DOG)–Rec. Mar.


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Last: Enoploclytis sp. Beikirch and Feldmann, 1980, Austin Formation, Travis County, Texas, USA.

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First and Last: Uncinia posidoniae, Liassic, lower Toarcian, Holzmaden, Baden-Württemberg, Germany.

**Infra-order** THALASSINIDEA Latreille, 1831


First: Magil? bonjouri (Etallon, 1861), Lower Jurassic, Europe (Glaessner, 1969).

Extant


First: Jaxa kuemeli Bachmayer, Miocene, Australia (Glaessner, 1969).

Extant

F. CALLIANASSIDAE Dana, 1852 J. (MLM)–Rec. Mar.

First: Protocalmannassa Beurlen, 1930 (Glaessner, 1969).

Extant


Extant

Comment: The U. clypeata from the Bathanion of England was referred to the Mecochiridae by Woods (1928).

**Infra-order** PALINURA Latreille, 1803


?First and Last: Cancrinos claviger Münster, 1839, Solnhofen Limestone, Bavaria, Germany (Glaessner, 1969).


First: ?Proeryon hartmanni (Von Meyer, 1835), Liassic, lower Toarcian, Holzmaden, Baden-Württemberg, Germany.


Comment: Rathbun (1919) assigned fragments from the Lower Miocene of the West Indies to this family.


This family was recognized by Glaessner (1969), (and by Sepkoski, 1982) but was not listed by Schram (1986). Unfortunately, Schram did not indicate where he would place the two included genera Coleia and Helleocaris.


Last: Coleia sp., Lower Cretaceous, India (Glaessner, 1969).


First: Palaeopemphix Gemmellaro, 1890 (three species from the Lower Permian Sosio Limestone of Sicily). Protoctiliotsis antiqua Birshtein, 1958, uppermost Permian, Siberia, was placed in the Erymidae by Schram (1980), but he subsequently (1986) declared that it ‘seems to be a glypheid’. Otherwise the earliest records are of Litogaster ?Lower and Middle Triassic of Germany (Glaessner, 1969).


Comment: Glaessner (1969, p. 436) considered that the Palaeopemphix material needs re-examination before assignment to the order Decapoda.

**F. MECOCHIRIDAE Van Straelen, 1925**

First: *Pseudoglyphea* Oppel, 1861, Triassic (Glaessner, 1969).

Last: *Meyeria* M'Coy, 1849, Campanian, cosmopolitan (Glaessner, 1969); Genus indet. mecochirid, Austin Formation, lower CMP, Travis County, Texas, USA (Beikirch and Feldmann, 1980).

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**F. PEMPHICIDAE Van Straelen, 1928**

First and Last: *Pemphix* von Meyer, 1840, including *Pemphix sueurii* (Desmarest, 1822), or *Pseudopemphix* Wüst, 1903, including *Pseudopemphix albertii* (von Meyer, 1840), both Europe (Glaessner, 1969).

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**F. PALINURIDAE Latreille, 1803**


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**F. POLYCHELIDAE Wood-Mason, 1874**

First: *Willemoesiocris ovalis* Van Straelen, 1925, Middle Jurassic, France (Glaessner, 1969). Extant

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**F. SCYLLARIDAE Latreille, 1825**

**Arthropoda (Crustacea excluding Ostracoda)**

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<td>23. Parthenopidae</td>
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<td>LLY</td>
<td>24. Atelecyclidae</td>
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<tr>
<td>ASH</td>
<td>25. Cancridae</td>
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<tr>
<td>CRD</td>
<td>26. Caridinae</td>
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<td>LLO</td>
<td>27. Carpillidae</td>
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<tr>
<td>LLN</td>
<td>28. Geryoniidae</td>
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<td>29. Gonyolidae</td>
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<tr>
<td>TRE</td>
<td>30. Pinnothidae</td>
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<td>31. Portunidae</td>
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<td>32. Potamidace</td>
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<td>CFR</td>
<td>33. Retropulicidae</td>
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<tr>
<td>EDI</td>
<td>34. Costacoplomidae</td>
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<tr>
<td>VAR</td>
<td>35. Xanthidae</td>
</tr>
<tr>
<td>STU</td>
<td>36. Gecarcinidae</td>
</tr>
</tbody>
</table>

**Fig. 18.2**

**First:** Scyllarides punctatus Woods, 1925 and Scyllarella gardneri Woods, 1925, Gault, England, UK. Extant

F. TETRACHELIDAE Beurlen, 1930 Tr (u.) Mar.

**First and Last:** Tetrachela raiblana (Bronn, 1858), Upper Triassic, southern Europe (Glaessner, 1969).

**Infra-order ANOMALA Boas, 1880**


**First:** Paguristes whitteni Bishop, 1983, Coon Creek Formation, Mississippi, USA. Extant


**First:** Coenobita? sp. Martin, 1883, ?Lower Miocene, Java. Extant

F. PAGURIDAE Latreille, 1803 J. (PLB)–Rec. Mar. (see Fig. 18.2)

**First:** Palaeopagurus deslongchampsi Van Straelen, 1925, Liassic, France (Glaessner, 1969). Extant

F. GALATHEIDAE Samouelle, 1819 J. (BAJ)–Rec. Mar.

**First:** Palaemundiopsis moutieri Van Straelen, 1925 (Glaessner, 1969).


**First:** Haumuriaegla glaessneri Feldmann, 1984, North Canterbury, New Zealand.


**First:** Porcellana antiqua, A. Milne Edwards, 1862, Cenomanian, France (Glaessner, 1969). Extant


**First:** Blepharipoda occidentalis Randall, 1840, Oligocene, North America (Glaessner, 1969).

**Infra-order BRACHYURA Latreille, 1803**

**Section DROMIACEA De Haan, 1833**

**First and Last:** The earliest fossil referred to the Brachyura, albeit tentatively, is *Imocaris tuberculata* Schram and Mapes, 1984, Chesterian, Imo Formation, Arkansas, USA.

F. EOCARCINIDAE Withers, 1932  J. (PLB) Mar.

**First and Last:** *Eocarcinus praecursor* Withers, 1932, lower Lias, England, UK (Glaessner, 1969).


**First:** *Prosopon* von Meyer, 1835, *Pithonoton* (*Pithonoton*) von Meyer, 1842, or *Coelopus Étállon*, 1861, all mid-Jurassic. **Extant**

**Comment:** Stratigraphy from Glaessner (1969).


**First:** *Mesodromilites glaber* Woodward, 1898, Albion (Gault), Folkestone, Kent, England, UK (Wright and Collins, 1972). **Extant**

**First:** *La Meseta Formation*, Seymour Island, Antarctica. **Extant**

F. DYNOMENIDAE Ortmann, 1892  J. (TTH)–Rec. Mar.

**First:** *Cyclothyreus reussi* (Gemmellaro, 1870), Tithonian, Moravia, Czechoslovakia (Glaessner, 1969). **Extant**


**First:** *Homolodromia chaneyi* Feldmann and Wilson, 1988, La Meseta Formation, Seymour Island, Antarctica. **Extant**


**First:** *Diaulax* sp. Glaessner, 1931, Portlandian. **Extant**


**First and Last:** *Mesodromilites glaber* Woodward, 1898, Albion (Gault), Folkestone, Kent, England, UK (Wright and Collins, 1972). **Extant**


**First:** *Heeia villersensis* (Hée, 1924), Villers-sur-Mer, France, and Wilmington, Devon, England, UK (Wright and Collins, 1972). **Extant**


**First:** *Gastrodorus neuhausensis* (von Meyer, 1864), Upper Jurassic, Germany (Glaessner, 1969). **Extant**

**Comment:** Some authors (notably Glaessner, 1969) regarded the Laterelliidae and the Homoliidae as a single family.


**First:** *Dakotacancer* Rathbun, 1917, including *Dakotacancer overanus* Rathbun, 1917, lower CMP, Mississippi, USA; *Avitelmesus* Rathbun, 1923, including *Avitelmesus grappoideus* Rathbun, 1923, upper Senonian, Tennessee, USA; *Tetracarcinus* Weller, 1905, including *Tetracarcinus subquadratrus* Weller, 1905, lower CMP, New Jersey to Wyoming, USA. **Extant**

**Last:** *Dakotacancer australis* Rathbun, 1935 and *Tetracarcinus subquadratrus* Weller, 1905, Coon Creek Formation, Mississippi, USA (Bishop, 1983).


**First:** *Heeia villersensis* (Hée, 1924), Villers-sur-Mer, France, and Wilmington, Devon, England, UK (Wright and Collins, 1972). **Extant**


**First:** *Dakrotacancer* Rathbun, 1917, including *Dakotacancer overanus* Rathbun, 1917, lower CMP, Mississippi, USA; *Avitelmesus* Rathbun, 1923, including *Avitelmesus grappoideus* Rathbun, 1923, upper Senonian, Tennessee, USA; *Tetracarcinus* Weller, 1905, including *Tetracarcinus subquadratrus* Weller, 1905, lower CMP, New Jersey to Wyoming, USA. **Extant**

**Last:** *Dakotacancer australis* Rathbun, 1935 and *Tetracarcinus subquadratrus* Weller, 1905, Coon Creek Formation, Mississippi, USA (Bishop, 1983).


**First:** *Heeia villersensis* (Hée, 1924), Villers-sur-Mer, France, and Wilmington, Devon, England, UK (Wright and Collins, 1972). **Extant**


**First:** *Gastrodorus neuhausensis* (von Meyer, 1864), Upper Jurassic, Germany (Glaessner, 1969). **Extant**

**Comment:** Some authors (notably Glaessner, 1969) regarded the Laterelliidae and the Homoliidae as a single family.


**First:** *Torynomma* Woods, 1953, Albian including *Torynomma quadra* Woods, 1953, upper Albian, Australia (Glaessner, 1969). **Extant**

Section EUBRACHYURA de St Laurent, 1980

Subsection HETEROTREMATA Guinot, 1977


**First:** ‘*Gebia’ controversa* Tribolet, 1874, Switzerland (Förster, 1968). **Extant**

**Comment:** This record is based on claws. The earliest completely known species is *Paramexocarcinus hexagonalis* Van Straelen, 1936, Hauterivian, Marnes (near Auxerre), Yonne, France (Wright and Collins, 1972). **Extant**


**First:** *Sodakus tatankayotankaensis* Bishop, 1978, Mobridge Member, Pierre Shale, South Dakota, USA. **Extant**

**Comment:** *Orithopsis bonnigi* Carter, 1872, Albion, England, UK, was referred to this family (e.g. Glaessner, 1969), but Wright and Collins (1972, p. 66–8) questioned the validity of this species, and synonymized it with *Necrocarcinus tricarinatus* Bell, 1863 (Calappidae).


**First:** *Typilobus trispinosus* Lörrenthey, 1909, Egypt (Glaessner, 1969). **Extant**


**First:** *Mithracia libinoides*, Weller, 1858, Lower Eocene, England, UK (Glaessner, 1969). **Extant**

**Comment:** Glaessner (1969, p. 502) reported fragmentary claws of *Stenocrinops* Desmarest, 1823, from the ?Upper Cretaceous, Arkansas, USA.


**First:** *Parthenope Weber, 1795, Middle Eocene (Glaessner, 1869). **Extant**


**First:** *Montezumella fraasi* Lörrenthey, 1907, Mokattam, Egypt. **Extant**
Arthropoda (Crustacea excluding Ostracoda)

F. CANCRIDAE Latreille, 1819  
First: Lobocarcinus Reuss, 1857, e.g. Lobocarcinus paulinowurtembergensis (von Meyer, 1847), Middle Eocene, Egypt.  
Last:  

F. CARCINERETIDAE Beurlen, 1930  
Last: Ophthalmoplax Rathbun, 1935, including Ophthalmoplax stephensoni Rathbun, 1935, Texas, USA.

F. CARPILIIDAE Ortmann, 1894  
First: Caloxanthus americanus Rathbun, 1935, uppermost Albian, Texas, USA (Wright and Collins, 1972).  Extant

F. GERYONIDAE Colosi, 1923  

F. GONEPLACIDAE MacLeay, 1838  
First: The following taxa occur in the Lower Palaeocene: Branchioplax Rathbun, 1916, Martinezicancer Van Straelen, 1939, Martezia (L.) stenzeli Woodward, 1873, (Deshayesites callidiscus Subzone), Isle of Wight, England, UK.  Extant
Comment: A Maastrichtian record of Goniocypoda H. Woodward, 1867, is doubtful (Glaessner, 1969). This genus may belong to the Hexapodidae.

F. PINNOTHERIDAE De Haan, 1833  
First: Pinnixa White, 1846, including Pinnixa eocenica Rathbun, 1825, Lower Eocene, Washington, USA (Glaessner, 1969). Also Pinnixa (Palaeopinnixa) porornata Collins and Morris, 1976, Lower or Middle Eocene, Scotland Beds, Spa, Barbados.  Extant

F. PORTUNIDAE Rafinesque, 1815  
Comment: Glaessner (1969) records other Eocene portunids, but none of these is specifically from the Lower Eocene.

F. RETROPLUMIDAE Gill, 1894  
First: Archaeopus antennatus Rathbun, 1908, ?Lower–Upper Cretaceous, California, USA.  Extant

F. COSTACOPLUMIDAE St Laurent, 1989  

F. XANTHIDAE MacLeay, 1838  
First: Cardisoma Latreille, 1825, Pliocene, Fiji (Glaessner, 1969).  Extant

F. GECARCINIDAE MacLeay, 1838  
First: Loerentheya Beurien, 1929, including Loerentheya carinata Beurien, 1929, Middle Eocene, Hungary.  Extant

F. HEXAPODIDAE Miers, 1886  
First: Anthracophausia dunsiana Peach, 1908, Cements tone

Order WATERSTONELLIDEA Schram, 1981

F. WATERSTONELLIDAE Schram, 1979  
C. (VIS) Mar.

Order EOCARIDACEA Brooks, 1962

Schram (1986, p. 104) described this as ‘a sort of catchall order, whose membership has slowly shrunk through the years as forms become better understood and assigned elsewhere’.

F. EOCARIDIDAE Brooks, 1962  
First: Eocaris oervigi (Brooks, 1962a), Middle Devonian, Rhenish Massif, Germany.  Last: Devonocaris designate (Van Straelen, 1943), Belgium.  Extant

F. ANTHRACOPHAUSIIDAE Brooks, 1962  
First: Anthracophausia dunsiana Peach, 1908, Cementstone
### Order LOPHOGASTRIDA Boas, 1883


**First and Last:** *Essoidia epiceron* Schram, 1974, Francis Creek Shale, Mazon Creek, NE Illinois, USA.

**Order** LOPHOGASTRIDA Boas, 1883


**First:** *Peachocaris strongi* (Brooks, 1962), Francis Creek Shale, Mazon Creek, NE Illinois, USA.

**Last:** *Peachocaris acanthouraea* Schram, 1984b, Missourian, Hushpuckney Shale, Crescent, Iowa, USA.

**F. LOPHOGASTRIDA Schram, 1986**

**First:** *Lophogaster voultensis*, Secretan and Riou, 1986, La Voulte-sur-Rhône, Ardeche, France.

**Comments:** Schram (1986, p. 124) discussed *Dollocaris ingens* Van Straelen, 1923 and *Kilianicaris lerichei* Van Straelen, 1923 from the same locality under this taxon, but remarks that they ‘are nothing but poorly preserved carapaces’. They are now identified as belonging in the Thylacocephala (see Arduini and Pinna, 1989).
**Order** PYGOCEPHALOMORPHA Beurlen, 1930

**F. EUCOPEIIDAE** Dana, 1852  
Tr. (ANS)–Rec. Mar./FW

First: *Schimperella beneckei* and *Schimperella kessleri* Bill, 1914, Triassic, Grès à Voltzia, Alsace, France.  
Extant Comment: Schram (1986, p. 124) discussed alternative assignments for this genus. The two species may be synonymous. Otherwise the first occurrence is *Eucopia praecursor* Secretan and Riou, 1986, Callovian, La Voulte-sur-Rhône, France.

**Order** PYGOCEPHALIDAE Brooks, 1962

**F. PYGOCEPHALOMORPHA** Beurlen, 1930

**F. TELLIOCARIDIDAE** Brooks, 1962  
C. (TOU)–P. (ROT) Mar./FW

First: *Pseudotealliocaris palinscosari* Schram, 1988, Kinderhookian, Lower Pocono Formation.  
Last: *Mamayocaris jepseni* Brooks, 1962, from the Lower Permian of Oklahoma, USA.

**F. NOTOCARIDIDAE** Brooks, 1962  
P. (ROT–ZEC) FW

First: *Notocaris tapscotti* (Woods, 1923), Lower Permian, South Africa.  
Last: *Paulocaris pachoecoi* Clarke, 1920, Upper Permian, Brazil.  
Comment: *Paulocaris* may be a pygocephalid (Briggs and Clarkson, 1990). These Permian taxa are in need of restudy.

**F. JEROMETICHENORIIDAE** Schram, 1978  
P. (KUN) FW

First and Last: *Jerometichenoria grandis* Schram, 1978, Kungur Stage, Irensky Horizon, Komai Republic, former USSR.
**Order** MYSIDA Boas, 1883 J. (CLV)-Rec. Mar./FW

**First:** Siriella antiqua Secretan and Riou, 1986, La Voulte-sur-Rhône, Ardeche, France.

**Comment:** Possible mysidan fossils are rare (Schram, 1986). Elder ungulatus Münster, 1839 and Francocaris grimmi Broili, 1917, Solnhofen Limestone, Bavaria, Germany, may belong here, but Schram (1986, p. 124) regarded them as ‘too poorly preserved to permit an unqualified assignment’.

**Extant**

**Order** EDRIOPHTHALMA Leach, 1815 (see Fig. 18.3)

**Suborder** ISOPODA Latreille, 1817

**Infra-order** FLABELLIFERA Sars, 1882

A number of flabelliferan isopods have been described from the fossil record and remain unassigned to families (e.g. Hessler, 1969).

**F. ARCHAEONISCIDAE** Haack, 1918 J. (TTH)-K. (?SEN) Mar.IFW

**First:** Archaeoniscus brodiei Milne Edwards, 1843, occurs in the Purbeck Beds of England, UK, the Serpulit of northwestern Germany and in the Abu Ballas Formation of Egypt (Barthel and Boettcher, 1978).

**Last:** Archaeoniscus texanus Wieder and Feldmann, 1992, ? Austin Chalk, Texas.

**F. CIROLANIDAE** Dana, 1853 K. (NEO)-Rec. Mar.

**First:** Cirolana enigma Wieder and Feldmann, 1992, Lakota Formation, South Dakota, USA.

**Comment:** A revision of species referred to Palaega might confirm older occurrences (Wieder and Feldmann, 1992).

**Extant**

**F. SEROLIDAE** Dana, 1853 ?Tr. (ANS)-Rec. Mar.

**First:** Anhelkocephalon handlirschi Bill, 1914, Triassic, Gres cl Voltzia, Alsace, France, may belong here (Schwebel et al., 1983).

**Extant**


**First:** Isopodites triasinus (Picard, 1858), Triassic, Germany.

**Extant**


**First:** Proidotea haugi Racovitza and Sevastos, 1910, Lower Oligocene–Middle Oligocene, Romania.

**Extant**

**Comment:** Anhelkocephalon handlirschi Bill, 1914, Triassic, Gres à Voltzia, Alsace, France shows some similarity to the Idoteidae as well as to the Serolidae (Schwebel et al., 1983).


**First:** Protamphisopus reichelti Gaessner and Malzahn, 1962, Upper Permian of Germany (Schram, 1986, p. 151).

**Extant**


**First:** Hesslerella shermani Schram, 1970, Francis Creek Shale, Mazon Creek, NE Illinois, USA.

**Last:** Palaeophreatoicus sojanensis Birshtein, 1962, Kazanian, Iva Gora, Soyama River, former USSR, or Palaeocrangon problematicus (von Schlotheim, 1820), Permian, Germany, and ? England, UK.

**Comment:** The relative ages of these Permian occurrences are not clear. The taxa were reviewed by Schram (1980).

**Infra-order** ONISCIDEA Latreille, 1803

**Section** DIPLOCHETA Vandel, 1957 F. LIGIIDAE Brandt, 1883 T. (PRB)-Rec. Terr.

**First:** Ligidium splendidum Strouhal, 1940, Baltic amber (Keilbach, 1982).

**Extant**

**Section** SYNOCHEATA Legrand, 1946

**Superfamily** TRICHONISCOIDEA Sars, 1899 F. TRICHONISCIDAE Sars, 1899 T. (PRB)-Rec. Terr.

**First:** Trichonisus Brandt, 1833, Upper Eocene (Hessler, 1969).

**Extant**

**Superfamily** ONISCOIDEA Dana, 1852 F. ONISCIDAE Brandt, 1851 T. (PRB)-Rec. Terr.

**First:** Oniscus Linne, 1758, Upper Eocene, Europe (Hessler, 1969). Oniscus convexus Koch and Berendt, 1854 occurs in the Baltic amber (Keilbach, 1982).

**Extant**


**First:** Protosphaeoniscus tertiarius Schmalfuss, 1980, Baltic amber.

**Extant**


**First:** Porcellio Latreille, 1804, including three species from Baltic amber (Keilbach, 1982).

**Extant**


**First:** Eubelum rusingaense Morris, 1979, Lower Miocene, Rusinga Island, Lake Victoria, Kenya.

**Infra-order** UNCERTAIN F. URDIDAE Kunth, 1870 J. (BTH)-K (APT) Mar.

**First:** Urda Münster, 1840 (Hessler, 1969; range from Sepkoski, 1982).

**Suborder** AMPHIPODA Latreille, 1816


**Infra-order** GAMMARIDEA Latreille, 1803


**Superfamily GAMMAROIDEA Leach, 1814**

*F. GAMMARIDAE* Leach, 1814

T. (RUP)–Rec. Mar./FW

First: *Jubeogammarus alsaticus* (Van Straelen, 1924), *Cammarus* sp., and *Condicio gammarus retzi* (Maikovsky, 1941), all Lower Oligocene, France (Karaman, 1984).

Comment: The familial placement of *Codicio gammarus* is uncertain (Karaman, 1984).

*F. ACANTHOGAMMARIDAE* Garjej, 1901

T. (MES)–Rec. FW

First: *Hellenis saltatorius* Petuninikov, 1914, Lower Miocene, Baku region, Caspian Basin or e.g. *Andrussovia bogacevi* Derzhavin, 1927, Middle Miocene, Caucasus (Karaman, 1984).

Comment: The familial placement of *Hellenis* is uncertain (Bousfield, 1982).

*F. PONTOGAMMARIDAE* Bousfield, 1977


First: *Prægemelina andrussovi* Derzhavin, 1927, and *P. archangelskii* Derzhavin, 1927, Middle Miocene, Grozny, Caucasus (Karaman, 1984).

Comment: The familial placement of *Prægemelina* and *P. archangelskii* is uncertain (see Schram et al., 1986).

**Superfamily HADZIOIDEA Karaman, 1932**

*F. MELITIDAE* Bousfield, 1973

T. (RUP)–Rec. Mar./FW


**Superfamily COROPHIOIDEA Dana, 1849**

*F. COROPHIIDAE* Dana, 1849

Q. (PLE)–Rec. Mar.

First: *Corophium volutator*, Quaternary, England, UK (Bousfield, 1982).

Comment: This record is based on a trace fossil.

**Order HEMICARIDEA Schram, 1981**

**Suborder CUMACEA Kröyer, 1846**


**Suborder TANAI DACEA Dana, 1853**

**Infra-order ANTHRACOCARIDOMORPHA Sieg, 1980**

*F. ANTHRACOCARIDIDAE* Schram, 1979

C. (VIS)–P. (UFI)–Tr. (RHT) Mar.

First: *Anthracocaris scotica* (Peach, 1882), Glencarthurm, Scotland, UK, Calciferous Sandstone Series. This taxon also occurs in the coeval Granton shrimp-bed, Edinburgh (Briggs et al., 1991).

Last: *Ophthalmapseudes rhenanus* (Malzahn, 1957), Kamp–Lintfort, Germany, Zechstein 1, Lower Permian.

Comment: Schram et al. (1986) pointed out that *Ophthalmapseudes* sp. (Végh and Bachmayer, 1965) from the RHT of Hungary, eventually may be determined to be more akin to *Jurapseudes*.


**Superfamily JURAPSEUDOIDEA Schram et al., 1986**

*F. JURAPSEUDIDAE* Schram et al., 1986


First and Last: *Jurapseudes friedericianus* (Malzahn, 1965) Middle Jurassic (Dogger, lineatum Zone), Germany, and *J. acutirostris* (Sachariowa-Kowatschewa and Bachmayer, 1965), Middle Jurassic (Dogger), Germany.

Comments: The relative stratigraphical levels of these two species are uncertain (see Schram et al., 1986).

**Infra-order APSEUDOMORPHA Sieg, 1980**

**Suborder SPELAEOPHRACEA Gordon, 1957**


**Infra-order TANAI DACEA Dana, 1853**

**Superfamily CRETITANAOIDEA Schram et al., 1986**

*F. CRETITANIDAE* Schram et al., 1986

K. (HAU) Mar.

First and Last: *Cretitainus giganteus* (Malzahn, 1979), Lower HAU, Hannover, Germany.

**Suborder SPELAEOPHACEA Gordon, 1957**


First and Last: *Acadiocaris novascotica* (Copeland, 1957), Mississippian, Canada.

**Class PHYLLOPODA Latreille, 1825**

**Subclass PHYLLOCARIDA Packard, 1879**

**Order ARCHAEOSTRACA Claus, 1888**

**Suborder CERATIOCARIDINA Clarke, 1900**

*F. CERATIOCARIDIDAE* Salter, 1860


First: *C.? scanica* (Moberg and Segerberg, 1906), Sweden, and *C. spp., Yukon* (additional less well-constrained records (Rolfe, pers. comm.) are listed in Bate et al., 1967).


*F. ECHINOCARIDIDAE* Clarke, 1900


*F. PEPHRICARIDIDAE* van Straelen, 1933

D. (FAM) Mar.

First and Last: *Pephr icaris horripilata* Clarke, 1898, Upper
Devonian, Chemung, Alfred, Allegany County, New York, USA (Rolfe, 1969).

F. ARISTOZOIDAE Gürich, 1929

First: Aristozoe Barrande, 1872, ?Lower Ordovician, Upper Silurian, Europe, Asia, Canada.


Suborder RHINOCARINA Clarke, 1900

F. RHINOCARIDIDAE Hall and Clarke, 1888

First and Last: Shale, Porter Creek, Cuyahoga County, Ohio, USA.

F. CANADASPIDIDA Novozhilov, 1960

F. RHABDOURAEDAE Schram and Malzahn, 1984

P. (GUA) Mar.

First and Last: Rhabdoura bentzi (Malzahn, 1958), Zechstein 1, Niederrhein, Germany.

Subclass CEPHALOCARIDA Sanders, 1955

Order BRACHYPODA Birseit, 1960

Comment: Dala, from the Upper Cambrian of Sweden, was once thought to be related to the Cephalocarida, but this view is no longer held (Müller, 1983).

Order LIPOSTRACA Scourfield, 1926

D. (FRA) FW

First and Last: Lepidocaris rhyniensis Scourfield, 1926, Rhynie Chert, Aberdeenshire, Scotland, UK.

Subclass SARSOSTRACA Tasch, 1969

Order ANOSTRACA Sars, 1867

F. ARTEMIIDAE Grochowski, 1896

Q. (PLE)–Rec. FW


Extant

F. BRANCHIPODIDAE Simon, 1886

?T. (PRB)–Rec. FW


Extant

Comment: Schram (1986, p. 375) argued that the Palaeozoic records of Anostraca (Tasch, 1969) are unconvincing, although he illustrated (p. 376) a possible example from the Upper Silurian Kokomo Limestone (LUD/PRD) of Indiana. An undetermined anostracan has been described from the 7BRM/APT Koonwarra Fossil Bed, Victoria, Australia (Jell and Duncan, 1986). Schram (1986) regarded the undescribed anostracan from the Miocene Barstow Formation of California (Palmer, 1957) as representing a new family.

Subclass CALMANOSTRACA Tasch, 1969

Order NOTOSTRACA Sars, 1867

F. TRIOPSIDAE Keilhack, 1910 C. (STE)–Rec. FW

First: Triops ornatus (Goldenberg, 1873), Stephanian, Saarbrücken, Germany (Tasch, 1969).

Extant

Comment: Schram (1986, p. 360) remarked that fossil notostracans ‘are few, incompletely known, and essentially indistinguishable from the modern types’.

Order KAZACHARTHRAN Novozhilov, 1957

F. KETMENIIIDAE Novozhilov, 1957 Tr. (u.)–J. (l.)


Last: Ketenema schultzi Chernyshev, 1940, Almatium gusevi Chernyshev, 1940, Illeia spinosa Chernyshev, 1940, Jeanrogerium sornayi Novozhilov, 1959, Kungulja tchakabaei Novozhilov, 1957, Kysyllamia tchiliensis Novozhilov, 1957 and Panacanthocaris ketmenia Novozhilov, 1957, all Lias,
Ketmen Mountains, Kazakhstan, former USSR (Tasch, 1969).

Order CONCHOOSTRACA Sars, 1867

Suborder LAEVICAUDATA Linder, 1945
K. (l.)—Rec.

This suborder is incorrectly called 'Laeviscaudata' in Tasch (1969), and 'Laeviscauda' in Schram (1986) (see Fryer, 1987).

F. LYNECEIDAE Stebbing, 1902 K. (l.)—Rec. FW

Superfamily SPINICAUDATA

This suborder is called Spinicauda in Schram (1986).

Superfamily LIMNADIOIDEA Baird, 1849
F. LIMNADIIDAE Baird, 1849 C. (BSK/MOS)—Rec. FW

Superfamily CYZICOIDEA Baird, 1849
F. CYZICIDAE Stebbing, 1910 D. (l.)—Rec. FW

F. ASMUSSIIDAE Kobayashi, 1954 D. (l.)—K. (u.) FW


Superfamily ESTHERIELLOIDEA Kobayashi, 1954
F. ESTHERIELLIDAE Kobayashi, 1954 C. (BSK/MOS)—K. (NEO) FW

Comment: Tasch (1969, p. 157) listed two subgenera from the Upper Carboniferous, but their relative ages are not clear.


Superfamily LEAIIOIDEA Raymond, 1946
D. (EIF/GIV)—K (NEO) FW

Last: Japanoleaia rectangula (Yokahama, 1894), Neocomian, Yuasa, Japan (Tasch, 1969).

Superfamily VERTEXIOIDEA Kobayashi, 1954
F. VERTEXIIDAE Kobayashi, 1954 C. (BSK/MOS)—Tr (u.) FW


Comment: Tasch (1969) recorded the range of this family as Lower Carboniferous—Upper Triassic, but listed no genus with a range older than Upper Carboniferous (Westphalian); Schram (1986) followed Tasch (1969).

F. LIMNADOPSIDAE Tasch, 1961 C. (l.)—Rec. FW

Extant Comments: Tasch (1969, p. 162) regarded Belgalimnadiopsis Novozhilov, 1958 from the Lower Devonian of Belgium, as 'inadequately documented; doubtful'.

F. PEMPHILIMNADIOPSIDAE Tasch, 1961 C. (u.) FW
First and Last: Pemphelimnadiopsis ortoni (Clarke, 1900), Pennsylvanian, Carolton, Ohio, USA (Tasch, 1969).

F. IPSILONIIDAE Novozhilov, 1953 D.—K. (ALB/APT) FW (see Fig. 18.4)


Order CLADOCERA Latreille, 1829

Suborder EUCLADOCERA Erikson, 1932

Superfamily DAPHNOIDEA Straus, 1820 (= Anomopoda)

F. DAPHNIIDAE Straus, 1820 K. (NEO)—Rec. FW
First: Ephippia from the early Cretaceous of Mount Ukha, Mongolia, are attributed to this family (Smirnov, 1992).

Comment: Daphniid carapaces occur in the Triassic, West Africa (Tasch, 1969).


F. MOINIDAE Goulden, 1968 K. (NEO)—Rec. FW
First: Ephippia from the early Cretaceous of Mount Ukha, Mongolia, are attributed to this family (Smirnov, 1992).

Comment: Daphniid carapaces occur in the 7BRM/APT Koonwarra Fossil Bed, Victoria, Australia (Jell and Duncan, 1986). Other occurrences of daphniid ephippia are reviewed by Fryer (1991).

F. PROCYHDORIDAE Smirnov, 1992 K. (NEO) FW

Order PENTASTOMIDA Rudolphi, 1819

Class MAXILLOPODA Latreille, 1817

?Order PENTASTOMIDA Rudolphi, 1819 Terr.

The affinities and status of the parasitic pentastomids are uncertain. Some authorities assign them to a separate phylum, but there is evidence that they are highly modified crustaceans (Grygier, 1983; Abele et al., 1989). An unnamed marine form resembling recent parasitic Pentastomida has
been described from the Tremadoc of Öland, Sweden (Andres, 1989).

**Order** ORSTENOCARIDA, Müller and Walossek, 1988

**First and Last:** *Bredocaris admirabilis* Müller, 1983, *Peltura* Zone, Alum Shale Formation, Västergötland, Sweden.

**Subclass** COPEPODA Milne Edwards, 1840

**Order** HARPACTICOIDA Sars, 1903

**Suborder** OLIGOARTHA Lang, 1948

**Infra-order** PODOGENNONTA Lang, 1948

**Superfamily** CLETODOIDEA Lang, 1948

**First:** *Cletocamptus* Schmankevitsch, 1875, Middle–Upper Miocene, Mojave Desert, California, USA (Palmer, 1960).

**Extant**

**Order** MONSTRILLOIDA Sars, 1903

**Order** CYCLOPOIDA Burmeister, 1834

**First and Last:** *Genus undet.* Middle–Upper Miocene, Mojave Desert, California, USA (Palmer, 1960).
**Class Thecostraca** Gruvel, 1905

Since the publication of *The Fossil Record* (Harland et al., 1967) and of the *Treatise* Vol. R (Newman et al., 1969), there have been a number of reviews of the systematics of some, or all, of the groups which constitute the cirripedes in the widest sense of the term. These include the classifications of Bowman and Abele, 1982; Tomlinson, 1969; Newman and Ross, 1976; Zevina, 1980; Zullo, 1983; Buckeridge, 1983; Schram, 1982, 1986; and Newman, 1987. Where they overlap, the various classifications use broadly similar lists of families and differ principally in the range of forms included within the Cirripedia, and the taxonomic status accorded to this and to other groups within the higher-order classification. Unless otherwise stated the classification used here follows that of Schram (1986) with modifications based on Newman (1987). The Order Apoda Darwin, 1854, which had an uncertain status in earlier classifications, is no longer recognized (see Newman, 1982, p. 200).

**Subclass FASCETOTECTA** Grygier, 1984

*First: Kabatarina pattersoni* Cressey and Boxshall, 1989, Santana Formation, Serro do Araripe, Ceara, Brazil.

*Comment: These parasitic copepods were found in the gills of the teleost fish *Cladocyclus gardneri* Agassiz.*

**Order Siphonostomatoida** Thorell, 1859

*F. Dichelethiidiae* Dana, 1853

*First: Kabatarina pattersoni* Cressey and Boxshall, 1989, Santana Formation, Serro do Araripe, Ceara, Brazil.

*Comment: These parasitic copepods were found in the gills of the teleost fish *Cladocyclus gardneri* Agassiz.*

**Class Thecostraca** Gruvel, 1905

The position of the enigmatic Y-larvae (Fascetotecta) is uncertain’ (Schram, 1986, p. 539). They have no fossil record.

**Extant**

**Subclass ASCOTHORACICA** Lacaze-Duthiers, 1880

No body fossils have been attributed to the Ascothoracica but some trace fossils attributed to the group have been recorded from the Upper Cretaceous. Many characters of the Order are interpreted as primitive and may indicate that the origins of the group lie far back in geological time (Schram, 1986; Newman, 1982, 1987; see Grygier, 1990 on similarity of nauplii to those of Cirripedia).
**Order SYNAGOGOIDA** Wagin, 1976

**Comments:** Unnamed conical borings in the tests of the echinoid *Echinocorys* were considered by Madsen and Wolff (1965) to be identical to the borings of the extant genus *Ulophysema*. The material came from the Upper Cretaceous (TUR—MAA) of north Jutland. There is no other fossil record.

**Order LAUROIDIDA** Wagin, 1976

**Comments:** Gall-like deformations in Cretaceous octocorals have been interpreted as the cysts of ascothoracic chitinous body fossil has also been recorded from the Upper Cretaceous (CMP-MAA), (Voigt, 1959, 1967) but there is no other fossil record.

**Subclass RHIZOCEPHALA** F. Müller, 1862
The wholly parasitic rhizocephalans have no known fossil record. The classification and evolutionary relationships within the group, which includes seven families in two orders, are not clear and there are a number of genera of uncertain status since their lack of a kentrogon stage has yet to be properly confirmed. Relationships with other cirri pedes sin. lato were discussed by Newman (1982, 1987) and could imply that the group has had a long history but, as noted by Schram (1986), there is also the possibility that they are polyphylectic. Two genera are exclusively fresh water in their occurrence.

**Subclass CIRRIPEEDIA** Burmeister, 1834

**Superorder ACROTHORACICA** Gruvel, 1905
The fossil record of the Acrothoracica is dominated by trace fossils which have been linked with the superorder, and in some cases with families on the basis of burrow morphology. Burrow characters, including the presence or absence of calcareous cement deposits, have also been used to recognize two ichnofamilies (Zapfillididae and Rogellididae). More recently Grygier and Newman (1985) compared some described traces with extant forms and showed that in some cases a calcareous rostral plate, which is an apparently primitive feature of some species in this superorder, may be preserved; as they pointed out, this preservation of body parts has considerable nomenclatural significance. The palaeontology of the group undoubtedly needs extensive review in the light of their discoveries. A chitinous body fossil has also been recorded from the Upper Cretaceous (Turner, 1973).

**Order PYGOPHORA** Berndt, 1907

**First:** *Zapfella* sp. in platyceratid gastropods, Lower Devonian, ?New Scotland Formation, Athens, New York (Baird et al., 1990).

**Order APYGOPHORA** Berndt, 1907

**Comments:** Tomlinson’s (1969) recognition of Carboniferous trypetesids has been shown to be erroneous by Seilacher (1969) who considered that trypetesid burrowing strategies evolved in the early Mesozoic and illustrated burrows, with lateral expansions, from the Trochitenkalk of Crailsheim in Germany.

**Superorder THORACICA** Darwin, 1854

**Order PEDUNCULATA** Lamarck, 1818

**Suborder CYPRILEPADOMORPHA** Newman et al., 1969

**First and Last:** *Cypripleis holmi* Wills, 1962, Schicht K, Oesel, Estonia, former USSR.

**Suborder HETERALEPADOMORPHA** Newman, 1987

**Comments:** *Priscanserramarinus barnetti* Collins and Rudkin, 1981, from the Middle Cambrian Burgess Shale of British Columbia, has been compared with the heteralepadids. Briggs (1983) urged caution in the interpretation of this fossil. The family has no other fossil record. The suborder includes five other extant families.

**Suborder PRAELEPADOMORPHA** Tschernyshew, 1930

**First:** *Praeles papwortii* Tschernyshew, 1930, Donetz and Kusnetz Basins, former USSR.

**Comments:** Two other species have also been recorded from rocks of a similar age in the former USSR. There is no other fossil record.

**Suborder LEPADOMORPHA** Pilsbry, 1916
The name Lepadomorpha is used by Newman (1987) and here in a more restricted sense than in most previous classifications.


**First:** *Trilasmis (Poecilasma) curryi* Withers, 1953, Middle Barton Beds, Barton, Hampshire, England, UK.  Extant


**First:** *Lepas stenzeli* Withers, 1953, Claiborne Group, Texas, USA.  Extant


**First:** *Oxynaspis eocenica* (Withers, 1953), Upper Bracklesham Beds, Selsey Bill, Sussex, England, UK (Withers, 1953).  Extant
Arthropoda (Crustacea excluding Ostracoda)

F. DOSIMIDAE Memmi, 1983
First: Dosima latiscutis Zullo, 1973, Puente Formation, Los Angeles, California, USA (Weisbord, 1980).

Comments: The family is here recognized and separated from the Lepadidae (in contrast to Schram, 1986). However, Memmi’s (1983) transfer of the Dosimidae and Oxynaspididae to the Scalpelloidea (= Scalpellomorpha herein) is not followed.

Suborder IBLOMORPHA Leach, 1825
First: Praelepas damrowi Schram, 1975 from the Mazon Creek fauna has been reinterpreted, placed in the new genus Illilepas, and suggested to have affinities with the iblids (Whyte, in prep.).

Suborder SCALPELLOMORPHA Pilsbry, 1916
First: Pabulum spathiforme Whyte, 1976 from the upper Brigantian (c. (VIS)) of Yorkshire, England, UK, and Fife, Scotland, UK, may not be a barnacle. The next record of a scalpellid is ?Neolepas augurata (Buckeridge and Grant-Mackie, 1985), upper Aratauran to lower Ururoan J. (SIN/PLB), New Caledonia. If the acrothoracic rostral plate is derived from a scalpellid ancestor, then a pre-early Devonian divergence is implied for the two groups.

Suborder STRAMENTIDAE Withers, 1920
First: Stramentum syriacum (Dames), 1874, ?Albian, Lebanon (Withers, 1935).
Last: Loriculina fosteri Buckeridge, 1983, Gingin Chalk, Molecape Hill, Western Australia.

Order SESSILIA Lamarck, 1818
Suborder BRACHYLEPADOMORPHA Withers, 1923
First: Pycnolepas tithonica (Withers), 1935, Red and White Limestone, Tithonian, Stramberg, Moravia, Czechoslovakia (Withers, 1935).

Suborder VERRUCOMORPHA Pilsbry, 1916
First: Proverruca nodosa (Withers, 1935), Chalk detritus (probably Chalk Marl), Charing, Kent, England, UK.

Extant

Suborder BALANOMORPHA Pilsbry, 1916
Superfamily CHIONELASMATOIDEA Buckeridge, 1983
First: Chionelasmus darwini (Pilsbry), Kaiatan T. (BRT), New Zealand (Buckeridge, 1983).

Extant

Superfamily CORONULOIDEA Newman and Ross, 1976
First: Pachydiadema cretaceum (Withers), 1£6, Sweden (Withers, 1935).

Extant
First: Eopopeia eosimplex Buckeridge, 1983, Port Willunga Beds (Aldingan), South Australia.

Superfamily BALANOIDEA Leach, 1817
First: Solidobalanus spp., McBean Formation, Claibornian, Georgia, USA (Zullo, 1984).

Extant

F. BALANIDAE Leach, 1817 (BRT)—Rec.

First: Megabalanus tintinnabulum (Lineaus), 1767, Hungary (Davadie, 1963).

Class THYLACOCEPHALA Pinna, Arduini et al., 1982

The Thylacocephala are generally regarded as a separate extinct class of crustaceans. Their nature, assigned taxa and higher taxonomy are reviewed by Rolfe (1985), Arduini and Pinna (1989) and Schram (1990) respectively. A familial taxonomy has yet to be attempted; hence the ranges are given for orders.

Order CONCaviCARida Briggs and Rolfe, 1983

First: Unnamed species from the Lower Silurian Brandon Bridge Formation of Wisconsin, USA (Mikulic et al., 1985a,b).

Last: Protozoa damesi Roger, 1946, P. hilgendorfii Dames, 1886, Pseudoerichthus cretaceus Dames, 1886, Lebanon.

Order CONCHyloCARIDA Secretan, 1983

?€ (CRF)—J. (TTH) Mar.

First: Silesicaris nasuta Gürich, 1926, Lower Cambrian, Poland.

Last: Clausocaris lithographica (Oppenheim, 1888), Solfhofen Limestone, Bavaria, Germany.

Comment: The assignment of Silesicaris here (Arduini and Pinna, 1989; Schram, 1990) is based on carapace alone, and may not be reliable.

REFERENCES


Barthel, K. W. and Boettcher, R. (1978) Abu Ballas Formation (Tithonian/Berriasian; Southwestern Desert, Egypt) a significant liostratigraphic unit of the former 'Nubian Series'. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, 18, 153–66.


Animals: Invertebrates


Walossek, D. and Müller, K. J. (1990) Upper Cambrian stem-
The classification of the Ostracoda is in a state of flux; a revision of the *Treatise on Invertebrate Paleontology*, Part Q, is presently being undertaken under the co-ordination of the two senior contributors. Some minor families are excluded herein and not all higher taxonomic relationships have been elucidated prior to the publication of this revision. The classification herein is based on Moore (1961), Hartmann and Puri (1974) and the present contributors' observations and those of unspecified Part Q revision authors. Classification schemes adopted by colleagues in the former USSR are in many cases radically different from that outlined herein; for example, see the 'Treatises' on Cainozoic (Nikolaeva et al., 1989) and Palaeozoic (Abushik et al., 1990) ostracods, respectively (the Mesozoic volume is in press). In particular, Russian colleagues often recognize many more families of ostracods than we identify herein.

The Ostracoda are regarded as a distinct Class of the Crustacea, distinguished as they are by their bivalved carapace which is pierced by pores and into which the entire animal can be withdrawn when the carapace is closed.

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**Class** OSTRACODA Lairesille, 1802

**Order** BRADORIIDA Raymond, 1935

The taxonomy of this heterogeneous (almost certainly polyphyletic) group is particularly contentious; many taxa which have been assigned to the group may belong outside the Ostracoda. The groupings and ranges given below are very conservative by some standards; in particular, large numbers of Chinese taxa (genera) have yet to be satisfactorily assessed and assigned with any degree of confidence to their respective families.

**F. BRADORIIDAE** Matthew, 1902

First: e.g. *Bradoria scrutator* Matthew, 1899, CRF, Nova Scotia, Canada.


**Intervening:** STD.

**F. HIPPONICHARIONIDAE** Sylvester-Bradley, 1961

First: e.g. *Hipponicharion eos* Matthew, 1886, St John Group, New Brunswick, Canada.


**Intervening:** STD.

**F. CAMBRIIDAE** Li, 1975

First: e.g. *Cambria sibirica* Neckaja and Ivanova, 1956, ATB, eastern Siberia, former USSR.

Last: All species are of Lower Cambrian age.

**F. KUNMINGELLIDAE** Huo and Shu, 1985

First: e.g. *Kunmingella maxima* Huo, 1956, CRF (Chungchusso Formation), Yunnan Province, China.

Last: All species are of early Cambrian age.

**F. HAOIIDAE** Shu, 1990

First: e.g. *Uskarella prisca* Koneva, 1978, CRF, Kazakhstan.

Last: *Septadella jackmanae* Stubblefield, 1933, TRE, Gloucestershire, England, UK.

**Intervening:** Rare and discontinuous.

**F. SVEALUTIDAE** Öpik, 1968


Last: e.g. *Anabarochilina ventriculosa* Abushik, 1960, MER, eastern Siberia, former USSR.

**F. COMPTALUTIDAE** Öpik, 1968

First: e.g. *Aristaluta gutta* Öpik, 1961, Devoncourt Limestone, Boomerangian, Queensland, Australia.
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**Fig. 19.1**

**Last:** All species are of Middle Cambrian age.

**Order** PHOSPHATOCOPIDA Müller, 1964

**Suborder** VESTROGOTHIINA Müller, 1982

**F. VESTROGOTHIIDAE** Kozur, 1974

**First:** Vestrogothia longispinosa Kozur, 1974, erratic boulder, STD, Sellin, Rügen, Germany.

**Last:** Vestrogothia spinata Müller, 1964, Peltura minor Zone, Sweden.

**Intervening:** MNT.

**F. FALITIDAE** Müller, 1964

**First:** e.g. Falites fala Müller, 1964, Agnostus and Olenus zones, Sweden.

**Last:** Falites angustiduplicata Müller, 1964, Peltura scarabaeoides Zone, Sweden.

**F. OEPIKALUTIDAE** Jones and McKenzie, 1980

**First:** e.g. Zepaera rete Fleming, 1973, Beetle Creek Formation, Templetonian 'stage', Duchess area, Queensland, Australia.

**Last:** e.g. Oepikaluta dissuta Jones and McKenzie, 1980, Current Bush Limestone, Undillan 'stage', Georgina Basin, Australia.

**F. MONASTERIIDAE** Jones and McKenzie, 1980

**First and Last:** Monasterium oepiki Fleming, 1973, Beetle
Creek Formation, Templetonian ‘stage’, Duchess area, Queensland, Australia.

**Suborder HESSLANDONINA Müller, 1982**

**F. HESSLANDONIDAE Müller, 1964**

€ (LEN–MNT) Mar.


*Last:* e.g. Hesslandona unisulcata Müller, 1982, Agnostus pisiformis Zone, Västergötland, Sweden.

**Intervening:** ?SOL, MEN.

**Order LEPERDITICOPIDA Scott, 1961**

**F. LEPERDITIIDAE Jones, 1856**


*First:* Eoleperditia ambiguus Berdan, 1976, Kanosh Shale, Pogonip Group, Chazyan, Utah, USA.

*Last:* Probably Herrmannina famesiana Schevtschow, 1971, upper Fam, Tataria, near Perm, former USSR. Abushik (1979) also records Moellerita from the Upper Devonian of the Siberian Platform, former USSR.

**Intervening:** LLN-RFS.

**Comments:** The records from the ?Upper Cambrian of the USA of supposed leperditiids (Frederickson, 1946; Palmer, 1954) are not yet confirmed by modern studies, and neither is the record of ‘Lower’(= Middle) Ordovician leperditiids from Greenland (Poulsen, 1937). Similarly, the records of leperditiids from the basal part of the Ordovician (Arenig ?) of Oklahoma (e.g. Harris, 1957, 1960) need to be reappraised before they can be used with confidence in modern stratigraphy.

**F. ISOCHILINIDAE Swartz, 1949**

O. (?ARG)–D. (u.) Mar.

*First:* Tirisochilina juabaria Berdan, 1976, Juab Limestone, Pogonip Group, Chazyan, Utah, USA.

*Last:* Abushik (1979) says that Hogmochilina occurs in the Upper Devonian of Spitsbergen. This refers to H. elliptica (Solle, 1935).

**Intervening:** ?LLN1–D2.

**Order ERIDOSTRACODA Adamczak, 1961**

The taxonomic position and rank of this group is particularly controversial. Some opinions hold that the ‘Eridostraça’ may be an extinct group of marine branchiopods; others, that they are a part of the ostracod group Palaeocopida.

**F. ERIDOCONCHIDAE Henningsmoen, 1953**


*First:* Conchoprimitia gammae Opik, 1935, Toila Formation, Ontik Regional ‘series’, Estonia, former USSR.

*Last:* Conchoprimitia tolli (Bonnema, 1909), Kukruse Regional ‘stage’, middle part of the Viru ‘series’, Estonia, former USSR.

**Intervening:** LLN–RAW.

**Superfamily HOLLINACEA Swartz, 1936**

**F. EUPRIMITIIDAE Henningsmoen, 1953**


*First:* Euprimia novum Sarv, 1959, Kunda ‘stage’, Baltoscandia.


**Intervening:** LLN–RAW.

**F. TVAERENELLIDAE Jaanusson, 1957**


*First:* Tvarenella modesta Sarv, 1957, Kunda ‘stage’, Baltoscandia.

*Last:* Eoaquapulex frequens (Steusloff, 1894), upper (Porkuni) part of Harju ‘series’, Baltoscandia.

**Intervening:** LLN–RAW.

**F. CTENONOTELLIDAE Schmidt, 1941**


*First:* Tallinnellina palmata Krause, 1889, middle part of Ontik ‘series’, Baltoscandia.
Last: *Steustlophia neglecta* Sarv, 1959, upper (Rakvere) part of Viru 'series', Baltoscandia.

Intervening: LLN₁—MRB.

**F. TETRADELLIDAE** Swartz, 1936


First: *Glossomorphites bocki* (Opik, 1935), middle part of Ontiik 'series', Baltoscandia.

Last: *Tetradella plicatula* (Krause, 1892), top (Porkuni) part of the Harju 'series', Baltoscandia.

Intervening: LLN₁—RAW.

**F. SARVINIDAE** Schallreuter, 1966


First: *Egorovella dejecta* Ivanova, 1959, Lower Volcinsk Formation, Middle Ordovician, Siberia, former USSR.

Last: *Egorovella poricostata* (Kanygin, 1965), upper (Nabala) part of Viru 'series', Baltoscandia.

Intervening: LLN₁—RAW.

**F. EGOROVELLIDAE** Schallreuter, 1966


First: *Egorovella aëctica* Ivanova, 1959, lower Volcinsk Formation, Middle Ordovician, Siberia, former USSR.

Last: *Egorovella pericosata* Kanygin, 1965, upper Kalycanskian Formation, Middle Ordovician, Siberia, former USSR.

**F. SOANNELLIDAE** Kanygin, 1977 O. (l./m.) Mar.

First: *Fuscinullina pectinata* Kanygin, 1967, Sienskian Formation, Lower Ordovician, Cher Mountains, Siberia, former USSR.

Last: *Sibiretella furcata* Kanygin, 1967, Kalycanskian Formation, Middle Ordovician, Cher Mountains, Siberia, former USSR.

**F. DOLBORELLIDAE** Melnikova, 1976

O. (l./m.)—S. (?TEL) Mar.

First: *Planiprimites solitius* Kanygin, 1967, Sienskaya Formation, Lower Ordovician, Cher Mountains, Siberia, former USSR.

Last: *Costaegera hastata* Abushik, 1960, upper LLY, Siberia, former USSR.

Intervening: O. (u.)—?FRO.

**F. HOLLINIDAE** Swartz, 1936


First: *Aloculatia hartmanni* Schallreuter, 1976, Skagen Limestone, Baltoscandia.


Intervening: ?MRB—ASS.

**F. HOLLINELLIDAE** Bless and Jordon, 1971

S. (LDF/PRD)—Tr. (?GRI) Mar.

First: *Hollinmella originalis* Lundin, 1965, Herryhouse Formation, Oklahoma, USA.

Last: *Hollinmella* sp. of Bless and Jordon 1972, lowermost Triassic, Australia.

Intervening: GED—7TAT.

**Superfamily** PRIMITIOPSAACEA Swartz, 1936

F. PRIMITIOPSISIDAE Swartz, 1936


First: *Anisocyamus multiplorata* (Harris, 1957), Mdlsh Formation, Oklahoma, USA.

Last: *Coryellina indicata* Sohn, 1954, Leonard Formation or Word Formation, Texas, USA.

Intervening: LLN₁—ART.

**F. VENTRIGYRIDAE** Gründel, 1977


First: *Ventrigrinus sulcatus* (Kanygin, 1965), Sakkyryskaya Svita (lower part), NE Siberia, former USSR.

Last: *Zenkopsis enormis* (Zenkova, 1975), Demidske Beds, Ural Mountains, former USSR.

Intervening: LLN₁—LDF.

**F. BUBNOFFIOSIDAE** Schallreuter, 1964


First: *Bubnoffiosis bubnoffi* Schallreuter, 1964, middle (Idavere/Johvi) part of Viru 'series', Baltoscandia.

Last: *Lembittites incognitus* (Sidaraviene, 1975), upper (Nabala) part of Viru 'series', Baltoscandia.

Intervening: LON—ACT.

**Superfamily** BEYRICHIACEA Matthew, 1886

F. CRASPEDOBOLBINIDAE Martinsson, 1962


First: *Bolbineosula pineaulti* Copeland, 1974, Becsce Formation, Anticosti Island, Canada.

Last: *Copelandella novascotia* (Jones and Kirkby, 1884), Horton Bluff Formation, lower Mississippiian, Nova Scotia, Canada (Bless and Jordon, 1971).

Comments: Other Lower Carboniferous, possibly amphitoxotine (?craspedobolinid) taxa are *Malinia spinosa* Jones, 1989, Bonaparte Basin, Australia and *Armilla sibirica* Bushina, 1975, Kolymian Basin, former USSR.

Intervening: IDW—D. (?u.).

**F. TREPOSELLIDAE** Henningsmoen, 1954


First: *Loutriella jupiterensis* Copeland, 1974, Becsce Formation, Anticosti Island, Canada.


Intervening: IDW—FRS.

**F. BEYRICHIIDAE** Matthew, 1886

O. (ASH)—C. (IVO) Mar.

First: *Fallaticella schaeferi* Schallreuter, 1984, Öjlemyrflint erratic boulder, ASH, Gotland, Sweden (Schallreuter, 1989). This is the only known pre-Silurian beyrichiacean species.

Last: *Pseudoleperditia tuberculifera* Schneider, 1956 (sensu Ivanova et al., 1975; see Jones, 1989, p. 29), Kizel Horizon, upper Tournaisian, south Urals, former USSR.

Comments: Inclusion in this family of a number of possibly (i.e. very diffusely) dimorphic, more *Ochseaarina*-like and possibly paraparchitid-like Russian genera (e.g. see Tschigova, 1977 and Abushik et al., 1990) would extend its stratigraphical range to younger horizons in the Carboniferous; however, based on evidence from literature sources alone, the taxonomic position of such forms remains uncertain.

Intervening: RHU—HAS.

**Superfamily** NODELLACEA Becker, 1968
F. NODELLIDAE Zaspelova, 1952


Superfamily KIRKBYACEA Ulrich and Bassler, 1906
F. AMPHISSTITIDAE Knight, 1928


Intervening: EIF–ROT.

F. ARCYZONIDAE Kesling, 1961

First: Chironiptrum bilinearis Copeland, 1977, Delorme Formation, District of McKenzie, NW Canada.
Last: Carinaknightina carinata Sohn, 1970, Mianwali Formation, west Pakistan.

Intervening: EMS–?CHD.

F. KIRKBYIDAE Ulrich and Bassler, 1906
D. (SIG)–Tr. (SCY) Mar.

First: Villozona aspera (Polenova, 1974), Valneviskii Horizon, Novaya Zemlya, former Arctic USSR.
Last: Carinaknightina carinata Sohn, 1970, Mianwali Formation, west Pakistan.

Intervening: EMS–?ZEC.

F. KELLETTINIDAE Sohn, 1954

First: Kindella sp. 1 of Becker and Wang, 1992, Bojiwan Formation, Guizhou Province, China.
Last: e.g. Kellettina vidriensis Hamilton, 1942, Leonard Formation or Word Formation, Glass Mountains, Texas, USA.

Intervening: ARU–ART.

Superfamily TRIBOLBINACEA Sohn, 1978
F. TRIBOLBINIDAE Sohn, 1978
S. (LDF)–P. (ZEC) Mar.

First: ?Kolmodinia grandis (Kolmodin, 1869), Eke Beds, Gotland, Sweden.

Intervening: C. (I., u.), ROT.

Superfamily DREPANELLACEA Ulrich and Bassler, 1923

Many authors hold that the six ‘drepellancean’ families listed below are not palaeocopes; rather, that they constitute a major separate taxonomic group, the Order Binodicipa Schallreuter, 1972, containing two superfamilies, the Drepellanacea (families Drepellidae, Bolliidae and Quadrijugatoridae) and Aechminacea (families Aechminidae, Spinigeritidae and Richinidae).

F. DREPANELLIDAE Ulrich and Bassler, 1923

Last: Duplexibollia duplex (Krause, 1892), upper (Porkuni) part of Harju ‘series’, Baltoscandia.

Intervening: ARG–RAW.

F. BOLLIDAE Boucek, 1936

First: Klimphores kuempers Schallreuter, 1992, middle part of Ontik ‘series’, Baltoscandia.

Intervening: LLN1–KAZ.


Last: Harpabollia harparum (Troedsson, 1918), upper (Porkuni) part of Harju ‘series’, Baltoscandia.

Intervening: ?COS–RAW.

F. AECHMINIDAE Boucek, 1936
O. (LLO)–C. (?VRK) Mar.

Last: Mammoïdes mamillatus Bradfield, 1935, Deese Formation?, middle Pennsylvanian, Oklahoma, USA.

Intervening: ?COS–?MEL.

F. SPINIGERITIDAE Schallreuter, 1980


Intervening: ?PUS–?TEL.


Last: Richina selenicristata Stover, 1956, Windom Shale Member, Moscow Formation, Hamilton Group, New York, USA.

Intervening: LLN1–?EIF.

Order PALAEOCOPIDA?

Superfamily BARYCHILINACEA Ulrich, 1894

Last: Monotiopeura auriculata Guber and Jaanusson, 1964, Whitewater Formation, Richmond Group, Ohio, USA.

Intervening: LLN1–?PUS.

Comment: This family has traditionally been assigned to the Kloedenellacea (=Platycopina); in his revision of that superfamily Adamczak (1991) maintains that the monotiopleurids (and the platycopids) are palaeocopes.

# Animals: Invertebrates

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**Fig. 19.2**

First: *Lomatopisthia mclishi* (Harris, 1957), Mclish Formation, Oklahoma, USA.

Last: *Lomatopisthia auricula* (Harris, 1957), Pooleville Member, Bromide Formation, upper CRD, Oklahoma, USA.

Intervening: Lower CRD—lower CRD.

Comment: Adamczak (1991) considers that this family is synonymous with the Monotiopleuridae.

**F. BARYCHILINIDAE Ulrich, 1894**

S. (FRO)—P. (ART) Mar. (Fig. 19.2)

First: *Neckajatia modesta* (Neekaja, 1958), Svenconys Formation, Lithuania, former USSR.

Last: *Ellipsella obliqua* Coryell and Rogatz, 1932, Arroyo Formation, Texas, USA.

Intervening: IDW—SAK.

**Superfamily** UNCERTAIN

F. KIRKBYELLIDAE Sohn, 1961


Intervening: PRD—?VRK.

F. CARDINIFERELLIDAE Sohn, 1953

C. (?PND—ALP) Mar.

First: *Cardiniferella bowsheri* Sohn, 1953, Helms Formation, Chesterian, Texas, USA.

Last: *Cardiniferella ringwoodensis* (Harris and Jobe, 1956), Manning Zone, Chesterian, Oklahoma, USA.
**Fig. 19.2**

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<th>Arthropoda (Crustacea: Ostracoda)</th>
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### F. SCROBICULIDAE Posner, 1951

**Order** LEIOCOPA Schallreuter, 1973

**Superfamily** APARCHITACEA Jones, 1901

**Family** SCROBICULIDAE Posner, 1951

**D. (EMS) - P. (TAT) Mar.**

**First:** *Dorcatatum* sp. 3 of Feist and Groos-Uffenorde 1979, Calcaires à polyplis siliceux, Montagne Noire, France.

**Last:** *Placidea lutkevichi* (Spizharsky, 1939), Tatarian, Russian Platform, former USSR.

**Intervening:** EIF - KAZ.

### F. LEPERDITELLIDAE Ulrich and Bassler, 1906

**O. (ARG) - CRD Mar.**

**First:** *Leperditella valida* Harris, 1957, Joins Formation, Oklahoma, USA.

**Last:** *Leperditella tumida* (Ulrich, 1892), Pooleville Member, Bromide Formation, upper CRD, Oklahoma, USA.

**Intervening:** LLN1 - lower CRD.

**Comment:** This family is herein tentatively referred to the Palaeocopida; its systematic position is problematic.

### F. APARCHITIDAE Jones, 1901

**O. (ARG) - D. (EMS) Mar.**

**First:** *Longidorsa rectelloides* Schallreuter, 1985, Lower Ordovician (BIII-B; upper ARG), Baltoscandia.


**Intervening:** LLN1 - SIG.

### F. SCHMIDTELLIDAE Neckaja, 1966

**O. (LLN1) - D. (GED) Mar.**

**Superfamily** PARAPARCHITACEA Scott, 1959

**F. APARCHITIDAE Scott, 1959**

**D. - P. Mar.**

The systematics of this group is in an extremely confused...
state. The family occurs in the Devonian, Carboniferous (Mississippian and Pennsylvanian) and Permian, but at present it is not possible to give a more exact range.

**Intervening:** C.

F. **JAANUSSONIDAE** Schallreuter, 1971


**First:** *Kayina hybosa* Harris, 1957, Mountain Lake Member, Bromide Formation, lower CRD, Oklahoma, USA.

**Last:** *Jaanussonia unicerata* Schallreuter, 1971, upper (Porkuni) part of Harju ‘series’, Baltoscandia.

**Intervening:** upper CRD–RAW.

**Order** MYODOCOPIDA Sars, 1866  
**Suborder** MYODOCOPINA Sars, 1866

F. **RUTIDERMATIDAE** Brady and Norman, 1896  
Mar. Extant

F. **SARSIELLIDAE** Brady and Norman, 1896  
Mar. Extant

F. **PHILOMEDIDAE** Müller, 1912  

**First:** *Philomedes donzei* Neale, 1976, VLG, Vocontian Trough, Provence, France. Extant

**Intervening:** Very discontinuous, HAU–HOL.

F. **CYPRIDINIDAE** Baird, 1850  
S. (?GOR)–Rec. Mar.

**First:** ‘Cyprinid’ gen. et sp. nov. A of Siveter et al., 1987, La Lande Murée Formation, Mayenne, Laval area, Brittany, France.

**Last:** *Cypridella nasuta* Glebovskaja, 1939, Lower Permian, northern Urals, former USSR.

**Intervening:** Discontinuous, FAM–C. (u.).

**Comment:** Some representatives show close similarities to bolbozoids.

F. **CYPRELLIDAE** Sylvester-Bradley, 1961  
C. (VIS) Mar.

**First and Last:** Poorly known and rare group; needs revision. All known species appear to be of probable Viséan age; for example, *Cyrella chrysalidea* De Koninck, 1841, Lower Carboniferous (VIS) Limestone, Visé, Belgium.

F. **CYPROSINIDAE** Whidhorne, 1890  

**First:** Possibly *Cyprosina* sp. of Chapman, 1904, Silurian, Victoria, Australia.

**Last:** *Cyprosina whidbornei* Jones and Kirkby, 1874, Dinantian Limestone, near Torquay, Devon, England, UK.

**Intervening:** None?

**Comment:** Very rare. Taxonomic position uncertain.

F. **RHOMBINIDAE** Sylvester-Bradley, 1951  

**First:** *Palaeophilomedes* ?neuvillensis Casier, 1988, ‘Montagne Shales’, Belgium.

**Last:** *Palaeophilomedes bairdiana* (Jones and Kirkby, 1874), Dinantian Limestone, Little Island, near Cork, Republic of Ireland.

**Intervening:** Very rare?

**Comment:** Poorly known group; taxonomic position uncertain.

F. **HALOCYPRIDAE** Dana, 1852 Mar. Extant

**Comment:** All supposed fossil records of halocyprids (such as *Conchoecia*) belong to other myodocopid genera.

F. **POLYCOPIDAE** SARS, 1866  

**First:** ‘Discoidella’ *spaerula* (Griindel, 1961), Gattendorfia ‘stage’, Thuringia, Germany. Extant

**Intervening:** Very discontinuous, SCY–HOL.

**Comment:** Carboniferous records dubious.

F. **HALOCYPRIDAE** Dana, 1852  
Mar. Extant

**Comment:** All supposed fossil records of halocyprids (such as *Conchoecia*) belong to other myodocopid genera.

F. **ENTOMOCONCHIDAE** Brady, 1868  
S. (?TEL/SHE)–P. (ASS) Mar.

**First:** *Elpezoe borealis* Copeland, 1964, Alien Bay Formation, Canyon Fiord Region, Ellesmere Island, District of Franklin, Canada.

**Last:** *Elpezoe orbiculata* Kotschetkova and Gusseva, 1972, ASS, Bashkiria, Urals, former USSR.

**Intervening:** Very discontinuous, ?WHI–NOG.

F. **THAUMATOCYPRIDIDAE** Muller, 1906  

**First:** *Thaumatomma piscifrons* Kornicker and Sohn, 1976, Limestone of early late Permian age, Idhra, Greece. Extant

**Intervening:** Very discontinuous, SCY–HOL.

**Comment:** Carboniferous records dubious.

F. **HALOCYPRIDAE** Dana, 1852  
Mar. Extant

**Comment:** All supposed fossil records of halocyprids (such as *Conchoecia*) belong to other myodocopid genera.

Suborder CLADOCOPINA Sars, 1866

F. **POLYCOPIDAE** SARS, 1866  

**First:** ‘Discoidella’ *spaerula* (Gründel, 1961), Gattendorfia ‘stage’, Thuringia, Germany. Extant

**Intervening:** Discontinuous, IVO–HOL.

F. **‘ENTOMOZOIDAE’** Prihyl, 1950  

**First:** *Thaumatomma pischirons* Kornicker and Sohn, 1976, Limestone of early late Permian age, Idhra, Greece. Extant

**Intervening:** Very discontinuous, SCY–HOL.

**Comment:** Carboniferous records dubious.
Arthropoda (Crustacea: Ostracoda)

Arnsbergian) Cravenoceratiodes nitidus Marine band (E2b2 Chronozone), Namurian, from near Littledale, Lancashire, England, UK, but the material is too poorly preserved for further identification.

**Intervening:** LDF–PND.

**Comment:** Possibly belong to the Cladocopina or Halocypridina. This family requires a new name (see note, under Family Bolbozoidae, on the type species of Entomozoe).

F. RHOMBOENTOMOZOIDAE Grundel, 1962

S. (GOR)–C (IVO/CHD) Mar.

**First:** Rhomboentomozoe rhomboidea (Barrande, 1872), Kopanina Formation, Bohemia, Czechoslovakia.

**Last:** Franklinella mempeii (Kummerow, 1939), highest TOU or lowest VIS, Germany.

**Intervening:** Discontinuous, LDF–HAS/IVO.

**Comment:** Poorly known group occurring in the same fades as ‘entomozoids’; taxonomic position uncertain.

Order PODOCOPIDA Muller, 1894

Suborder PLATYCPINAE Sars, 1866

Some authors (e.g. Becker, 1990; Adamczak, 1991) consider that the Suborder Platycoquina have (via the monotiopleurids) a closer affinity to the palaeocopes rather than to the Podocopida.

**Superfamily** KLOEDENELLACEA Ulrich and Bassler, 1908

F. KLOEDENELLIDAE Ulrich and Bassler, 1908

S. (TEL)–C (HAS) Mar.

**First:** Nyhamnella musculimonstrans Adamczak, 1966, Visby Beds, Gotland, Sweden.

**Last:** Dizygopleura mehli Morey, 1935, Bushberg Formation, Kinderhookian ‘series’, lower Mississippian, Missouri, USA.

**Intervening:** SHE–FAM.

F. CAPELLINIDAE Egorov, 1950

S. (SHE)–Tr. (ANS) Mar.

**First:** Gotlandella cornuta (Krause, 1891), Jaani Regional ‘stage’, Estonia, former USSR.

**Last:** Reubenella avnimelechi Sohn, 1970, Escalada Formation, northern Spain.

**Intervening:** WHI–SPA.

**Comment:** Adamczak (1991) regards this taxon as a subfamily of the Cytherellidae.

F. CYTHERELLIDAE Sars, 1866

**First:** Cytherella jenensis Kozur, 1968, lower Muschelkalk, eastern Germany.

**Intervening:** LAD–HOL.

Suborder METACOPINA Sylvester-Bradley, 1961

**Superfamily** TLHIPSURACEA Ulrich, 1894

F. HEALDIIDAE Harlton, 1933

S. (FRO)–J. (TOA) Mar.

**First:** Cyrtocypris inornata Copeland, 1974, Jupiter Formation, Anticosti Island, Quebec, Canada.

**Last:** Ogmoconcha convexa Boomer, 1991, Mochras Borehole, near Harlech, North Wales, UK.

**Intervening:** TEL–PLB.

F. TLHIPSURIDAE Ulrich, 1894


**First:** Conbathella inornata Copeland, 1974, Bescie Formation, Anticosti Island, Quebec, Canada.

**Last:** Possibly Polyzygia neodevonica (Matern, 1929) and other FRS thlipsurids, Dinant Basin, Belgium (Becker, 1971).

**Intervening:** IDW–GIV.

**Comment:** No undoubted Ordovician or Carboniferous members of this family are known.

Suborder PODOCOPINA Sars, 1866

**Superfamily** BAIRDIOCYPRIDACEA Shaver, 1961

F. BAIRDIOCYPRIDIDAE Shaver, 1961

**First:** Arcuaria sineclivula Neckaja, 1958, Middle Ordovician, north-western part of Russian Platform.

**Last:** Praepilatina homosibirica Becker, 1991, Escalada Formation, northern Spain.

**Intervening:** O. (u.)–S. (?VRK).

F. PACHYDOMELLIDAE Berdan and Sohn, 1961


**First:** Hesslandites ellipsiformis (Hessland, 1949), (and other ‘Bythocypris’ species), Lower Grey Orthoceras Limestone, Siljan District, Sweden.

**Last:** Microchelinella sp. of Sohn, 1970, Mianwali Formation, Pakistan.

**Intervening:** LLN1–P. (u.).

**Superfamily** BAIRDIAE Sars, 1888


**First:** Bairdiacypris incurvata Kraft, 1962, Einburg Formation, lower/middle CRD, Shenandoah Valley, Virginia, USA.

**Intervening:** O. (upper CRD)–HOL.

F. BEECHERELLIDAE Ulrich, 1894


**First:** Cypridacanthoidea virginiensis Kraft, 1962, Edinburg Formation, lower/middle CRD, Shenandoah Valley, Virginia, USA.

**Intervening:** O. (upper CRD)–P. (ROT).

**Superfamily** CYPRIDACEA Baird, 1845

F. MACROCYPRIDIDAE Muller, 1912


**First:** Macrosarisa exquisita (Kaye, 1964), APT, UK.

**Intervening:** ALB–HOL.

F. CYPRIDIDAE Baird, 1845

J. (m.)–Rec. FW.

**First:** Djungarica ?yunnanensis Ye et al., 1977, Upper Member of Hepingxiang Formation, Middle Jurassic, Jiangxiu of Changxin, Yulong County, Yunnan Province, China.

**Intervening:** J. (u.)–HOL.
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Fig. 19.3

**F. CANDONIDAE** Kaufmann, 1990  
J. (KIM)—Rec. FW.  
*First*: *Cetacella inermis* Martin, 1958, borehole, Thoren, north of Hannover, Germany.  
*Intervening*: TIH—HOL.  
*Extant*

**F. ILYOCYPRIDIDAE** Kaufmann, 1990  
J. (BTH)—Rec. FW.  
*First*: *Cyprideis* sp. of Oertli, 1957, upper BTH, Route Nationale 42, 14.5 km east of Boulogne, France.  
*Intervening*: CLV—HOL.  
*Extant*

**F. NOTODROMADIDAE** Kaufmann, 1990  
T. (Eoc.)—Rec. FW.  
*First*: *Cyprigos ephraimensis* Swain, 1964, Colton Formation, Eocene, Utah, USA.  
*Intervening*: Discontinuous to HOL.  
*Extant*

**F. PARACYPRIDIDAE** Sars, 1923  
Tr. (ANS)—Rec. Mar.  
*First*: *Triassocypris pusilla* (Kozur, 1968), Germany.  
*Intervening*: LAD—HOL.  
*Extant*

**F. PONTOCYPRIDIDAE** Müller, 1894  
*First*: *Liastina lanceolata* (Apostolesc, 1959), upper rariocostatum Zone, uppermost SIN (Lophodentina striata ostracod zone of Boomer, 1991), Mochras Borehole, near Harlech, North Wales, UK.  
*Extant*
### Arthropoda (Crustacea: Ostracoda)

#### Key for both diagrams

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<td>TAT</td>
<td>DARWINULACEA Brady and Norman, 1889</td>
<td>Darwinulidae sp. of Sohn, 1985, Bluestone Formation, West Virginia, USA. Extant</td>
<td>PLB–HOL.</td>
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<td>KAZ</td>
<td>CYTHERACEA Baird, 1850</td>
<td>Sida nettgauensis Gründel, 1966, lower ALB, Nettgau Borehole 6/59, Saxony, Germany. Extant</td>
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<td>UFI</td>
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<td>Praeschuleridea pseudokinkellinella Bate and Coleman, 1975, middle TOA, Empingham, Leicestershire, England, UK. Extant</td>
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<td>Cushmanidea serangodes Krutak, 1961, Yazoo Clay, Alabama, USA. Extant</td>
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**Superfamily** DARWINULACEA Brady and Norman, 1889

**F. DARWINULIDAE Brady and Norman, 1889**

First: *Darwinula* sp. of Sohn, 1985, Bluestone Formation, West Virginia, USA. Extant

Intervening: PLB–HOL.

**Superfamily** CYTHERACEA Baird, 1850

**F. CYTHERIDAE Baird, 1850**

First: *Sida nettgauensis* Gründel, 1966, lower ALB, Nettgau Borehole 6/59, Saxony, Germany. Extant

Intervening: RHU–HOL.

**F. CYTHERIDEIDAE Sars, 1925**

J. (TOA)–Rec. Mar./Brackish/FW

First: *Praeschuleridea pseudokinkellinella* Bate and Coleman, 1975, middle TOA, Empingham, Leicestershire, England, UK. Extant

Intervening: AAL–HOL.

**Comment:** Although such Carboniferous genera as *Basslerella* Kellett, 1935 are considered by some to belong to this family, this is not accepted here. Rather, they are regarded as Cytheracea incertae sedis. Family includes Schulerideidae Mandelstam, and Cuneocytheridae Mandelstam.

**F. NEOCYTHERIDEIDAE Puri, 1957**

T. (Eoc.)–Rec. Mar./Brackish

First: *Cushmanidea serangodes* Krutak, 1961, Yazoo Clay, Alabama, USA. Extant

Intervening: Oli.–HOL.

**Intervening:** Discontinuous to HOL.

**F. BYTHOCYTHERIDAE Sars, 1926**


First: *Sylthere vonhachi* Schallreuter, 1978, top (Porkuni) part of the Harju 'series', Baltoscandia. Extant
F. ROCKALLIIDAE Whatley et al., 1982
First: Arcacythere eccentrica (Whatley et al., 1982), Waipawan Stage, DSDP Site 207, Lord Howe Rise, off New Zealand. Extant
Intervening: YPR—HOL.
F. CYTHERURIDAE Müller, 1894
Tr. (SCY)—Rec. Mar./Brackish
This family is in the process of being revised, and a number of Triassic cytheracean families are being accommodated within it. At present, it is not possible to give a first species for the family, but there are a number of SCY candidates. Extant
Intervening: ANS—HOL.
F. ENTOCYTHERIDAE Hoff, 1942
FW/Commensal Extant
North American, subterranean and commensal on other Crustacea. Not known fossil.
F. EURYCIDAE Puri, 1954
Intervening: HAU—HOL.
F. KLIELLIDAE Schafer, 1954
FW/Subterranean Extant
F. KRITHIDAE Mandelstam, 1958
First: Krithe sp. 1 of Colin, 1973, upper CEN, Fournet, Dordogne, France. Extant
Intervening: TUR—HOL.
F. LEPTOCYTHERIDAE Hanai, 1957
T. (BRT)—Rec. Mar./Brackish
First: Callistocythere kaata (Hornibrook, 1952), Kaitaan and Runungan stages, Jackson’s Paddock, New Zealand. Extant
Intervening: PRB—HOL.
F. LIMNOCYTHERIDAE Klie, 1938
First: Microcythere moresiana Stephenson, 1935, Middle Miocene, Louisiana, USA. Extant
Intervening: LAN2—HOL.
F. PARADOXOSTOMATIDAE Brady and Norman, 1889
K. (MAA)—Rec. Mar./Brackish
First: Paracythereis ?praegracilis Herrig, 1964, upper MAA, eastern Germany. Extant
Intervening: DAN—HOL.
F. PECTOCYTHERIDAE Hanai, 1957
First: Praemunseyella ornata Bate, 1972, Toolonga Calcilutite, Carnarvon Basin, Western Australia. Extant
Intervening: CMP—HOL.
F. PROGONOCYTHERIDAE Sylvester-Bradley, 1948
J. (BAJ)—K. (SAN) Mar.
First: Acanthocythereis (Protoacanthocythere) faveolata Bate, 1963, Kirton Shale, Kirton Lindsey, Lincolnshire, England, UK. Last: Majungaella annula Bate, 1972, Lower Toolonga Calcilutite, Carnarvon Basin, Western Australia. Extant
Intervening: BTH—APT.
Intervening: TUR–HOL.

Order PODOCOPIDA

Suborder and Superfamily UNCERTAIN

F. CARBONITIDAE Swain, 1976
C. (SPK)–P. (75AK/KUN) Non-mar.

First: Carbonita n. sp. of Sohn, 1985, Bluestone Formation, West Virginia, USA.

Last: Gutschickia convexa Tasch, 1963, Leonardian, Kansas, USA.

Intervening: KIN–ASS.

F. GEISINIDAE Sohn, 1961
D. (EMS)–P. (ART) Mar.


Last: Knoxilla simplex Xie, 1983, Maokou Formation, Szechwan, China.

Intervening: Discontinuous, EIF–SAK.


First: Rishona sardinula Reynolds, 1978, Receptaculites Limestone, New South Wales, Australia.

Last: Risuna sp. of Braun, 1966, Hume Formation, Norman Wells area, western Canada.

Intervening: EIF.

F. TRICORNIDAE Blumenstengel, 1965
O. (ONN)–Tr. (ANS) Mar.


Intervening: PUS–SPA.

Comments: Some researchers (e.g. Schallreuter) regard this family as Metacopina, other authors (e.g. Becker) assign it to the Cytheracea (Podocopida) or even (e.g. Becker and Bless, 1990) to the Drepanellacea (Palaeocopida).

REFERENCES

All relevant references except those listed below are to be found in Kempf’s Index and Bibliography of Non-marine (1980) and Marine Ostracoda (1984–1988).

Abushik, A. F. (1979) Order Leperditicopida, in Ostracoda, with a list of species, particularly noticing those which have as yet been discovered within the bounds of the club. Proceedings Koninklijke Nederlandse Akademie van Wetenschappen, ser. B, 90, 1–30.


Animals: Invertebrates


ARTHROPODA (EUTHYCARCINOIDEA AND MYRIAPODA)

A. J. Ross and D. E. G. Briggs

Superclass EUTHYCARCINOIDEA Gall and Grauvogel, 1964 (see Fig. 20.1)

The euthycarcinoids are generally considered to be a primitive group of uniramians (Schram and Rolfe, 1982). They were previously assigned to the crustaceans (Gall and Grauvogel, 1964), merostomoids (Schram, 1971) and trilobitoids (Starobogatov, 1988). The classification followed here is that of Schram and Rolfe (1982). An undescribed euthycarcinoid has been recorded from the Upper Silurian of Western Australia (K. J. McNamara and N. H. Trewin, in preparation).

F. EUTHYCARCINIDAE Handlirsch, 1914

First: Kottixerxes gloriosus Schram, 1971, and Smithixerxes juliarum Schram and Rolfe, 1982, Carbondale Formation, Mazon Creek, Illinois, USA.

Last: Synastra brookvalensis Riek, 1964, Hawkesbury Sandstone, New South Wales, Australia.

Superclass MYRIAPODA Latreille, 1796

For general comments see Chapter 21 (Superclass Hexapoda), paragraph two. The earliest undoubted myriapods occur in the Upper Silurian of the UK. A possible marine myriapod-like uniramian occurs in the Lower Silurian Brandon Bridge Formation of Wisconsin, USA (Mikulic et al., 1985a,b). An earlier, more equivocal example (Cambropodus gracilis) was described from the Middle Cambrian Wheeler Formation of Utah, USA (Robison, 1990).

The classification and the authors of higher taxa are taken mainly from Hoffman (1969), supplemented with later papers.

ACKNOWLEDGEMENTS

J. Hannibal, P. A. Selden, W. D. I. Rolfe and E. A. Jarzemowski kindly supplied information and comments.
358

Animals: Invertebrates

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**Key for both diagrams**

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<tr>
<th>CRETACEOUS</th>
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<td>E. Euthycarcinidae</td>
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<td>S. Scolopendrididae</td>
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<th>JURASSIC</th>
<th>AMYNILYSPEDIDA Hoffman, 1969</th>
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<tr>
<td>F. AMYNILYSPEDIDAE Hoffman, 1969</td>
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<td>C. (ACROGLOMERIDAE Fritsch, 1899)</td>
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<td>F. SPIROBOLIDAE Bollman, 1893</td>
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**Comment:** Hoffman (1969) assigned *Glomeropsis* to the Amnilyspedidae. Hannibal and Feldmann (1981) provided no definitive statement regarding its affinities, but rejected it from the Amnilyspedidae.

**Order SPHAEROTHERIIDA Brandt, 1833**

**Comment:** The order is extant, but the assignment of this specimen is uncertain.

F. *Sphaerotheriidae* Fritsch, 1899

**First and Last:** *Glomeris denticulata* Menge, 1854, Baltic amber (Keilbach, 1982).

**F. GLOMERIDAE (GLOMERIDIDAE) Leach, 1815**

**T. (PRB)–Rec. Terr.**

**First:** *Glomeris denticulata* Menge, 1854, Baltic amber (Keilbach, 1982).

**Order AMYNILYSPEDIDA Hoffman, 1969**

**F. AMYNILYSPEDIDAE Hoffman, 1969**

**First and Last:** *Amynilyspes typicus* Fritsch, 1899, Saarland, Germany (Forster, 1973).

**F. ‘SPHAERHERPESTIDAE’ Fritsch, 1899**

**First and Last:** *Glomeropsis ovalis* Fritsch, 1899, Gasköhle Formation, Nyřany, Czechoslovakia (Hoffman, 1969).
**F. ATOPETHOLIDAE** Chamberlin, 1918  
**First:** Gobiulus sabulosus Dzik, 1975, and Gobiulus sp. Dzik, 1975, Barun Goyot Formation, Gobi Desert, Mongolia.  
**Extant Comment:** Dzik (1975) tentatively assigned Gobiulus to this family.  

**F. XYLOIJULIDAE** Cook, 1895  
C. (WES B)–Tr. (SCY) Terr.  
**First and Last:** Xylojulus sigillarum (Dawson, 1860), Joggins, Nova Scotia, Canada (Hoffman, 1969).  

**F. PLAGIASCETIDAE** Hoffman, 1969  
C. (WES D) Terr.  
**First and Last:** Plagiasceatus lateralis Hoffmann, 1963, Allegheny Series, Linton Mine, Jefferson County, Ohio, USA.  

**F. ANTHRACOJULIDAE** Hoffman, 1969  
C. (WES D) Terr.  
**First and Last:** Anthracojulus pictus Fritsch, 1899, Gasköhle Formation, Nyřany, Czechoslovakia (Hoffman, 1969).  
**Comment:** Secretan (1980) noted that this family may be...
represented in the Stephanian at Montceau-les-Mines, France.

Order POLYZONIIDA Cook, 1895
First: Polyzonium sp. Bachofen-Echt, 1942, Baltic amber (Keilbach, 1982).
Extant
First: Siphonocybe sp. Shear, 1981, Dominican amber, Dominican Republic.
Extant
Order JULIDA Brandt, 1833
First: Julius laevigatus Koch and Berendt, 1854, Baltic amber (Keilbach, 1982).
Extant
First: Blaniulus sp. Menge, 1856, Baltic amber.
Extant
Extant
Order SPIROSTREPTIDA Cook, 1895
F. UNNAMED C. (u.)–Rec. Terr.
First: Archicambala dawsoni (Scudder, 1868).
Comment: Doubtful record of this extant order (Hoffman, 1969).
Order CALLIPODIDA Bollman, 1893
F. DORYPETALIDAE Verhoeff, 1900 T. (?RUP/CHT)–Rec. Terr.
Extant
Order CHORDEUMIDA Cook, 1895
First: Craspedosoma angulatum Koch and Berendt, 1854 and C. affine Koch and Berendt, 1854, Baltic amber (Keilbach, 1982).
Extant
Order POLYDESMIDA Pocock, 1887
F. POLYDESMIDAE Leach, 1815 T. (PRB)–Rec. Terr.
First: Polydesmus sp. Menge, 1856, Baltic amber.
Extant
First: Docodesmus brodzinskyi Shear, 1981, Dominican amber, Dominican Republic.
Extant
Order UNCERTAIN
F. ‘PROGLOMERIDAE’ Fritsch, 1899 C. (WES D) Terr.
First and Last: Archiscudderia paupera Fritsch, 1899, Gasköhle Formation, Nýřany, Czechoslovakia (Hoffman, 1969).

Class PAUROPODA Lubbock, 1866
No fossil record.
Class SYMPHYLA Ryder, 1880
Order SCOLOPENDRELLIDA Hoffman, 1969
F. SCOLOPENDRELLIDAE Shear and Bonamo, 1988 D. (GIV) Terr.
First and Last: Devonobius delta Shear and Bonamo, 1988 D. (GIV) Terr.
Order SCUTIGEROMORPHA (SCUTIGERIDA) Pocock, 1895
First: Scutigera illigeri (Koch and Berendt, 1854) and S. leachii (Koch and Berendt, 1854), Baltic amber (Keilbach, 1982).
Extant
Order LITHOBIOMORPHA (LITHOBIIDA) Pocock, 1895
F. LITHOBIIDAE Leach, 1814 T. (PRB)–Rec. Terr.
First: e.g. Lithobius marillosus Koch and Berendt, 1854, Baltic amber (Keilbach, 1982).
Extant
Order GEOPHILOMORPHA (GEOPHILIDA) Pocock, 1895
F. GEOPHILIDAE Newport, 1844 T. (PRB)–Rec. Terr.
First: Calciphilus abboti Chamberlin, 1949 (family uncertain) is Cainozoic and not Cretaceous as stated in Hoffman (1969); see Shear and Bonamo (1988).
F. GEOPHILIDAE Newport, 1844 T. (PRB)–Rec. Terr.

Order SCOLOPENDROMORPHA (SCOLOPENDRIDA) Pocock, 1865

F. UNNAMED C. (WES D) Terr.

First: Mazoscolopendra richardsoni Mundel, 1979, Carbon-dale Formation, Mazon Creek, Illinois, USA.

F. SCOLOPENDRIDAE Newport, 1844 T. (PRB)–Rec. Terr.

First: Scolopendra pravita Menge, 1854, Baltic amber (Keilbach, 1982).

F. CRYPTOPIDAE (CRYPTOPSIDAE) T. (PRB)–Rec. Terr.

First: Cryptops sp. Bachofen-Echt, 1942, Baltic amber (Keilbach, 1982).

Class/Order ARTHROPLEURIDA Waterlot, 1934

F. ARTHROPLEURIDAe Scudder, 1885 C. (NAM A –STE) Terr.

First: Diplichnites cuithensis Briggs et al., 1979, Limestone Coal Group, Isle of Arran, Scotland, UK. This record is based on a trackway attributed to Arthropleura.


First: Eoarthropleura devonica Størmer, 1976, Nellen-köpfchen-Schichten, Alken an der Mosel, Germany.

Last: 'Tiphoscorpio' hueberi, Ontoera Formation, New York, USA (Selden and Shear, 1992).

REFERENCES


In the first edition of *The Fossil Record*, Crowson *et al.* (1967) only included the stratigraphical ranges of insect superfamilies and higher taxa; in this work we have attempted a listing of all families which have a pre-Quaternary fossil record, for the latter, see Buckland and Coope (1991). For ease of reference, the families are listed alphabetically within their orders. Alternative names, spelling variations and groups included are given in parentheses.

Period, epoch and stage abbreviations follow Harland *et al.* (1982); however, we have used the European nomenclature for the Upper Carboniferous. We have attempted to give ranges of families and orders to stage level, but this has often proved impossible because of the absence of accompanying detailed stratigraphical information. Thus ages of Permian localities follow Wootton (1981). For C.I.S. locality names we have used the English transliteration unless an alternative is better known, e.g. Transbaikalia instead of Zabaikale. Where there is some uncertainty as to the exact age of species, e.g. those in Baltic amber, we have made a decision as indicated below. For first and last occurrences, an example is given where there is more than one species of the same age. We have distinguished between the author of a species and a reference in which the species is mentioned by giving the latter as 'in'. We have also used 'in' for references where specimens are figured but undescribed.

The insect part of the *Treatise* by F. M. Carpenter appeared while this work was in press. However, it is based on published work up to 1983, and therefore we have surveyed the literature in detail from January 1984 up to December 1991, although some of the ranges in Dmitriev and Zherikhin (1988) may be based on unpublished material. The ranges given here should be supplemented by Carpenter (1992) which gives the authors of higher taxa documented before 1984 (we have only included the authors of families described after 1983) and much more information besides on the occurrence of fossil insects.

The *Treatise* arrangement of classes is followed; however, Kukalová-Peck (1987a) unites Collembola and Protura in the Parainsecta and includes Diplura in the Insecta s.s. A phylogenetic classification of these and other extant hexapods is discussed by Kristensen (1991). For common names of orders see Jarzembowski (1990b). The earliest hexapod is as for Collembola. The Class/Order Protura is Recent only. Most insects are terrestrial, but Wootton (1988) gives a useful overview of the geological history of aquatic insect groups. 'Terr.' has been used below in the broadest sense, including aerial or freshwater adults or larvae/nymphs.

To keep this list up to date please send your reprints on fossil insects to AJR.

**Acknowledgements** – Many thanks to all those who have commented on the manuscript and sent us reprints, particularly: Dr A. P. Rasnitsyn, Dr Y. A. Popov, Dr D. E. Schcherbakov, Professor Y. Hong, Dr J. Zhang, Professor R. G. Martins-Neto, Dr A. V. Gorokhov, Dr U. Spahr, Dr V. A. Blagoderov, Dr A. G. Ponomarenko, Dr L. N. Pritykina, Dr N. D. Sinichenkova, Dr I. D. Sukacheva and Dr V. V. Zherikhin. This is PRIS contribution No. 228 for E.A.J.
Megasecoptera | Strepsiptera | 367 | 1 | 419
Miomoptera | Thysanoptera | 378 | 2 | 394
Monura | Trichoptera | 366 | 3 | 419
Neuroptera | Zoraptera | 417 | 4 | 395
Odonata | Zygoptera | 369 | 5 | 366
Orthoptera |
Palaeodictyoptera |
Phasmatodea |
Phthiraptera |
Plecoptera |
Protelytroptera |
Protodonata |
Protorthoptera |
Pscocoptera |
Raphidioptera |
Siphonaptera |

**Superclass** HEXAPoda (Insects *sensu lato*)

**Class/Order** COLEMBOLA D. (SIG)–Rec.


F. ENTOMOBRYIDAE P. (ROT)–Rec. Terr.

Extant
### Arthropoda (Hexapoda; Insecta)

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| Key for both diagrams
| COLLEMBOLA       |                  |                                 |           |                              |                      |                     |
| 1. Entomobryidae |                  |                                 |           |                              |                      |                     |
| 2. Hypogastruridae |                |                                 |           |                              |                      |                     |
| 3. Isotomidae    |                  |                                 |           |                              |                      |                     |
| 4. Neanuridae    |                  |                                 |           |                              |                      |                     |
| 5. Poduridae     |                  |                                 |           |                              |                      |                     |
| 6. Protentomobryidae |            |                                 |           |                              |                      |                     |
| 7. Sminthuridae  |                  |                                 |           |                              |                      |                     |
| 8. Tomoceridae   |                  |                                 |           |                              |                      |                     |
| 9. Campodeidae   |                  |                                 |           |                              |                      |                     |
| 10. Ocelliidae   |                  |                                 |           |                              |                      |                     |
| 11. Testajapygidae |             |                                 |           |                              |                      |                     |
| 12. Machilidae   |                  |                                 |           |                              |                      |                     |
| 13. Triassmachilidae |           |                                 |           |                              |                      |                     |
| 14. Dasylectidae |                  |                                 |           |                              |                      |                     |
| 15. Ateluridae   |                  |                                 |           |                              |                      |                     |
| 16. Lepidotrichidae |             |                                 |           |                              |                      |                     |
| 17. Lepismatidae |                  |                                 |           |                              |                      |                     |
| 18. Asthenohymenidae |           |                                 |           |                              |                      |                     |
| 19. Biarmohymenidae |          |                                 |           |                              |                      |                     |
| 20. Diaphanopteridae |         |                                 |           |                              |                      |                     |
| 21. Elmoidae     |                  |                                 |           |                              |                      |                     |
| 22. Martynoviidae |                  |                                 |           |                              |                      |                     |
| 23. Namurodiaphiade |              |                                 |           |                              |                      |                     |
| 24. Parabrodiidae |                  |                                 |           |                              |                      |                     |
| 25. Pseudachorutes |                |                                 |           |                              |                      |                     |
| 26. Podura fuscata |                |                                 |           |                              |                      |                     |
| 27. Protentomobrya walkeri |          |                                 |           |                              |                      |                     |
| 28. Tomocerus cf. minor |         |                                 |           |                              |                      |                     |
| 29. Ocellia articulicornis |         |                                 |           |                              |                      |                     |
| 30. Testajapyx thomasi Kukalová-Peck (1987), Carbondale Formation, Mazon Creek, Illinois, USA. |
| 31. Testajapidae (SCARABAEODA; insects sensu stricto) | | | | | | |

**Fig. 21.1**


First:
- e.g. *Hypogastrura* (*Ceratophylla*) sp., *in* Lawrence (1985), Baltic amber, Gdańsk, Poland.

Extant


First:

Extant


First:
- *Pseudachorutes* sp., *in* Lawrence (1985), Baltic amber, Gdańsk, Poland.

Extant


First:
- *Podura fuscata*, *in* Spahr (1990), Baltic amber.

Extant

F. PROTENTOMOBRYIDAE K. (CMP) Terr.

First and Last:
- *Protentomobra walkeri* *in* Spahr (1990), Canadian amber, Canada.


First:
- *Sminthurinus* sp., *in* Lawrence (1985), Baltic amber, Gdańsk, Poland.

Extant


First:
- e.g. *Tomocerus* cf. *minor*, *in* Lawrence (1985), Baltic amber, Gdańsk, Poland.

Extant

Class/Order DIPLURA C. (WES D) Rec. Terr.

First as for Testajapygidae.


First:
- *Campodea darwinii* *in* Spahr (1990), Baltic amber.

Extant


First and Last:
- *Ocellia articulicornis*, *in* Spahr (1990), Baltic amber.


First and Last:
- *Testajapyx thomasi* Kukalová-Peck (1987), Carbondale Formation, Mazon Creek, Illinois, USA.

Class INSECTA (SCARABAEODA; insects sensu stricto) D. (EMS?) Rec.
First as for Archaeognatha. The Lower Devonian \textit{Rhyniognatha hirsti} in Kukalová-Peck (1991) is a possible myriapod.

\textbf{Subclass APTERYGOTA} s.s. (LEPISTMATONA; primitively wingless insects; THYSANURA s.l. of older classifications) \(D.\) (EMS?)–Rec.

First as for Archaeognatha.

\textbf{Order ARCHAEOGNATHA (MACHILIDA \textit{pars})} \(D.\) (EMS?)–Rec. Terr.

\textbf{First:} \textit{Gaspea palaeoentognathae} (nomen nudum) Labandeira \textit{et al.} (1988), Battery Point Formation, Gaspé Peninsula, Canada. This species has not been placed in a family. Jeram \textit{et al.} (1990) do not consider that this species is a fossil hexapod. Extant

\begin{itemize}
  \item F. \textbf{MACHILIDAE} \(K\) (u.?–Rec. Terr.
  \item F. \textbf{TRIASSOMACHILIDAE} Tr. (u.) Kukalová-Peck (1991) considers \textit{Triassomachilis} to be a mayfly nymph.
\end{itemize}

\textbf{Order MONURA (MACHILIDA \textit{pars})} C. (u.)–P. Terr.

Only one recognized family.

\begin{itemize}
  \item F. \textbf{DASYLEPTIDAE} C. (u.)–P. Terr.
  \item First: e.g. \textit{?Dasyleptus} sp. Kukalová-Peck (1985), Carbondale Formation, Mazon Creek, Illinois, USA.
  \item Last: e.g. \textit{Leiododasypus sharoui}, in Labandeira and Beall (1990), Kansas, USA.
\end{itemize}

\textbf{Order ZYGENTOMA} (THYSANURA s.s.; LEPISMATIDA) C. (WES D)–Rec. Terr.

\textbf{First:} \textit{Ramsdelepidion schusteri} Kukalová-Peck (1987), Carbondale Formation, Mazon Creek, Illinois, USA. Kukalová-Peck (1987) did not place this species in a family. Extant

\begin{itemize}
  \item F. \textbf{ATELURIDAE} T. (Oli.)–Rec. Terr.
  \item F. \textbf{LEPIDOTRICHIDAE} (LEPIDOTHRICIDAE) K. (u.)–Rec. Terr.
  \item F. \textbf{LEPISTEMATIDAE} K (u.)–Rec. Terr.
\end{itemize}

\textbf{Subclass PTERYGOTA} (SCARABAEONA; winged insects) C. (NAM A)–Rec. Terr.

The Order Archaeoptera is based on crustacean rather than insect remains (Rodendorf, 1972). First as for Protorthoptera.

\textbf{Cohort PALAEOPTERA} C. (NAM B)–Rec. Terr.

First as for Megasecoptera.

\textbf{Order DIAPHANOPTERODEA} (DIAPHANOPTERIDA) C. (NAM B)–Rec. Terr.

First as for Namurodiaphidae.

\begin{itemize}
  \item F. \textbf{ASTHENOHYMENIDAE} (DOTERIDAE) \(P.\) Terr.
  \item e.g. \textit{Doter minor}, in Hubbard (1987), Kansas, USA.
  \item F. \textbf{BIARMOHYMENIDAE} \(P.\) Terr.
  \item F. \textbf{DIAPHANOPTERIDAE} C. (u.) Terr.
  \item F. \textbf{ELMOIDAE} \(P.\) Terr.
  \item F. \textbf{MARTYNOVIIDAE} \(P.\) Terr.
\end{itemize}

F. \textbf{NAMURODIAPHIDAE} Kukalová-Peck and Brauckmann, 1990 C. (NAM B) Terr. Extant

\textbf{First and Last:} \textit{Namurodiapha sippelorum} Kukalová-Peck and Brauckmann (1990), Vorhalle Beds, Hagen-Vorhalle, Germany.

\begin{itemize}
  \item F. \textbf{PARABRODIIDAE} C. (u.) Terr.
  \item F. \textbf{PARELMOIDAE} P. (ROT) Terr.
  \item F. \textbf{PERMOHYMENIDAE} P. (ART) Terr.
\end{itemize}

\textbf{Order EPHEMEROPTERA} (EPHEMERIDA, PLECTOPTERA) C. (WES C)–Rec. Terr.

Data taken from Hubbard (1987), unless stated otherwise. First as for Bojophlebiidae. The Triassomachilidae may prove to belong here (see Order Archaeognatha).

\begin{itemize}
  \item F. \textbf{AENIGMEPHEMERIDAE} J. (u.) Terr.
  \item First and Last: \textit{Aenigmephemera demoulini}, Karatau, Kazakhstan, former USSR.
  \item F. \textbf{AMETROPODIDAE} K. (APT)–Rec. Terr.
\end{itemize}

\textbf{Extant}

\begin{itemize}
  \item F. \textbf{BAETIDAE} T. (PRB)–Rec. Terr.
  \item First: e.g. \textit{Baetis gigantea}, Baltic amber. Sinichenkova (1985a, 1989) included the Jurassic genus \textit{Mesobaetis} in the Siphlonuridae, but Hubbard (1987) placed it in the Baetidae without discussion. Here, we have followed Sinichenkova (1985a, 1989).
  \item F. \textbf{BOJOPHLEBIIDAE} Kukalová-Peck, 1985 C. (WES C) Terr.
\end{itemize}

\textbf{Extant}

\begin{itemize}
  \item F. \textbf{BOJOPHLEBIIDAE} Kukalová-Peck, 1985 C. (WES C) Terr.
  \item First and Last: \textit{Bojophlebia prokopi}, Whetstone Horizon, Bohemia, Czechoslovakia. Klyuge (1989), however, considers that the ‘nymph’ of this species may belong in another order, ‘probably Thysanura’.
  \item F. \textbf{EPEOROMIMIDAE} (EPEOROMIDAE) J. (I.)–K. (I.) Terr.
  \item First: e.g. \textit{Epeoromimus kazlauskasi}, western Siberia, former USSR.
  \item Last: e.g. \textit{Epeoromimus cretaceus}, Transbaikalia, former USSR.
  \item F. \textbf{EPHEMERELLIDAE} J. (I.)–Rec. Terr.
  \item First: e.g. \textit{Clephemera clava} Lin (1986), south China. The systematic position of this species is doubtful. Extant
  \item F. \textbf{EPHEMERIDAE} (ICHTHYBOTIDAE) K. (APT)–Rec. Terr.
\end{itemize}
Arthropoda (Hexapoda; Insecta)

First: e.g. Australiphemera revelata McCafferty (1990), Santana Formation, Ceará, Brazil. The Upper Jurassic 'Ephemera' deposita Weyenbergh does not belong to this family (McCafferty, 1990).

F. EUTHYPOCIIDAE K. (l.)–Rec. Terr.
First: e.g. Pristiplocia rupestris McCafferty (1990), Santana Formation, Ceará, Brazil.

F. HEPTAGENIIDAE (ECYDURIDAE, ECYDONYURIDAE) T. (PRB)–Rec. Terr.
First: e.g. Heptagena (Kageronia) fusigrisea, in Klyuge (1986), Baltic amber.

F. HEXAGENITIDAE (PAEDEPHEMERIDAE, STENODICRANIDAE) J. (l.)–K. (l.) Terr.
First: e.g. Siberiogenites angustatus, Transbaikalia, former USSR.
Last: e.g. Protoligoneuria limai, in McCafferty (1990), Santana Formation, Ceará, Brazil.

F. JARMILIDAE P. (ROT) Terr.
First and Last: Jarmila eiongata, Czechoslovakia.

F. LEPTOPHLEBIIDAE J. (1.)–Rec. Terr.
First: e.g. Mesoneta antiqua, Transbaikalia, former USSR.

F. LITOPHLEBIIDAE (XENOPHLEBIIDAE) Tr. (u.) Terr.
First and Last: Litophlebia optata, Molteno Formation, Bird's River, South Africa. Hubbard (1987) believes this is a megasecopteran.

F. MESEPHEMERIDAE (PALINGENIOPSIDAE) P. (ZEC)–J. (TTH) Terr.
First: Paliningiopsis praecox, former USSR.
Last: e.g. Mesephemera lithophila, Lithographic Limestone, Solnhofen, Germany.

F. MESTROPECTOPTERIDAE P.–Tr. Terr.
e.g. Mesoplectopteron longipes, western Europe.

F. METRETOPODIDAE T. (PRB)–Rec. Terr.
First: e.g. Metretopus henningseni, Baltic amber.

F. MISTHODOTIDAE (EUDOTERIDAE) P. (ROT) Terr.
e.g. Misthodotes obtusus, Wellington Formation, Kansas, USA.

First: Potamanthellus rubiensis, Ruby River Basin, Montana, USA.

F. OBORIPHLEBIIDAE P. (ROT) Terr.
e.g. Oboriphlebia moravica, Czechoslovakia.

F. OLIGONEURIDAE (ISONYCHIIDAE) K. (APT)–Rec. Terr.
First: Colocus indivicus McCafferty (1990), Santana Formation, Ceará, Brazil. McCafferty (1990) transferred the previously supposed oldest species Protoligoneuria limai to the Hexagenitidae.

F. PALINGENIIIDAE J. (u.)–Rec. Terr.
First: Mesogenesia petersae, Transbaikalia, former USSR.

F. POLYMITARCIDAE (POLYMITARCYIDAE) K. (APT)–Rec. Terr.
First: Caririnympha mandibulata Martins-Neto and Caldas (1990), Santana Formation, Ceará, Brazil.

F. POTAMANTHIDAE K. (l.)–Rec. Terr.
First: e.g. Potamandea (?) sp. 1 McCafferty (1990), Santana Formation, Ceará, Brazil.

F. PROTEREISMATIDAE P. (ROT) Terr.
e.g. Protereisma permium, Wellington Formation, Kansas, USA.

F. SIPHLONURIDAE J. (l.)–Rec. Terr.
First: e.g. Mogzonurus elevatus, Transbaikalia, former USSR.

F. SYNTONOPTERIDAE C. (WES D) Terr.
e.g. Syntoneoptera schucherti, in Carpenter (1988), Carbondale Formation, Mazon Creek, Illinois, USA. Carpenter (1988), however, preferred to place this family in Order Uncertain because important body structures, such as the mouthparts, are not yet known.

First: Archaeobehningia edmundsi, in Sinichenkova (1989), Udinskaya Formation, Transbaikalia, former USSR. Sinichenkova (1989) transferred this genus from the Behningiidae thus reverting the latter family back to Recent only.

F. TRIPLOSOBIDAE C. (STE) Terr.
First and Last: Triplosoba pu/Chella, Commentry, France.

Order MEGASECOPTERA (MISCHOPTERIDA) C. (NAM B)–P. Terr.
First as for Brodiopteridae, although Xenoptera riojanaensis ('Xenopteridae') may be older. The Upper Triassic Litophlebiidae (Ephemeroptera) may prove to belong to this order.

F. ALECTONEURIDAE P. Terr.
F. ANCHINEURIDAE C. (u.) Terr.
F. ANCOPTERIDAE P. Terr.
F. ARCIONEURIDAE P. Terr.
F. ASPIDOTHORACIDAE C. (WES D–STE) Terr.
First: Aspidothorax aestalis Brauckmann (1991), Piesberg, Osnabrück, Germany.
Last: Aspidothorax triangularis, in Brauckmann (1991), Commentry, France.

F. BARDHOYMENIDAE C. (NAM B)–P. (KUN) Terr.
First: Sylvohymen peckae Brauckmann (1988b), Vorhalle Beds, Hagen-Vorhalle, Germany.
**Fig. 21.2**

Last: e.g. *Bardohymen magnipennifer, in* Brauckmann (1988b), Urals, former USSR.

**F. BRODIIDAE** C. (u.) Terr.

**F. BRODIOPTERIDAE** C. (NAM B–WES A) Terr.

**First:** Brodioptera stricklani Nelson and Tidwell (1988), Manning Canyon Shale Formation, Utah, USA.

**Last:** Brodioptera cumberlandensis, in Nelson and Tidwell (1988), USA.

**F. CARBONOPTERIDAE** C. (WES D)

**First and Last:** Carbonoptera furcaradii, in Brauckmann (1991), Neuenkirchen, Saarland, Germany.

**F. CAULOPTERIDAE** P. Terr.

**F. CORYDALOIDIDAE** C. (u.) Terr.

**F. ENGISOPTERIDAE** P. Terr.

**F. FORIRIIDAE** C. (u.) Terr.

**F. FRANKENHOLZIIDAE** C. (WES D)

**First and Last:** Frankenholzia culmanni, in Brauckmann (1991), Grube Frankenholz, Saarland, Germany.

**F. HANIDAE** P. Terr.

**F. ISCHNOPTILIDAE** C. (u.) Terr.

**F. MISCHOPTERIDAE** C. (u.) Terr.

e.g. *Mischoptera douglassi, in* Shear and Kukalová-Peck (1990), Carbondale Formation, Mazon Creek, Illinois, USA.
Fig. 21.2

F. MORAVOHYMENIDAE P. Terr.

F. PROTOHYMENIDAE C. (u.)—P. Terr.

First: *Sunohymen xishanensis* Hong (1985c), Shanxi Formation, Xishan, Shanxi, China.

F. SCYTOHYMENIDAE P. Terr.

F. SPHECOPTERIDAE C. (u.) Terr.

F. VORKUTIIDAE C. (u.)—P. Terr.

F. 'XENOPTERIDAE' Pinto, 1986 C. (NAM) Terr.

First and Last: *Xenoptera riojaensis* Pinto (1986), Malanzan Formation, Malanzan, Argentina. It is uncertain as to whether this formation is of Lower or Upper Carboniferous age. This family name is a junior homonym of Xenopteridae Riek (Orthoptera).

Order ODONATA (LIBELLULIDAE)

P. (ROT)—Rec. Terr.

Earliest families: Ditaxineuridae and Kennedyidae, although some authors include the Protodonata in this order.

F. AESCHNIDIIDAE J. (u.)—K. (u.) Terr.

First: e.g. *Hebeiaeschnidia fengningensis* in Hong (1985d), Hebei, China.

Last: *Aeschnidopsis flindersiensis* in Rozefelds (1985), Queensland, Australia.

F. AESHNIDAE (AESCHNIDAE) J. (u.)—Rec. Terr.

Extant

F. AKTASSIIDAE J. (u.)—K. (l.) Terr.

F. AMPHIPTERYGIDAE (STELLOOPTERIDAE)

J. (TTH)—Rec. Terr.

First: *Steleopteron deichmulleri*, in Ponomarenko (1985b), Lithographic Limestone, Solnhofen, Germany. Extant

F. ARCHITHEMISTIDAE J. (l.)—J. (u.) Terr.

First: e.g. *Dorsettia laeta* Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK.

F. ASIOPTERIDAE J. (u.) Terr.

F. BATKENIIDAE Tr. (u.) Terr.
### Fig. 21.3

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**F. CALLIMOKALTANIIDAE**  P. (ZEC)  Terr.  Extant

**F. CALOPTERYGIDAE**  T. (Eoc)–Rec.  Terr.  Extant

**F. CAMPTEROPHLEBIIDAE**  Tr. (RHT)–J. (u.)–Rec.  Terr.  Extant

**F. CHLOROLESTIDAE**  T. (Oli.)–Rec.  Terr.  Extant

**F. COENAGRIONIDAE**  (COENAGRIIDAE)  K. (HAU)–Rec.  Terr.  Extant

**F. COORDULIIDAE**  K. (I.)–Rec.  Terr.  Extant

**F. DITAXINEURIDAE**  P.  Terr.

**F. EUPHAEIDAE**  (EPALLAGIDAE)  T. (LUT/BRT)–Rec.  Terr.
**Arthropoda (Hexapoda; Insecta)**

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**Key for both diagrams**

9. Peramgrionidae 22. Sieblossidae 32. Archaeomacromanidae 44. Lycocercidae

**Fig. 21.3**

First: e.g. *Epallagites avus*, in Nel (1988b), Green River Formation, Colorado, USA.  
Extant

**F. EUTHEMISTIDAE** J. (u.)–K. (HAU) Terr.  
First: e.g. *Euthemis multivernosa*, in Jarzembowski (1990a), Karatau, Kazakhstan, former USSR.  
Last: *Euthemis sp.*, Jarzembowski (1990a), Lower Weald Clay, Capel, Surrey, England, UK. Pritynkina (pers. comm.) considers that this species belongs in the Oreopectidae.  

**F. GOMPHIDAE (GOMPHINIDAE, PROTOLINDENIIDAE)** J. (u.)–Rec.  
Terr.  
First: e.g. *Sinogamphus taushanensis*, in Hong (1985d), north China.  
Extant

**F. HEMEROSCOPIIDAE** K. (l.) Terr.  

**F. HETEROPHELBIIDAE** J. (l.–u.) Terr.  
First: e.g. *Heteroblebi sp.*, Whalley (1985), Lower Lias, Charnouth, Dorset, England, UK.  

**F. ISOPHELBIIDAE** J. (l.)–K. (l.) Terr.  

First: *Dinosamarura tugnica*, in Pritynkina (1985), Transbaikalia, former USSR.  

**F. ITALOPHELBIIDAE** Whalley, 1986a  
Tr. (RHT) Terr.  
First and Last: *Italophlebia gerasuttilii* Whalley (1986a), ArgiUiti di Riva di Solto Formation, Bergamo, Italy.  

**F. KALTANONEURIDAE** P. (ZEC) Terr.  

**F. KARATAWIIDAE** J. (l.–u.) Terr.  
First: e.g. *Karatawia sibirica*, in Pritynkina (1985), Ust-Balei, Siberia, former USSR.  
Last: e.g. *Karatawia turanica*, in Pritynkina (1985), Karatau, Kazakhstan, former USSR.  

**F. KENNEDYIDAE** P. (ROT)–Tr. Terr.  

**F. LESTIDAE** T. (LUT/BRT)–Rec. Terr.  
First: *Petrolestes hendersoni*, in Nel (1986), Green River Formation, Ute Trail, Colorado, USA.  
Extant

**F. LIASSOGOMPHIDAE** J. (l.) Terr.  

First: e.g. *Epallagites avus*, in Nel (1988b), Green River Formation, Colorado, USA.  
Extant

**F. LITOPHELBIIDAE** Whalley, 1986a  
Tr. (RHT) Terr.  
First and Last: *Italophlebia gerasuttilii* Whalley (1986a), ArgiUiti di Riva di Solto Formation, Bergamo, Italy.  

**F. KALTANONEURIDAE** P. (ZEC) Terr.  

**F. KARATAWIIDAE** J. (l.–u.) Terr.  
First: e.g. *Karatawia sibirica*, in Pritynkina (1985), Ust-Balei, Siberia, former USSR.  
Last: e.g. *Karatawia turanica*, in Pritynkina (1985), Karatau, Kazakhstan, former USSR.  

**F. KENNEDYIDAE** P. (ROT)–Tr. Terr.  

**F. LESTIDAE** T. (LUT/BRT)–Rec. Terr.  
First: *Petrolestes hendersoni*, in Nel (1986), Green River Formation, Ute Trail, Colorado, USA.  
Extant

**F. LIASSOGOMPHIDAE** J. (l.) Terr.  

First: *Dinosamarura tugnica*, in Pritynkina (1985), Transbaikalia, former USSR.  

**F. ITALOPHELBIIDAE** Whalley, 1986a  
Tr. (RHT) Terr.  
First and Last: *Italophlebia gerasuttilii* Whalley (1986a), ArgiUiti di Riva di Solto Formation, Bergamo, Italy.  

**F. KALTANONEURIDAE** P. (ZEC) Terr.  

**F. KARATAWIIDAE** J. (l.–u.) Terr.  
First: e.g. *Karatawia sibirica*, in Pritynkina (1985), Ust-Balei, Siberia, former USSR.  
Last: e.g. *Karatawia turanica*, in Pritynkina (1985), Karatau, Kazakhstan, former USSR.  

**F. KENNEDYIDAE** P. (ROT)–Tr. Terr.  

**F. LESTIDAE** T. (LUT/BRT)–Rec. Terr.  
First: *Petrolestes hendersoni*, in Nel (1986), Green River Formation, Ute Trail, Colorado, USA.  
Extant

**F. LIASSOGOMPHIDAE** J. (l.) Terr.  

First: *Dinosamarura tugnica*, in Pritynkina (1985), Transbaikalia, former USSR.  

**F. ITALOPHELBIIDAE** Whalley, 1986a  
Tr. (RHT) Terr.  
First and Last: *Italophlebia gerasuttilii* Whalley (1986a), ArgiUiti di Riva di Solto Formation, Bergamo, Italy.  

**F. KALTANONEURIDAE** P. (ZEC) Terr.  

**F. KARATAWIIDAE** J. (l.–u.) Terr.  
First: e.g. *Karatawia sibirica*, in Pritynkina (1985), Ust-Balei, Siberia, former USSR.  
Last: e.g. *Karatawia turanica*, in Pritynkina (1985), Karatau, Kazakhstan, former USSR.  

**F. KENNEDYIDAE** P. (ROT)–Tr. Terr.  

**F. LESTIDAE** T. (LUT/BRT)–Rec. Terr.  
First: *Petrolestes hendersoni*, in Nel (1986), Green River Formation, Ute Trail, Colorado, USA.  
Extant
F. LIASSOPHLEBIIDAE J. (l.) Terr.
e.g. Liassophlebia pseudomagnifica Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK.

First: Condalia woottoni Whalley and Jarzembowski (1985), Lithographic Limestone, Montsech, Spain. This species is a libelluloid, but may not belong to this family. Extant

Extant

F. MESOPHLEBIIDAE Tr. – K. (APT) Terr.
First: e.g. Mesophlebia antinodalis, in Rozefelds (1985), Coal Measures, Ipswich, Australia.

Extant

F. OREOPTERIDAE J. (1.) – K. (1.) Terr.

Extant

F. PERMAESCHNIDAE P. (ZEC) Terr.
E.g. Gondvanoptilon brasiliense, in Martins-Neto (1987a), Irati Formation, São Paulo, Brazil.

F. PERMAESCHNIDAE P. (ZEC) Terr.
Extant

Extant

Extant

Oldest species from the Hagen Beds of Germany, see Dictyoneuridae and Graphiptilidae.

F. ARCHAEMEGAPTILIDAE C. (u.) Terr.

First: e.g. Jugobreperia sippelorum Brauckmann et al., 1985, Vorhalle Beds, Hagen-Vorhalle, Germany.
Last: e.g. Breyeria boulei, in Brauckmann et al., 1985, Commeny, France.


F. DIATHEMIDAE P. (KUN) Terr.
e.g. Diathemidia monstruosa, in Riek and Kukalova-Peck (1984), Koshelevo Formation, Suxsun, Perm, former USSR.

F. DIAPHANEURIDAE C. (NAM B) – P. Terr.
First: e.g. *Schmidtopteron adictyon*, in Brauckmann (1988a), Hagen Beds, Schmiedestrasse, Germany.

**F. ELMOBORIIDAE** P. Terr.

**F. EUBLEPTIDAE** C. (u.) Terr.

**F. EUGEREONIDAE** C. (u.)–P. Terr.

Last: e.g. *Eugereon boeckingi* in Shear and Kukalova-Peck (1990), Germany.

**F. FOUQUEIDAE** C. (u.) Terr.

**F. GRAPHIPTILIDAE** (PATTEISKYIDAE) C. (NAM B–STE) Terr.

First: *Pattisikya buackaerti*, in Brauckmann (1988a), Hagen Beds, Schmiedestrasse, Germany.

Last: e.g. *Graphiptilus heeri*, in Brauckmann et al. (1985), Commentry, France.

**F. HOMOIOPTERIDAE** C. (NAM B–STE) Terr.

First: *Homoioptera vorhallensis*, in Brauckmann et al. (1985), Vorhalle Beds, Hagen-Vorhalle, Germany.

Last: e.g. *Homoioptera gigantea*, in Riek and Kukalova-Peck (1984), Commentry, France.

**F. LITHOMANTEIDAE** (LITHOMANTIDAE) C. (NAM B–STE) Terr.

First: *Lithomantis varius* Brauckmann et al., 1985, Vorhalle Beds, Hagen-Vorhalle, Germany.

Last: e.g. *Macroptera jariai*, in Brauckmann et al., 1985, Alto do Pejao, Portugal.

**F. LYCOCERCIDAE** C. (u.) Terr.

e.g. *Lycocerus goldenbergi* in Shear and Kukalová-Peck (1990), Commentry, France.

**F. MECYNOSTOMATIDAE** C. (STE) Terr.

First and Last: *Meynostoma (=Mecynostoma) dohrni* in Shear and Kukalová-Peck (1990), Commentry, France.

**F. MEGAPTILIDAE** C. (NAM B–P. (KAZ) Terr.

First: *Namurotypus sippeIi*, Vorhalle Beds, Hagen-Vorhalle, Germany.

Last: e.g. *Arctotypus sinuatus*, Iva-Gora, Archangelsk, former USSR.

**F. PARALOGIDAE** C. (WESA)–P. (ART) Terr.

First: *Oligotypus britannicus* (nomen nudum), Lower Coal Measures, Staffordshire, England, UK.

Last: e.g. *Oligotypus tilyardi*, Wellington Formation, Elmo, Kansas, USA.

**F. TRIADOTYPIDAE** Tr. (SCY–u.) Terr.

First: *Triadotypus guillaumei*, Bunter Sandstone, France.

Last: e.g. *Triadotypus sogdianus*, Sogd, Fergana, former USSR.

**Cohort** NEOPTERA C. (NAM A)–Rec. Terr.

First as for Protorthoptera.

**Superorder** POLYNEOPTERA (GRYLLONES; Orthopteroid orders) C. (NAM A)–Rec. Terr.

First as for Protorthoptera.

**Order** BLATTODEA (BLATTIDA, BLATTIDEA, BLATTARIAE, BLATTOIDEA) C. (WES A)–Rec. Terr.

We have followed Schneider’s (1984) classification of the Palaeozoic Blattoidea; Durden (1984) gave an alternative classification. The Eocene Parallelophoridae consists of the anal fields of other cockroach families (Lutz, 1984).

**F. ARCHIMYLACRIDAE** C. (WES A)–P. (ART) Terr.


**F. ARCHOBLLATTINIDAE** C. (WES–STE) Terr.

**F. BLABERIDAE** T. (PRB)–Rec. Terr.

Extant

**F. BLATTELIDAE** (PHYLLODROMIIDAE) K. (u.)–Rec. Terr.

**F. BLATTIDAE** K. (l.)–Rec. Terr.
### Animals: Invertebrates

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**Fig. 21.4**

**First:** e.g. *Methana?* sp. Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.  
**Extant**

F. **BLATTULIDAE** J. (l.–u.) Terr.

**First:** e.g. *Mesobblattula sincera* Lin (1986), south China.

F. **COMPSOBLATIIDAE** C. (STE)–P. (ROT) Terr.

**Last:** e.g. *Compsobblatta frankel*, in Schneider (1984), Thüringer, Germany.

F. **CORYDIIDAE** (POLYPHAGIDAE) K. (l.)–Rec. Terr.

**Extant**

F. **DIECHOBBLATINIDAE** P. (ROT)–J. (u.) Terr.

F. **LATIBBLATIDAE** J. (u.) Terr.

F. **MESOBLATINIDAE** C. (STE)–K. (u.) Terr.

F. **MYLACRIDAE** C. WES–P. (ZEC) Terr.

**First:** e.g. figured but undescribed in Jarzembowski (1989a), Farrington Formation, Writhlington, Avon, England, UK.

F. **NECYMYLACRIDAE** C. (WES B–STE) Terr.

**First:** e.g. *Necymylacris handlirschi*, in Schneider (1984), Mercer group, Brookville, USA.

**Last:** e.g. *Necymylacris* sp. in Schneider (1984), former USSR.

F. **PHYLOBLATIDAE** C. (WES)–P. Terr.

**First:** e.g. *Phyloblatta?* sp. Brauckmann and Willmann (1990), Weiterstadt 1 borehole, Rhine Valley, Germany.
Arthropoda (Hexapoda; Insecta)

F. POROBLATTINIDAE C. (WES)–K. (u.) Terr.  
First: *Poroblatta duffienxi*, in Schneider (1984), Lens, France.

F. RAPHIDIOMIMIDAE J. (u.) Terr.  
First: *e.g. Kinklidoblatta morini*, in Schneider (1984), Nord-Pas-de-Calais, France.

F. SPILOBLATTINIDAE C. (WES)–Tr. (u.) Terr.  
First: *e.g. Kinklidoblatta morini*, in Schneider (1984), Nord-Pas-de-Calais, France.

F. SUBIOBLATTIDAE P. (ROT)–J. (u.) Terr.  
Last: *Subioblatta karatavica*, in Schneider (1984), Karatau, Kazakhstan, former USSR.

F. UMENOCOREIDAE K. (l.) Terr.  
We have followed Ponomarenko (pers. comm.) in considering that this family belongs to this order.

Order CALONEURODEA (CALONEURIDA)  
C. (u.)–P. Terr.  
We do not consider that the Lower Cretaceous family Mesogrammatidae Hong, 1985d belongs in this order, because the only known specimen does not show the ordinal characters as given by Burnham (1984). This family probably belongs in the Orthoptera.

F. AMBONEURIDAE C. (u.) Terr.  
F. ANOMALOGRAMMATIDAE P. Terr.  
F. APSIDONEURIDAE C. (u.)–P. (ART) Terr.  
First: *e.g. Apsidoneura sottyi* Burnham (1984), Montceau-les-Mines, France.  
Last: *Apsidoneura flexa*, in Burnham (1984), Wellington Formation, Elmo, Kansas, USA.

F. CALONEURIDAE C. (u.) Terr.  
First and Last: *Caloneura dawsoni*, in Burnham (1984), Commentry, France.

F. EUTHYGRAMMATIDAE P. Terr.  
F. PALEUTHYGRAMMATIDAE P. Terr.  
e.g. *Paleuthygramma tenuis* in Kukalová-Peck (1991), Urals, former USSR.
F. **PERMOBIELLIDAE** C. (u.)—P. Terr.

F. **PLEISIOGRAMMATIDAE** P. Terr.

F. **SYNOMALOPTILIDAE** P. Terr.

e.g. *Synomaloptila longipes* in Kukalova-Peck (1991), Urals, former USSR.

**Order** **DERMAPTERA (FORFICULIDA)**

J. (SIN)—Rec. Terr.

First as for Protodiplatyidae.

F. **DIPLATYIDAE** T. (LMI)—Rec. Terr.

**Extant**

**First:** *Diplatys (Syndiplatys) protoflavicollis* Sakai and Fujiyama (1989), Seki, Sado Island, Japan.

F. **FORFICULIDAE** T. (THA)—Rec. Terr.

**First:** *Forficula paleocaenica* Willmann (1990), Mo-clay, Knuden, Denmark.

F. **LABIDURIDAE** T. (PRB)—Rec. Terr.

**Extant**

**First:** *Semenoviola obliquotruncata* in Popham (1990), Turkestan, former USSR.

F. **LABIIDAE** J. (u.)—Rec. Terr.

**Extant**

**First:** *Brevicula gradus* Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK.

F. **PROTODIPLATYIDAE** (PROTODIPLATIDAE)

J. (SIN)—K. (l.) Terr.

**Extant**

**First:** *Brevicula gradus* Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK.
**Arthropoda (Hexapoda; Insecta)**

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**Key for both diagrams**

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**Order of Orthoptera**

**Extant**

**Order Grylloblattodea (Grylloblattidae pars)** P. (ZEC)–Rec. Terr. (see Fig. 21.5)

Some authors regard this order as Recent only; however, Storozhenko (1988, 1991) would also include a number of families which we have retained in the Protorthoptera.

**Order Blattogryllidae** P. (ZEC)–K. (L.) Terr.

**First** Protoblattogryllus zajsanicus Storozhenko (1990b), Akkolka Formation, Karaungur, Kazakhstan, former USSR.

**Last** Parablattogryllus obscurus Storozhenko (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR.

**Order Geinitziidae** Tr. (u.)–J. (u.) Terr.

**First** e.g. Fletchizia picturata, in Martins-Neto (1991), Molteno Formation, Natal, South Africa.

**Extant**

**Order Oecanthoperliidae** Storozhenko, 1988 K. (L.) Terr.

**First and Last** Oecanthoperla sibirica Storozhenko (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR.
Order ISOPTERA (TERMITIDA) K. (BER)—Rec. Terr.
First as for Hodotermitidae.

F. HODOTERMITIDAЕ K. (BER)—Rec. Terr.
First: Meiatermes berterani Lacasa-Ruiz and Martínez-Delclòs (1986), Lithographic Limestone, Montsech, Spain.
Extant

F. KALOTERMITIDAЕ (CALOTERMITIDAЕ) K. (u.)—Rec. Terr.
First: Termite nest in Rohr et al. (1986), Javelina Formation, Big Bend National Park, Texas, USA. The Lower Cretaceous Hebeitermes (=Hopeitermes) weichangensis in Hong (1985d) is a cockroach hindwing (Blattodea).
Extant

F. MASTOTERMITIDAЕ K. (u.)—Rec. Terr.
Extant

Extant

Extant

Order MANTODEA (MANTIDA, MANTEODEA) K. (1.)—Rec. Terr.
For new fossil families and species, see Gratshev and Zherikhin (in press).

F. CHAETESSIDIDAЕ (CHAETESSIDIDAЕ) K. (1.)—Rec. Terr.
Extant

F. MANTIDAЕ (MANTEIDAE) T. (Oli.)—Rec. Terr.
Extant

Order MIOMOPTERA (PALAEOMANTEIDA) C. (u.)—J. (1.) Terr.
Kukalová-Peck (1991) considers this order belongs to the Oligoneoptera.

F. ARCHAEMIOPTERIDAЕ C. (u.)—P. Terr.
F. METROPATORIDAЕ C. (u.) Terr.
F. PALAEOMANTEIDAE C. (u.)—P. Terr.
F. PALAEOMANTISCIDAE P. (ROT) Terr.
F. PARASIALIDAE P. (ZEC) Terr.
F. PERMOSIALIDAE (PERMOSIALIDIDAЕ, EPIMASTACIDAE) P.—J. (1.) Terr.
Order ORTHOPTERA (GRYLLIDA, TITANOPTERA) C. (STE)—Rec. Terr.
First as for Oedisciidae.

Extant

Extant

First and Last: Adumbratomorpha tettigonioides Gorokhov (1987c), Chekarda, former USSR.

First and Last: Archaeoptenomena cretacea (nomen nudum) Martins-Neto (1987b), Santana Formation, Ceará, Brazil.

e.g. Baissopteryllus sharovii, in Gorokhov (1985), Zaza Formation, Baisa, Buryat ASSR, former USSR.

F. BINTONIELLIDAЕ Gorokhov, 1985 K. (1.) Terr.
e.g. Baissogryllus sharovi, in Gorokhov (1985), Zaza Formation, Baisa, Buryat ASSR, former USSR.

First and Last: Bouretia elegans (nomen nudum) Martins-Neto (1987b), Santana Formation, Ceará, Brazil.

F. ELCANIDAЕ J. (l.)—K. (l.) Terr.
First: e.g. Elcana liasina, in Zessin (1987), Lower Lias, Strensham, Worcestershire, England, UK.
Last: e.g. Eubaissettidae sharovi Gorokhov (1966a), Gurvaneren Formation, Mongolia.

F. EUMASTACIDAЕ J. (u.)—Rec. Terr.
Extant

F. GIGATITANIDAЕ Tr. (u.) Terr.
F. GRYLLACRIDAЕ (GRYLLACRIDAЕ) K. (u.)—Rec. Terr.
The Triassic Xenogryllacris reductus and Jurassic Jurassobatea gryllacroides listed in Martins-Neto (1991) do not belong in this family.
Extant

F. GRYLLAVIDAЕ Gorokhov, 1986b Tr. (u.) Terr.
e.g. Paragryllacrus curtatus Gorokhov (1986b), Madygen, former USSR.

F. GRYLLIDAЕ (ENEOPTERIDAЕ, OECANTHIDAЕ, MYRMECOPHILIDAЕ, TRIGONIDIIDAЕ) K. (l.)—Rec. Terr.
First: e.g. Gryllospeculum mongolicum Gorokhov (1985), Bon-Tsagan, Mongolia.
Extant

F. GRYLLOTALPIDAE K. (APT)—Rec. Terr.
First: e.g. Palaeoscapteriscops cretacea Martins-Neto (1991), Santana Formation, Ceará, Brazil.
Extant

F. HAGLIDAЕ Tr. (u.)—J. (u.) Terr.
First: e.g. Hagloptera intermedia Gorokhov (1986b), Madygen, former USSR.

F. HAGLOEDISCHIIDAE Gorokhov, 1986b Tr. (u.) Terr.
First and Last: Hagloedischia primitiva Gorokhov (1986b), Madygen, former USSR.

First and Last: Haglotettigonia egregia Gorokhov (1988b), River Vitim, former USSR.

F. LOCUSTAVIDAE Tr. Terr.
F. LOCUSTOPSEIDAE (LOCUSTOPSIDAE) Tr. (SCY)–K. (CEN) Terr.
First: Praelocustopsis mirabilis, Siberia, former USSR.
Last: Zeunerella arborea, in Ansgorse (1991), Kzyl Dzhar, Kazakhstan, former USSR.

F. MESOEDISCHIIDAE Gorokhov, 1987b Tr. (u.) Terr.
e.g. Mesoedischia kirgizica Gorokhov (1987b), Madygen, former USSR.

F. MESOGRAMMATIDAE Hong, 1985d K. (1.) Terr.
First and Last: Mesogramma divaricata Hong (1985d), north China. See Caloneurodea.

F. PARATITANIDAE Tr. (u.) Terr.
F. PERMELCANIDAE P. (ART)–Tr. (u.) Terr.
First: Promartynovia venicosta, in Zessin (1987), Wellington Formation, Elmo, Kansas, USA.
Last: e.g. Meselcana permiana Gorokhov (1987b), Madygen, former USSR.

F. PHASOMIMIDAE J. (I.)–Rec. Terr.
First: Paraphasmomima sharovi Zherikhin (1985a), Iya, Irkutsk Basin, former USSR.
Last: e.g. Promastacaoides albertae, in Martins-Neto (1991), Paskapoo Formation, Alberta, Canada.

F. PROMASTACIIDA T. (Eoc.) Terr.
Gorokhov (1988a) transferred the Palaeocene genus Promastacaoides to the Phasomimidae.

F. PROPARAGYLLACRIDIDAE Tr. Terr.
e.g. Paragryllacia sharovi Gorokhov (1987c), Madygen, former USSR.

F. PROPHALANGOPSIDAE J. (I.)–Rec. Terr.
First: Prophaulax mirabilis, Siberia, former USSR.
Last: e.g. Deinovitimia insolita Gorokhov (1989), Zaza Formation, Baisa, Buryat ASSR, former USSR.

F. PROTOGRYLLIDAE Tr. (u.)–J. (u.) Terr.
First: Protogryllus stormbergensis, in Martins-Neto (1991), Stormberg Series, South Africa.
Last: e.g. Falsispeculum karataucicus, in Gorokhov (1985), Karatau, Kazakhstan, former USSR.

F. PRUVOSTITIDAE (TETAVIDAE) P. (ART)–Tr. (u.) Terr.
First: Paroedischia recta, Wellington Formation, Elmo, Kansas, USA.
Last: e.g. Provitimia pectinata, in Martins-Neto (1991), Madygen Formation, Madygen, former USSR.

First: e.g. Cratodactylus ferreirai Martins-Neto (1990), Santana Formation, Ceara, Brazil. Extant

F. TRIASSOMANTEIDAE (TRIASSOMANTIDAE) Tr. (u.)–J. (SIN) Terr.

F. XENOPTERIDAE Tr. (u.) Terr.
e.g. Xenoferganella pini Gorokhov (1989), Madygen, former USSR.
F. AEROPLANIDAE Tr. Terr.
*e.g.* Aeroplana mirabilis, *in* Rozefelds (1985), Australia.

**Last:** Chresmoda aquatica Martinez-Delclòs (1989b), Lithographic Limestone, Montsech, Spain.
Some authors regard this family as belonging in other orders or as Order *incertae sedis*.

**First:** Cretophasma araripensis Martins-Neto (1989), Santana Formation, Ceará, Brazil.
**Last:** *e.g.* Cretophasma nagrei, *in* Martins-Neto (1989), Kzyl-Dzhar, Karatau, Kazakhstan, former USSR.

F. NECROPHASMATIDAE J. (u.) Terr. (Fig. 21.6)

F. PHASMATIDAE T. (PRB)–Rec Terr.

**Extant**

F. PHYLLIIDAE (PHYLLIDAE) T. (PRB)–Rec. Terr.

**Extant**

F. PROCHRESMODIDAE Tr. (u.)–K. (l.) Terr.

**Order** PLECOPTERA (PERLIDA, PERLARIA)

P. (KUN)–Rec. Terr.

Oldest species from Chekarda (former USSR), see Palaeonemouridae, Perlopseidae and Tshekardoperlidae.
Most data are taken from Sinichenkova (1987).
Arthropoda (Hexapoda; Insecta)

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**Fig. 21.6**

**F. BALEYOPTERYGIDAE** Sinichenkova, 1985b

First: *Baleyopteryx alta*, Kuznetsk Basin, Mongolia.

Extant

**F. CAPNIIDAE** T.? (Mio.)–Rec. Terr.

First: *Dipsoperla serpentina*, Transbaikalia, former USSR.

Extant

**F. CHLOROPERLIDAE** K. (I.)–Rec. Terr.

First: *Dipsoperla serpentina*, Transbaikalia, former USSR.

Extant

**F. EUSTHENIIDAE** P. (ZEC)–Rec. Terr.

First: *Stenoperlidium pernianum*, Australia.

Extant

**F. EUXENOPERLIDAE** P. (ZEC)–Tr. (u.) Terr.

First: *Euxenoperla simplex*, Middle Beaufort Series, Natal, South Africa.

Last: *Gondwanoperlidium argentinarum*, Potrevislos Formation, Mendoza, Argentina.

**F. GRIPPOPTERYGIDAE** K. (APT)–Rec. Terr.

First: *Eodinotoperla duncanae* Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia. Extant


First: *Lycoleuctra lupina*, Transbaikalia, former USSR.

Extant

**F. MESOLEUCTIDAE** Tr. (u.)–J. (m.) Terr.

First: *Mesoleuctra gracilis*, Mongolia.

**F. NEMOURIDAE** K. (I.)–Rec. Terr.

First: *Nemourisca diligens*, Transbaikalia, former USSR.

Extant


First: *Uralonympha varica*, Chekarda, former USSR.

Last: *Palaeonemoura clara*, Kuznetsk Basin, Mongolia.

**F. PALAEOPERLIDAE** P. (ZEC) Terr.

First: *Palaeoperla exacta*, Kuznetsk Basin, Mongolia.
Fig. 21.7

F. PERLARIOPISEIDAE Sinichenkova, 1985b  
Tr. (u.)–K. (l.) Terr.  
First: e.g. Fritaniopsis brevicaulis, former USSR.  
Last: e.g. Accretonemoura radiata, Mongolia.

F. PERLIDAE T. (PRB)–Rec. Terr.  
First: Perla prisca, Baltic amber.  
Extant

F. PERLOODIAE J. (u.)–Rec. Terr.  
First: Derancheperla collaris Sinichenkova (1990b), Arhangay Aymag, Mongolia.

F. PERLOPSEIDAE P. (KUN) Terr.  
e.g. Perlopsis flicornis, Chekarda, former USSR.

F. PLATYPERLIDAE J. (l.)–K. (l.) Terr.  
First: e.g. Platyperla platypoda, former USSR.  
Last: Platyperla parricidalis Sinichenkova (1990a), Polosatik, Transbaikalia, former USSR.

F. SIBERIOPERLIDAE Tr. (u.)–K. (l.) Terr.  
Last: e.g. Flexoperla flexuosa, Transbaikalia, former USSR.

First: e.g. Gurvanopteryx effeta, Mongolia.  
Extant

F. TSHEKARDOPERLIDAE Sinichenkova, 1987  
P. (KUN) Terr.  
e.g. Tshekardoperla expulsa, Chekarda, former USSR.

Order PROTELYTROPTERA (PROTELYTRIDA)  
P. Terr.

F. APACHELYTRIDAE P. (ART) Terr.  
First and Last: Apachelytron transversum, in Shear and Kukalova-Peck (1990), Obora, Moravia, Czechoslovakia.

F. ARCHELYTRIDAE P. Terr.

F. DERMELYTRIDAE P. (TAT) Terr.

F. ELYTRONEURIDAE P. Terr.

F. LABIDELYTRIDAE (STENELYTRIDAE)  
Kukalová-Peck, 1988  
P. (TAT) Terr.  
e.g. Labidelytron enervatum in Kukalová-Peck (1988), Belmont, New South Wales, Australia.
Arthropoda (Hexapoda; Insecta)

F. MEGELYTRIDAE P. Terr.
F. PERMELYTRIDAE P. Terr.
F. PERMOPHILIDAE P. (TAT) Terr.
F. PLANELYTRIDAE P. Terr.
F. PROTELYTRIDAE P. Terr.

F. MEGEL YTRIDAE P. Terr.
F. PERMELYTRIDAE P. Terr.
F. PERMOPHILIDAE P. (TAT) Terr.
F. PLANELYTRIDAE P. Terr.
F. PROTELYTRIDAE P. Terr.

e.g. Protelytron permianum, in Jarzembowski (1990b), Wellington Formation, Elmo, Kansas, USA.

F. PROTOCOLEIDAE P. (TAT) Terr.

F. PLANELYTRIDAE P. Terr.

F. PROTOCOLEIDAE P. (TAT) Terr.

F. PERMOPHILIDAE P. (TAT) Terr.

Order PROTORTHOPTERA s.l. (STHAROPODINA,
PARAPLECOPTERA, GERARIDA,
BLATTINOPSODEA, HYPOPERLIDA,
GRYLLOBLATTIDA pars)

C. (NAM A)-Tr. Terr.

We have followed the traditional broad definition of this order sensu F. M. Carpenter. See Rodendorf and Rasnitsyn (1980) for an alternative classification. First as for Paoliididae.

F. ADELONEURIDAE C. (u.) Terr.
F. AENIGMATOIDIDAE C. (u.) Terr.
F. ANTHRACOPTILIDAE C. (u.) Terr.
F. ANTHRACOTHREMMIDAE C. (u.) Terr.

First: e.g. Kochopteron hoffmannorum, in Brauckmann et al. (1985), Vorhalle Beds, Hagen-Vorhalle, Germany.

Last: e.g. Cacurgus spilopterus, in Brauckmann et al. (1985), Carbondale Formation, Mazon Creek, Illinois, USA.

F. APITHANIDAE C. (u.) Terr.
F. ARCHIPROBNIDAE (ARCHIPROBNISIDAE) P. Terr.

F. ATACTOPHLEBIIDAE P. (KAZ) Terr.

e.g. Atactophlebia termitoides, in Storozhenko (1990a), Kama River, former USSR.

F. BLATTINOPSIDAE C. (u.)-P. Terr.


First: e.g. Kochopteron hoffmannorum, in Brauckmann et al. (1985), Vorhalle Beds, Hagen-Vorhalle, Germany.

Last: e.g. Cacurgus spilopterus, in Brauckmann et al. (1985), Carbondale Formation, Mazon Creek, Illinois, USA.

F. CAMPTONEURITIDAE P. Terr.
F. CHELOPERIDAE P. Terr.
F. CNEMIDOLESTIDAE C. (u.) Terr.
F. CYMBOPSIDAE P. Terr.
F. DEMOPTERIDAE P. Terr.
F. EPIDEIGMATIDAE C. (u.) Terr.
F. EUCAENIDAE C. (WES D) Terr.

First and Last: Eucanaeus ovalis, in Baird et al. (1985), Carbondale Formation, Mazon Creek, Illinois, USA.

F. EURYMISCIDAE P. Terr.
F. EURYPTILONIDAE P. Terr.
F. EVENKIDAE C. (u.) Terr.
F. GERARIDAE C. (u.) Terr.

F. MEGAKHOSARIDAE P. Terr.

F. HADONOMIDAE C. (u.) Terr.
F. HAPALOPTERIDAE C. (u.) Terr.
F. HAVLATIIDAE P. Terr.
F. HERBSTIALIDAE C. (u.) Terr.
F. HERDINIDAE C. (u.) Terr.

e.g. Herdinia mirificus, in Shear and Kukalova-Peck (1990), Carbondale Formation, Mazon Creek, Illinois, USA.

F. HETEROPTILIDAE P. Terr.
F. HOMALOPHLEBIIDAE C. (u.) Terr.
F. HOMOEODICTYIDAE P. Terr.
F. HYPOPERLIDAE P. Terr.
F. IDELIIDAE C. (u.)–Tr. (m.) Terr.
F. ISCHNONEURIDAE C. (u.) Terr.
F. JABLONIIIDAE P. Terr.

F. LIOMOPTERIDAE P. Terr.

F. LEMMATOPHORIDAE P. (ROT–ZEC) Terr.

First: Lemmatophora typa in Kukalova-Peck (1991), Wellington Formation, Elmo, Kansas, USA.

Last: Karaungirella minuta Storozhenko (1991), Karaungur, Kazakhstan, former USSR.

F. LIOMOPTERIDAE P. Terr.

F. MEGAKHOSARIDAE P. Terr.

E.g. Megahkosa rodendorji, in Martins-Neto (1987a), Boituva, Brazil.

F. OMALIIDAE C. (u.) Terr.
F. PACHYTYLOPSIDAE C. (u.) Terr.
F. PAOLIIDAE C. (NAM A–WES A) Terr.


Last: e.g. Zdenekia occidentalis Laurentiaux-Vieira and Laurentiaux (1986b), micaceous schists, Charbonnages de Ressaux, Belgium.

F. PERMARRHAPHIDAE P. Terr.
F. PERMOTERMOPSIDAE P. Terr.
F. PHENOPTERIDAE P. Terr.
F. PROBNIDAE P. Terr.
F. PROEDISCHIDAE C. (u.) Terr.
Animals: Invertebrates

First and Last: Proedischia mezzalirai, in Martins-Neto (1987a), Boituva, Brazil.

F. PROTEMBIIDAE P. Terr.
F. PROTOKOLLARIIDAE C. (u.) Terr.
F. PROTOPHASMATIDAE C. (u.) Terr.
F. PROTOPROSBOLOIDEA C. (NAM B) Terr.

First and Last: Protoprosbole straeleni, in Brauckmann (1988a), Charleroi Coal Basin, Belgium.
Arthropoda (Hexapoda; Insecta)

F. PSOROPTERIDAE P. Terr.
F. SHEIMIIDAE P. Terr.
F. SKALICIIDAE P. Terr.
F. SPANIODERIDAE C. (u.) Terr.
F. STEGOPTERIDAE P. Terr.
F. STENONEURIDAE C. (u.) Terr.
F. STENONEURITIDAE C. (u.) Terr.
F. STEREOPTERIDAE P. Terr.
F. STREPHOCLADIDAE C. (u.)-P. Terr.
F. STREPHONEURIDAE P. Terr.
F. STYGNIDAE C. (u.) Terr.
F. SYLVAPHLEBIIDAE P. Terr.
F. THORONYSIDAE C. (u.) Terr.
F. TILLYARDEMBIIDAE P. Terr.
F. TOMIIDAE P. Terr.

Superorder PARANEOPTERA (Hemipteroid orders)
P. (ROT)-Rec. Terr.

Order HEMIPTERA (CIMICIDA) P. (ROT)-Rec. Terr.

Earliest families: Archescytinidae, Boreoscytidae, Ingruidae and Prosbolopseidae.

First: e.g. Acanthosoma sp. Fujiyama (1987), Abura, Hokkaido, Japan.

First: e.g. Acixites immodesta Hamilton (1990), Santana Formation, Ceará, Brazil.

F. ADELGIDAE K. (u.)-Rec. Terr.


The earlier records in Boucot (1990) are extremely doubtful.

F. ALYDIDAE J. (u.)-Rec. Terr.

First: Berendtaphis cimicoides, in Heie (1985), Baltic amber.

First: e.g. Eoanthocoris cretaceus Popov (1990), Turga Formation, Transbaikalia, former USSR.

First: Paleapsylloides oligocaenica, in Bekker-Migdisova (1985b), Baltic amber.

First: e.g. Sunaphis shandongensis Hong and Wang (1990), Laiyang Formation, Shandong, China.


First: Aradus nicholasi Popov (1989), Bon-Tsagan, Mongolia.

F. ARCHEGOCIMICIDAE (ARCHAEGOCIMICIDAE, EONABIDAE, DIATILLIDAE) J. (SIN)-K. (l.) Terr.
Last: e.g. Sondalia kovalevi Popov (1988b), Godymoyskaya Formation, Onokhoy, Chita, former USSR.

F. ARCHESCYTINIDAE P. (ROT-ZEC) Terr.
First: e.g. Archescytina permiana, in Wootton and Betts (1986), Wellington Formation, Elmo, Kansas, USA.
Last: e.g. Protopincombea obscura, in Bekker-Migdisova (1985a), New South Wales, Australia.

F. ARCHIJASSIDAE J. (u.)-K. (l.) Terr.
Last: Archijassus? plurieris Zhang (1985), Laiyang Formation, Laiyang, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age. Shcherbakov (pers. comm.) considers that this species does not belong in this family and that this family belongs in the Hylicellidae.

F. BELOSTOMATIDAE Tr. (u.)-Rec. Terr.

F. BERNAEIDAE K. (l.) Terr.


Last: Megaleurodes megocellata Hamilton (1990), Santana Formation, Ceará, Brazil. Shcherbakov (pers. comm.) considers that this species does not belong in this family.

F. CANADAPHIDAE K. (l.)-u.) Terr.
First: Nuuraphis gemma Vengerek (1991), Bon-Tsagan, Mongolia.
Last: e.g. Canadaphis carpenteri, in Heie (1987), Canadian amber, Cedar Lake, Manitoba, Canada.

First: e.g. Carsidarina hooleyi, in Bekker-Migdisova (1985b), Bembridge Marls, Isle of Wight, England, UK.


F. CERCOPIDAE K. (u.)-Rec. Terr.
First and Last: Cercopion reticulata Hamilton (1990), Santana Formation, Ceará, Brazil.
F. CHILIOCYCLIDAE Tr. (u.) Terr.
F. CICADELLIDAE (ASSIDAE, SPINIDAE, JASCOPIDAE, APHRODIDAE, COELEIDAE, EUSCELIDAE, ASSIDAE, MACROPSIDAE, TETTIGELLIDAE) K. (l.)–Rec. Terr.
First: e.g. Mesococcus lutarius Zhang (1985), Laiyang Formation, Laiyang, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age. Extant
First: e.g. Mesococcus lutarius Zhang (1985), Laiyang Formation, Laiyang, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age. Extant
F. CICADOPROSBOLIDAE Tr. (u.)–K. (l.) Terr.
Last: e.g. Architettix compacta Hamilton (1990), Santana Formation, Ceanl, Brazil. Extant
F. CIXIIDAE K. (BRM)–Rec. Terr.
F. COLEOSCYTIDAE P. (ZEC) Terr.
F. COREIDAE (CORIZIDAE, RHOPALIDAE) J. (u.)–Rec. Terr.
First: e.g. Hebeicoris xinboensis Hong (1985d), north China. Extant
F. COREIDAE J. (l.)–Rec. Terr.
First: e.g. Venacorixa xiangzhongensis Lin (1986), south China. Extant
F. CREAPHIDIDAE Shcherbakov and Vengerek, 1991 Tr. (CRN) Terr.
First and Last: Creaphis theodora Shcherbakov and Vengerek (1991), Madygen Formation, Dzhalou-Tcho, South Fergana, former USSR. Extant
F. CUNEOCORIDAE J. (l.) Terr.
F. CURVICUBITIDAE Hong, 1984b Tr. (m.) Terr.
First and Last: Curvicubitus triassicus Hong (1984b), Tongchuan Formation, Jinshuoguan, Shaanxi, China. Kozlov (1988) transferred this family from the Lepidoptera. Extant
First: e.g. Clavicornis cretaceus Popov (1986), Gurvaneren Formation, Mongolia. Extant
F. DELPHACIDAE (ARAEOPIDAE) K. (APT)–Rec. Terr.
Extant
F. DERBIDAE Tr. (u.?)–Rec. Terr.
First: Sanctipaulus mendesi, in Martins-Neto (1987a), Santa Maria Formation, Rio Grande do Sul, Brazil. Shcherbakov (pers. comm.) considers that this species does not belong to this family. Extant
F. DIASPIDIDAE T. (PRB)–Rec. Terr.
Extant
F. DICTYOPHARIDAE K. (SAN)–Rec. Terr.
First: Netutela announciator, in Martins-Neto (1988a), Siberian amber, Taimyr, former USSR. Extant
Extant
F. DRECANOSPIDIDAE (CALLAPHIDAE) J. (u.?)–Rec. Terr.
First: Jurocallis longipes, in Heie (1987), Karabastau Formation, Karatau, Kazakhstan, former USSR. Extant
F. DUNSTANIIDAE P. (ZEC)–J. (u.) Terr.
F. DYSMORPHOPTILIDAE (EOSCARTERELLIDAE, DISMORPHOPTILIDAE) F. (ZEC)–J. (u.) Terr.
First: e.g. Antonaphis brachycera, in Heie (1987), Siberian amber, Taimyr, former USSR. Last: Schizoneurites sp., in Heie (1985), Willershausen, Germany. Extant
F. ENICOCORIDAE (XISHANIDAE, MESOLYGAEIDAE) J. (u.)–K. (l.) Terr.
e.g. Mesolygaeus laiyangensis, in Zhang (1991b), China and Mongolia. Comment: The name Enicocoridae has date priority over Xishanidae and Mesolygaeidae; the latter was used erroneously by Hong and Wang (1990) and Zhang (1991b). Extant
F. ERIOCOCCIDAE T. (PRB)–Rec. Terr.
First: e.g. Kuenowicoccus pietazeniukae Koteja (1988b), Baltic amber. Extant
F. FLATIDAE T. (PRB)–Rec. Terr.
First: Figured but undescribed in Gomez Pallerola (1986), Lithographic Limestone, Montsech, Spain. Shcherbakov (pers. comm.) considers that these specimens do not belong in this family. Extant
F. FULGORIDAE K. (?) (BER)–Rec. Terr.
First: Figured but undescribed in Gomez Pallerola (1986), Lithographic Limestone, Montsech, Spain. Shcherbakov (pers. comm.) considers that these specimens do not belong in this family. Extant
F. FULGORIDAE J. (l.–u.) Terr.
First: e.g. Valvifulgoria tiantungensis Lin (1986), Guangxi, China. Comments: Zhang (1989) transferred the Miocene species in Hong (1985b) to the genus Limois in the Fulgoridae. Shcherbakov (pers. comm.) considers that this family belongs in the Cixiidae. Extant
F. GELASTOCORIDAE K. (? (APT)–Rec. Terr.
First: Gelastocorid indet. Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia. Popov
### Arthropoda (Hexapoda; Insecta)

#### Tertiary

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#### Cretaceous

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Fig. 21.9
(pers. comm.) considers that these specimens belong in the Nuacoridae.

F. GENAPHIDIDAE J. (u.) Terr.


F. GERRIDAE T. (Pal.)–Rec. Terr. Extant

F. GRANULIDAE Tr. m. Terr.

F. GREENIDEIDAE T. (LMI)–Rec. Terr.

First: e.g. *Aphis* macrostyla, in Heie (1987), Radoboj, Croatia.

F. HEBRIDAE T. (CHT)–Rec. Terr. Extant

First: e.g. ?Hebrus* sp., in Spahr (1988), Mexican amber, Chiapas, Mexico.


First: e.g. *Petiolaphis laiyangensis* Hong and Wang (1990), Laiyang Formation, Shandong, China.

F. HYDROMETRIDAE T. (Pa1.)–Rec. Terr. Extant

F. HYLICELLIDAE Tr. (u.)-K. (u.) Terr.

F. IGNOTALIDAE (IGNATOLIDAE) P. (ZEC) Terr.


First: e.g. *Scytoineurella major* in Shcherbakov (1984), Chekarda, former USSR.


First and Last: *inka minuta* Koteja (1989), Siberian amber, Taimyr, former USSR.

F. IPSVICIIDAE Tr. (u.)–K. (l.) Terr.

First: *Ipsuvia jonesi* in Kukalova-Peck (1991), Australia. *Apheloscyta xiangdongensis* Un (1986) was originally placed in this family; however, this genus belongs in the Scytinopteridae, see Shcherbakov (1984).

F. ISOMETOPIDAE T. (CHT)–Rec. Terr. Extant

F. ISSIDAE K. (u.)–Rec. Terr. Extant

F. KARABASIIDAE Popov, 1985 J. (l.)–K. (u.) Terr.

First: *Tegulicicada plana* in Popov (1989), Shiti Formation, Guangxi, China.

F. KARANABIDAE J. (u.) Terr.

Popov (pers. comm.) considers that this family belongs in the Mesovellidae.

F. KERMESIDAE T. (PRB)–Rec. Terr. Extant

First: e.g. *Cinara limnogena* Zhang (1989), Shanwang Formation, Shanwang, China.

F. LACHNIDAE T. (Mio.)–Rec. Terr.

First: e.g. *Cinara limnogena* Zhang (1989), Shanwang Formation, Shanwang, China.


First and Last: *Lalax mutabilis* Hamilton (1990), Santana Formation, Ceará, Brazil.

Comment: Shcherbakov (pers. comm.) considers that this family belongs in the Cixiidae.

F. LASYIDAE K. (APT)–Rec. Terr.

First: e.g. *Lalax mutabilis* Hamilton (1990), Santana Formation, Ceará, Brazil.

Comment: Shcherbakov (pers. comm.) considers that this family belongs in the Cydnidae.

F. LEPTOPODIDAE T. (CHT)–Rec. Terr. Extant

F. LEIOPHYLLIDAE (LITHENTOMIDAE, ASIENTOMIDAE) P. (ZEC) Terr.

First: e.g. *Liadopsylla geinitzi* in Bekker-Migdisova (1985b), Upper Lias, Dobbentin, Germany.

F. LYGAEIDAE J. (?–Rec. Terr.


F. MAGNACICADIIDAE Tr. (m.) Terr.

F. MALMOPSYLLIDAE Bekker-Migdisova, 1985b J. (u.) Terr.

First and Last: *Malmopsylla karatavica* Bekker-Migdisova (1985b), Karabastau Formation, Karatau, Kazakhstan, former USSR.

F. MARGARODIDAE T. (PRB)–Rec. Terr. Extant

First: Figured in Koteja (1990), Baltic amber.

F. MATSUOCIDAE K. (l.)–Rec. Terr.

First: e.g. *Eomatuscoccus sakachewa* Koteja (1988a), Zaza Formation, Baisa, Buryat ASSR, former USSR.

F. MEMBRACIDAE T. (Oli.)–Rec. Terr. Extant


F. MESOGEREONIDAE Tr. (u.) Terr.

First: e.g. *Mesogereon superbum* in Kukalova-Peck (1991), Queensland, Australia.

F. MESOPENTACORIDAE J. (TOA)–K. (l.) Terr.

Last: e.g. *Corienta transbaicalica* Popov (1990), Turga Formation, Transbaikalia, former USSR.

F. MESOTREPHIDAE K. (u.) Terr.

F. MESOTREPHIDAE K. (u.) Terr.

F. MESOTREPHIDAE K. (u.) Terr.

F. MESOTREPHIDAE K. (u.) Terr.

F. MICROPHYSIDAE K. (u.)–Rec. Terr. Extant

F. MICOATIDAE T. (?–Rec. Terr.


F. MICOATIDAE T. (?–Rec. Terr.

First: *Duncanovelia extensa* Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia. Extant

F. MICOATIDAE T. (?–Rec. Terr.

First: Duncanovelia extensa Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia. Extant

F. MICOATIDAE T. (?–Rec. Terr.

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F. MICOATIDAE T. (?–Rec. Terr.

First: Duncanovelia extensa Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia. Extant

Arthropoda (Hexapoda; Insecta)

F. MINDARIDAE K. (u.)—Rec. Terr.
First: Nordaphis sukatchevae, in Heie (1987), Siberian amber, Taimyr, former USSR.

F. MIRIDAE J. (u.)—Rec. Terr.

First: Monophlebus irregularis, in Koteja (1990), Baltic amber.

F. NABIDAE J. (m.? )—Rec. Terr.
First: Sinanabis brevipes Zhang (1986b), Hebei, China.
Comment: The position of this species is doubtful. Popov (pers. comm.) considers that it belongs in the Mesovellidae.

F. NAUCORIDAE (APHLEBOCORIDAE, APOPNIDAE, ATOPOSITIDAE) Tr. (u.)—Rec. Terr.
Extant

F. NEOPSYLLOIDIDAE Bekker-Migdisova, 1985b J. (u.) Terr.
e.g. Neopsylloides turutanovae Bekker-Migdisova (1985b), Karatau, Kazakhstan, former USSR.

F. NEPIDAE J. (u.)—Rec. Terr.
Extant

F. NOTONECTIDAE Tr. (u.)—Rec. Terr.
Extant

First: e.g. Protorthezia aurea Koteja (1987), Baltic amber, Poland.

F. OVIPAROSIPHIDAE K. (1.) Terr.
e.g. Oviparosiphum jakovlevi, in Heie (1987), Mongolia. This family may be synonymous with the Drepanosiphidae, see Jarzembowski (1989b).

F. PACHYMERIDIIDAE (PSYCHROCORIDAE, HYPOCIMICIDAE, SISYROCORIDAE) J. (SIN)—K. (1.) Terr.
First: e.g. gen. et sp. nov. 3A Whalley 1985, Lower Lias, Charmouth, Dorset, England, UK.
Last: e.g. Pachycoridium letum Popov, 1986, Madygen Formation, Fergana, former USSR.

F. PALAEOAPHIDIDAE K. (1.-u.) Terr.
e.g. Caudaphis spinalis Zhang et al. (1989), Laiyang Formation, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as early Cretaceous in age.
Last: e.g. Palaeoaphis archimelia, in Heie (1985), Canadian amber, Cedar Lake, Manitoba, Canada.

First: e.g. Asiooress costalis, in Gomez Pallerola (1984), Dzhil Formation, Issyk-Kul, Kirgizia, former USSR.
Last: e.g. figured but undescribed in Jazzembowski (1984), Lower Weald Clay, Capel, Surrey, England, UK.

F. PARAKNIGHTIIDAE P. (ZEC)—Tr. (u.) Terr.

First: e.g. Germaphis dryoides, in Heie (1985), Baltic amber. Heie (1985) listed the Upper Cretaceous Palaeoforda taymyrensis as systematic position unknown.

Extant

F. PEREBORIIDAE (PEREBORIDAE) P. (ZEC) Terr.
e.g. Scytophara extensa, in Shcherbakov (1984), Kargala, former USSR.

Extant

F. PHYMATIDAE T. (RUP)—Rec. Terr.
Extant

Extant

F. PINCOMBEIDAE (PINCOMBAEIDAE) P. (ZEC)—Tr. (u.)
First: e.g. Pincombea mirabilis, in Bekker-Migdisova (1985b), Belmont, New South Wales, Australia.
Last: Madygenopsyllidium djailautshoense Bekker-Migdisova (1985b), Madygen Formation, Fergana, former USSR.

First: Electrococcus canadensis, in Koteja (1989), Canadian amber, Cedar Lake, Manitoba, Canada.

F. PRICECORIDAE K. (APT) Terr.
First and Last: Pricecoris beckerae, in Martins-Neto (1987a), Codó Formation, Maranhão, Brazil.
Comment: Popov (pers. comm.) considers that this family belongs in the Cydnidae.

F. PROBASCANIIIDAE (PROBASCANIONIDAE) J. (I.) Terr.
e.g. Probascian megacephalum, in Ponomarenko and Schultz (1988), Upper Lias, Dobbertin, Germany.

F. PROCERCOPIDAE J. (I.)—K. (u.) Terr.

F. PROGONOCIMICIDAE (ACTINOSCYTINIDAE, CICADOCORIDAE, ACTINESCYTINIDAE, EOCIMICIDAE) P. (ZEC)—K. (u.) Terr.
First: e.g. Actinoscytina belmontensis, in Wootton and Betts (1986), Warner’s Bay, New South Wales, Australia.

F. PROPREOCORIDAE J. (I.) Terr.
Comment: Popov (pers. comm.) considers that this family belongs in the Cydnidae.

First and Last: Prosolecidida gondwanica Pinto (1987b), Irati Formation, Rio Grande do Sul, Brazil.
Comment: Shcherbakov (pers. comm.) considers that this family belongs in the Prosolbiidae.
Fig. 21.10

F. PROSBOLIDAE (CICADOPSYLLIDAE, PERMOGLYPHIDAE, PERMOCICADOPSIDAE, SOJANONEURIDAE) P. (ZEC)–Tr. (u.) Terr.

First: e.g. *Permocicada integra* in Shcherbakov (1984), Ivango-Gora Beds, Archangelsk, former USSR.

Last: e.g. *Sinisbole juvenis* Lin (1986), Hunan, China.

Comment: Shcherbakov (pers. comm.) considers that this species belongs in the Hylicellidae.

F. PROSBOLOPSEIDAE (PROSBOLOPSIDAE, IVAIIDAE, MUNDIDAE) P. (ROT–ZEC) Terr.

Last: e.g. *Prosboloneura kondomensis*, in Shcherbakov (1984), Kuznetsk Formation, Kaltan, Kuznetsk Basin, former USSR.

F. PROTOCORIDAE J. (l.) Terr.

e.g. *Pallicoris firmis* Lin (1986), Guangxi, China.

Comment: Popov (pers. comm.) considers that this species belongs in the Pachymeridiidae.

F. PROTOPSYLLIDIIDAE (EOPSYLLIDIIDAE, PERMOPSYLLIDAE, PERMAPHIDOPSEIDAE) P. (ZEC)–K. (l.) Terr.

First: e.g. *Permopsyllidium mitchelli*, in Bekker-Migdisova (1985b), New South Wales, Australia.

Last: *Aphidulum stenoptilium* Shcherbakov (1988a), Bon-Tsagan, Mongolia.


Extant
### Arthropoda (Hexapoda; Insecta)

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**Key for both diagrams**

5. Procercoptidae 23. Serpentivenidae  41. Aphidiidae
6. Progonocimiidae 24. Shurabellidae  42. Amphinomidae
7. Proprococoidae 25. Serpentividae  43. Archipsocidae
9. Proboleidae  27. Stenoviidae  45. Caeciliidae
11. Proprococidae 29. Tajmyrakrotidae  47. Edgariackiidae
13. Pseudoscalididae 31. Tettigometrididae  49. Elipsocidae
15. Psychodidae  33. Tingidae  51. Lachesillidae
16. Pyrrhocoridae 34. Tingidae  52. Lepidopsocidae
17. Reduviidae  35. Tingidae  53. Liposcelidae
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Fig. 21.11

Comment: Shcherbakov (pers. comm.) considers that this species belongs in the Procercopidae.

F. SERPENTIVENIDAE (SERPENTIVENIDAE)  
Shcherbakov, 1984  
P. (ZEC)—Tr. (u.) Terr.
Last: e.g. Serpentivena tigrina Shcherbakov (1984), Madygen Formation, southern Fergana, former USSR.
First: Tinaphis sibirica Vengerek (1989), Itatskaya Formation, Yenisey River, Siberia, former USSR.

F. SHAPOSHNIKOVIIDAE J. (u.)—K. (u.) Terr.
Last: e.g. Shaposhnikovia electri in Heie (1987), Siberian amber, Taimyr, former USSR.
First: e.g. Shurania sibirica Popov (1985), Kuznetsk Basin, former USSR.

F. SHURABELLIDAE J. (l.–m.). Terr.
Last: e.g. Shurania altaica Popov (1988a), Bakhar Formation, Gobi Altai, Mongolia.
Arthropoda (Hexapoda; Insecta)

  e.g. *Sinaphidum epichare* Zhang et al. (1989), Laiyang Formation, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age. Vengerek (pers. comm.) considers that this family belongs in the Oviparosiphidae.

F. STENOVICIIDAE P. (ZEC)–Tr. (u.) Terr.


F. TAJMYRAPHIDIDAE (TAYMYRAPHIDIDAE) K. (u.) Terr.
  e.g. *Tajmyraphis beckermigdisova*, in Heie (1987), Siberian amber, Taimyr, former USSR.

F. TETTIGARTIDAE Tr. (u.?)–Rec. Terr.
  First: e.g. *Quadrisbole vieta* Lin (1986), Hunan, China.
  Comment: Shcherbakov (pers. comm.) considers that this species and *Lacunisbole ligonis* Lin (1986) do not belong in this family.

F. TETTIGOMETRIDAE T. (PRB)–Rec. Terr.
  Extant

F. THAUMASTELLIDAE K. (APT)–Rec. Terr.
  Extant

F. THELAXIDAE T. (PRB)–Rec. Terr.
  First: *Palaeothelaxes setosa*, in Heie (1987), Baltic amber.
  Extant

  First: e.g. *Sinulocader drakei* Popov (1989), Bon-Tsagan, Mongolia.
  Extant

F. TRIASSOCORIDAE Tr. (u.) Terr.

  Extant

  First: e.g. *Urochela pardinis* Zhang (1989), Shanwang Formation, Shanwang, Shandong, China.
  Extant

  Comment: Zherikhin (pers. comm.) considers that this family belongs in the Lophioneuridae.

F. XYLOCOCCIDAE (XYLOCCIDAE) K. (l.)–Rec. Terr.
  First: *Baisococcus victoriae*, in Koteja (1989), Zaza Formation, Baisa, Buryat ASSR, former USSR.
  Extant

Order PHYTHIRAPTERA (ANOPLURA, MALLOPHAGA) T. (PRB)–Rec. Terr.
  First: Eggs in Boucot (1990), Baltic amber. These eggs cannot be determined to family level.
  Extant
  Comment: There are no pre-Quaternary family records of this order.

Order PSOCOPTERA (PSOCIDA, CORRODENTIA) P. (ROT)–Rec. Terr.
  F. AMPHIENTOMIDAE K. (u.)–Rec. Terr.
  Extant

  Extant

F. ARCHIPSOCIDAE T. (PRB)–Rec. Terr.
  Extant

F. ARCHIPSYLLIDAE P. (ZEC)–K. (l.) Terr.
  F. CAECILIIDAE T. (PRB)–Rec. Terr.
  Extant

  Extant

  First and Last: *Edgariekie una* Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.
  Comment: Zherikhin (pers. comm.) considers that this family belongs in the Lophioneuridae.

F. ELECTRENOMIDAE T. (PRB) Terr.
  F. ELIPSOCIDAE K. (u.)–Rec. Terr.
  Extant

F. EPIPSOCIDAE T. (PRB)–Rec. Terr.
  Extant

F. LACHESILLIDAE K. (u.)–Rec. Terr.
  Extant

F. LEPIDOPSOCIDAE T. (PRB)–Rec. Terr.
  Extant

F. LIPOSCELIDAE T. (PRB)–Rec. Terr.
  Extant

F. LOPHIONEURIDAE P. (ROT)–K. (u.) Terr.
  Comment: Some authors consider that this family does not belong in this order.

F. MARTYNOPSOCIDAE P. Terr.

  Extant

  Extant

  Extant

  Extant

F. PERMOPSOCIDAE P. Terr.

F. PSEUDOPISOCIDAE P. Terr.

F. PHILOTARSIDAE T. (PRB)–Rec. Terr.
  Extant

  Extant

F. PSEUDOCAECILIIDAE T. (PRB)–Rec. Terr.
  Extant

F. PSOCIDAE T. (PRB)–Rec. Terr.
F. PSOCIDIIDAE  P. Terr.
F. PSYLLIPSOCIDAE  K. (u.)–Rec. Terr.
F. SPHAEROPSOCIDAE  K. (u.)–Rec. Terr.
F. SURIJOKOPSOCIDAE  P. Terr.

F. TRICHOPSOCIDAE  T. (PRB)–Rec. Terr.
F. TROGIIDAE  K. (u.)–Rec. Terr.
F. ZYGOPSOCIDAE  P. Terr.

Order THYSANOPTERA (THRIPIDA)
P. (ROT)–Rec. Terr.

Extant
Extant
Extant
Extant
Arthropoda (Hexapoda; Insecta)

F. AEOLOTHRIPIDAE (AEOTHRIPIDAE)  
K. (u.)—Rec. Terr.  
**Extant**

F. HETEROTHRIPIDAE  
J. (u.)—Rec. Terr.  
**Extant**

F. KARATAOTHRIPIDAE  
J. (u.)  Terr.  
F. LIASSOTHRIPIDAE  
J. (u.)  Terr.  
F. MEROTHRIPIDAE  
T. (PRB)—Rec. Terr.  
**Extant**

F. PALAEOTHRIPIDAE  
T. (Eoc.)  Terr.  
F. PERMOTHRIPIDAE  
P. (ROT)  Terr.  
F. PHLAEOOTHRIPIDAE  
T. (PRB)—Rec. Terr.  
**Extant**

F. THRIPIDAE  
K. (u.)—Rec. Terr.  
**Extant**

Order ZORAPTERA  
T. (Oli.)—Rec. Terr.  
Only one fossil record.

F. ZOROTYPIDAE  
T. (Oli.)—Rec. Terr.  
**Extant**


Superorder OLIGONEOPTERA (Holometabola, Endopterygota, Scarabaeiformes)  
C. (u.?)—Rec. Terr.  
First as for Raphidioptera.

Order COLEOPTERA (SCARABAEIDA)  
P. (ROT)—Rec. Terr.  

F. ACANTHOCNEMIDAE  
(ACANTHOCUEMIDAE)  
J. (l.?)—Rec. Terr.  
**Extant**

First: Artinama qinghuoensis Lin (1986), south China.  
Comment: Ponomarenko (pers. comm.) considers that this species belongs in the Elateridae.

F. ADEMOSYNIDAE  
Tr. (u.)—K. (l.)  Terr.  
**Extant**

First: e.g. Ademosynoides juxta Lin (1986), south China.

F. ADERIDAE (CIRCAEIDAE)  
T. (PRB)—Rec. Terr.  
**Extant**

F. ACANTHOCNEMIDAE  
(ACANTHOCUEMIDAE)  
J. (l.?)—Rec. Terr.  
**Extant**

F. APIONIDAE  
K. (l.)—Rec. Terr.  
**Extant**

F. ARTEMATOPIDAE  
T. (?PRB)—Rec. Terr.  
**Extant**

F. ASIOCOLEIDAE  
P.  Terr.  
F. ASPIDIPHORIDAE  
T. (PRB)—Rec. Terr.  
**Extant**

F. ATTELABIDAE  
K. (l.)—Rec. Terr.  
**Extant**

F. BOSTRYCHIDAE  
T. (YPR)—Rec. Terr.  
**Extant**

F. BRENTHIDAE (BRENTIDAE)  
T. (Oli.)—Rec. Terr.  
**Extant**

F. BRUCHIDAE  
J. (m.?)—Rec. Terr.  
**Extant**

First: Mesoloria longala Zhang (1986b), northern Hebei, China.  
Comment: Ponomarenko (pers. comm.) considers that this species does not show any structures attributable to this family.

F. BUPRESTIDAE (ELECTRAPATIDAE)  
J. (m.)—Rec. Terr.  
**Extant**

F. BYRRHIDAE  
J. (l.)—Rec. Terr.  
**Extant**

F. BYTURIDAE  
T. (?PRB)—Rec. Terr.  
**Extant**

F. CANTHARIDAE  
K. (APT)—Rec. Terr.  
**Extant**


F. CARABIDAE (PAUSSIDAE)  
J. (SIN)—Rec. Terr.  
**Extant**

First: e.g. figured but undescribed, in Whalley (1985), lower Lias, Charmouth, Dorset, England, UK.

F. CATINIIIDAE (CANTITIDAE)  
Tr. (u.)—K. (l.)  Terr.  
**Extant**

F. CATOPIDAE  
T. (PRB)—Rec. Terr.  
**Extant**

F. CERAMBYCIDAE  
K. (l.)—Rec. Terr.  
**Extant**

F. CEROPHYTIDAE  
K. (l.)—Rec. Terr.  
**Extant**

F. CERYLONIDAE  
K. (u.)—Rec. Terr.  
**Extant**

F. CHRYSOMELIDAE  
J. (u.)—Rec. Terr.  
**Extant**

F. CICINDELIDAE  
T. (PRB)—Rec. Terr.  
**Extant**

F. CISIDAE  
T. (PRB)—Rec. Terr.  
**Extant**

F. CLAMBIDAE  
**Extant**

F. CLERIDAE  
T. (PRB)—Rec. Terr.  
**Extant**
**Animals: Invertebrates**

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**Fig. 21.13**

**F. COCCINELLIDAE** K. (I.)—Rec. Terr.  
*Extant*  
*Last:* e.g. *Bolbonectes intermedius* Ponomarenko (1987), Byankinskaya Formation, Bolboy, former USSR.

**F. COPLYDIIDAE** K. (I.)—Rec. Terr.  
*Extant*  

*First:* e.g. *Timarchopsis sainshandensis* Ponomarenko (1987), Khamarkhoburinskaya Formation, Tushilga, Mongolia.

**F. CORYLIDAE** (ORTHOPERIDAE)  
T. (PRB)—Rec. Terr.  
*Extant*  

**F. CRYPTOPHAGIDAE** K. (SAN)—Rec. Terr.
**F.** ARTHROPODA (HEXAPODA; INSECTA)

397

**F.** CUCUJIDAE K. (u.)–Rec. Terr. Extant

**F.** CUPEDIDAE (CUPESIDAE, TRIADOCUPEDIDAE) Tr. (m.)–Rec. Terr. Extant

First: **Chengdecupes shiluoense** Hong (1985d), north China. Extant

**F.** CURCULIONIDAE J. (?SIN)–Rec. Terr. Extant

First: gen. et sp. indet. Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK. Comment: Zherikhin (pers. comm.) considers that this specimen does not belong in this family.

**F.** CYBOCEPHALIDAE T. (?PRB)–Rec. Terr. Extant

First: e.g. **Mesogyrus sibiricus** Ponomarenko (1985a), former USSR. Extant

**F.** DASCILLIDAE J.–Rec. Terr. Extant

**F.** DERMESTIDAE T. (Pal.)–Rec. Terr. Extant

**F.** DRYOPIDAE T. (PRB)–Rec. Terr. Extant

**F.** ELATERIDAE J. (SIN)–Rec. Terr. Extant

First: e.g. **Sucinimontia infleta**, Perkovsky (1990), Zaza Formation, Baisa, Buryat ASSR, former USSR. Extant

**F.** ELMIDAE T. (Eoc.)–Rec. Terr. Extant

First: e.g. **Liadytes major** Ponomarenko (1985a), Ust-balei, Irkutsk Basin, Siberia, former USSR. Last: e.g. **Liadytes dajensis** Ponomarenko (1987), Glushkovskaya Formation, Daya River, former USSR. Comment: Crowson (1985) preferred to treat this genus as **Adephaga incertae sedis.** Extant

**F.** F. LIMNICHIDAE T. (PRB)–Rec. Terr. Extant

**F.** LIADYTIDAE (LYADYTIDAE) J. (I.)–K. (I.) Terr. Extant

**F.** LIMNICHIDAE T. (PRB)–Rec. Terr. Extant

**F.** LOPHOCATERIDAE J. (u.)–Rec. Terr. Extant

**F.** LUCANIDAE T. (LUT/BRT)–Rec. Terr. Extant

First: Figured but undescribed in Lutz (1988), Messel Formation, Grube Messel, Germany. Extant

**F.** LUCANIDAE T. (PRB)–Rec. Terr. Extant

**F.** LYCIDAE T. (PRB)–Rec. Terr. Extant

**F.** LYCTIDAE T. (PRB)–Rec. Terr. Extant

**F.** LYMEXYLONIDAE (LYMEXYLIDAE, LYMEXILIDAE) T. (PRB)–Rec. Terr. Extant

First: **Heterocrites kobdoensis** Ponomarenko (1986a), Gurvaneren Formation, Mongolia.
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Fig. 21.14

Animals: Invertebrates
Arthropoda (Hexapoda; Insecta)

F. MELANDRYIDAE  K. (u.)—Rec.  Terr.  Extant

F. MELOIDAE  T. (PRB)—Rec.  Terr.  Extant

F. MELYRIDAE (MALACHIIDAE) K. (u.)—Rec.  Terr.  Extant

F. MICROMALTHIDAE  T. (Oli.)—Rec.  Terr.  Extant

F. MORDELLIDAE  J. (u.)—Rec.  Terr.  Extant

F. MYCETOPHAGIDAE  T. (PRB)—Rec.  Terr.  Extant

F. NEMONYCHIDAE (EOBELIDAE) J. (u.)—Rec.  Terr.  Extant

First:  e.g. Eobelus longipes, Karabastau Formation, Galkini, Kazakhstan, former USSR.

F. NITIDULIDAE  J. (m.)—Rec.  Terr.  Extant

First:  e.g. Sinonitidulina luanpingensis, in Hong (1985d), north China.

Comment:  Ponomarenko (pers. comm.) considers that this species does not show structures attributable to this family.

F. NOSODENDRIDAE  T. (Eoc.)—Rec.  Terr.  Extant

F. NOTERIDAE  T. (Pal.)—Rec.  Terr.  Extant

F. OBOROCOLEIDAE  P.  Terr.

F. OOEDEMERIDAE  J.?—Rec.  Terr.  Extant

Comment:  Ponomarenko (pers. comm.) considers that the Mesozoic records of this family are doubtful.

F. OXYCORYNIDAE  K.? (APT)—Rec.  Terr.  Extant

F. PARAHYGROBIIDAE  J. (u.).  Terr.

First and Last:  Parahygrobia natans, in Zherikhin (1985b), Uda, Transbaikalia, former USSR.

F. PASSALIDAE  K. (?APT)—Rec.  Terr.  Extant

F. PASSANDRIDAE  T. (Eoc.)—Rec.  Terr.  Extant

F. PELTIDAE (OSTOMIDAE, OSTOMATIDAE)  J.—Rec.  Terr.  Extant

First:  e.g. Anhuistoma hyla Lin (1985), Hanshan Formation, Hanshan, China.

Comment:  Ponomarenko (pers. comm.) considers that this species does not show structures attributable to this family.

F. PERMOCUPEDIDAE  P.  Terr.

e.g. Kaltanicupes ponomarenkoi Pinto (1987a), Irati Formation, Porto Alegre-Uruguayana, Rio Grande do Sul, Brazil.
F. SCHIZOPHORIDAE (SCHIZOCOLEIDAE) Tr. (u.)–K. (u.) Terr.
First: e.g. Shijingocoleus margacrispus Lin and Mou (1989), Xiaoping Formation, Guangzhou, China.

F. SCIRRITIDAE (HELODIDAE) K. (APT)–Rec. Terr.
First: Helodid indet. Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia. Extant

F. SCIRYMAENIDAE K. (I.)–Rec. Terr. Extant

F. SERROPALPIDAE Tr. (PRB)–Rec. Terr. Extant

F. SILPHIDAE J. (l.)–Rec. Terr.
First: e.g. Mercata festira Lin (1986), Guangxi, China. Extant

F. SILVANIDAE T. (PRB)–Rec. Terr. Extant

F. SPHINIDAE T. (PRB)–Rec. Terr. Extant

F. STAPHYLINIDAE Tr.? (RHT)–Rec. Terr.
First: Figured but undescribed, in Gore (1988), Newark Supergroup, Culpeper Basin, Virginia, USA. Extant

F. TALDYCUPEIDAE (TALDYCUPEIDAE) P.–J. (m.)
Last: Yuxianocoleus hebeiense Hong (1985a), Xiahuayuan Formation, Hebei, China. Extant

F. TENEBRIONIDAE (ALLECULIDAE) Tr.?–Rec. Terr. Extant

Comment: Zherikhin (pers. comm.) considers that the Mesozoic records of this family are doubtful.

F. THROSCIDAE (TRIXAGIDAE) K. (l.)–Rec. Terr. Extant

F. TRACHYPACHIDAE (TRACHYPACHIDAE, TRACHYPACHYIDAE) Tr. (u.)–Rec. Terr.
First: Sogdodromeus altus, Madygen Formation, Madygen, Batken, former USSR. Extant

F. TRIPLIDAE Tr. (u.)–K. (l.) Terr.
e.g. Triplus macroplatus, Madygen Formation, south Fergana, former USSR. Extant

F. TRICOLEIDAE Tr. (u.)–K. (l.) Terr.

F. TROGOSSITIDAE (TROGOSITIDAE) J. (u.)–Rec. Terr. Extant

F. TSHEKARDOCOLEIDAE P. Terr.
e.g. Votocoleus submissus in Kukalova-Peck (1991), Moravia, Czechoslovakia. Extant


F. ACARTOPHTHALMIDAE T. (PRB)–Rec. Terr. Extant

F. ACROCERIDAE J. (u.)–Rec. Terr. Extant

F. AGROMYZIDAE T. (LUT/BRT)–Rec. Terr. Extant

F. ANISOPODIDAE (PROTOLBIOGASTRIDAE, MYCETOBIIDAE, RHYPHIDAE, OLBIOGASTRIDAE) J. (l.)–Rec. Terr. Extant

F. ANTHOMYIIDAE T. (PRB)–Rec. Terr. Extant

First: Anthomyia sp., Baltic amber.

F. ARCHISARGIDAE J. (u.) Terr. Extant

F. ARCHITENDIPEDIDAE Tr. Terr. Extant

F. ARCHIZELMIRIDAE J. (u.)–Rec. Terr. Extant

F. ASILIDAE K. (APT)–Rec. Terr. Extant

First: e.g. Araripogon axelrodi Grimaldi (1990), Santana Formation, Ceará, Brazil. Extant

F. ASIOCHAOBORIDAE Hong and Wang, 1990 K. (l.) Terr. e.g. Asiochaoborus tenuous Hong and Wang (1990), Laiyang Formation, Shandong, China. Extant

F. AULACIGASTRIDAE T. (PRB)–Rec. Terr. Extant

First: Protaulacigaster electrica, Baltic amber. Extant

F. TRIAPLIDAE Tr. (u.)–K. (l.) Terr.
First: Succiniasteia carpenteri, in Spahr (1989), Baltic amber. Extant

F. AULARCICASTRIDAe T. (PRB)–Rec. Terr. Extant

First: Protulacigaster electrica, Baltic amber. Extant

F. BIBIONIDAE (PLECIIDAE, PENTHETRIIDAE, HESPERINIDAE) K. (?APT)–Rec. Terr. Extant

First: Described but unnamed in Grimaldi (1990), Santana Formation, Ceará, Brazil. Extant

F. BLEPHARICERIDAE (BLEPHAROCERIDAE) K. (CEN)–Rec. Terr. Extant
### Arthropoda (Hexapoda; Insecta)

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Fig. 21.15
F. BOHOLDOYIDAE Kovalev, 1985
J. (l.)–K. (l.) Terr.
First: Boholdoya alata Kovalev, in Kalugina and Kovalev (1985), Transbaikalia, former USSR.
Last: e.g. ?Boholdoya thoracica Kovalev (1990), Tuva, former USSR.

F. BOMBYLIIDAE (MYTHICOMYIIDAE, SYSTROPIDAE, PHTHIRIIDAE, USIIDAE)
J (m.)–Rec. Terr.
First: e.g. Crosaphis anomala, in Kovalev (1983), Ipswich Series, Mt. Crosby, Australia.

F. CALLIPHORIDAE (SARCOPHAGIDAE)
K. (u.)–Rec. Terr.
First: e.g. Cretaphormia fowleri, in Grimaldi (1990), Edmonton Formation, Alberta, Canada.

F. CALLIPHRIDAE (SARCOPHAGIDAE)
K. (u.)–Rec. Terr.
First: e.g. Cretaphormia fowleri, in Grimaldi (1990), Edmonton Formation, Alberta, Canada.

F. CANTHYLOSCELIDAE (HYPEROSCELIDIDAE)
J. (m.)–Rec. Terr.
First: e.g. Prohyperoscelis jurassicus Kovalev, in Kalugina and Kovalev (1985), former USSR.

F. CARNIDAE T. (PRB)–Rec. Terr.
First: Meoneurites enigmaticus, Baltic amber.

F. CERATOPHAGIDAE (LEPTOCONOPIDAE)
K. (APT)–Rec. Terr.
First: e.g. Choroliinnobia ostera, in Un (1986), Hunan, China.

F. CHAMAEMYIIDAE T. (PRB)–Rec. Terr.
First: e.g. Retinitus nervosus, in Grimaldi (1990), Siberian amber, former USSR.

F. CHLOROPIDAE K. (u.)–Rec. Terr.
First: e.g. Gephyromyiella electrica, Baltic amber.

F. CHYROMYIIDAE (CHYROMYIIDAE)
T. (PRB)–Rec. Terr.
First: e.g. Eoplichthys primitiva, in Kovalev (1990), Upper Lias, Germany.
Last: e.g. Eomycetophila asymetrica Kovalev (1990), Daya, Transbaikalia, former USSR.

F. CROSAPHIDAE Kovalev, 1983
Tr. (u.)–J. (u.) Terr.
### Arthropoda (Hexapoda; Insecta)

| HOL | 1. Pleciodictyidae  
| PLI | 2. Pleciofungivoridae  
| UMI | 3. Pleciomimidae  
| MMI | 4. Procrampomonomyiidae  
| LMI | 5. Procteotiophilidae  
| CHT | 6. Prototipidae  
| RUP | 7. Prototipididae  
| BRB | 8. Protomphralidae  
| LUT | 9. Protoligoneuridae  
| YPR | 10. Propteocidae  
| THA | 11. Protorhyphididae  
| DAN | 12. Protoscatopsidae  
| MAA | 13. Pseudopomyzidae  
| CMP | 14. Psilidae  
| SAN | 15. Psychodidae  
| CON | 16. Ptychopteridae  
| TUR | 17. Rhaetomyiidae  
| CEN | 18. Rhagionidae  
| CHT | 19. Richardiidae  
| RUP | 20. Scatophagidae  
| BRB | 21. Scatopsidae  
| LUT | 22. Sciadoceridae  
| YPR | 23. Sciaridae  
| THA | 24. Sciomyzidae  
| DAN | 25. Sepsidae  
| MAA | 26. Siberhyphidae  
| CMP | 27. Simuliidae  
| SAN | 28. Sinotendipedidae  
| CON | 29. Sphaeroceridae  
| TUR | 30. Stratiomyidae  
| CEN | 31. Syrphidae  
| CHT | 32. Tabanidae  
| RUP | 33. Tachinidae  
| BRB | 34. Tanyderidae  
| LUT | 35. Tanyderophryneidae  
| YPR | 36. Tephritidae  
| THA | 37. Therevidae  
| DAN | 38. Thaumaleidae  
| MAA | 39. Xylomyidae  
| CMP | 40. Xylophagidae  
| SAN | 41. Xylophagidae  
| CON | 42. Xylophagidae  
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| CEN | 44. Xylophagidae  
| CHT | 45. Xylophagidae  
| RUP | 46. Xylophagidae  
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| LUT | 48. Xylophagidae  
| YPR | 49. Xylophagidae  

**Fig. 21.16**

**F. EREMOCHAETIDAE (BREMOCHAETIDAE)**

J. (u.)–K. (l.) Terr.

*First:* e.g. *Pareremochaetus minor*, in Kovalev (1989a), Kazakhstan, former USSR.

*Last:* e.g. *Eremochaetosoma mongolicum* Kovalev (1986), Gurvanereren Formation, Mongolia.

**F. GLOSSINIDAE**

T. (Oli.)–Rec. Terr.

**Extant**

*First and Last:* *Graclitiipula asiatica* Hong and Wang (1990), Laiyang Formation, Shandong, China.

**F. GRACILITIPULIDAE** Hong and Wang, 1990

K. (l.) Terr.
F. HELEOMYZIDAE (HELOMYZIDAE) 
T. (PRB)—Rec. Terr. Extant
First: e.g. Chaetohelomyza electrica, Baltic amber.
F. HIPPOBOSCIDA T. (Oli.)—Rec. Terr. Extant
F. HYPERPOLYNEURIDAE Tr. Terr. Extant
F. LAURENTIPTERIDAE (PSEUDODIPTERIDAE) 
Tr. (m.)—J. (I.) Terr.
First: Laurentiptera gallica, in Wootton and Ennos (1989), Vosges, France.
Last: Ijapsyche sibirica, in Wootton and Ennos (1989), former USSR.
F. MESOPHANTASMATIDAE J. (u.) Terr.
F. MESOSCIOPHILIDAE (ALLACTONEURIDAE pars, FUNGIVORITIDAE pars) 
J. (m.—k. (?)) Terr.
First: e.g. Mesosciophilina irinae Kovalev, in Kalugina and Kovalev (1985), Garvaner Formation, Mongolia.
F. MICROPEZIDAE (CALOBATIDAE) 
T. (PRB)—Rec. Terr. Extant
First: e.g. Electrobata tertiaria, in McAlpine (1990), Baltic amber.
F. MEGAMERINIDAE T. (PRB)—Rec. Terr. Extant
First: Palacotanypeza spinosa, Baltic amber.
F. MUSCIDAE T. (?PRB)—Rec. Terr. Extant
e.g. 'Musca' longipes, Baltic amber.
F. MYCETOPHILIDAE (FUNGIVORITIDAE, BOLITOPHILIDAE, ARACHNOCAMPIDAE, LYGISTORRHINIDAE, KEROPLATIDAE, DITOMYIIDAE, MANOTIDAE, MACROCERIDAE, DIADOCIDIIDAE) J.? (SIN)—Rec. Terr. Extant
First: Prodocidia spectra Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK. Blagoderov (pers. comm.) considers that this species does not belong in this family.
F. MYDAIDAE T. (Oli.)—Rec. Terr. Extant
F. MYDIDAE T. (Oli.)—Rec. Terr. Extant
F. NEMESTRINIDAE J. (u.)—Rec. Terr. Extant
F. NEUROCHAETIDAE T. (PRB)—Rec. Terr. Extant
First: e.g. Anthoclusia gephyrea, in Spahr (1989), Baltic amber.
F. ODINIIDAE T. (PRB)—Rec. Terr. Extant
First: Protodinia electrica, Baltic amber.
F. OESTRIDAE T. (PRB)—Rec. Terr. Extant
First: Novoberenidia baltica, Baltic amber.
F. OLIGOPHRYNEIDAE J. (I.) Terr.
F. OPOMYZIDAE T. (Oli.)—Rec. Terr. Extant
F. OITIDAE (ULIDIIDAE) T. (Oli.)—Rec. Terr. Extant
F. PACHYNEURIDAE (CRAMPTONOMYIIDAE) J. (u.)—Rec. Terr. Extant
F. PALAEOLIMNOBIIDAE Zhang et al., 1986 K. (I.)
e.g. Palaeolimmobia laiyangensis Zhang et al. (1986), Laiyang Formation, Laiyang, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age.
F. PALAEOPHORIDAE J. (u.) Terr.
F. PALAEOPLECIIDAE J. (I.) Terr.
F. PALAEOSTRATIOMYIIDAE (PALAEOSTRIOMYIIDAE) J. (u.)—K. (I.) Terr. Last: e.g. Stratiomyopsis robusta Hong and Wang (1990), Laiyang Formation, Shandong, China.
F. PALLOPTERIDAE T. (PRB)—Rec. Terr. Extant
First: e.g. Pallopterites electrica, Baltic amber.
e.g. Paratendipes laiyangensis Hong and Wang (1990), Laiyang Formation, Laiyang, Shandong, China.
F. PARAXYMYIIDAE J. (m.—u.) Terr.
F. PERISSOMMATIDAE J. (m.)—Rec. Terr. Extant
First: Palaeoperissomma collessi Kovalev, in Kalugina and Kovalev (1985), former USSR. Extant
F. PERMOTANYDERIDAE P. (TAT) Terr.
e.g. Permotanyderus ableptus, in Willmann (1989b), Warner's Bay, New South Wales, Australia.
F. PERMOTIPULIDAE P. (ZEC). Terr.
e.g. Permotipula patricia, in Willmann (1989a), Warner's Bay, New South Wales, Australia.
### Arthropoda (Hexapoda; Insecta)

**Fig. 21.17**

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**Fig. 21.17**

1. Jurinidae
2. Permoberothidae
3. Polycytlidae
4. Uskatelytridae
5. Agaoniidae
6. Anaxyelidae
7. Andreinidae
8. Anthophoridae
9. Aphididae
10. Apidae
11. Archaeocnepididae
12. Argidae
13. Armaniidae
14. Austroniidae
15. Baisoniidae
16. Bethylidae
17. Bethylonymidae
18. Blasticotomidae
19. Braconidae
20. Cephidae
21. Ceraphronidae
22. Chalcididae
23. Chrysididae
24. Cimbicidae
25. Cretevaniidae
26. Cynipidae
27. Diapriidae
28. Diprionidae
29. Dryinidae
30. Electrotomidae
31. Embolemidae
32. Encyrtidae
33. Eoichneumonidae
34. Ephialtidae
35. Eulophidae
36. Eumenidae
37. Eupelmidae
38. Eurytomidae
39. Evanidae
40. Falsiformicidae
41. Figitidae
42. Formicidae
43. Gasteruptiidae
44. Gigastricidae
45. Halictidae
46. Heloridae
47. Ibaliidae
48. Ichneumonidae
49. Jurapriidae
Animals: Invertebrates

First: Metopina goeleti Grimaldi (1989), New Jersey amber, Kinkora, New Jersey, USA.

F. PHRAGMOLIGONEURIDAE J. (l.) Terr.
F. PIOPHILIDAE T. (Oli.)–Rec. Terr.

F. PIPUNCULIDAE K. (u.)–Rec. Terr.

F. PLATYPEZIDAE (OPETIIDAE) K. (1.)–Rec. Terr.
First: e.g. Palaeopetia laiyangensis Zhang (1987), Laiyang Formation, Laiyang, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age.

F. PLATYSTOMATIDAE T. (PRB)–Rec. Terr.
First: Scholastes joordi, English amber, Norfolk, England, UK.

F. PLECIODICTYIDAE J. (l.) Terr.
F. PLECIODICTYIDAE (PLICIOFUNGIVORIDAE, ALLACTONEURIDAE pars, FUNGIVORITIDAE pars) J. (l.)–K. (l.) Terr.
First: e.g. Archihesperinus phryneoides, in Kovalev (1987), Issyk-Kul, Kirgizia, former USSR.
Last: e.g. Bryanlaz lepida Kovalev (1990), Daya, Transbaikalia, former USSR.

F. PROCRAMPTONOMYIIDAE Kovalev, 1985 J. (1.-u.) Terr.
First: e.g. Procramptonomyia sibirica Kovalev, in Kalugina and Kovalev (1985), Transbaikalia, former USSR.

F. PRONEOTTIOPHILIDAE T. (PRB) Terr.
First and Last: Proneottiophilum extinctum, Baltic amber.

F. PROTENDIPEDIDAE J. (u.) Terr.
e.g. Protendipes huabeiensis Zhang (1986b), northern Hebei, China.

F. PROTEMPIPIDAE J. (u.) Terr.

F. PROTEMPIPIDAE J. (u.)–K. (l.) Terr.

F. PROTEMPIPIDAE J. (l.)–K. (l.) Terr.
First: e.g. Archiplicomia obtusipennis, in Kalugina and Kovalev (1985), former USSR.

F. PROTEMPIPIDAE J. (l.)–K. (l.) Terr.
First: e.g. Prototephytaphus ovisimilis, in Kalugina and Kovalev (1985), Upper Lias, Dobbertin, Germany.
Last: Prototephytaphus major Kovalev (1990), Daya, Transbaikalia, former USSR.

F. PROTOPSCATOPSIDAE J. (m.–u.) Terr.
First: Mesoscatopse rohdendorfi Kovalev, in Kalugina and Kovalev (1985), former USSR.

F. PSEUDOPOMYZIDAE T. (PRB)–Rec. Terr.
First: Eopseudopomyza kuehnei, Baltic amber.

First: Electrochyliza succini, Baltic amber.

F. PSYCHODIDAE (PHLEBOTOMIDAE) J. (m.?–u.)–Rec. Terr.
First: Eopericoma zherichini Kalugina, in Kalugina and Kovalev (1985), Transbaikalia, former USSR.


F. SCIOYMYZIDAE K. (BER)–Rec. Terr.

First: Protoptyrgma electricum, Baltic amber.

F. SIBERHYPIDAE Kovalev, 1985 J. (m.)–Rec. Terr.
First and Last: Siberhyphus lebedevi Kovalev, in Kalugina and Kovalev (1985), former USSR.

F. SIMULIIDAE J. (m.)–Rec. Terr.
First: Simulimima grandis, in Crosskey (1991), Ichetuiisk Formation, Transbaikalia, former USSR.

First and Last: Sinotendipes tuanwangensis Hong and Wang (1990), Laiyang Formation, Shandong, China.
**Arthropoda (Hexapoda; Insecta)**

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**Fig. 21.18**

**F. SPAHEROCERIDAE** T. (PRB)–Rec. Terr.  
First: *Copromyza* sp., Baltic amber.  
Extant

**F. STRATIEMYIDAE (STRATIEMYIIDAE, STRATIEMYRIIDAE)** K. (BER)–Rec. Terr.  
First: e.g. Dipterous larva: species 1, Whalley and Jarzembski (1985), Lithographic Limestone, Montsech, Spain.

**F. SYRPHIDAE** K. (u.)–Rec. Terr.  
Extant

**F. TABANIDAE** K. (APT)–Rec. Terr.  
Extant

**F. TACHINIDAE** T. (PRB)–Rec. Terr.  
Extant  
First: e.g. *Electrotachina smithii*, Baltic amber.
Animals: Invertebrates

F. TANYDERIDAE Tr. (u.)-Rec. Terr. Extant
F. TANYDEROPHRYNEIDAE J. (l.)-Rec. Terr. Extant
F. TEPHRITIDAE T. (Mio.)-Rec. Terr. Extant
F. TETHINIDAE T. (Mio.)-Rec. Terr. Extant
F. THAUMALEIDAE (THAUMALAEIDAE) K. (I.)-Rec. Terr. Extant
First: Mesothaumalea fossilis Kovalev (1989b), Baley Series, Dai, Transbaikalia, former USSR. Extant
F. THEREVIDAE K. (?APT)-Rec. Terr. Extant
First: Described but unnamed, in Grimaldi (1990), Santana Formation, Ceará, Brazil. Extant
F. TIPULIDAE (LIMONIIDAE, ARCHITIPULIDAE, EOASILIDAE, CYLINDROTOMIDAE) Tr. (u.)-Rec. Terr. Extant
F. TIPULODICTYIDAE J. (l.)-Rec. Terr. Extant
F. TIPULOPLECIIDAE J. (u.)-Rec. Terr. Extant
F. TRICHERIDAE J. (l.)-Rec. Terr. Extant
First: Eotrichocera christinae Kalugina, in Kalugina and Kovalev (1985), Transbaikalia, former USSR. Extant
F. TRICOSCELIDAE (TRICOSCELIDIDAE) T. (Oli.)-Rec. Terr. Extant
F. VERMILEONIDAE (PROTOBRACHYCERONIDAE) J. (TOA)-Rec. Terr. Extant
First: Protobrachyceron lusinum, in Ponomarenko and Schultz (1988), Upper Lias, Dobbertin, Germany. Extant
F. XYLOMYIDAE K. (u.)-Rec. Terr. Extant
F. XYLOPHAGIDAE (RACHICERIDAE, COENOMYIIDAE) K. (u.)-Rec. Terr. Extant
F. VERMILEONIDAE (PROTOBRACHYCERONIDAE) J. (TOA)-Rec. Terr. Extant
F. VERSILEONIDAE (PROTODLATOMIDAE) J. (Oli.)-Rec. Terr. Extant
Order GLOSSELYTRODEA (JURINIDA) P. (I.)-Rec. Terr. Extant
Last as for Polycyttellidae.

First: Archaeocynips villosa Rasnitsyn and Kovalev (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR. Extant

First: Archaeocynips villosa Rasnitsyn and Kovalev (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR. Extant

First: Archaeocynips villosa Rasnitsyn and Kovalev (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR. Extant

First: Archaeocynips villosa Rasnitsyn and Kovalev (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR. Extant

F. ARGIDAE T. (Oli.)-Rec. Terr. Extant
F. ARMANIIDAE K. (u.)-Rec. Terr. Extant
e.g. Armания robusta, in Wilson (1987), Alska Formation, Magadan, former USSR. Extant
F. AUSTRONIIDAE (TRUPOCHALCIDII) K. (I.)-Rec. Terr. Extant
F. BAISSODIDAE K. (I.)-Rec. Terr. Extant
e.g. ?Baissodes longus Rasnitsyn (1986), Gurvaner Forma
tion, Mongolia. Extant
F. BETHYLIDAE K. (I.)-Rec. Terr. Extant
First: Cretobethylellus lucidus Rasnitsyn (1990), Pavlovka, former USSR. Extant
F. BETHYLONYMIDAE J. (u.)-Rec. Terr. Extant
e.g. Bethylonymus sibiricus in Zherikhin (1985b), Uda, Transbaikalia, former USSR. Extant
F. BLASTICOTOMIDAE T. (Oli.)-Rec. Terr. Extant
F. BRACONIDAE (BRACONIDAE) K. (I.)-Rec. Terr. Extant


F. AGAONIDAE (AGAONTIDAE) T. (Oli.)-Rec. Terr. Extant
F. ANAXYELIDAE J. (u.)-Rec. Terr. Extant
First: e.g. Xaxexis longhuaensis (Hong, 1985d) comb. nov., north China. New generic name from Pagliano and Scaramozzino (1990).
F. ANDRENIDAE T. (PRB)-Rec. Terr. Extant
First: Described but unnamed, in Grimaldi (1990), Santana Formation, Ceará, Brazil. Extant
e.g. Archaeocynips villosa Rasnitsyn and Kovalev (1988), Zaza Formation, Baisa, Buryat ASSR, former USSR. Extant
F. ARGIDAE T. (Oli.)-Rec. Terr. Extant
F. ARMANIIDAE K. (u.)-Rec. Terr. Extant
e.g. Armания robusta, in Wilson (1987), Alska Formation, Magadan, former USSR. Extant
F. AUSTRONIIDAE (TRUPOCHALCIDII) K. (I.)-Rec. Terr. Extant
F. BAISSODIDAE K. (I.)-Rec. Terr. Extant
e.g. ?Baissodes longus Rasnitsyn (1986), Gurvaner Formation, Mongolia. Extant
F. BETHYLIDAE K. (I.)-Rec. Terr. Extant
First: Cretobethylellus lucidus Rasnitsyn (1990), Pavlovka, former USSR. Extant
F. BETHYLONYMIDAE J. (u.)-Rec. Terr. Extant
e.g. Bethylonymus sibiricus in Zherikhin (1985b), Uda, Transbaikalia, former USSR. Extant
F. BLASTICOTOMIDAE T. (Oli.)-Rec. Terr. Extant
F. BRACONIDAE (BRACONIDAE) K. (I.)-Rec. Terr. Extant
Arthropoda (Hexapoda; Insecta)

First: Eobraconus inopinatus, in Rasnitsyn (1985), Mongolia.

Extant

F. CEPHIDAE K. (L.)—Rec. Terr.

First: e.g. Mesoscothopus sibiricus, Zaza Formation, Baisa, Buryat ASSR, former USSR.

Comment: Pagano and Scaramozzino (1990) transferred the Upper Jurassic Cephenopsis mirabilis Hong (1985c) to incertae sedis.

F. CERAPHRONIDAE K. (u.)—Rec. Terr.

Extant

F. CHALCIDIDAE (CHALCIDAE) K. (APT)—Rec. Terr.

Extant

F. CHRYSIDIDAE K. (L.)—Rec. Terr.

First: Dahurochrysis veta Rasnitsyn (1990), Turga, former USSR.

Extant

F. Cimbicidae T. (PRB)—Rec. Terr.

Extant

F. CRETEVANIIDAE K. (HAU—u.)—Rec. Terr.


Last: e.g. Cretevania minor, Siberian amber, Taimyr, former USSR.


First: Protimaspis costalis, Canadian amber, Cedar Lake, Manitoba, Canada.

Extant

F. DIAPRIIDAE K. (APT)—Rec. Terr.

First: Cretacoformica explicata Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.

Extant

F. Diprionidae T. (PRB)—Rec. Terr.

Extant

F. DRYINIDAE K. (L.)—Rec. Terr.

Extant

F. ELECTROTOMIDAE T. (PRB) Terr.

First and Last: Electrotoma succini, Baltic amber.

Extant


First: e.g. Ampulicomorpha succinalis, Baltic amber.

Extant


First: Propelma rohdendorfi, Baltic amber.

Extant

F. EOICHRONUMONIDAE Jell and Duncan, 1986 K. (L.)—Terr.

e.g. Eoicrheonum duncanae Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.

F. EPHIALTITIDAE (KARATAIDAE) J. (L.)—K. (APT) Terr.

First: e.g. Sippelipterus lassinus Zessin (1985), Upper Lias, Tongrube, Germany.

Last: Karataus kourios Sharkey, in Darling and Sharkey (1990), Santana Formation, Ceará, Brazil.

F. EULOPHIDAE (APELIDAE) K. (u.)—Rec. Terr.

Extant


Extant


Extant


First: e.g. Evania (Parevania) brevis, Baltic amber.

Extant

F. FALSIFORMICIDAE K. (u.)—Rec. Terr.

e.g. Falsiformica cretacea, Siberian amber, former USSR.

F. FIGITIDAE K. (u.)—Rec. Terr.

Extant

F. FORMICIDAE (DOLICHODERIDAE, PALEOSMINTHURIDAE) K. (APT)—Rec. Terr.

First: Cariridris bipetiolata Brandao and Martins-Neto, in Brandao et al. (1989), Santana Formation, Ceará, Brazil.

Extant

F. GASTERUPTIIDAE (AULACIDAE, KOTUJELLIDAE) K. (L.)—Rec. Terr.

First: e.g. Manlaya laevinota Rasnitsyn (1986), Gurvanerener Formation, Mongolia.

Extant

F. GIGASIRICIDAE J. (L.—u.) Terr.


Extant

F. HELORIDAE J. (u.)—Rec. Terr.

Extant

F. IBALIIDAE K. (u.)—Rec. Terr.

Extant


First: e.g. Tarechora petriolata, in Hong (1988), Sahai Formation, Kezuo, China; Zaza Formation, Baisa, Buryat ASSR, former USSR.

Extant

F. JURAPRIIDAE J. (u.)—Terr.

First and Last: Jurapria sibirica, in Zherikhin (1985b), Uda, Transbaikal, former USSR.

F. KARATAVITIDAE J. (L.—u.) Terr.

F. MAIMETSHIDAE K. (SAN)

First and Last: Maimetscha arctica, Siberian amber, Taimyr, former USSR.

F. MASARIDAE K. (L.)—Rec. Terr.

Extant

F. MEGACHILIDAE T. (PRB)—Rec. Terr.

Extant

F. MEGALYRIDAE J. (1.)—Rec. Terr.

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F. MEGALYRIDAE J. (1.)—Rec. Terr.

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F. MEGALYRIDAE J. (1.)—Rec. Terr.

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F. MEGALYRIDAE J. (1.)—Rec. Terr.

Extant
Animals: Invertebrates

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Fig. 21.19
Arthropoda (Hexapoda; Insecta)

F. MEGASPILIDAE K. (l.)–Rec. Terr. **Extant**

F. MELITTIDAE (CTENOPLECTRIDAE) T. (PRB)–Rec. Terr. **Extant**

First: e.g. Ctenoplectrella dentata, Baltic amber. **Extant**

F. MESOSERPHIDAE J. (l.)–K. (l.) Terr. **Extant**

F. MUTILLIDAE (CRETAVIDAE) K. (u.)–Rec. Terr. **Extant**

First: e.g. Cretavus sibiricus, in Manley and Poinar (1991), Siberia, USSR. Rasnitsyn in Darling and Sharkey (1990) transferred the Lower Cretaceous Mesomutilla aptera Zhang (1985) to Vesponina (Apocrita) incertae sedis. **Extant**

F. MYMARIDAE K. (u.)–Rec. Terr. **Extant**

First: e.g. Triadomerus bulbosus, Canadian amber, Medicine Hat, Canada. **Extant**

F. MYMAROMMATIDAE K. (u.)–Rec. Terr. **Extant**

First: e.g. Archaeromma minutissima, Canadian amber, Alberta, Canada. **Extant**

F. MYRMICIDAE (PSEUDOSIRICIDAE) J. (m.–u.) Terr. **Extant**

F. ORUSSIDAE K. (u.)–Rec. Terr. **Extant**

First: Mesorussus taimyrensis, Siberian amber, Taimyr, former USSR. **Extant**

F. PAMPHILIIDAE J. (u.)–Rec. Terr. **Extant**

First: Juralyda udensis, in Zherikhin (1985b), Uda, Transbaikalia, former USSR. **Extant**

F. PARARCHEXYELIDAE J. (m.–u.) Terr. **Extant**

F. PARORYYSSIDAE (PARORYSIDAE) J. (u.)–K. (l.) Terr. **Extant**

F. PELECNIDAE (PELECINOPTERIDAE) K. (1.)–Rec. Terr. **Extant**

First: Isocpinus baissieux, River Vitim, former USSR. **Extant**

F. PLATYGASTRIDAE T. (Pal.)–Rec. Terr. **Extant**

F. POMPILIDAE K. (l.)–Rec. Terr. **Extant**

First: Pompilopterus ciliatus, Zaza Formation, Baisa, Buryat ASSR, former USSR. **Extant**

F. PRAEALUCIDAE (ANOMOPTERELLIDAE) J. (u.)–K. (APT) Terr. **Extant**

First: Palaeathalia laiyangensis Zhang (1985), Laiyang Formation, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age. **Extant**

F. TENTHREDINIDAE K. (l.)–Rec. Terr. **Extant**

First: Palaethalia laiyangensis Zhang (1985), Laiyang Formation, Shandong, China. We have followed Hong and Wang (1990) in regarding this formation as Lower Cretaceous in age. **Extant**

F. TETRACAMPIDAE K. (CMP)–Rec. Terr. **Extant**

First: e.g. Baemorphus dubitata, Canadian amber, Cedar Lake, Manitoba, Canada. **Extant**
F. THYSANIDAE  T. (CHT)–Rec.  Terr.

F. TIPHIIDAE (TIPHIIDAE, METHOCIDAE)
K. (APT)–Rec.  Terr.

First:  Architiphia rasnitsyni  Darling, in Darling and Sharkey (1990), Santana Formation, Ceará, Brazil.

F. TORYMIDAE  K. (u.)–Rec.  Terr.

Extant

F. TRICHOGRAMMATIDAE  K. (CMP)–Rec.

First:  Enneagmus pristinus, Canadian amber, Cedar Lake, Manitoba, Canada.

Extant

F. TRIGONALIDAE (ICHNEUMOMIMIDAE)
K. (l.)–Rec.  Terr.

Extant
Arthropoda (Hexapoda; Insecta)

16. Permopanorpidae
17. Protoperopanorpidae
18. Protoperopanorpidae
19. Protoopanorpidae
20. Protoopanorpidae
21. Protoopanorpidae
22. Robakopanorpidae
23. Tomochoristidae
24. Xenochoristidae
25. Corydalidae
26. Euchanlididae
27. Sialidae
28. Tychtodelopteridae

MEGALOPTERA
25. Corydalidae
26. Euchanlididae
27. Sialidae
28. Tychtodelopteridae

NEUROPTERA
25. Corydalidae
26. Euchanlididae
27. Sialidae
28. Tychtodelopteridae

First: e.g. Darbigonalus capitatus Rasnitsyn (1986), Gurvaner Formation, Mongolia.
F. VANHORNIIDAE K. (u.?)–Rec. Terr. Extant
F. VESPIDAE K. (l.)–Rec. Terr. Extant
First: e.g. Priorvepsa buitata Carpenter and Rasnitsyn (1990), Zaza Formation, Baisa, Buryat ASSR, former USSR.
F. XYELIDAE Tr. (u.)–Rec. Terr. Extant
First: e.g. Figured but undescribed in Kukalová-Peck (1991), Australia.
F. XYELOTOMIDAE J. (m.–)–K. (l.) Terr. Extant
Last: e.g. ?Undatoma undurgensis Rasnitsyn (1990), Undurga, former USSR.
F. XYELYDIDAE (XYELIDIDAE) J. (l.–)–K. (l.) Terr. Extant
Last: Sinoprylyda meileyingensis Hong (1987), Jiufutang Formation, Kezuo, China.
F. XYLOCOPIDAE T. (Oli.)–Rec. Terr. Extant
F. CASTNIIDAE T. (RUP)–Rec. Terr. Extant
First: Dominicus castnioides Tindale (1985), Florissant, Colorado, USA.
F. COPROMORPHIDAE T. (RUP)–Rec. Terr. Extant
First: Copromorpha fossilis, Bembridge Marls, Isle of Wight, England, UK.
F. COSSIDAE T. (?RUP)–Rec. Terr. Extant
First: e.g. Elachistites inclusus, Baltic amber.
F. EOLEPIDOPTERIGIDAE (EOLEPIDOPTERYGIDAE) J. (u.–)–K. (APT). Terr. Extant
First: e.g. Eolepidopterix jurassica, Transbaikalia, former USSR.
Last: e.g. Datopterix rasnitsyni, Daya River, Transbaikalia, former USSR.
F. GEOMETRIDAE T. (RUP)–Rec. Terr. Extant
First: e.g. Geometridites laerroriformis, Bembridge Marls, Isle of Wight, England, UK.
F. LOPHOCRONGIDAE K. (t.)–Rec. Terr. Extant
First: Prolepidopterix jurassica, Transbaikalia, former USSR.
F. OLEPIDOPTERIGIDAE (EOLEPIDOPTERYGIDAE) J. (u.–)–K. (APT). Terr. Extant
First: e.g. Eolepidopterix jurassica, Transbaikalia, former USSR.
Last: e.g. Datopterix rasnitsyni, Daya River, Transbaikalia, former USSR.
F. GEOMETRIDAE T. (RUP)–Rec. Terr. Extant
First: e.g. Geometridites laerroriformis, Bembridge Marls, Isle of Wight, England, UK.
F. LOPHOCRONGIDAE K. (t.)–Rec. Terr. Extant
First: Prolepidopterix jurassica, Transbaikalia, former USSR.
First: Rhiodinella nympha, Colorado, USA.

F. LYMANTRIIDAE T. (MES) – Rec. Terr. Extant
First: Figured but undescribed, in Cavallo and Galletti (1987), gypsumiferous marls, Alba, Italy.

F. LYONETIIDAE T. (PRB) – Rec. Terr. Extant
First: Auleptera cockerelli, Baltic amber.

F. MICROPTERIGIDAE (MICROPTERYGIDAE) J. (u.) – Rec. Terr. Extant
First: Auliepterix mirabilis Kozlov (1989), Kazakhstan, former USSR.

F. NEPTICULIDAE J. (u.) – Rec. Terr. Extant
First: e.g. Neorinopsis sepulta, Aix-en-Provence, France.

First: e.g. Cerurites wagneri, Willershausen, Germany.

F. OECOPHORIDAE (SYMMOCIDAE) T. (PRB) – Rec. Terr. Extant
First: e.g. Borkhausenites bachofeni, Baltic amber.

First: e.g. Praepapilio colorado, Colorado, USA.

F. PTEROPHORIDAE T. (RUP) – Rec. Terr. Extant
First: e.g. Epinomeuta truncatipennella, Baltic amber.

We have followed the traditional classification including stemgroups Antiophora (Diptera plus Siphonaptera plus Mecoptera) and Mecopteroidea (Amphiesmenoptera (Trichoptera plus Lepidoptera) plus Antiophora) in the Mecoptera; i.e. Mecoptera as given here (s.l.) is paraphyletic with respect to Amphiesmenoptera, Diptera and Siphonaptera. Most data are taken from Willman (1978, 1989b). Families marked with an asterisk are considered not to belong to the Mecoptera (s.l.) (Willmann, 1989b).

F. AGETOPANORPIDAE (CHORISTOPSYCHIDAE, TYCHTOPSYCHIDAE) P. (ROT) – J. (l.) Terr. Extant
First: e.g. Agetopanorpa maculata, Wellington Formation, Elmo, Kansas, USA.

First: e.g. Aneuretopsyche rostrata Rasnitsyn and Kozlov (1990), Mikhailovka, former USSR.

F. ANORMOCHORISTIDAE* P. (ART) Terr. Extant
First and Last: Anormochorista oligoclada, Wellington Formation, Elmo, Kansas, USA.

F. AUSTROPANORPIDAE T. (Pal.) Terr. Extant
First and Last: Austropanorpa australis, Redbank Plains Series, Redbank Plains, Queensland, Australia.

F. BELMONTIIDAE P. (TAT) Terr. Extant
First: e.g. Belmontia mitchelli, Belmont Beds, Belmont, New South Wales, Australia.

F. BITTACIDAE J. (u.) – Rec. Terr. Extant
First: Probittacus avitus, Karatau, Kazakhstan, former USSR.

F. CHORISTIDAE K. (APT) – Rec. Terr. Extant
First: Cretacochorista parva Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.
Arthropoda (Hexapoda; Insecta)

First: Choristopanorpa bifasciata, Beacon Hill, New South Wales, Australia.
Last: Choristopanorpa drinnani Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.

F. CIMBROPHLEBIIDAE T. (THA) Terr.
First and Last: Cimbrophlebia bittaciformis, Mo-clay, north Jutland, Denmark.

First and Last: Cyciopterina autumnalis in Carpenter (1987), I1jinsk Formation, Kuznetsk Basin, former USSR.

F. CYCLORISTIDAE* P. (ROT) Terr.
First and Last: Cyciorista convexicosta, Kaltan, Kuznetsk Basin, former USSR.

F. DINOPANORPIDAE T. (LMI) Terr.
First and Last: Dinopanorpa megarche, former USSR.

F. DOBBERTINIIDAE* J. (TOA) Terr.
First and Last: Dobbertinia reticulata, Upper Lias, Dobbertin, Germany.

F. EOMEROPIDAE (NOTIOTHAUMIDAE) Tr. (u.)-Rec. Terr.
First: e.g. Pronotiothauma neuropteroides, Madygen Formation, Madygen, former USSR. Extant

F. HOLCORPIDAE T. (Oli.) Terr.
First and Last: Holcorpa maculosa, Florissant, Colorado, USA.

F. KALTANIDAE* P. (ROT–ZEC) Terr.
First: e.g. Altajopanorpa kaltanica, Kuznetsk Basin, former USSR.
Last: e.g. Altajopanorpa iljinskiensis, Iljinsk Formation, Kuznetsk Basin, former USSR.
The Lower Cretaceous Cretacechorista qilianshanensis Hong et al. (1989) does not agree with the family definition as given by Martynova (1962). Zherikhin (pers. comm.) considers that it belongs in the Blattodea: Raphidiomimidae.

F. LITHOPANORPIDAE P. (ART–ZEC) Terr.
First: Lithopanorpa pusilla, Wellington Formation, Elmo, Kansas, USA.
Last: Lithopanorpa kuznetskiensis, Gramoteino Formation, Kuznetsk Basin, former USSR.

F. MARIMEROBIIDAE* P. (KUN) Terr.
First and Last: Marimerobius splendens, Chekarda, former USSR.

e.g. Martynopanorpa angustata, Archangelsk, former USSR.

First: e.g. Mesopanorpodes belmontensis, Warner’s Bay, New South Wales, Australia.
Last: Prochoristella leongatha Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.

F. MESOPSYCHIDAE Tr. (u.)–K. (l.) Terr.
First: Mesopsyche triareolata, Ipswich Beds, Ipswich, Australia.
Last: Undisa dobrokhotova Sukacheva (1990a), Transbaikalia, former USSR.

First and Last: Muchoria reducida, Transbaikalia, former USSR.

F. NANNOCHEMORISTIDAE P. (TAT)–Rec. Terr.
First: e.g. Nannochoristella reducida, Warner’s Bay, New South Wales, Australia. Extant

F. NEORTHOPHLEBIIDAE Tr. (u.)–J. (TOA) Terr.
First: e.g. Archebittacus exilis, Ipswich Series, Mt. Crosby, Australia.
Last: e.g. Neorthophlebia maculipennis, Upper Lias, Dobbertin, Germany.

F. NEOPARACHORISTIDAE Tr. (u.)–K. (APT) Terr.
First: e.g. Neoparachorista reducida, Warner’s Bay, New South Wales, Australia. Extant

F. NEOPARACHORISTIDAE Tr. (u.)–K. (APT) Terr.
First: e.g. Neoparachorista reducida, Warner’s Bay, New South Wales, Australia. Extant

F. ORTHOPHLEBIIDAE Tr. (u.)–K. (l.) Terr.
First: e.g. Orthophlebia curta, Sogjuty, former USSR.

F. PANORPIDAE T. (PRB)–Rec. Terr.
First: e.g. Panorpa mortua, Baltic amber. Extant

F. PANORPIDAE T. (PRB)–Rec. Terr.
First: e.g. Panorodes brevicauda, Baltic amber. Extant

F. PERMOCENTROPIDAE P. (ZEC) Terr.
First and Last: Permocentropus philopotamoides Iva-Gora, Archangelsk, former USSR.

F. PERMOCHEMORISTIDAE (MESOCHORISTIDAE) P. (ROT)–J. (l.) Terr.
First: e.g. Mesochorista javorskyi, Kuznetsk Basin, former USSR.

F. PERMOMEROPIDAE* P. (ROT–ZEC) Terr.
e.g. Permomerope nanus, Warner’s Bay, New South Wales, Australia.

F. PERMOPANORPIDAE P. (ART)–Tr. (u.) Terr.
First: e.g. Permapanorpa inaequalis, Wellington Formation, Elmo, Kansas, USA.
Last: e.g. Neopermapanorpa mesembria, Ipswich Series, Mt. Crosby, Queensland, Australia.

First: e.g. Petrocorista pronata, Kaltan, Kuznetsk Basin, former USSR.
Last: e.g. Petrocorista elegantula, Tichjie Gory, former USSR.
F. PROTOMEROPIDAE* (PLATYCHORISTIDAE)  
P. (ASS–ZEC) Terr.  
**First:** Pseudomeropera gallei Kukalová-Peck and Willmann (1990), Ričany, Czechoslovakia.  
**F. PROTOPANORPIDAE** P. (ART) Terr.  
**First and Last:** Protopanorpa permiana, Wellington Formation, Elmo, Kansas, USA.  
**F. PSEUDOPOLYCENTROPIDAE** (PSEUDOPOLYCENTROPIDIDAE, PSEUDOPOLYCENTROPODIDAE)  
J. (SIN–u.) Terr.  
**First:** Pseudopolycentropus prolatipennis Whalley (1985), Lower Lias, Charmouth, Dorset, England, UK.  
**Last:** Pseudopolycentropus latipennis, Karatau, Kazakhstan, former USSR.  
**F. ROBINJOHNIIDAE** P. (TAT) Terr.  
**First and Last:** Robinjohnia tillyardi, Warner’s Bay, New South Wales, Australia.  
**F. TOMIOCHORISTIDAE** P. (ROT) Terr.  
e.g. Tomiochorista minuta, Kaltan, Kuznetsk Basin, former USSR.  
**F. TRIASSOCHORISTIDAE** Willmann, 1989b  
Tr. (u.) Terr.  
**First and Last:** Triassochorista nana, Ipswich Series, Mt. Crosby, Queensland, Australia.  
**F. XENOCHORISTIDAE** P. (TAT)–T. (u.) Terr.  
**First:** Xenochorista sobrina, Warner’s Bay, New South Wales, Australia.  
**Last:** Xenochoristella hillae, Ipswich Series, Mt. Crosby, Queensland, Australia.  
**Order MEGALOPTERA (CORYDALIDA)**  
P. (ZEC)–Rec. Terr.  
**F. CORYDALIDAE** K. (l.)–Rec. Terr.  
**Extant**  
**F. EUCHAULIODIDAE** Tr. (u.) Terr.
**Arthropoda (Hexapoda; Insecta)**

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**1. Siyridae**
**2. Solenoptilidae**
**3. Alloraphidiidae**
**4. Baissopteridae**
**5. Fajjanopteridae**
**6. Inocelliidae**
**7. Letopalopteridae**
**8. Mesoraphidiidae**
**9. Raphidiidae**
**10. Sinoraphidiidae**
**11. Sojanoraphidiidae**
**12. Ctenophthalmidae**

**25. Cladochoristidae**
**26. Dysoneridae**
**27. Ecnomidae**
**28. Electralbertidae**
**29. Glossosomatidae**
**30. Goeridae**
**31. Mengeidae**
**32. Hydrobiosidae**
**33. Hydropsychidae**
**34. Hydroptilidae**

**39. Microptysmatidae**
**40. Molannidae**
**41. Necrotauliidae**
**42. Odontoceridae**
**43. Philoptomidae**
**44. Phylganeidae**
**45. Polycentropodidae**
**46. Prohyacophilidae**
**47. Prosepididontidae**

**First and Last: Euchauliodes distinctus** in Kukalova-Peck (1991), South Africa.

F. **SIALIDAE** K. (APT)–Rec. Terr.

F. **Tychtodeopteridae** P. (ZEC) Terr.

**Order NEUROPTERA (PLANIPENNIA, MYRMELEONTIDA)** P. (ZEC)–Rec. Terr.

F. **Allopteridae** Zhang, 1991a K. (l.) Terr.

**Fig. 21.21**

First and Last: *Euchauliodes distinctus* in Kukalova-Peck (1991), South Africa.

F. **SIALIDAE** K. (APT)–Rec. Terr.

Extant

F. **ASCALAPHIDAE** K. (APT)–Rec. Terr.

First: *Cratopteryx robertosantosi* Martins-Neto and Vulcano (1989), Santana Formation, Ceará, Brazil. Extant


e.g. *Babinskaia pulchra* Martins-Neto and Vulcano (1989), Santana Formation, Ceará, Brazil.

F. **BEROTHIDAE** K. (APT)–Rec. Terr.

First: e.g. *Araripeberotha fairchildi* Martins-Neto and Vulcano (1990), Santana Formation, Ceará, Brazil. Extant

F. **BRONGNIARTIILLIDAE** J. (l.)–K. (BER) Terr.
Animals: Invertebrates

First: e.g. Actinophlebia intermixta, in Whalley (1988), Upper Lias, Gloucestershire, England, UK.

Last: e.g. Pterinoblattina pluma, in Whalley (1988), Durlston Formation, Durlston Bay, England, UK.

F. CHRYSOPIDAE (MESOCHRYSOPIDAE, MESOCHRYSOPSIDAE) J. (TOA)—Rec. Terr.
First: Liassochrysa stigmatica Ansorge and Schlüter (1990), Upper Lias, Dobbertin, Germany.

Extant

F. CONIOPTERYGIDAE J. (u.)—Rec. Terr.
Extant

F. HEMEROBIIDAE K. (APT)—Rec. Terr.
Extant

F. KALLIGRAMMATIDAE J. (TOA)—T. (Pal.) Terr.

F. MANTISPIDAE J. (u.)—Rec. Terr.
First: Promantispa similis, Kazakhstan, former USSR, in Nel (1988a), Karatau, Extant

First: e.g. Sibithone dichotoma Ponomarenko (1984), Ichetuy Formation, Buryat ASSR, former USSR.

F. MESOBEROTHIDAE (PROBEROTHIDAE) Tr. (u.)—Rec. Terr.
First: e.g. Prohemerobius oshinensis Ponomarenko (1984), Zhargalanska Formation, Kobdos Aymak, Mongolia.

F. MESOPOLYSTOECHOTIDAE Tr. (?CRN)—Rec. Terr.
First: e.g. Lithosmylidia lineata, in Lambkin (1988), Mt. Crosby Formation, Mt. Crosby, Queensland, Australia. Extant

F. POLYSTOECHOTIDAE Tr. (?CRN)—Rec. Terr.
First: Lithosmylia lineata, in Lambkin (1988), Mt. Crosby Formation, Mt. Crosby, Queensland, Australia. Extant

F. PALAEMEROBIIDAE P. (ZEC) Terr.

First: Panfiliova acuminata, in Makarkin (1990), Karatau, former USSR.

F. PERMITHONIDAE (ARCHEOSMYLIDAE, PERMOPSYCHOPIDAE) P. (ZEC)—J. (TOA) Terr.
First: e.g. Permipsythone panfifioi, in Martins-Neto (1987a), Itarit Formation, Porto Alegre-Uruguay, Rio Grande do Sul, Brazil.

Last: e.g. Archeosmylus complexus Whalley (1988), Gloucestershire, England, UK.

F. POLYSTOECHOTIDAE Tr. (?CRN)—Rec. Terr.
First: Lithosmylia lineata, in Lambkin (1988), Mt. Crosby Formation, Mt. Crosby, Queensland, Australia. Extant

First: e.g. Prohemerobius oshinensis Ponomarenko (1984), Zhargalanska Formation, Kobdos Aymak, Mongolia.

F. PSYCHOPSIDAE Tr. (u.)—Rec. Terr.
First: e.g. Triassopsychops superba, in Schlüter (1986), Ipswich, Queensland, Australia. Extant

F. SOLICIDOPSIDAE P. (ZEC) Terr.

Extant

F. SIALIDOPSIDAE P. (ZEC) Terr.

F. ALLORAPHIDIIDAE K. (u.)—Rec. Terr.
First: Archeraphidia yakoulewii Ponomarenko (1988), Mongolia.

Last: Alloraphidia dorfii, Redmond Formation, Knob Lake District, Canada.

F. BAISSOPTERIDAE (BAISSORAPHIDIIDAE) J. (TOA)—Rec. Terr.

Last: e.g. Bassoptera longissima Ponomarenko (1988), Bon-Tsagan, Mongolia.

F. FATJANOPTERIDAE C. (u.)—Rec. Terr.
Extant

Order RAPHIDIOPTERA (RAPHIDIIDA)
C. (u.)—Rec. Terr.
Most data are taken from Oswald (1990). First as for Fatjanopteridae, although the ordinal position of this family is doubtful. First definite raphidiopteran as for Sojanoraphidiidae.

First: e.g. Archeraphidia yakoulewii Ponomarenko (1988), Mongolia.

Last: Alloraphidia dorfii, Redmond Formation, Knob Lake District, Canada.
F. LETOPALOPTERIDAE P. (ZEC) Terr.
e.g. Letopaloptera albardiana, former USSR.
The ordinal placement of this family is doubtful.

F. MESORAPHIDIIDAE (MESORAPHIDIIDAE)
J. (SIN)–K. (I.) Terr.
Last: e.g. Mesoraphidia sp. Whalley (1988), Lower Weald Clay, Capel, Surrey, England, UK.

F. RAPHIDIIDAE K. (APT)–Rec. Terr.
First: Raphidia brasilienis Nel et al. (1990), Santana Formation, Ceára, Brazil.

F. SINORAPHIDIIDAE J. (u.) Terr.
First and Last: Sinoraphidia viridis, Gansu, China.

F. SOJANORAPHIDIIDAE P. (ZEC) Terr.
First and Last: Sojanoraphidia rossica, former USSR.

Order SIPHONAPTERA (PULICIDA)
Boucot (1990) discusses the Cretaceous records of this order.

Extant

F. HYSTRICHOPSYLLIDAE T. (PRB)–Rec.
Extant

F. PULICIDAE K. (APT)–Rec. Terr.
First: e.g. Pulicid indet. 1, Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.
Extant

F. SAUROPHTHIRIDAE Ponomarenko, 1986b
K. (I.) Terr.
e.g. Sauropthirioides mongolicus Ponomarenko (1986b), Gurvaneren Formation, Mongolia. The position of this family is doubtful.

Order STREPSIPTERA (STYLOPIDA)
Data was taken from Kathirithamby (1989). First as for Myrmecolacidae.

Extant

Extant

F. MENGEIDAE T. (PRB) Terr.
e.g. Mengea tertiaria, Baltic amber.

First: Stichotrema eocaenicum, Brown Coal, Halle-an-der-Saale, Germany.
Extant

Order TRICHOPTERA (PHRYGANAEIDA, PHYRGANEIDA) P. (ART)–Rec. Terr.
We have followed the traditional classification, including stem group Amphiesmenoptera (Trichoptera plus Lepidoptera), i.e. Trichoptera as given here (s.l.) are paraphyletic with respect to Lepidoptera. Ranges taken from Kulicka and Sukacheva (1990). First as for Micro-ptysmatidae. Baltic amber records taken from Spahr (1989).

Extant

F. BAISSOFERIDAE J. (u.)–K. (I.) Terr.

F. BERAIEIDAE T. (PRB)–Rec. Terr.
First: Beroades pectinatus, Baltic amber.
Extant

F. BRACHYCENTRIDAE T. (PRB)–Rec. Terr.
First: Brachycentrus labialis, Baltic amber.
Extant

F. CALAMOCERATIDAE K. (APT)–Rec. Terr.
First: e.g. Calamoceratid pupa indet. Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.
Extant

F. CLADOCHORISTIDAE P. (u.)–Tr. (u.) Terr.


Extant

F. BAISSOFERIDAE J. (u.)–K. (I.) Terr.

F. BERAIEIDAE T. (PRB)–Rec. Terr.
First: Beroades pectinatus, Baltic amber.
Extant

F. BRACHYCENTRIDAE T. (PRB)–Rec. Terr.
First: Brachycentrus labialis, Baltic amber.
Extant

F. CALAMOCERATIDAE K. (APT)–Rec. Terr.
First: e.g. Calamoceratid pupa indet. Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.
Extant

F. CLADOCHORISTIDAE P. (u.)–Tr. (u.) Terr.

Extant

Extant

F. BAISSOFERIDAE J. (u.)–K. (I.) Terr.

F. BERAIEIDAE T. (PRB)–Rec. Terr.
First: Beroades pectinatus, Baltic amber.
Extant

F. BRACHYCENTRIDAE T. (PRB)–Rec. Terr.
First: Brachycenturus labialis, Baltic amber.
Extant

F. CALAMOCERATIDAE K. (APT)–Rec. Terr.
First: e.g. Calamoceratid pupa indet. Jell and Duncan (1986), Koonwarra Fossil Bed, south Gippsland, Australia.
Extant
References:


Grashkev, V. G. and Zherikhin, V. V. (in press) [New fossil mantids (Insects, Mantidae).] *Paleontologicheski Zurnal*.


22

**BRACHIOPODA**


The initial review of the first and last familial occurrences within the phylum (Ager et al., 1967) post-dated publication of the first edition of the brachiopod part of the *Treatise on Invertebrate Paleontology* (Williams et al., 1965). Range coverage was uneven. Data for nine superfamilies of inarticulate and three superfamilies of rhynchonellide were provided with limited familial information, while only superfamily data were reported for the orthides and strophomenides. Fuller information was listed for 30 families of spire-bearing brachiopod (including two families of thecideides) and 14 families of terebratulides. Moreover, since publication of the *Treatise*, there has been an accelerated proliferation of taxa (see Grant, 1980) together with a move towards cladistic classification within the group (Carlson, 1989; Holmer, 1991c). Consequently, data now are presented here for over 275 families across over 50 superfamilies. The split of the phylum into three classes, the Lingulata, Inarticulata and Articulata, is followed (Gorjansky and Popov, 1986).

Since the *Treatise*, there has been no comparable review of the phylum; moreover, few of the main groups within the phylum have been revised, as a whole, to account for new data. Accordingly, some contributors have not included data pertaining to post-*Treatise* families, while others have attempted to include as many verifiable families as possible. Most authors have presented data within accepted taxonomic structures; however, in a few cases, families have been listed alphabetically or in order of stratigraphical appearance.

There are many unresolved problems of correlation relevant to both well-known and less well-known faunas and their horizons, which, together with the uneven precision of taxonomic structure across the phylum, have presented major problems. Nevertheless, the project is finite and the information is presented within inevitable stratigraphical and systematic constraints. The *Treatise* (Williams et al., 1965) remains the main source reference for the phylum while Doescher (1981 and updates) provides important generic lists and bibliographic data.

**Acknowledgements** – DATH and MAP thank Drs L. E. Holmer and L. E. Popov for their detailed comments on the non-articulate groups and Professor A. D. Wright for his comments on the Orthida. DATH thanks Professor P. G. Baker for detailed comments and new information on the Thecideida, Professor N. M. Savage for comments on the Palaeozoic Rhynchonelloidea and Dr R. E. Grant for detailed comments on the Stenoscismatoidea; DATH and ALJ thank Dr C. H. C. Brunton for his comments on the Spiriferida. CHCB thanks Dr P. R. Racheboeuf for helpful comments on the chonetid section, and Dr R. E. Grant for comments on the productid section. CDP is grateful to Drs D. E. Lee and E. F. Owen for their comments on the post-Palaeozoic Rhynchonelloida. Professor Rong Jia-yu commented on parts of the entire manuscript. DATH thanks Professor D. L. Bruton for facilities at the Paleontologisk Museum, Oslo during final compilation and editing of the chapter, and Rex Doescher for access to his Brachiopod Bibliographic File in the Department of Paleobiology, Smithsonian Institution, Washington DC.

**Phylum** BRACHIOPODA Duméril, 1806

**THE NON-ARTICULATE BRACHIOPODS**

This informal grouping includes the classes Lingulata and Inarticulata of Gorjansky and Popov (1985).

**Class** LINGULATA Gorjansky and Popov, 1985

**Order** LINGULIDA Waagen, 1885

**Superfamily** LINGULOIDEA Menke, 1828

The classification of the Linguloidea is difficult, compounded by numerous generic assignments based only on outline and shape and not on internal morphology. Future revision may require substantial changes of some familial assignments and range data.


**First**: Not positively known, since many pre-Devonian species are poorly documented, particularly the interiors
which are needed to confirm assignments; for example *Lingula* sp. from the Upper Whitehouse of the Girvan district, SW Scotland (Harper, 1984) may be better assigned to the pseudolingulins (Holmer, 1991b). The first is probably *Apsilingula parkesensis* Williams, 1977, Mandagery Sandstone, New South Wales, Australia (Williams, 1977).

**Extant**

F. **OBOLIDAE** King, 1846


First: There are many cosmopolitan occurrences of *Linguella*: precise relative ages of the majority of older species being in doubt and not better constrained than lower Cambrian. The first is probably *Linguella linguata* Pelman, 1977, Tiusser Formation and *L. variabilis* Pelman, 1977, Erkeky Formation of the Siberian Platform, former USSR (Pelman, 1977).

Last: *Trigonoglossa scotica* (Davidson, 1860), Harden Beds (Middle Border Group), Black Metals Marine Band (Limestone Coal Group) and Calmy Limestone (Upper Limestone Group), Midland Valley of Scotland (Graham, 1970). *Lachrymula pringlei* Graham, 1970, Skipsey’s Marine Band, Midland Valley of Scotland, is only doubtfully referred to the obolids.

F. **ELKANIIDAE** Walcott and Schuchert, 1908


First: Probably *Elkania hamburgensis* (Walcott, 1884), Upper Cambrian, Nevada, USA (Ulrich and Cooper, 1938) or possibly *Broeggeria salteri* (Holl, 1865), Upper Cambrian, Malvern Hills, England, UK (Cocks, 1978).


F. **LINGULASMATIDAE** Winchell and Schuchert, 1893


First: *Lingulasma crassum* (Eichwald, 1829), Kunda rocks, east Baltic (Popov and Pushkin, 1986).

**Fig. 22.1**

**F. LINGULELLOTRETIDAE Koneva, 1983**

Є. (CRF)—О. (ARG) Mar.

**First:** *Lingulellotreta ergalievi* Koneva, 1983, Lower Cambrian, Malyi Karatau, southern Kazakhstan, former USSR (Gorjansky and Koneva, 1983).

**Last:** *Mirilingula aff. mutabilis* Popov, 1983, Lower Ordovician, Malyi Karatau, southern Kazakhstan (Koneva and Popov, 1983).

**F. ZHANATELLIDAE Koneva, 1986**

Є. (CRF—MER) Mar.

**First:** *Kyrshabaktella bellii* (Pelman, 1977), Lower Cambrian, Siberian Platform (Koneva, 1986).

**Last:** *Zhanatella rotunda* Koneva, 1986, Selety Horizon, Kazakhstan (Koneva, 1986).

**F. ANDOBOLIDAE Kozłowski, 1930** О. (?LLN/LLO) Mar.

**First and Last:** *Andobolus jackowskii* Kozłowski, 1930. This family is monotypic and apparently restricted to the Ordovician of Bolivia, South America (Kozłowski, 1930).

**F. PATERULIDAE Cooper, 1956**

О. (ARG)—Д. (PRA) Mar.

**First:** *Paterula sp.*, Volkov rocks, east Baltic (Gorjansky, 1969).

**Order** ACROTRETIDA Kuhn, 1949

**Suborder** ACROTRETIDINA Kuhn, 1949

**Superfamily** ACROTRETIOIDEA Schuchert, 1893

F. ACROTRETIDAE Schuchert, 1893

**First:** Linarssonia sp., uppermost Atdabanian, Sinija River, Siberian Platform, former USSR (Rozanov and Sokolev, 1984).

**Last:** Opisconidion arcticum Ludvigsen, 1974, Michelle Formation, northern Yukon is the last described species (Ludvigsen, 1974), but there are records of torynelasmatines from the Adorf Stufe (FRS) of Germany (Langer, 1971).

F. EOCONULIDAE Rowell, 1965

**First:** Although the genus has been reported from the upper Cambrian (Popov, in Holmer, 1989) the earliest records to date are from Lower Ordovician rocks, for example, Eoconulus cryptomyus Gorjansky, 1969, Volkhov rocks, west Estonia, former USSR (Biernat, 1973).  

**Last:** Eoconulus sp., Kildare Limestone Formation, County Kildare, Republic of Ireland (McClean, 1988).

F. CURTICIDAE Walcott and Schuchert, 1908

**First:** Curticia minuta Bell, 1941, Holm Dal Formation, Greenland (Zell and Rowell, 1988) and Dresbachian, Colorado, USA (Rowell and Bell, 1961).

**Last:** Curticia elegantula Walcott, 1905, Franconian, Minnesota, USA (Rowell and Bell, 1961).

F. ACROTHELIDAE Walcott and Schuchert, 1908

**First:** A number of species of Acrothele are known from rocks of early Cambrian age but are poorly constrained; better constrained is Spinulothlele dubia (Walcott, 1912), Pecla Formation, Nevada, USA (Rowell, 1977).  

**Last:** There are a number of TRE species of Orbitule recorded, for example, O. contraria (Barrande, 1868) from Czechoslovakia and O. bicornis Biernat, 1973 from the Holy Cross Mountains (Biernat, 1973); definitely Orbitule undulosa (Barrande, 1868), Klabava Formation, Bohemia, Czechoslovakia (Mergl, 1981).

F. BOTSFORDIIDAE Schindewolf, 1955

**First:** Botsfordia caelata (Hall, 1847), uppermost Atdabanian, Sinija River, Siberian Platform, former USSR (Rozanov and Sokolev, 1984).

**Last:** B. epigona Mergl, 1988, lower Middle Cambrian, Morocco (Mergl, 1988).

**Superfamily** DISCINOIDEA Gray, 1840


**First:** Schizocrania salopiensis Williams, 1974, upper Llanvirn, Shelve Inlier, Shropshire (Williams, 1974).

**Last:** Possibly Schizocrania? helderbergensis (Hall, 1892), lower Helderberg Group, eastern USA.

**Superfamily** SIPHONOTRETOIDEA Kutorga, 1848

F. SIPHONOTRETIDAE Kutorga, 1848

**First:** Dysoristus belli Pelman, 1977, Lenian, Siberian Platform may be the oldest (Pelman, 1977); definitely Schizambon reticulatus MacKinnon, 1976, Elandinskii Horizon, Altai Mountains (Aksarina and Pelman, 1978).

**Last:** Multispinula drummuckensis Harper, 1984, South Threave Formation, Girvan district, SW Scotland, UK (Harper, 1984).

**Order** PATERINIDA Rowell, 1965

**Superfamily** PATERINOIDEA Schuchert, 1893

F. PATERINIDAE Schuchert, 1893

**First:** Aldanotrema sunnaginensis Pelman, 1977, Tommotian, Siberian Platform (Pelman, 1977).

**Last:** Dictyotites fredriki Holmer, 1989, Furudal Limestone, Dalarna, Sweden and D. perforata Cooper, 1956, Pratt Ferry Formation, Alabama, southern Appalachians, USA, are approximately coeval; the tentative record of the genus from the Dalby Limestone, Dalarna, Sweden may be the latest occurrence (Holmer, 1989).

**Class** INARTICULATA Huxley, 1869

**Order** CRANIOPSIDA Gorjansky and Popov, 1985

**Superfamily** CRANIOPSIOIDEA Williams, 1963

F. CRANIOPSIDAE Williams, 1963

**First:** O. (TOM)–O. (LLO/CRD) Mar.

**Comment:** This family was elevated to a separate Order of the Class Inarticulata by Gorjansky and Popov (1985).

**First:** Pseudopholidops pusilla (Eichwald, 1829), Kukruse rocks, East Baltic (Popov and Pushkin, 1986).

**Last:** Possibly Craniops cf. hamiltoniae (Hall, 1860), Bedford Shales, Bedford, Ohio, USA.

**Order** TRIMERELLIDA Gorjansky and Popov, 1985

This group was given ordinal status by Gorjansky and Popov (1985).

**Superfamily** TRIMERELLOIDEA Davidson and King, 1872


**First:** Palaetrimellera superba Nikitin and Popov, 1984, Bestamak Formation, Bestamak, Chingiz Range, Kazakhstan, former USSR (Nikitin and Popov, 1984).

**Last:** The group declined within the Ludlow; nevertheless Trimerella lindstroemi Dall, 1870, Klinteberg Beds, Gotland together with T. ohiensis Meek, 1871, Niagara Group, New York, USA, and T. grandis Billings, 1862, Guelph Group, Ontario, Canada and others are locally common during this epoch.


**First and Last:** Ussunia incredibilis Nikitin and Popov, 1984, Bestamak Formation, Bestamak, Chingiz Range, Kazakhstan, former USSR (Nikitin and Popov, 1984).
F. ADENSUIDAE Popov and Rukavishnikova, 1986  
O. (PUS) Mar.


Order CRANIIDA Waagen, 1885

Gorjansky and Popov (1985) have given this group ordinal status.

Superfamily CRANIOIDEA Menke, 1828


First: Cambrian records, for example, Philhedra columbiana (Walcott, 1908), Middle Cambrian of British Columbia inadequately known; Pseudocrania petropolitana (Pander, 1830), Volkov rocks, east Baltic may be oldest (Gorjansky, 1969). [DATH] Extant

POSITION AND STATUS UNCERTAIN

The following four orders probably have more in common with the Articulata than the non-articulate groups.

Order KUTORGINIDA Kuhn, 1949

Gorjansky and Popov (1985) tentatively parked the kutorginids between their non-articulates and the articulates.

Superfamily KUTORGINOIDEA Schuchert, 1893


First: Khusatigina primaria Ushatsinskaya, 1987, uppermost Tommotian, Salany-Gol Rivulet, west Mongolia (Ushatsinskaya, 1987) and possibly Kutorgina peculiaris (Tate), upper Tommotian or lower Atdabanian, South Australia (Daily, 1956) or K.? anglica Cobbold and Pocock, 1934, Malvern Quartzite, England, UK (Rushton, 1974).

Last: There are a number of poorly constrained Middle Cambrian Kutorgina species, but Kutorgina amazzacca Aksarina, 1978, Mundybashskii Horizon, Altai Mountains (Aksarina and Pelman, 1978) may be youngest.


Order OBOLELLIDA Rowell, 1965

Gorjansky and Popov (1975) classified the calcareous-shelled obolellides with the articulate families.

Superfamily OBOLELLOIDEA Walcott and Schuchert, 1908


Last: Probably Alisina sibirica (Aksarina, 1978), Mundybashskii Horizon, Altai Mountains (Aksarina, 1978) or species of Trematobolus, for example, T. simplex (Vogel, 1962), Murero Formation, Zaragoza, Spain.

Order CHILEIDA Popov and Tikhonov, 1990

Popov and Tikhonov (1990) questionably assigned this order to the Inarticulata.

Superfamily CHILEIDOIDEA Popov and Tikhonov, 1990


First: Chile mirabilis Popov and Tikhonov, 1990, Botomian rocks, Alai Range, south Kirgizia, former USSR (Popov and Tikhonov, 1990).


Order NAUKATIDA Popov and Tikhonov, 1990

Popov and Tikhonov (1990) assigned this order to the Articulata.

Superfamily NAUKATOIDEA Popov and Tikhonov, 1990


Class ARTICULATA Huxley, 1869

Order ORTHIDA Schuchert and Cooper, 1932

Suborder ORTHIDINA Schuchert and Cooper, 1932

Superfamily BILLINGSELLIOIDEA Schuchert, 1893


Superfamily NISUSIOIDEA Andreeva, 1987


First: Nisusia festinata (Billings, 1861), Virginia, USA (Cooper, 1936).

Last: Nisusia sulcata Rowell and Caruso, 1985, Middle Cambrian, Utah, USA (Rowell and Caruso, 1985) or Nisusia desisi Bell, 1965, Middle Cambrian, Montana, USA (Bell, 1965).

Superfamily PROTORTHOIDEA Cooper, 1976

This family was raised to a superfamily by Cooper (1976) who described the earliest species of three new genera (Glyptoria, Israelaria, Psiloria) from rocks of early Cambrian age.
Formation, Bohemia, Czechoslovakia (Havlicek, 1977).

**Superfamily ORTHOIDEA** Woodward, 1852

F. **EOORTHIDAE** Walcott, 1908

**First:** Possibly *Diraphora venzaffi* Wolfart, 1974, Lower Cambrian, Iran (Wolfart, 1974).

**Last:** *Jivinella slaviki* (Kloucek, 1915), Klaba Formation, Bohemia (Havlíček, 1977).

F. **HESPERONOMIIDAE** Ulrich and Cooper, 1936

**First:** Ulrich and Cooper (1936) recorded four species of *Hesperonomia*, for example, *H. planidorsalis*, Sarbach Formation (Lower Ordovician, middle T.RE), Alberta, Canada.

**Last:** Possibly *Hesperonomia orientalis* (Su, 1976), Middle Ordovician, Inner Mongolia (Nei et al., 1976).

F. **ORTHIDIELLIDAE** Ulrich and Cooper, 1936

**First:** Probably *Orthidium gemmiculum* (Billings, 1865), Upper Canadian rocks, Quebec, Canada (Cooper, 1956).

**Last:** Probably *Ortheydium bellulum* Ulrich and Cooper, 1938, Upper Pogonip Group, Nevada, USA (Cooper, 1956).

**Comment:** *Portranella angulocostellata* Wright, 1964, Portrane Limestone, Portrane, eastern part of Irish Republic (Wright, 1964) has been assigned to the Enteletida (Hiller, 1968).

F. **TOXORTHIDAE** Rong, 1984


F. **ORTHIDAE** Woodward, 1852

**First:** Probably *Orthidium gemmiculum* (Billings, 1865), Upper Canadian rocks, Quebec, Canada (Cooper, 1956).

**Last:** Probably *Ortheydium bellulum* Ulrich and Cooper, 1938, Upper Pogonip Group, Nevada, USA (Cooper, 1956).

**Comment:** *Portranella angulocostellata* Wright, 1964, Portrane Limestone, Portrane, eastern part of Irish Republic (Wright, 1964) has been assigned to the Enteletida (Hiller, 1980).

F. **LEIORIDAE** Cooper, 1976

**First and Last:** *Leioria bentori* Cooper, 1976, Nimra Formation, southern Negev, Israel (Cooper, 1976).

F. **ALIMBELLIDAE** Andreeva, 1960

**First and Last:** *Alimella armata* Andreeva, 1960, TRE, Urals, former USSR (Andreeva, 1960).

F. **BOHEMIELLIDAE** Havlicek, 1977

**First:** Many species of the genera assigned to this family by Havlicek (1977) first occurred in the middle Cambrian. Stratigraphical records are too imprecise to name the first: as an example, *Bohemiella romingeri* (Barrande, 1879), Jince Formation, Bohemia, Czechoslovakia (Havlíček, 1977).

**Last:** *Shiragia biloba* Kobayashi, 1935, Chuangia Zone, South Korea (Kobayashi, 1935).

F. **RANORTHIDAE** Havlicek, 1977


**Last:** *Eodalmenella socialis* (Barrande, 1879), Šárka Formation, Bohemia, Czechoslovakia (Havlíček, 1977).

F. **NANORTHIDAE** Havlicek, 1977

**First:** *Nanorthis hamburgensis* (Walcott, 1884), Nevada and Colorado, USA (Ulrich and Cooper, 1938).

**Last:** *Trondorthis strandi* Neuman, 1974, Holonda Limestone, Trondheim Region, Norway, or *Trondorthis bifurcatus* (Cooper, 1956), Antelope Valley Limestone, Nevada, USA (Neuman and Bruton, 1974).
THE PUNCTATE ORTHIDES

This diverse group, probably derived polyphyletically from the non-punctate orthides, is considered in terms of two superfamilies following Havliček (1977).

Order ENTELETIDA Waagen, 1884

Superfamily ENTELETIDEOIDEA Waagen, 1884

F. ENTELETIDAE Waagen, 1884

First: Enteletes lamarcki (Fischer von Waldheim, 1825), Westphalian, Spain, Austria, and the former USSR (Martinez-Chacon, 1979).


F. DRABOVIIDAE Havliček, 1950

First: Notothrissa notaonconcha Havliček, 1977, Bolivia (Havlíček and Branisa, 1980).

Last: Enteletes minor Havliček, 1951, Bohemia, Czechoslovakia (Havlíček, 1951).

F. PORAMBORTHIDAE Havliček, 1951

O. (TRE)--Mar.

First: Poramborthis grimmi (Barrande, 1879), or Poramborthis anomala Havliček, 1977, both Tencice Formation (lower TRE), Bohemia, Czechoslovakia (Havlíček, 1977).


Superfamily PLECTORTHOIDEA Schuchert and Le Vene, 1929

According to Havliček (1977), the families Plectorthidae, Finkelnburgiidae and Skenidiidae are members of this superfamily, previously treated as separate families within the superfamily Orthidea of the Treatise.

F. FINKELNBURGIIDAE Schuchert and Cooper, 1931

First: Finkelnburgia buttsi Ulrich and Cooper, 1938, Upper Cambrian, Virginia, USA (Ulrich and Cooper, 1932).

Last: Probably fercia rongi Baarli, 1988, Solvik Formation, Askar, southern Norway (Baarli, 1988).

F. SCHIZOPHORIIDAE Schuchert and Le Vene, 1929

First: Possibly Villicundella mosetici (Levy and Nullo, 1974), ASH, San Juan Province, Argentina (Levy and Nullo, 1974).

Last: Proschizophoria personata (Zeiler, 1857), LOK and SIG, Europe (Maillieux, 1912).

F. LINOPORELLIDAE Schuchert and Cooper, 1931

First: Linoporella marina Xu and Liu, 1984 from the Meitan Formation, northern Guizhou, SW China or Protoskenidioides revelata Williams, 1974 from the Myton Flags, Shelve district, England, UK (Williams, 1974).

Last: Linoporella carinata (Hall, 1843), near cosmopolitan distribution in rocks of FRS age.

F. DICOELOSIIDAE Cloud, 1948

O. (PUS)--Mar.

**Last:** *Teichertina fitzroyensis* Veevers, 1959, Sadler Formation, Fitzroy Basin, Australia (Veevers, 1959).

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**F. KAYSERELLIDAE** Wright, 1965

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**First:** *Kayserella costulata* Lenz, 1977, Lower Devonian, Yukon, USA (Lenz, 1977).

**Last:** *Kayserella lepida* (Schnur, 1853), EIF, the Eifel, Germany and Moravia, Czechoslovakia (Havlíček, 1977).

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**F. SAUKRODICTYIDAE** Wright, 1964

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**First:** *Saukrodictya porosa* (Havlíček, 1977), Libeň and Letná formations, Czechoslovakia (Havlíček, 1977).

**Last:** *Saukrodictya arcana* Havlíček, 1977, Želkovic Forma­tion, Hýskov, Czechoslovakia (Havlíček, 1977).

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**F. MYSTROPHORIDAE** Schuchert and Cooper, 1931

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**First:** Probably *Visbyella* sp. nov. Temple, 1987, lower LLY, Wales, UK (Temple, 1987).

**Last:** *Biernatium emanuelensis* (Veevers, 1959), FRS, Fitzroy Basin, Australia (Havlíček, 1977).

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**F. HYPSOMYONIIDAE** Wright, 1965

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**First and Last:** *Hypsomonia stainbrooki* Cooper, 1955, 'Independence Shale', Iowa, USA (Cooper, 1955).
F. HARKNESSELLIDAE Bancroft, 1928
Last: Reuschella sp., Portrane Limestone, Co. Dublin, Republic of Ireland (Wright, 1964) and R. sp., Dolhir Formation, Glyn Ceiriog, North Wales (Hiller, 1980); Reuschella inexpectata Temple, 1968, Hirniant rocks overlying the Keisley Stage, Keisley, Cumbria, England, UK (Temple, 1968) has been assigned to Dysprosorthis (Rong, 1984).

F. HETERORTHIDAE Schuchert and Cooper, 1931
First: Tissintia prototypa (Williams, 1949), Didymograptus bifidus Shales and equivalent units at Builth, Llandeilo and Shelve, Wales, UK (Lockley and Williams, 1981).
Last: Platytorthis opercularis (Verneuil, 1845), EIF, Brittany, Germany and the Ural Mountains (Harper et al., 1969).

F. RHIPIDOMELLIDAE Schuchert, 1913
O. (CRD)–P. (TAT) Mar.
Last: Although common in the Lower Permian, Rhipidomella is rare in the higher parts of the system; Rhipidomella sp. from the middle Productus Limestone of the Salt Range may be youngest (Grant, 1970).

Suborder CLITAMBONITIDINA Öpik, 1934

Superfamily CLITAMBONITOIDEA Winchell and Schuchert, 1893
First: Protambonites soror (Barrande, 1879) and Protambonites kolahi (Havlíček, 1977), Holoubkov and Březany, respectively, Trenice Formation, Czechoslovakia (Havlíček, 1977).
Last: Eremovechia cloudi Cooper, 1956, Arline Formation, Blount, Appalachians, USA (Cooper, 1956).

F. CLITAMBONITIDAE Winchell and Schuchert, 1893
First: Apomatella ingrica (Pahlen, 1877), Volkhov Stage, Estonia and Russia, former USSR (Hints, 1990).
Last: Vellamo silurica Öpik, 1934 and Ilmarinia ponderosa Öpik, 1934, Porkuni Stage, Estonia, former USSR (Öpik, 1934).

Superfamily GONAMBONITOIDEA Schuchert and Cooper, 1931
First: Antigonambonites planus (Pander, 1830), Latorp Stage, Estonia and Russia, former USSR (Öpik, 1934).

First: Possibly Kullervo sp., Ffairfach Group, Mid-Wales, UK (Lockley and Williams, 1981) or Kullervo lacunata Öpik, 1934 and Kullervo sp. nov., Uhaku Stage, Estonia, former USSR (Rõõmusoks, 1970).
Last: Kullervo complectens (Wiman, 1907), 'West Baltic Leptaena Limestone', Hulterstad, Öland, Sweden and K? sp., Langøyene and Langara formations, Oslo Region, Norway (Cocks, 1982).

Suborder TRIPLESIIDINA Moore, 1952

Superfamily TRIPLESIOIDEA Schuchert, 1913
F. TRIPLESIIDAE Schuchert, 1913
First: Onychoplecia kindlei Cooper, 1956, Table Head Formation, Newfoundland, Canada (Cooper, 1956).
Last: Plectotrema lindstroemi Ulrich and Cooper, 1936a, Hemse Beds, Gotland (Bassett and Cocks, 1974). [DATH]

Order UNCERTAIN

Suborder DICTYONELLIDINA Cooper, 1956

Superfamily EICHWALDIOIDEA Schuchert, 1893
F. EICHWALDIIIDAE Schuchert, 1893
First: Eichwaldia subtrigonalis Billings, 1858, Rockland Formation, Ontario, Canada (Billings, 1858).
Last: Dictyonella sp., Middle Devonian (GIV), northern Balkhash area, former USSR (Kaplun, 1967).

F. ISOGRAMMIDAE Schuchert and LeVene, 1929
First: Several species of Isogramma are known from rocks of Viséan age, for example, I. germanica Paeckelmann, 1930, Lower Carboniferous, Austria, Germany, Lower Moscow Basin, and the Ukraine, former USSR; in Britain Isogramma sp. A, Dinwoodie Beds, southern Scotland, UK is the oldest (Brand, 1970).
Last: Isogramma lobatum Cooper and Grant, 1975, Cathedral Mountain Formation, west Texas, USA (Cooper and Grant, 1975). [DATH]

Order STROPHOMENIDINA Öpik, 1934

Suborder STROPHOMENIDINA Öpik, 1934

This group is similar to that in the Treatise (A. Williams, in Williams et al., 1965) except that the Thecospiroidae and the Bactryniidae have been removed to the Spiniferida.

Superfamily PLECTAMBONITOIDEA Jones, 1928

The classification within this superfamily follows the recent revision by Cocks and Rong (1989).

F. PLECTAMBONITIDAE Jones, 1928
First: Plectella uncinata (Pander, 1830), B1 Beds with Corynetopus, Maekula, Estonia, former USSR (Öpik, 1933).

F. TAFFIIDAE Schuchert and Cooper, 1931
First: May be Leptella? exigua Clark, 1917, Shumardia Zone of Beekmantown Group (TRE), Levis, Quebec, Canada (Cooper, 1956); but definitely Lower ARG, for example, Schedophyla striata (Xu et al., 1974), lower Meitan Formation, Guizhou, China (Xu et al., 1974).


First: Bimuria superba Ulrich and Cooper, 1942, Arline Formation, Tennessee, USA (Cooper, 1956).

Last: Bimuria youngiana (Davidson, 1871), Craighead Limestone, Girvan, Scotland, UK (Williams, 1962).


First: Syndielasma bisetatum Cooper, 1956, upper Pogonip Group, Nevada, USA (Cooper, 1956).


First: Leptellina (Leptellina) occidentalis Ulrich and Cooper, 1938, upper Pogonip Group, Nevada, USA (Ulrich and Cooper, 1938).


First: Tetradontella? aquiloides Fu, 1975, Xiliangsi Formation, Shaanxi, China (Fu, 1975).

Last: Gromus glabrata Spjeldnæs, 1957, Arenstad Formation, Oslo, Norway (Spjeldnæs, 1957).


First: Bilobia virginiensis Cooper, 1956, Edinburg Formation, Virginia, USA (Cooper, 1956).

Last: Xenambonites undosus Cooper, 1956, Pratt Ferry Formation, Alabama, USA (Cooper, 1956).

Last: Jonesia mariaformis (Lenz, 1977), Road River Formation, Yukon, Canada (Lenz, 1977).


First: Hesperomena leptellinoidea Cooper, 1956, Antelope Valley Limestone, Nevada, USA (Cooper, 1956).

Last: A number of species of Kassinella occur within the middle Ashgill (Cocks and Rong, 1989) including Kassinella (Kassinella) moneta (Barrande, 1879), Kráľův Úvěr Formation, Kosov, Czechoslovakia (Havlíček, 1967).


First: Sowerbyella antiqua Jones, 1928, Ffairfach Group, Llandeilo, Wales, UK (Williams et al., 1981).

Last: Plectodonta (Dalejdidiscus) comitans (Barrande, 1879), Daleje Shales, Prague, Czechoslovakia (Havlíček, 1967).

Superfamily STROPHOMENOIDEA King, 1846

The classification within this superfamily is unsatisfactory and needs revision. As pointed out by Cocks (1978), since denticles appeared polyphyletically in four different strophomenide stocks, then the superfamily Stropheodontoidea used by some authors for these brachiopods should not be employed. The classification here generally follows Williams (in Williams et al., 1965), but has been somewhat modified according to, e.g. Harper and Boucot (1978), Havlíček (1967). For ease of reference the families without denticles are listed first (Christianiidae to Strophomenidae) and these are followed by those with denticles (Amphistriphidae to Strophonellidae).


First: Christianiella sulcata Williams, 1962, Stirchill Limestone, Girvan, Scotland, UK (Williams, 1962).

Last: Christianiella aff. tenuicincta (M'Coy, 1846), Langøyene Formation, Oslo, Norway (Cocks, 1982).


First: Leptaenoida gotlandica Hedström, 1917, Upper Visby Beds, Gotland, Sweden (Bassett and Cocks, 1974).

Last: Leptaeniscus concava (Hall, 1857), Haragan Formation, Oklahoma, USA (Amsden, 1958).


First: Macrocoelia llandeiloensis (Davidson, 1871), Lower Flags and Grits of Ffairfach Group, Llandeilo, Wales, UK (Williams et al., 1981).

Last: Drummuckina donax (Reed, 1917), Lady Burn Starfish Beds, Girvan, Scotland, UK (Cocks, 1978).


First: Strophomena deficiens Reed, 1917, Balclatchie Mudstones, Girvan, Scotland, UK (Williams, 1962).


Last: Devonampistriphia alvata (Hall, 1863), Schoharie Grit, New York, USA (Harper and Boucot, 1978).
**F. DOUVILLINIDAE** Caster, 1939  
Last: Douvillella arcuata (Hall, 1857), Lime Creek Beds, Rockford, Iowa, USA (Harper and Boucot, 1978).

**F. LEPTOSTROPHIIDAE** Caster, 1939  

**F. PHOLIDOSTROPHIIDAE** Stainbrook, 1943  

**F. SHALERIIDAE** Williams, 1965  
Last: Shaleria rigida (de Koninck, 1876), Grés de Gdoumont, Gedinne, Belgium (Harper and Boucot, 1978).

**F. STROPHOEONTIDAE** Caster, 1939  
Last: Strophonelloides reversa (Calvin, 1878), Hackberry Group, Rockford, Iowa, USA (Harper and Boucot, 1978).

**F. STROPHONELLIDAE** Caster, 1939  
First: Eostrophonella ethen (Bancroft, 1949), Gasworks Mudstone, Haverfordwest, Dyfed, Wales, UK (Williams, 1951).  
Last: Strophonella (Quasistrophonella) bohemica (Barrande, 1848), Konéprusy Limestone, Prague, Czechoslovakia (Havlíček, 1967).  
[LRMC]

**Superfamily DAVIDSONIOIDEA** King, 1850  
In general, the classification scheme of Havlíček (1967) is followed, with the possible addition of the Eocramatidae. Relationships between the various families are rather obscure, and so they are listed here in alphabetical order.

**F. CHILIDIOPSIDA** Boucot, 1959  
First: Gacella insolita Williams, 1962, Stinchar Limestone, Girvan, Scotland, UK (Williams, 1962).  
Last: Pulisia mosquensis Ivanov, 1925, SPK, Moscow Basin, former USSR (Sarytcheva and Sokolskaya, 1952).

**F. DAVIDSONIIIDAE** King, 1850  
First: Biconostrophia fragilis (Barrande, 1879), Konéprusy Limestone, Prague, Czechoslovakia (Havlíček, 1967).  
?F. EOCRAMATIIDAE** Williams, 1974  
Comment: It is uncertain whether or not these genera, which have a bilobed cardinal process, but whose shell structure is unknown, should be assigned to the Strophomenoida, Orthoidea or Davidsonioida, but the latter seems most probable.

**F. MEEKELLIDAE** Stehli, 1954  
First: Orthotettina thomasi (Sarytcheva and Sokolskaya, 1952), SPK, Tarussky, Moscow Basin, former USSR (Sarytcheva and Sokolskaya, 1952).  
Last: Geyerella americana Girty, 1909, Capitan Formation (early KAZ, in age), Texas, USA (Cooper and Grant, 1974).

**F. ORHTOTETIDAE** Waagen, 1884  
First: Orthotetes keokuk (Hall, 1858), Keokuk Limestone (Chadian), Keokuk, Iowa, USA (Weller, 1914).  

**F. SCHUCHERTELLIDAE** Williams, 1953  
First: Aesopomum aseopum (Barrande, 1879), Lockhov Limestone, Lockhov, Prague, Czechoslovakia (Havlíček, 1967).  
Last: Goniarella permiana (Stehli, 1954), Bone Spring Formation, Texas, USA (Cooper and Grant, 1974).

**F. STREPTORHYNCHIDAE** Stehli, 1954  
First: Aesopomum aseopum (Barrande, 1879), Konéprusy Limestone, Konéprusy, Czechoslovakia (Havlíček, 1967).  
Last: Tropidolasma gregarium Girty, 1909, Capitan Formation, Texas, USA (Cooper and Grant, 1974).  
[CHCB and LRMC]

**Suborder CHONETIDINA** Muir-Wood, 1955  
There has been no complete revision of the suborder since the Treatise (1965), so those families are followed here, with the addition of the Rugsoschonetiidae, Strophochonetidae and Anopliidae, elevated from their subfamilies in the Treatise.

**Superfamily CHONETOIDEA** Bronn, 1862  
F. CHONETIDAE Bronn, 1862  
First: Dawsonellidae canadensis (Billings, 1874), New Scotland Beds, northern Appalachians, USA (Boucot and Harper, 1968).
**Animals: Invertebrates**

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<table>
<thead>
<tr>
<th>SIN</th>
<th>1. Rugosochonetidae</th>
<th>23. Buxtoniidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>HET</td>
<td>2. Strophochonetidae</td>
<td>24. Dictyoclostidae</td>
</tr>
<tr>
<td>RHT</td>
<td>3. Anoplidiidae</td>
<td>25. Linoproductidae</td>
</tr>
<tr>
<td>CRN</td>
<td>5. Chonostrophiidae</td>
<td>27. Lytioniidae</td>
</tr>
<tr>
<td>LAD</td>
<td>6. Daviesiellidae</td>
<td>28. Poikilosakidae</td>
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<tr>
<td>ANS</td>
<td>7. Strophalosidae</td>
<td>29. Brevicameriidae</td>
</tr>
<tr>
<td>SCY</td>
<td>8. Teguliferidae</td>
<td>30. Camarellidae</td>
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<tr>
<td>KAZ</td>
<td>10. Tschernyschewiidae32. Eostrophiidae</td>
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<td>UFI</td>
<td>11. Artocladidae</td>
<td>33. Hueneellidae</td>
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<tr>
<td>KUN</td>
<td>12. Aulostegiidae</td>
<td>34. Lycophoriidae</td>
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<tr>
<td>ART</td>
<td>13. Sinuatellidae</td>
<td>35. Parastrophiidae</td>
</tr>
<tr>
<td>ASS</td>
<td>15. Scacchinellidae</td>
<td>37. Syntrophiidae</td>
</tr>
<tr>
<td>GZE</td>
<td>16. Richthofeniidae</td>
<td>38. Syntrophospidae</td>
</tr>
<tr>
<td>KAS</td>
<td>17. Productellidae</td>
<td>39. Tetralobulidae</td>
</tr>
<tr>
<td>MOS</td>
<td>18. Leioproductidae</td>
<td>40. Enantiosphoridae</td>
</tr>
<tr>
<td>BSH</td>
<td>19. Overtoniidae</td>
<td>41. Gypidulidae</td>
</tr>
<tr>
<td>SPK</td>
<td>20. Marginiferidae</td>
<td>42. Pentameriidae</td>
</tr>
<tr>
<td>VIE</td>
<td>21. Productiidae</td>
<td>43. Stricklandiidae</td>
</tr>
<tr>
<td>TOU</td>
<td>22. Echinococonchidae</td>
<td>44. Angusticardiidae</td>
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**Last:** *Quinuenella glabra* Waterhouse, 1975, Chhidru Formation, Nepal.  
**Comment:** The rugosochonetids, strophochonetids and anoplids of the *Treatise* are removed from here.

F. **RUGOSOCHONETIDAE** Muir-Wood, 1962  
D. (EMS)–P. (CHX) Mar.

**First:** *Dagnachonetes (Luanquella) alcaldei* Racheboeuf, 1981, lower Moniello Formation, NW Spain.  
**Last:** *Rugaria aff. nisalensis* Waterhouse, 1978, Senja Formation, Nepal.

F. **STROPHOCHEFONETIDAE** Muir-Wood, 1962  

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**Last:** *Arachaeochonetes primigenius* (Twenhofel, 1914), Vaureen Formation, Anticosti Island, Canada (Racheboeuf and Copper, 1986).  
**Last:** *Chlupacina longispina* Havlíček and Racheboeuf, 1979, Chotec Limestone, lower *Pinacites juglen* Zone, Bohemia, Czechoslovakia (Racheboeuf, 1981).

F. **ANOPLIIDAE** Muir-Wood, 1962  

**First:** *Epilicanoplia collicula* (Foerste, 1909), Salina Formation, Indiana, USA (Boucot and Harper, 1968).  
**Last:** *Glabrichonetes kunauensis* Waterhouse, 1978, Senja Formation, Nepal.
F. EODEVONARIIDAE Sokolskaya, 1960
First: Davoustia davousti (Oehlert, 1887). St Cénéré Formation, Laval, France (Racheboeuf, 1976).

F. CHONOSTROPHIIDAE Muir-Wood, 1962
First: Chonostrophilla complanata (Hall, 1857), Tarratte Formation, Maine, USA (Boucot and Amsden, 1964).
Last: Chonostrophilla cynthiae Racheboeuf, 1987, Upper Blue Fjord Formation, Arctic Canada. Or, if proved, Chonostrophia reversa (Whitefield, 1802), Delaware Formation, Ohio, USA, possibly EIF.

F. DAVIESIELLIDAE Sokolskaya, 1960
Comment: Megachonetes Sokolskaya, 1950 was included in this family in the Treatise, with a range starting in the mid-Devonian and extending to the upper Carboniferous (MOS), but it is thought to be better assigned to the Rugosoconchidae. [CHCB]

Suborder PRODUCTIDINA Waagen, 1883
The 24 families included here are classified in four superfamilies, but unlike the Treatise (1965), the aulostegids are here treated as a superfamly, within which several previous strophalosioidean families now reside, as well as the Institinidae from the Productoida. The Richthofenioidae and the Lyttonioidea remain unsatisfactory. Since 1965, other families have been proposed and provide good groupings, such as McKellar's (1970) use of the Leioconchidae from the Productoidea. The Richthofenioidea retained within the Echinoconchidae. While authors such as Sarytcheva (1963), and Cooper and Grant (1975), have added families, the lack of any complete revision of the Productidina makes their inclusion here difficult.

Superfamily STROPHALOSIOIDEA Schuchert, 1913
F. STROPHALOSIOIDEA Schuchert, 1913
D. (EMS)–P. (CHX) Mar.
First: Ralia primigenia Lazarev, 1987, Oculipora angulata Zone, Gobi Altai, southern Mongolia.
Last: Marginalosia kalikotei (Waterhouse, 1975), Senja Formation, Nepal.
Comment: The Upper Permian Cyrtalosia circinata Termier and Termier, 1970 from Cambodia has no interarea and is thought to be an aulostegid.

F. TEGULIFERIDAE Muir-Wood and Cooper, 1960
C. (KAS)–P. (KUN) Mar.
First: Teguliferina armata (Girty, 1908), Hertha Limestone, Missouri, USA (Dunbar and Condra, 1932).
Last: Acritosia magnifica Cooper and Grant, 1975, Road Canyon Formation, Texas, USA.

F. CHONETELLIDAE Likharew, 1960
C. (KAS)–P. (CHX) Mar.
First: Chonetella dunbari Newell, 1934, Missourian, Oklahoma, USA. There is some doubt about the assignment of this species.

Superfamily AULOSTEGOIDEA Muir-Wood and Cooper, 1960
F. SPYRIDIOPHORIDAE Muir-Wood and Cooper, 1960
First: Spyridiophora distincta Cooper and Stehli, 1955, Neal Ranch, Texas, USA (Cooper and Grant, 1975).
Last: Spyridiophora reticulata (R. E. King, 1931), low Cathedral Mountain, Texas, USA (Cooper and Grant, 1975).
F. TSCHERNYSCHWEIIIDAE Muir-Wood and Cooper, 1960
First: Tschernyschewia inexpectans Cooper and Grant, 1975, Taylor Ranch, Texas, USA.
Last: T. typica or T. yakowlewi Stoyanow, 1910, Djulfa, Armenia.
Comment: In North America, members of the family are restricted to the Lower Permian, while in Eurasia they are mainly late Permian in age.
F. AULOSTEGIDAE Muir-Wood and Cooper, 1960
C. (GZE)–P. (CHX) Mar.
First: Limbella costellata Cooper and Grant, 1975, Uddenites Shale, Texas, USA.
Last: Megasteges nepalensis Waterhouse, 1975, Senja Formation, Nepal.
F. SINUATELLIDAE Muir-Wood and Cooper, 1960
First: Sinuatella sinuata (de Koninck, 1851), Visé, Belgium and England, UK (Brunton and Mundy, 1988).
Last: S. johnsoni Brunton and Mundy, 1988, lower Namurian, Northumberland, NE England, UK.
Comment: Demanet (1958) recorded the species from the Ivorian of Tournai, but the identification is doubted.
F. INSTITINIDAE Muir-Wood and Cooper, 1960
First: Institina plicatiliformis (Fredericks, 1932), Uralian, northern Russia, former USSR (Muir-Wood and Cooper, 1960).
F. SCACCHINELLIDAE Licharew, 1928
First: Scacchinella primitiva Cooper and Grant, 1975, Gaptank Formation, Texas, USA.
Last: Scacchinella variabilis Gemmellaro, 1897, Sosio Limestone, Sicily (Rudwick and Cowen, 1968).
Comment: The age of the Sosio Limestone remains in doubt.

Superfamily RICHTHOFENIOIDEA Waagen, 1885
F. RICHTHOFENIIDAE Waagen, 1885


**First:** Hercosia uddeni (Bose, 1916), Skinner Ranch Formation, Texas, USA (Cooper and Grant, 1975).

**Last:** Sestropoma cribriferum Cooper and Grant, 1975, Capitan Formation, Texas, USA.

**Superfamily** PRODUCTOIDEA Gray, 1840

F. PRODUCTELLIDAE Schuchert and Le Vene, 1929


**First:** Eoproductionella manakovae Rzhonsnitskaja, 1980, Pandzhhrutskiy Horizon, central Asia.

**Last:** Stictozoster leptus Grant, 1976, Rat Buri Limestone, Thailand.

**Comment:** This is one of the longer-ranging families, and is likely that some of the younger genera should reside elsewhere.

F. LEIOPRODUCTIDAE Muir-Wood and Cooper, 1960


**First:** Devonoproductus intermedius Cooper and Dutro, 1982, Sly Gap Formation, New Mexico, USA.

**Last:** Productina pectinoides (Phillips, 1836), Valdesta Formation, northern Spain (Prins, 1968).

**Comment:** Here the probable Lower Permian genus Jakutoproductus Kashirtsev, 1959 is considered as an overtonid.

F. OVERTONIIDAE Muir-Wood and Cooper, 1960

C. (HAS)–P. (CHX) Mar.

**First:** Overtonia borodenovensis (Tolmatchow, 1924), Taidon Formation, Kuznetsk, former USSR (Sarytcheva, 1963).

**Last:** Dorashamia abichi Sarytcheva, 1965, Djulfian, Transcaucasus, former USSR and Iran (Sarytcheva, 1965).

**Comment:** If Tolmatchoffia Frederiks, 1933 is accepted in this family there are species from the Kuznetsk Basin, former USSR, of early to mid TOU age.

F. MARGINIFERIDAE Stehli, 1954

C. (CHD)–P. (CHX) Mar.

**First:** Eomarginifera sp. Shephard-Thorn, 1963, Waulsortian Limestone, Limerick, Republic of Ireland.

**Last:** Spinomarginifera sp. Grant, 1970, Mianwali Formation, Salt Range, Pakistan.

**Comment:** Perhaps the earliest-named species is Eomarginifera cf. longispina (J. Sowerby, 1814) known from the Chadian of Derbyshire, England, UK, while Spinomarginifera cf. helica (Abich), recorded by Nakazawa et al. (1975) from the upper TAT of Nepal, is perhaps the youngest.

F. PRODUCTIDAE Gray, 1840


**First:** Productus garwoodi Muir-Wood, 1928, S2 Bryozoa Beds, Westmorland (Cumbria), England, UK.

**Last:** Productus carbonarius de Koninck, 1842, Quarterburn Marine Band, Westmorland (Cumbria), England, UK (Calver, in Owens and Burgess, 1965).

F. ECHINOCONCHIDAE Stehli, 1954


**First:** Caucasiproductus gretchishnikovae Lazarev, 1987, Indosipifer pseudowilliamsi Zone, Transcaucus, former USSR.

**Last:** Waagenoconcha gangeticus (Diener, 1897), Nangung Formation, Nepal (Waterhouse, 1978).

**Comment:** Lazarev’s species was placed in the Sentosisiidae McKellar 1970, within the Echinocochoidea sensu Lazarev, 1987.

F. BUXTONIIDAE Muir-Wood and Cooper, 1960

C. (IVO)–P. (LGT) Mar.

**First:** Dictyoclocestidae Stehli, 1954

**First:** ‘Cancrinella’ panderi (Auerbach, 1862), Cita, Donetz Basin, former USSR (Aizenverg, 1966) and Ovatia laevicosta (White, 1860), Taidon, Kuznetsk Basin, former USSR (Sarytcheva, 1963).

**Last:** Linoproductus superbus Reed, 1944, Senja Formation, Nepal (Waterhouse, 1978).

**Comment:** O. laevicosta reported by Nalivkin (1979) from the Fammenian of the Urals has yet to be confirmed.

F. LINOPRODUCTIDAE Stehli, 1954


**First:** Lincolnoprotus ashfelli Ferguson, 1971, Ashfell Limestone, northern England, UK.


**Comment:** Bagrasia Nalivkin, 1960 was doubtfully included here in the Treatise (1965) from Etroeungt beds in the former USSR, but is considered more likely to be a linoprotidic.

**Superfamily** LYTONIOIDEA Waagen, 1883

F. LYTONIIDAE Waagen, 1883


**First:** Keyserlingina filicis (Keyserling, 1891) and K. schellwieni Tschernevschchew, 1902, Schwagerina Limestone, Urals, former USSR.

**Last:** Oldhamia transcaucascica (Stoyanov, 1915), Djulfian, Transcaucus, former USSR (Sarytcheva, 1965) and Lyttonia.
substrate, not the specimens, seems to be spinose, the slightly younger than P. 

**F. POIKILOSAKIDAE** Williams, 1953


**First:** Poikilosakos plana (Ivanova, 1936), Moscow Basin, former USSR (Sarytcheva, 1952).
**Last:** Cardinocrania indica Waagen, 1885, Chhidru Formation, (Cephalopod Bed), Salt Range, Pakistan.

**Comment:** Poikilosakos petaloides Watson, 1917, from the Plattsmouth Limestone, USA (Dunbar and Condra, 1932) is slightly younger than P. plana.

F. SPINOLYTTONIIDAE Williams, 1965: invalid

**Comment:** This family has only one genus and, since the substrate, not the specimens, seems to be spinose, the family is invalid.

**Order** PENTAMERIDA Schuchert and Cooper, 1931

**Superfamily** PORAMBONITOIDEA Davidson, 1853

F. BREVICAMERIDAE Cooper, 1956

O. (LLO—CRD) (includes Parallelelasmatidae) Mar.

**First:** Brevicamera camerata Cooper, 1956, Pratt Ferry Formation, Alabama, USA.
**Last:** Vaga sinualis Sapelnikov and Rukavishnikova, 1973, upper CRD, Chu-ili Mountains, Kazakhstan, former USSR (Sarytcheva, 1952).

F. CAMARELLIDAE Hall and Clarke, 1894


**First:** Idiostrophina perfeta Ulrich and Cooper, 1936b, Mystic Conglomerate, Quebec, Canada.
**Last:** Bleshidium triste Havliček, 1990, Přidolí Formation, Beroun, Czechoslovakia (Havliček and Štorch, 1990).

F. CLARKELLIDAE Schuchert and Cooper, 1931


**First:** Syntrophina alata Severgina, 1985, TRE, Gorny Altai, former USSR (Sarytcheva, 1952).
**Last:** Yangeteella poloi (Martelli, 1901), Kuniutan Formation, Hubei Province, China.

F. EOSTROPHIIIDAE Ulrich and Cooper, 1936


**First and Last:** Cambrostrophia cambria (Walcott, 1908), Middle Cambrian, Utah, USA.

F. HUENELLIDAE Schuchert and Cooper, 1931


**First:** Huenella abnormis (Walcott, 1912), Deep Creek Limestone, Wyoming, USA (Walcott, 1912).

F. LYCOPHORIIDAE Schuchert and Cooper, 1931


**First and Last:** Lycophoria nucella (Dalman, 1828), Lower Ordovician, Baltoscandia (Schuchert and Cooper, 1931).

F. PARASTROPHINIDAE Ulrich and Cooper, 1938


**First:** Parastrophina bilobata Cooper, 1956, Pratt Ferry Formation, Alabama, USA (Cooper, 1956).

F. HUENELLIDAE Schuchert and Cooper, 1931


**First:** Eoconchidium, Holorhynchus, Proconchidium and Tscherkidium are common in the middle Ashgill; they are represented by a number of species, for example, Proconchidium muensteri (St. Joseph, 1938), ASH, Ringerike, Norway.

F. POIKILOSAKIDAE Davidson, 1853


**First:** Porambonites? umbonatus Cooper, 1956, Pogonip Group, Nevada, USA.
**Last:** Definite Porambonites sp., Dolhir Formation, Glyn Ceiriog, North Wales, UK (Hiller, 1980), or possibly Noetlingia tscheffkini (de Verneuil, 1845), unreviewed Lower Silurian, Urals, former USSR (fide Biernat in Williams et al., 1965).

F. SYNTROPHIDS Schuchert, 1896


**First:** Syntrophia lateralis (Whitfield, 1886), middle ARG, Cassin Formation, Vermont, USA (Biernat in Williams et al., 1965).
**Last:** Xenelasmella perplexa Liu et al., 1984, middle Ordovician, Kunun and Altun Mountains, China (Liu et al., 1984) or Syntrophia gigantea Ross, 1987, Newfoundland, Canada (Ross and James, 1987).

F. SYNTROPHOPSISIDAE Ulrich and Cooper, 1936


**First:** Tcharella amgensis Andreeva, 1987, Kooteniella Zone, Amga River, Siberian Platform, former USSR (Andreeva, 1987).
**Last:** Rhysostraphia nevadensis Ulrich and Cooper, 1936b, upper Pogonip Group, Nevada, USA.

F. TETRALOBULIDAE Ulrich and Cooper, 1936


**First:** Tetrabolus? mundina (Walcott, 1905), lower Pogonip Group, Nevada, USA (Ulrich and Cooper, 1938).
**Last:** Tetrabolus huanghuaensis Wang, 1975, ARG, Yichang, south-west China.

**Superfamily** PENTAMEROIDEA M'Coy, 1844

F. ENANTIOPHENIDAE Torley, 1934


**First and Last:** Enantiosphen vicaryi (Davidson, 1882), GIV, Germany.

F. GYPIDULIDAE Schuchert and Le Vene, 1936


**First:** There are a number of records of the Gypidulidae from the lower WEN and an unconfirmed report from the upper LLY of the Hudson Bay Lowlands of Canada.
**Last:** There are a number of records of the genus Gypidula from the Upper Devonian (FRS); these include, Gypidula sublubrica Zhao, 1977, Hupeh Province, China, together with G. mimica Cooper and Dutro, 1982, G. stainbrooki Cooper and Dutro, 1982 and G. subcarinata Cooper and Dutro, 1982, New Mexico, USA (Cooper and Dutro, 1982).
**Fig. 22.4**

Last: *Bisulcata indianensis* Boucot and Johnson, 1979, Kenneth Limestone Member, Salina Formation, Logansport, Indiana, USA.

**F. STRICKLANDIIDAE** Schuchert and Cooper, 1931 O. (ASH)–S. (WEN) Mar.

First: *Prostricklandia prisca* Rukavishnikova, 1973, Kazakhstan, former USSR (Sapelnikov, 1977); the systematic position of *Prostricklandia* requires revision.

Last: *Costistricklandia* sp. of Bassett (1977) from *linnarssoni* Zone age beds (Sheinwoodian), near Llandeilo, Wales, UK. [LRMC and END]

Precise position uncertain

**F. ANGUSTICARDINIIDAE** Schuchert and Cooper, 1931 O. (ARG–ASH) Mar.

This group is better located within the parabombolites than the orthides where it possibly gave rise to the rhynchonellides (Jaanusson, 1971).

First: *Angusticardinia recta* (Pander, 1830) and *A. striata* (Pander, 1830), Latorp Stage, Estonia, former USSR (Rubel, 1961).

Last: *Apatorthis ultima* Opik, 1933, Pirgu Stage, Estonia, former USSR (Opik, 1933). [DATH]

**Order RHYNCHONELLIDA** Kuhn, 1949

The classification of Mesozoic and Cainozoic rhynchonellides used here is largely based on that proposed by Ager (1965) in the Treatise, but has been modified to include some of the less-tentative ideas put forward by Ager et al. (1972).

**Superfamily DIMERELLOIDEA** Buckman, 1918

**F. DIMERELLIDAE** Buckman, 1918 Tr. (CRN)–K. (HAU) Mar.

First: *Halorella rectifrons* (Bittner, 1884), CRN, Plesivec, Slovakia, Eastern Alps, Czechoslovakia (Ager, 1968) is an early species of numerous poorly dated species of *Halorella* and *Halorelloidea* known from the CRN and NOR worldwide (Ager, 1968). It is not certain which species of these two genera is the first of the Dimerellidae.

Last: *Peregrinella multicarinata* Lamarck, 1819, HAU, Drôme, south-west France (Biernat, 1957).

**Superfamily** RHYNCHONELLOIDEA Gray, 1848

No overall consensus on the classification of the Palaeozoic families of this group has emerged since publication of the *Treatise*; this together with the establishment of a large number of new Middle Palaeozoic genera without clear familial attachments has limited the precision of this part of the project. Palaeozoic members of the superfamily have been listed mainly in order of stratigraphical appearance. Tentative proposals by Ager et al. (1972) to extend the families Pugnacidae and Erymnariidae into the Mesozoic are not followed here; there is currently insufficient evidence to warrant adoption of these proposals.

F. ANCISTORHYNCHIDAE Cooper, 1956
Last: *Kriformylia seclusa* Rong and Yang, 1981, Xiangshuyuan Formation, NE Guizhou, China (Rong and Yang, 1981). The probable reassignment of this genus to the atrypides (J.-Y. Rong, unpublished data) may restrict this family to the Ordovician.

F. TRIGONIRHYNCHIIDAE McLaren, 1965


Last: *Tricoria hirpex* Cooper and Grant, 1976, Skinner Ranch Formation, west Texas (Cooper and Grant, 1976).

F. RHYNCHOTREMATAIDAE Schuchert, 1913

O. (CRD)—D. (GIV) Mar. (includes Lepidocyclidae)

First: *Rhyncotrema kentuckiense* Fenton and Fenton, 1922, Trenton Formation, Kentucky, USA, or *R. wisconsinense* Fenton and Fenton, 1922, Decorah Formation, Minnesota and Wisconsin, USA (Cooper, 1956).

Last: Possibly *Callipleura nobilis* (Hall, 1860), Hamilton Group, New York, USA.

F. OLIGORHYNCHIIDAE Cooper, 1956


First: *Oligorhynchia subplana gibbosa* Cooper, 1956, Lincolnshire Formation, Tennessee, USA or *O. conybeare* (Reed, 1917), Balclatchie Conglomerate, Girvan district, Scotland, UK (Williams, 1962).

Last: If *Rhyncotreta* is considered a member of this family, then *R. gansuensis* Fu, 1983, Putongyan Formation, NW China (Fu, 1993).

F. INNAECHIIDAE Baranov, 1980


First: *Lepidocycloides batikicus* Nikiforova, 1961, Upper Ordovician, Siberia, former USSR.

Last: *Alekseevaella salagaensis* (Rzonsnitskaja, 1967), Ural’tun Formation, Omulevskij Mountains, NE of former USSR.

F. EATONIIDAE Schmidt, 1965


First: *Clarkea* sp., upper Bani Sandstone Formation, Morocco (Destombes et al., 1985).

Last: Although there are records of *Costellirostra*, *Eucharitina*, *Pegmarhynchia* and *Tanerhynchia* species from the EMS, *Clarkea bulbishecki* Kaplin, 1968, EIF, North Pribalkhash, former USSR may be youngest (Kaplun, 1968).

F. LEPTOCOELIIDAE Boucot and Gill, 1956


First: *Ecoeloa hemisphaerica* (J. de C. Sowerby, 1839) from middle Llandovery localities in Wales and the Welsh Borderlands, UK (Cocks, 1978).

Last: Species of *Australocoeloa*, *Leptocoela* and *Pacificocoeloa* occur in EMS rocks in a number of parts of the world; *Pacificocoela infrequens* (Johnson, 1970) from EMS rocks in Nevada is one of the last (Boucot, 1975).

F. CAMAROTOECHIIDAE Schuchert and Le Vene, 1929


Last: *Paranorella aquilonia* Cooper and Grant, 1976, Bell Canyon Formation, west Texas (Cooper and Grant, 1976).

F. UNICNUILIDAE Rzhonsnitskaya, 1956


Last: Although several records of *Uncinunellina* from Upper Permian rocks, for example, *U. theobaldi* (Waagen, 1884), Salt Range, Pakistan, were considered youngest, Grant (1976) has transferred *Uncinunellina* to the Wellerellidae. Youngest may be *Hypothyridina cuboides* (J. de C. Sowerby, 1840), Upper Devonian, south Devon, England, UK.

F. KATUNIIDAE Xu and Yao, 1984


First: *Sulcatina sulcata* (Cooper, 1942), Waldron Shale, USA.

Last: *Terebratuloida davidsoni* Waagen, 1883, Wargal Limestone, Salt Range, Pakistan (Grant, 1976).

F. PUGNACIIDAE Rzhonsnitskaya, 1956


First: *Xeniopugnax modicus* (Barrande, 1847) and *X. lynx* (Barrande, 1879) from the Kopanina Formation, Bohemia, Czechoslovakia (Havlíček, 1982a).


F. PYGMAELLIDAE Baranov, 1977


First: Probably *Pygmaella pygmaea* Baranov, 1977, Sagyrian Horizon, in the NE of former USSR.


F. PHOENICITOECHIIDAE Havlicek, 1990


First and Last: This small family consists of three genera mainly occurring in the Konéprésy Limestone and coeval strata, Konéprésy area, Czechoslovakia; *Phoenicitoechia phoenix* (Barrande, 1847) and *Kotysex simulans* (Barrande, 1879) are representative (Havlíček, 1990).

F. ROZMANARIIDAE Havlicek, 1982


First: *Rackirhynchia lacerata* (Barrande, 1879) from the Konéprésy Limestone, Konéprésy, Czechoslovakia (Havlíček, 1990).

Last: *Hadjyrhyncha hadyensis* Havlíček, 1979 from the Hady Limestone, near Brno, Czechoslovakia (Havlíček, 1979).

F. DOGDOIDAE Baranov, 1982

D. (PRA—EIF) Mar.

First: Probably *Corvinopugnax bimbax* Havlíček, 1990 from the Vinatice Limestone, Konéprésy, Czechoslovakia.

Last: *Selennjachia abaimovae* Baranov, 1982, Seymchan Formation, Selennjak Range, former USSR and *Tatjanka trigona* Baranov, 1982, Seymchan Formation, Ulakhan-Sis Range, former USSR.

F. WELLERELLIDAE Likharev in Rzhonsnitskaya, 1956

First: Possibly Yakutijaella dubatolovi Baranov, 1977, Nelchenian Horizon, Selennyahk Range, in the NE of former USSR (Baranov, 1977) or Tetratomia amanshauseri (Dahmer, 1942) from the EIF of the Rhineland (Havlíček, 1961).


F. CAMEROPHORINIDAE Rzhonsnitskaya, 1958
First: Camarophorina pachyderma (Quenstedt, 1871), EIF, Germany (Schmidt, 1941).

Last: Camarophorina bijugata (Schnur, 1851), GIV, Moravia (Schmidt, 1941).

F. ALLORHYNCHIIDAE Cooper and Grant, 1976

Last: Several allorhynchiids occur high in the Bell Canyon Formation and coeval units in west Texas, USA (Cooper and Grant, 1976a), for example, Allorhynchus venustulum Cooper and Grant, 1976, Ptilorhynchus delicaturn Cooper and Grant, 1976, Deltarina magnicostata Cooper and Grant, 1976, and Fascicosta longaeva (Girty, 1909).

F. ANTISTRIXIDAE Johnson, 1972


F. YUNNANELLIDAE Rzhonsnitskaya, 1959
First: Possibly Schnurella schnuri (de Verneuil, 1840), Gerolstein, the Eifel, Germany (Schmidt, in Williams et al., 1965).

Last: Possibly Paraphorhynchus elongatum Weller, 1914, lower Mississippian, Mississipi Valley Basin, USA (Weller, 1914).

F. TETRACAMERIDAE Licharew in Rzhonsntsikaya, 1956
First: Rotaia subtrigona (Meek and Worthen, 1860), lower Mississippian, Illinois, USA (Carter, 1990).

Last: Tetracamara subcuneata (Hall, 1858), middle Mississippian, Indiana, USA (Carter, 1990).

F. RHYNCHOTRETRADIDAE Licharew in Rzhonsntsikaya, 1956
C. (TOU)–P. (ROT) Mar.
First and Last: Possibly Gonophoria monstrosa Yanishevskiy, 1910, Lower Carboniferous to Lower Permian, south Urals, former USSR (Licharew, 1957).

F. CARDIARINIDAE Cooper, 1956
First: Loborina lobata Balinski, 1982, Upper Devonian, Cracow Region, Poland (Grant, 1988).

Last: Lamiarina iota Grant, 1988, Upper Permian, Hydra Island, Greece (Grant, 1988).

F. PONTISIIDAE Cooper and Grant, 1976
First: Pontisia spp. have been reported from Pennsylvanian rocks in North America, for example, the Gaptank Formation of west Texas (Cooper and Grant, 1972); however, Pontisia leonica (Martínez-Chacon, 1979) from the Cantabrian Mountains, Spain, may be oldest.

Last: A number of pontisiids are present in the Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1976a), for example, Aphaurosia scutata Cooper and Grant, 1976; A. rotundata Cooper and Grant, 1976; Antidericus bicostatus Cooper and Grant, 1976; A. scutillovanus (Shumard, 1860) and Lirellaria costellata Cooper and Grant, 1976.

F. AMPHIDELLIDAE Cooper and Grant, 1976
First: Amphipella arcaria Cooper and Grant, 1976, base of Cathedral Mountain Formation, west Texas, USA (Cooper, and Grant, 1976a).

Last: A. attenuata Cooper and Grant, 1976, Road Canyon Formation, west Texas, USA (Cooper and Grant, 1976a).

F. PETASMATHERIDAE Cooper and Grant, 1976
P. (GUA) Mar.
First: Iotina minuta Cooper and Grant, 1976, Bone Spring Limestone, west Texas, USA (Cooper and Grant, 1976a).

Last: Petasmatherus opulus Cooper and Grant, 1976, Word and Cherry Canyon Formations, west Texas, USA (Cooper and Grant, 1976a).

F. RHYNCHONELLIIDAE Gray, 1848
Tr. (ANS)–K. (MAA) Mar.
First: Piarorhynchia trinodosi (Bittner, 1890), Werfener Schiefer and Muschelkalk of numerous localities in the Alps (Bittner, 1890; Ager et al., 1972).


F. SEPTIRHYNCHIIDAE Muir-Wood and Cooper, 1951
J. (CLV-KIM?) Mar.


F. CRYPTOPORIDAE, Muir-Wood, 1955
First: Cryptopora antiqua Bittner and Pisera, 1979, MAA Chalk facies of Mielnik, eastern Poland (Bittner and Pisera, 1979). The second oldest is a record of Cryptopora, possibly C. parvillima (Sacco, 1902), Palaeocene (DAN), Crimea, former USSR (Popiel-Barczyk, 1980).

Extant

F. BASILIOLIDAE, Cooper, 1959
First: Probolarina chathamensis Lee, 1978, Upper Palaeocene–lower Eocene, Chatham Islands, New Zealand (Lee, 1978). Other early species include Eohemithyris alexi Hertlein and Grant, 1944, Domengine Formation (Eocene),
California, USA (Cooper, 1959) and Probolarina brevirostris
Cooper, 1988, Castle Hayne Formation (Eocene), North Carolina, USA (Cooper, 1988). The earliest record of the
genus Aetheia which is arguably attributable to this family, is from the Eocene of Otago, New Zealand (Lee, 1978).

**Extant**

F. HEMITHYRIDIDAE, Rzhonsnitzkaya, 1956

First: Protegulorhynchia meridionalis Owen, 1980, Lower CMP, James Ross Island, Antarctica (Owen, 1980); next earliest is
*Teugelorynchus boongerooensis* McNamara, 1983, Boongerood Greensand (Lower Palaeocene–Lower Eocene), Western Australia (McNamara, 1983).

**Extant**


First: May be an unnamed species of *Hispanirhynchia*, Eocene, Habana Province, Cuba (Cooper, 1959), but definitely *Sphenaria sicula* (Seguenza, 1870), Pliocene, Sicily (Davidson, 1870).


First: Probably *Erymnia polymorpha* (Massalongo, 1850), Lower Eocene, Spiliceko, Verona, Italy (Cooper, 1959).

Last: May be *Erymnia cubensis* Cooper, 1959, Eocene, Matanzas Province, Cuba (Cooper, 1959). Poor dating and correlation make exact determination of first and last species impossible. [DATH and CDP]

**Superfamily** STENOSCISMAATOIDEA Oehlert, 1887

F. ATRIBONIIDAE Grant, 1965

First: Protostrinion alticum Gratsianova, 1967, Lower Devonian, Altai Range, Russia, former USSR.

Last: Ussuricamara majchensis Koczyrkevicz, 1969, upper Permian, southern Primoria, Russia, former USSR.

F. STENOSCISMATIDAE Oehlert, 1887

First: Coledium rhomboidale (Hall and Clarke, 1894) from the Logansport Limestone, Indiana, Grant, 1965.

Last: Species of *Stenosisma* are widespread in uppermost Permian rocks; a distinctive species from Dzhulfian rocks of
Armenia may be youngest (Grant, 1970) or more probably unnamed species from the Changxing Formation, China, or from the Episkopi Limestone, Greece (Dr R. E. Grant, pers. comm.).

**Superfamily** RHYNCHOPOROIDAE Muir-Wood, 1955

F. RHYNCHOPORIDAE Muir-Wood, 1955

First: Probably *Rhynchopora? morini* (Drot, 1964), FAM, Morocco (Brunton, 1971).


F. ARATELLIDAE Erlanger, 1986


**Last:** *Aratella dichotomians* (Abrahamians, 1954) or *A. aratica* (Abrahamians, 1957), lower TOU, Transcaucus, former USSR (Erlanger, 1986).

**Superfamily** POSITION UNCERTAIN

F. DISPHENIIDAE Grant, 1988 P. (ZEC)

The placement of this aberrant group requires clarification; it may be a rhynchonellide or terebratulide.

First and Last: *Disphenia myiodes* Grant, 1988 from the Upper Permian rocks of Hydra Island, Greece (Grant, 1988).

**Order** ATRYPIDA Rzhonsnitzkaya, 1960
(see F. 22.4)

**Suborder** LISSATRYPIDINA Twenhofel, 1914

**Superfamily** LISSATRYPOIDEA Twenhofel, 1914

F. LISSATRYPIDAE Twenhofel, 1914


F. PROTOZYGIDAE Copper, 1986

First: *Manespira* sp., Crown Point Formation, New York, USA (Copper, 1986).

Last: *Idiospira taupoensis* Fu, 1982, upper Beiguo shan Formation, China (Copper, 1986).

F. GLASSIIDAE Schuchert and Le Vene, 1928


Last: *Peratos beirichi* (Kayser, 1872), ‘Rotheisenstein’, Brilon, Germany or possibly *P. drevermanni* Maillieux, 1936, Schistes de Matagne, Belgium (Copper, 1986).

**Suborder** ZYGOSPIRIDINA Waagen, 1883

**Superfamily** ZYGOSPIROIDEA Waagen, 1883

F. ZYGOSPIRIDAE Waagen, 1883

First: *Anazyga matutina* (Cooper, 1956), Little Oak Formation, Lower CRD, Alabama, USA


First: *Tuvaella rackovskii* Chernyshev, 1937, Elevest Formation, Altai, former USSR.

Last: *Tuvaella gigantea buchtarmensi* Kulikov and Kozlov, 1978, Sazhaev Formation, Altai, former USSR.

**Suborder** ATRYPIDA Boucot, Johnson and Staton, 1964

**Superfamily** ATRYPOIDEA Gill, 1871

F. ATRYPIDAE Gill, 1871
First: Protatrypa malmoensis Boucot et al., 1964, lower LLY, Norway or Syphatrypa honora Copper, 1982, Manitoulin Formation, Ontario, Canada.

Last: Spinatrypa frequens (Weller, 1907), Glen Park Limestone, Missouri, USA.

F. ATRYPINIDAE McEwen, 1939

First: Sulcospira parva (Rukavishnikova, 1970), Dulankara Formation, Kazakhstan, former USSR.

Last: Atrypina proswani Johnson et al., 1973, Fauna F, Nevada, USA.

Superfamily PUNCTATRYPITOIDEA Rzhonsnitskaya, 1960

F. PUNCTATRYPIDAE Rzhonsnitskaya, 1960

First: Punctatrypa tumidula (Khodalevich, 1951), Saud Formation, eastern Urals, former USSR.

Last: Punctatrypa siehlj Johnson, 1975, Greifensteinerkalk, Germany.

Suborder DAVIDSONIIDAE King, 1850

Superfamily DAVIDSONIOIDEA King, 1850

F. DAVIDSONIIIDAE King, 1850

First: Gracianella praecrista Johnson, 1975, Greifensteinerkalk, Germany. (Ivanova, 1956, Safonov Horizon, Podolia, former USSR.)

Last: Vagrania (Desatrypa), upper Permian, for example, *M. roemerii* Weller, 1914, Mississippi Basin, USA.

F. MERISTIDAE Hall and Clarke, 1895

First: Species of *Merista*, for example, *M. typa* Hall, 1859, are common in rocks of WEN age in the Western Hemisphere (Boucot et al., 1969) or *Diacamaropsis parva* (Thomas, 1926), St Clair Limestone, Arkansas, USA (Amsden and Barrick, 1988).

Last: Several species of *Meristina* have been reported from Lower Carboniferous rocks, for example, *M. roemerii* Weller, 1914, Mississippi Basin, USA.

Superfamily ATHYRIDIDOIDEA Davidson, 1881

F. DIDYMOTHYRIDIDAE Modzalevskaya, 1977

First: Glassina laeviuscula (Sowerby, 1839), WEN, Welsh Borderland, UK (Cocks, 1978) or *G. usitata* Modzalevskaya, 1979, Mukshinian Horizon, Podolia, former USSR (Modzalevskaya, 1979).

Last: Buchanathyris westoni Talent, 1956, Buchan Caves Limestone, Victoria, Australia (Talent, 1956).

Superfamily PALAFERELLOIDEA Spiestersbach, 1942

F. PALAFERELLIDAE Spiestersbach, 1942

First: Gruenwaldtia sp., Wellersbach Horizon, lower EIF, Eifel, Germany.


F. KARPINSKIIDAE Poulsen, 1943

First: Tectatrypa tectiformis (Chernyshev, 1893), Severural Horizon, PRD, eastern Urals, former USSR or *Eokarpinskia naliivikii* (Nikiforova, 1937), Svetloroz Formation, Kazakhstan, former USSR.

Last: Vagninia (Desatrypa) desquamata (Sowerby, 1840), upper GIV, Devon, England, UK, or *Vagninia (Desatrypa) globosa* (Leidhold, 1928), Massenkalk, Germany. [PC]

Order SPIRIFERIDA Waagen, 1883

Suborder ATRYPINIDINA Boucot, Johnson and Staton, 1964

Superfamily MERISTELLOIDEA Waagen, 1883

F. MERISTELLIDAE Waagen, 1883


Last: Several species of *Meristina* have been reported from Lower Carboniferous rocks, for example, *M. roemerii* Weller, 1914, Mississippi Basin, USA.

F. MERISTIDAE Hall and Clarke, 1895

First: Species of *Merista*, for example, *M. typa* Hall, 1859, are common in rocks of WEN age in the Western Hemisphere (Boucot et al., 1969) or *Diacamaropsis parva* (Thomas, 1926), St Clair Limestone, Arkansas, USA (Amsden and Barrick, 1988).

Last: Several species of *Meristina* have been reported from Lower Carboniferous rocks, for example, *M. roemerii* Weller, 1914, Mississippi Basin, USA.

Superfamily ATHYRIDIDOIDEA Davidson, 1881

F. DIDYMOTHYRIDIDAE Modzalevskaya, 1977

First: Glassina laeviuscula (Sowerby, 1839), WEN, Welsh Borderland, UK (Cocks, 1978) or *G. usitata* Modzalevskaya, 1979, Mukshinian Horizon, Podolia, former USSR (Modzalevskaya, 1979).

Last: Buchanathyris westoni Talent, 1956, Buchan Caves Limestone, Victoria, Australia (Talent, 1956).

F. ATHYRIDIDAE Davidson, 1881

First: Possibly *Apheathryis guyuanensis* Fu, 1982, middle Ordovician, NW China (Fu, 1982).

Last: Many species of *Cleiothyridina* are reported from the upper Permian, for example, *C. capillata* (Waagen, 1883), upper part of Chhidru Formation, west Pakistan (Grant, 1970).

F. SPIRIFERELLIDAE Grunt, 1965

First: *Meristella mitchiganeense* Grabau, 1910, Amherstberg Dolomite, Michigan, USA.

Last: *Spirigerella* spp., Mianwali Formation, Salt Range and Trans-Indus Ranges, west Pakistan (Grant, 1970).

F. XENOSARIIDAE Cooper and Grant, 1976

First and Last: *Xenosaria exotica* Cooper and Grant, 1976, Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1976a).

F. DIPLOSPIRELLIDAE Schuchert, 1894

First: *Meristella mitchiganeense* Grabau, 1910, Amherstberg Dolomite, Michigan, USA.

Last: *Spirigerella* spp., Mianwali Formation, Salt Range and Trans-Indus Ranges, west Pakistan (Grant, 1970).

F. XENOSARIIDAE Cooper and Grant, 1976

First and Last: *Xenosaria exotica* Cooper and Grant, 1976, Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1976a).

F. DIPLOSPIRELLIDAE Schuchert, 1894

First: *Meristella mitchiganeense* Grabau, 1910, Amherstberg Dolomite, Michigan, USA.

Last: *Spirigerella* spp., Mianwali Formation, Salt Range and Trans-Indus Ranges, west Pakistan (Grant, 1970).
### Animals: Invertebrates

**Superfamily** NUCLEOSPIROIDEA Davidson, 1881

F. NUCLEOSPIRIDAE Davidson, 1881

S. (WEN) – Tr. (RHT)

**First:** Nucleospira pisiformis Hall, 1859, upper Clinton Group, New York, USA (Dale, 1953).

**Last:** Nucleospira cunctata Cooper and Grant, 1976, Cathedral Mountain Formation, Texas, USA (Cooper and Grant, 1976a) or possibly Amphitomella hemisphaeroidica (Klipstein, 1843), RHT, Eastern Alps (Grunt, 1989).

**Suborder** RETZIIDINA Boucot, Johnson and Staton, 1964

**Superfamily** RETZIOIDEA Waagen, 1883

F. RETZIIDAE Waagen, 1883


**First:** Leptospira costata (Hall, 1859), New Scotland Formation, New York, USA (Boucot et al., 1969).

**Last:** Plectospira sexplicata (White and Whitfield, 1862), Chemung Group, New York and Iowa, USA (Grunt, 1989).

F. NEORETZIIDAE Dagis, 1962


**First:** Possibly Eumetria subtrigonalis (Stainbrook, 1947), Percha Shale, New Mexico and Arizona, USA (Grunt, 1989).

**Last:** Neoretzia superbescens (Bittner, 1890), RHT, Crimea and the Caucasus, former USSR (Dagis, 1962).

F. RHYNCHOSPIRINIDAE Schuchert and Le Vene, 1929


**First:** Possibly Homoeospirella? sp., LLY, Haverfordwest, Wales, UK (Temple, 1987).

**Last:** Rhynchospirina cf. haidingeri Barrande, 1879, Hlubocepy Limestone, Czechoslovakia (Havlíček, 1956).

**Superfamily** ATHYRISINOIDEA Grabau, 1931

F. ATHYRISINIDAE Grabau, 1931

S. (PRD) – Tr. (NOR) Mar.

**First:** Possibly S quamathayris glacialis Modzalevskaya, 1981, Skala rocks, Podolia (Grunt, 1989).

**Last:** Probably Misolia noetlingii (Bittner, 1890), Sumra Formation, Arabia (Hudson and Jefferies, 1961).

F. METATHRYRISINIDAE Wang et al., 1981

**Suborder** **DAYIIDINA** Waagen, 1883

**Superfamily** **DAYIOIDEA** Waagen, 1883

**F. DAYIIDAE** Waagen, 1883


**First:** Possibly *Cyclospira? longa* Cooper, 1956, basal Ardwell Group, Girvan, SW Scotland, UK (Williams, 1962).

**Last:** *Dayia bohemia* Bouček, 1940, Upper Silurian rocks, Estonia and Podolia, former USSR (Rubel, 1977).

F. **ANOPLOTHECIDAE** Schuchert, 1894


**First:** *Coelospira saffordi* Foerste, 1903, Brownsport Formation, Tennessee, USA (Boucot and Johnson, 1967).

**Last:** *Coelospira camilla* Hall, 1867, Bois Blanc Formation, Lancaster, USA (Boucot and Johnson, 1967).

F. **KAYSERIIDAE** Boucot, Johnson and Staton, 1964


**First:** *Kayseria lens* (Phillips, 1841), Middle Devonian, SW England, UK.
Suborder KONINCKINIDINA Davidson, 1853
Superfamily KONINCKINOIDEA Davidson, 1853
F. KONINCKINIDAE Davidson, 1853
Tr. (LAD)–J. (SIN) Mar.
First: Bittner (1890) described a suite of koninckinids from the St Cassian Beds of the Italian Dolomites including Koninckina amoena Bittner, 1890 and Koninckinella triassina Bittner, 1890.
Last: Several koninckinids, including Bittner, 1893 and (Dagis, 1972).

Superfamily CADOMELLOIDEA Schuchert, 1893
F. CADOMELLIIDAE Schuchert, 1893
First: Cadomella davidsoni (Eudes Deslongchamps, 1854) and C. moorei (Davidson, 1876), Liassic, Somerset, England, UK (Davidson, 1876).
Last: Cadomella davidsoni (Eudes Deslongchamps, 1854), Liassic, Normandy, France (Davidson, 1876).

Suborder THECIDEIDINA Elliott, 1958
Baker's (1990) detailed revision of the group and its assignment to the Spiriferida are followed herein.

Superfamily THECOSPIROIDEA Bittner, 1890
F. THECOSPIRIDAE Bittner, 1890
Tr. (RHT)–Rec. Mar.
First: Thecospira semseyi Bittner, 1890, CRN, Hungary (Dagis, 1972).
Last: Thecospira haidingeri (Suess, 1854), RHT, Northern Alps and Carpathians (Benigni and Ferliga, 1989).

F. THECOSPIRELLIDAE Dagis, 1972
Tr. (CRN–NOR) Mar.
First: Probably Thecospirella locziyi (Bittner, 1912), CRN, Lienz area, Southern Alps (Bittner, 1912).
Last: Bitternella bittneri Dagis, 1974, NOR, south-eastern Pamir (Dagis, 1974).

F. HUNGARITHECIDAES Dagis, 1972
Tr. (CRN–RHT) Mar.
First: Hungaritheca andreaei (Bittner, 1890), CRN, Hungary (Dagis, 1972).
Last: Pamirotheca aulacothyridiformis Dagis, 1974, RHT, south-eastern Pamir (Dagis, 1974).

Superfamily THECIDEOIDEA Gray, 1840
F. ENALLOTHECIDEIDAE Baker, 1983
First and Last: Enallothecidea pygmaea (Moore, 1861) from the Cotswold area of southern England, UK (Baker, 1983).
F. THECIDEELLIIDAE Elliott, 1958
Tr. (RHT)–Rec. Mar.
First: Moorellina prima Elliott, 1953, RHT, Hirtenberg, Austria (Elliott, 1953).

F. BACTRYNIIDAE Williams, 1965
Tr. (RHT) Mar.
First and Last: Bactrynum bicarinatum Emmrich, 1855, Kossener Schichten of Austria (Rudwick, 1968).
F. THECIDEIDAE Gray, 1840
Tr. (RHT)–Rec. Mar.
First: Davidsonella rhetaea (Zugmayer, 1880) from the Rhaetian rocks of Waldegg, Austria (Zugmayer, 1880). Extant

Suborder SPIRIFERIDINA Waagen, 1883
Superfamily CYRTIOIDEA Fredricks, 1919 (1924)
F. CYRTIIDAE Fredricks, 1919 (1924)
First: Iliella minima Rukavischinkova, 1980, Choparskij Horizon, northern part of the Dulankar Mountains, Kazakhstan, former USSR (Appollonov et al., 1980).
Last: Probably Punguispirifer interruptus (Barrandé, 1879), EIF, Czechoslovakia (Havlíček, 1971b).

F. AMBOCOELIDAE George, 1931
S. (WEN)–Tr. (SCY) Mar.
First: Boucot (1975) reported a species of Plicoplasia, Cape Phillips Formation, Canadian Arctic; otherwise Ambothyris praecox Kozlowski, 1929, Ukraine or possibly Ambocelia operculifera Havlíček, 1959, Bohemia, Czechoslovakia (Havlíček, 1959).

Superfamily SPIRIFEROIDEA King, 1846
F. DELTHYRIDIDAES Waagen, 1883
Last: Possibly Tylothyris clarksvillensis (Winchell, 1865) from middle Mississippian rocks from the midcontinent of North America and elsewhere (Carter, 1990).

F. MUCROSPIRIFERIDAE Pitrat, 1965
First: Mucrospirifer mucronatus (Conrad, 1841), Romney Formation, Maryland, USA (Vokes, 1957).

F. FIMBRISSIPRIFERIDAE Pitrat, 1965
First: Fimbriospirifer charybdis (Barrandé, 1879), lower Devonian, Bohemia, Czechoslovakia (Havlíček, 1959).
Last: Fimbriospirifer venustus (Hall, 1860), Hamilton Formation, New York, USA (Cooper, 1944).

F. SPINOCYRTIIDAE Ivanova, 1959
First: Spinostryx affinis (Fuchs, 1929), lower Siegenian, Belgium (Vandercammen, 1963).
Last: Spinostryx strunianus (Gosselet, 1879), Couches d’Etrœungt, France (Vandercammen, 1956).
F. COSTISPIRIFERIDAE Termier and Termier, 1949
First: Costispirifer arenosus (Conrad, 1841), Oriskany Group, Maryland, USA (Vokes, 1957).
Last: Possibly Eudoxina species, for example E. subrotunda from the English River Sandstone, Iowa, USA (Carter, 1960).

F. CYRTOSPIRIFERIDAE Termier and Termier, 1949
Last: Tipispirifer oppilatus Grant, 1976, Ko Muk, Thailand (Grant, 1976).

F. SPIRIFERIDAE King, 1846
(includes Neospiriferidae Termier, 1975)
First: May be Palaespirifer karagatschicus (Sverbiloava, 1963), Upper Devonian, Kazakhstan, former USSR (Martynova and Sverbiloava, 1968). But if Glyptospirifer belongs to this family, then Glyptospirifer chui Grabai, 1931 (Hou and Xian, 1975) and Glyptospirifer chui cyrtinaoides Xian, 1978, lower–middle Devonian, China (Hou, 1979) may be the oldest.

F. BRACHYTHYRIDIDAE Fredericks, 1919 (1924)
First: Possibly Brachythyriss talicensis Khodalevich, 1959, Bauxite deposits, Urals, former USSR (Khodalevich and Breivel, 1959); otherwise Brachythyriss bisbeensis Staintbrook, 1947 and B. putilla Staintbrook, 1947, Percha Shale, New Mexico and Arizona, USA (Staintbrook, 1947) and also B. melioplicata Martynova and Sverbiloava, 1968, from the Upper Devonian, Kazakhstan, former USSR.
Last: Purdonella oligosangonis Termier et al., 1974, Wardak, central Afghanistan (Termier et al., 1974).

F. SPIRIFERELLIDAE Termier, Termier, Lapparent and Marin, 1975
First: Probably Spiriferella neglecta (Hall, 1858) from the Keokuk Limestone, Mississippi Valley Basin (Weller, 1914).
Last: There are a number of upper Permian species of Spiriferella, for example, Spiriferella spp. from the Hachtel Limestone and the Stephens Formation, New Zealand (Waterhouse, 1968).

Superfamily RETICULARIOIDEA Waagen, 1883
F. RETICULARIIDAE Waagen, 1883
S. (WEN)—P. (KAZ) Mar.
First: Probably Reticularioidea silurica Strusz, 1982 or Vadum copipense Strusz, 1982, Australian Capital Territory (Strusz, 1982).

F. ELythididae Fredericks, 1924
First: Elita (Elytha) saffordi Hall, 1859, Oriskany Group, Pennsylvania, USA (Cleaves, 1939).


F. MARTINIIDAE Waagen, 1883
Last: Notospirifer excelsus Waterhouse, 1968, N. microspinus Waterhouse, 1968, Arthuroon Group, New Zealand (Waterhouse, 1968) or if Mentzela belongs to the family, the last are Triassic (RHT), Mentzela kawhiana Trechmann, 1918, M. cf. ampla Bittner, 1890, Hokonui Hills, Kawhia, New Zealand (Marwick, 1953).

F. XENOMARTINIIDA Havlicék, 1957
First: Proreticularia carens (Barrande, 1879), basal LUD, Czechoslovakia (Havlíček, 1950).
Last: Obesaria obesa (Barrande, 1848), EIF, Czechoslovakia (Havlíček, 1959).

F. ANOMALORIIDAE Cooper and Grant, 1976
P. (GUA) Mar.
First and Last: Anomaloria anomala Cooper and Grant, 1969, Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1969).

Suborder SPIRIFERINIDINA King, 1846
This suborder includes the punctate spiriferides probably derived polyphyletically from the impunctate spiriferide group.

Superfamily SPIRIFERINOIDEA Davidson, 1884
F. SPIRIFERINIDAE Davidson, 1884
C. (TOU)—J. (LIA) Mar.
Last: Callospiriferina tumidus (von Buch, 1836), Liassic, Morocco (Rousselle, 1977).

F. RETICULARINIDAE Cooper and Grant, 1976
First: Reticularina hueconiana Cooper and Grant, 1976, Huego Canyon Formation, west Texas, USA (Cooper and Grant, 1976b).
Last: Reticularina phoxa Cooper and Grant, 1976, Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1976b).

F. CRENISPIRIFERIDAE Cooper and Grant, 1976
First: Crenispirifer sagus Cooper and Grant, 1976, Bone Spring Formation, west Texas, USA (Cooper and Grant, 1976b).
Last: Crenispirifer jubatus Cooper and Grant, 1976, Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1976b).

F. PARASPIRIFERINIDAE Cooper and Grant, 1979
First: Paraspiriferina amoena Cooper and Grant, 1976, Neal
Ranch Formation, west Texas, USA (Cooper and Grant, 1976b).

Last: Paraspiriferina setulosa Cooper and Grant, 1976, Word Formation, west Texas, USA (Cooper and Grant, 1976b).


First: Sarganostega prisca Cooper and Grant, 1976, Bone Spring Formation, west Texas, USA (Cooper and Grant, 1976b).

Last: Sarganostega pressa Cooper and Grant, 1976, Bell Canyon Formation, west Texas, USA (Cooper and Grant, 1976b).


First: Probably Xestotrema pulchrum (Meek, 1860), Park City and Phosphoria formations, Rocky Mountains, USA (Cooper and Grant, 1976b).

Last: Arionthia lamaria Cooper and Grant, 1976, Carlsbad, Capitan and Bell Canyon formations, west Texas (Cooper and Grant, 1976b).


First and Last: Yangkoxia planofolida, Y. qieermaensis, and Y. zhijinaensis Xu and Liu, 1983, from the Middle Triassic rocks of the South Qilian Mountains, China (Xu and Liu, 1983).

Superfamily SYRINNOTHECOIDEA Waagen, 1883


Last: Possibly Psioidea australis (Trechmann, 1918), P. nelsonensis (Trechmann, 1918), and P. conjuncta (Hector, 1879), Balfour Group, Hokonui Hills, New Zealand (Marwick, 1953) or perhaps Flabellocyrtia flabellum Chorowicz and Termier, 1975, Svilaja, former Yugoslavia (Chorowicz and Termier, 1975).


First and Last: Suesia costata Eudes Deslongchamps, 1854, Liassic (Ducque, 1933) and Suesia liasiana Eudes Deslongchamps, 1854, Domerian, Morocco (Dubar, 1948).


First: Bashkiriia gemma Nalivkin, 1979, Lower Carboniferous, Urals, former USSR.

Superfamily SYRINGOTHyroidea Massa et al., 1975


First: Syringothyris spissus Glenister, 1955, Moogocor Limestone, Western Australia (Glenister, 1955).

Last: Paecelkamella teneicostata Termier, 1975, Wardak, central Afghanistan (Termier et al., 1974) or Licharewia kaniensis Kulikov and Stepanov, 1975, Kanin Peninsula, former USSR (Stepanov et al., 1975). [AL]

Order TEREBRATULIDA Waagen, 1883 (see Fig. 22.6)

Suborder CENTRONELLIDINA Stehli, 1965

Superfamily STRINGOCEPHALOIDEA King, 1850


Last: Notothyris warthi Waagen, 1882, upper Productus Limestone, Pakistan, and Cryptocanthia compacta White and St John, 1867, Permian, Caucasus, former USSR (Waagen, 1882; Licharew, 1936).


First: Prorensellaria nylanderi Raymond, 1923, Heldberg Formation, Maine, USA (Cloud, 1942). Waldheimia maivei Davidson, 1881, WEN, England, UK, is a spiriferid (Cloud, 1942). There are no terebratulids in the British succession below the Ludlow Bone Bed.

Last: Girtyella intermedia Wellers, 1911, Chester Formation, Illinois, USA (Cooper, 1944).

F. STRINGOCEPHALIDAE King, 1850 D. (GIV) Mar.

First: Subrenselladia clagoli (Hall, 1891), Hamilton Formation, Pennsylvania, USA.

Last: Stringocephalus burtini Defrance, 1825, Europe and North America. Several other genera and species extend to the top of the GIV (Cloud, 1942; Cooper, 1944).


First and Last: Megantesis suessi Drevermann, 1901, PRA–EMS of Europe (Cloud, 1942).

Suborder TEREBRATULIDINA Waagen, 1883

Superfamily DIELASMATIDAE Schuchert, 1913


First: Brachygyga pentameroides Kozlowski, 1929 and Podolella renisselaeroides Kozlowski, 1929, Borszczow Formation, Poland. Earliest of Cryptonella series (Crypotnellinae and Cranaeninae) is Cryptonella melonica (Barrande, 1847), Upper Konéprusy Limestone, Bohemia, Czechoslovakia (Weller, 1911; Cloud, 1942). The Cryptonella series should probably be separated from the Dielasmatinae proper; they are ubiquitous in the Carboniferous and Permian.

Last: Dielasias brevifilum Waagen, 1882 and Hemiptychina himalayensis Davidson, 1862, upper Productus Limestone, Pakistan (Waagen, 1882) and Dielasia elongatum (Scholeth, 1816), Magnessian Limestone, and Upper Zechezt, western Europe; these are all late members of the Dielasmatinae. Of the Cryptonella series, last is Heteroelasia schumardianum Girty, 1908, Permian, west Texas, USA (Cooper, 1944).

F. TEREBRATULIDAE Gray, 1840 Tr. (LAD)–Rec. Mar.
First: ‘Terebratula’ *suborbieularis* Munster, 1841, ‘*T*. capsella’ Bittner, 1890, St Cassian Beds, Italian Alps (Bittner, 1890). Also *Plectochoncha aequiplicata* (Gabb, 1864), Triassic, Nevada, USA (Cooper, 1944).

**Extant**

**Comment:** ‘*Terebratula*’ *larimontana* Bittner, 1890, Muschelkalk, central Europe, is earlier, but is inadequately known (Bittner, 1890).


First: *Orthotoma liasina* (Friren, 1896), margaritatus Zone, western Europe (Muir-Wood, 1896).

Last: *Orthotoma spinatii* Rau, 1905, spinatum Zone, western Europe.


First and Last: *Cheniothyris morieri* (Eudes Deslongchamps, 1852), Europe, mainly England and France (Buckman, 1918).


First: *Dictyothyris coarctata* Parkinson, 1811, Jurassic, England, UK (Buckman, 1918).

Last: *Dictyothyris baudens* (Rollier, 1918), Jurassic, Europe (Makridin, 1964).


First and Last: *Tegulithyris bentleyi* (Davidson, 1851), Europe, mainly England, UK.


First: *Linguithyris bifida* (Rothpletz, 1886), Jurassic, western Europe (Buckman, 1914).

Last: *Pygites diphyoides* (d’Orbigny, 1849), Europe, mainly France and Switzerland, the Arctic and North Africa.

F. **DYSCOLIIDAE** Fischer and Oehlert, 1891 J. (CLV)–Rec. Mar.


**Extant**

F. **DIENOPIDAE** Cooper, 1983 J. (CLV) Mar.

First and Last: *Dienopterus trigera* (Eudes Deslongchamps, 1856), Europe, mainly France.

F. **HESPERITHYRIDIDAE** Cooper, 1983 J. (PLB) Mar.

First and Last: *Hesperithyris sinuosa* (Dubar, 1942), Domerian, Morocco.


First and Last: *Muirwoodella muirwoodae* Tchorschhevsky, 1974, Transcarpathians and former USSR.


First: *Viligothyris viligaensis* Dagis, 1968, northern Siberia, former USSR.

Last: *Bejrutella bejrutica* Tchorschhevsky, 1972, Lebanon and Syria.

**Superfamily** **CANCELLOTHYRIDOIDEA** Thomson, 1926


First: *Terebratulina elongata* Davidson, 1874, Greensand, England, UK.

**Extant**

**Suborder** **TEREBRATELLIDINA** Muir-Wood, 1955

**Superfamily** **ZELLERIOIDEA** Allan, 1940

F. **ZELLERIIDAE** Allan, 1940 Tr. (CRN)–K. (ALB) Mar.

First: *’Terebratula’ juliea* Bittner, 1890, *’T.’ paroniea* Tommasi, 1887, and *’T.’ woehrmanniana* Bittner, 1890, Carditaschichten, and *Camerothyris ramosauri* Suess, 1855, the Alps (Bittner, 1890).


First: *Apothyris* sp., Marrat Formation, Saudi Arabia (Cooper, 1989).

Last: *Apothyris abberans* Cooper, 1989, Jurassic, Saudi Arabia (Cooper, 1989).

**Superfamily** **TEREBRATELLOIDEA** King, 1850

F. **DALLINIDAE** Beecher, 1895 Tr. (NOR/RHT)–Rec. Mar.

First: *Eodallina peruviana* Elliott, 1959, Cerro de Pasco, Peru.

**Extant**

F. **MEGATHYRIDIDAE** Dall, 1870 K. (CEN)–Rec. Mar.


**Extant**


First: *Zittelina orbis* (Quenstedt, 1858), White Jura, Westphalia, Germany (Owen, 1980).


First: *Waconella wacoensis* (Roemer, 1852), Comanchean, Duck Creek Formation, Texas, USA (Owen, 1970).

**Extant**

F. **TEREBRATELLIDAE** King, 1850 K. (ALB)–Rec. Mar.

First: *Australiareulula artesiana* Elliott, 1960, Oodnadata, South Australia.

**Extant**


First: *Platidia eretaesa* Weller, 1907, New Jersey, USA.

**Extant**

F. **KRAUSSINIDAE** Allan, 1940 T. (Mio.)–Rec. Mar.

First: *Megerlia obita* (Michelotti, 1839), north Italy.

**Extant**

[Stefan]
Fig. 22.6

PRECISE POSITION UNCERTAIN
F. TROPIDOLEPTIDAE Schuchert, 1896

According to Jaanusson (1971) this group possesses cyrtomatodont teeth which, together with the presence of a loop, indicate a close affinity with the terebratulides, where it is better accommodated.

First: Tropidoleptus sp., LOK, Annapolis Valley, Nova Scotia, Canada (Boucot et al., 1969).

Last: Tropidoleptus carinatus (Conrad, 1839), Chemung Group, Chemung, New York, USA (Isaacson and Perry, 1977).

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The Phoronida are a phylum of tube-dwelling, vermiform lophophorates regarded as close relatives of brachiopods and bryozoans. Although cosmopolitan in their present-day distribution, only about 10 or 11 species distributed between two genera (*Phoronis, Phoronopsis*) are recognized (see Emig, 1982, 1985). Phoronids have no mineralized parts and are devoid of a body fossil record. However, living phoronids either burrow into soft sediment or bore into hard substrates, and various fossil burrows and borings have been attributed, with varying degrees of confidence, to the activities of phoronids. The range is plotted on the first bryozoan chart (Fig. 24.1) (see Chapter 24).

No family-level classification exists.

**Phylum** PHORONIDA Hatschek, 1888

??PC (RIP)??D. (SIG)–Rec. Mar.

First: **Skolithos**, Riphean, North Australia (Glaessner, 1969); "Formengruppe B" boring of Jux and Strauch (1965), Siegenian, Germany.

Comments: **Skolithos** Haldemann, 1840, a simple straight burrow, may be partly attributable to the Phoronida but, as Hantzschel (1975) emphasizes, this ichnogenus requires revision. Various borings can be attributed with more certainty to the Phoronida (see Voigt, 1975). While the earliest example may be an unnamed Devonian boring, the post-Palaeozoic ichnogenus **Talpina** von Hagenow, 1840 has been shown by Voigt (1975) to resemble closely the borings of modern *Phoronis ovalis*.

**REFERENCES**


BRYOZOA

P. D. Taylor

The Bryozoa are an exclusively colonial phylum of coelomate metazoans, closely related to brachiopods and phoronid worms. Most present-day bryozoans are marine and the majority of these secrete mineralized skeletons of calcium carbonate, usually calcite. As sessile members of the benthos, bryozoans have a good fossilization potential and are represented in the fossil record by an estimated 20000 or more species. Unfortunately, the taxonomy and stratigraphical distribution of fossil bryozoans are both poorly known. This compilation must therefore be treated as very provisional; it is no more than a starting point for subsequent improvement. Major problems inherent in the compilation include:

1. Uncertain taxonomic status of families. Relatively few bryozoan families are defined rigorously as monophyletic clades using autapomorphies. A great many are likely to be paraphyletic or even polyphyletic groupings.
2. Subjectivity of taxonomic rank. There is little or no consistency in what constitutes a family, either within or between orders of bryozoans.
3. Stratigraphical range uncertainty. Many fossil bryozoan faunas have yet to be adequately described, and so family ranges are likely to be underestimated. Furthermore, difficulties exist in dating some faunas, especially for the Upper Palaeozoic.

Ryland (1982) provides the most up-to-date family-level classification of living bryozoans. There is no equivalent work for extinct families; the original bryozoan Treatise (Bassler, 1953) has been revised only in part (Boardman et al., 1983).

The general lack of comprehensive monographic literature (cf. faunal studies) means that it is impossible to supply information about the presence/absence of families in intervening stages between their first and last occurrences.

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Class PHYLACTOLAEMATA Allman, 1856

This is a small class of exclusively freshwater bryozoans which lack mineralized skeletons. Only one phylactolaemate body fossil has been reported — Plumatellitites proliferus Fric, 1901 from the Cenomanian of Bohemia — but this indistinct fossil shows no certain phylactolaemate features (Mundy et al., 1981). However, all modern phylactolaemates produce chitinous resting bodies called statoblasts which are resistant and should have a reasonable fossilization potential. Until recently, the oldest statoblasts recorded were from the ‘late Tertiary’ of Arctic Canada. Apparent statoblasts have now been described by Vinogradov (1985) from the Jurassic of the former USSR, and by Jell and Duncan (1986) from the Cretaceous of Australia. If phylactolaemates are a primitive bryozoan class, as is often believed, finds of statoblasts from older rocks might be anticipated.

F. PLUMATELLIDAE Allman, 1856

First: Plumatella mongoliensis Vinogradov, 1985, Lower or Middle Jurassic, Jargalang Group, Jargalang, Mongolia; P. sibiriensis Vinogradov, 1985, P. sp., Lower or Middle Jurassic, Ichetuya Group, Novospasskoe settlement, Mukhor–Shibirskii region, Buryat, former USSR; P. sedimentata Vinogradov, 1985, Lower or Middle Jurassic, Cheremkovka Group, Irkutsk District, Olonkovsk region, Ust-Balei, former USSR.

Extant

F. LOPHOPODIDAE Rogick, 1935 Extant

F. CRISTATELLIDAE Allman, 1856

First: Cristatella mucedo Cuvier, 1798, Beaufort Formation, Arctic Canada (see Kuc, 1973; Matthews et al., 1990).

Extant

F. FREDERICELLIDAE Hyatt, 1868 Rec.

Order CTENOSTOMATA Busk, 1852
Ctenostomes are a primitive paraphyletic group of gymnolaemate bryozoans which lack mineralized skeletons. Most modern ctenostomes are marine, but some are inhabitants of brackish water or fresh water (see d’Hondt, 1983 and Hayward, 1985 for identification guides to modern taxa). The majority of families are unrepresented in the fossil record. However, preservation of ctenostomes as fossils can occur in two ways: some species are represented by the borings that they excavate in calcareous substrata (see Pohowsky, 1978); non-boring species can be preserved as natural moulds on the underside of oysters, serpulid worms or other organisms which have overgrown them ('bioimmuration', see Taylor, 1990). Unfortunately, a dual nomenclature has developed for boring ctenostomes; certain palaeontologists regard them as ichnofossils, whereas others treat them as body fossils because the borings accurately reproduce the external shapes of the zooids.

**Fig. 24.1**

| JURASSIC | | | | | | | CRETACEOUS | | | | | | | TERTIARY | | | | | | | QU. | HOL | PLE | | | | | | PLI | 3 | 15 | | | | | | UMI | 13 | | | | | | MMI | 13 | | | | | | LMI | 13 | | | | | | CHT | 13 | | | | | | RUP | 13 | | | | | | PRB | 17 | | | | | | BRT | 17 | | | | | | LUT | 32 | 37 | | | | | | YPR | 44 | 51 | | | | | | THA | 43 | | | | | | DAN | 43 | | | | | | MAA | 43 | | | | | | CMP | 43 | | | | | | SAN | 43 | | | | | | CON | 43 | | | | | | TUR | 43 | | | | | | CEN | 43 | | | | | | ALB | 43 | | | | | | APT | 43 | | | | | | BRM | 43 | | | | | | HAU | 43 | | | | | | VLG | 43 | | | | | | BER | 43 | | | | | | TTH | 43 | | | | | | KIM | 18 | | | | | | OXF | 6 | | | | | | CLV | 14 | | | | | | BTH | 14 | | | | | | BAJ | 14 | | | | | | AAL | 14 | | | | | | TOA | 12 | | | | | | PLB | 12 | | | | | | SIN | 12 | | | | | | HET | 12 | | | | | | | F. BENEDENIPORIDAE Delage and Hérouard, 1897 | Extant | Mar. |
| | | | | | | | | | | | | | | | | | F. HISLOPIIDAE Jullien, 1885 | Extant | FW |
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| | | | | | | | | | | | | | | | | | F. FLUSTRELLIDRIDAE Bassler, 1953 | Extant | Mar. |
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| | | | | | | | | | | | | | | | | | F. PALUDICELLIDAE Allman, 1844 | Extant | FW |
| | | | | | | | | | | | | | | | | | F. ARACHNIDIIDAE Hincks, 1880 | Tr. (LAD)–Rec. | Mar./FW |
**Bryozoa**

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<th>TRIASSIC</th>
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**Key for both diagrams**

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<td>2. Plumatellidae</td>
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<td>3. Cristatellidae</td>
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<td>11. Terebriporidae</td>
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<td>12. Penetantiidae</td>
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<td>CHEILOSTOMATA:</td>
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<td>ANASCA</td>
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<td>15. Aeteidae</td>
<td>43.</td>
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<td>16. Scrupariidae</td>
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<td>22.</td>
<td>17. Membraniporidae</td>
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<td>18. Electriidae</td>
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<td>28.</td>
<td>23. Calloporidae</td>
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**Fig. 24.1**

**Extant**

F. VICTORELLIDAE Hincks, 1880 **Extant** Mar./FW

F. PANOLICELLIDAE Jebram, 1985 **Extant** Mar.

F. SUNDANELLIDAE Jebram, 1973 **Extant** Mar.

F. MONOBRYOZONTIDAE Remane, 1936 **Extant** Mar.

F. AETHOZOONTIDAE d'Hondt, 1983 **Extant** Mar.

F. PACHYZOONTIDAE d'Hondt, 1983 **Extant** Mar.

F. VALKERIIDAE Hincks, 1880 **Extant** Mar.

F. MIMOSELLIDAE Hincks, 1877 **Extant** Mar.

F. TRITICELLIDAE Sars, 1874 **Extant** Mar.

F. BATHYALOZOONTIDAE d' Hondt, 1975 **Extant** Mar.

F. FARELLIDAE d'Hondt, 1983 **Extant** Mar.

F. AEVERRILLIIDAE Jebram, 1973 **Extant** Mar.

F. HYPOPHORELLIDAE Prenant and Bobin, 1956 **Extant** Mar.
F. VESICULARIIDIACEAE Hincks, 1880  Extant  Mar.
First:  Immengentia cruciata (Mägdefrau, 1937), Eisenerz-konglomerat des Mittelsantons, Lengede-Broistedt, Peine, Niedersachsen, Germany.
Comments: Monogeneric.
First:  Ropalonaria venosa Ulrich, 1879, Richmond Group, Ohio and Indiana, USA.
First:  Orbignyopora? capillaris (Dollhus, 1877), Rochester Limestone, Lockport, New York State, USA.
Last:  O. archiaci (Fischer, 1866), Astian, Italy (Pohowsky, 1978, p. 59).
Comments: Monogeneric.
Comments: Monogeneric.
First:  Haimeina michelini (Terquem, 1855), Kòssener Schichten, Marmorgraben bei Mittenwald, Germany (Pohowsky, 1978, p. 90).  Extant
Last:  C. lagaijii Pohowsky, 1978, Kaliman, Muddy Creek, Victoria, Australia.
Comments: Monospecific.

✓  Order CHEILOSTOMATA Busk, 1852
Cheilostomes are a seemingly monophyletic order of gymnolaemate bryozoans, which are mostly marine but also include a few brackish water species. All cheilostomes have mineralized skeletons of calcite or, less commonly, aragonite or a calcite:aragonite mix. In some families, however, mineralization is slight.
Cheilostomes are traditionally divided into two suborders: Anasca and Ascophorina. These are best regarded as organizational grades. Anascans are a primitive and paraphyletic group from which ascophorans have probably been derived polyphyletically. Detailed phylogenetic relationships are poorly understood throughout the order, and classification is in a state of flux (see Gordon, 1989). Hence the validity and ranges of many families must be viewed as highly tentative.

Suborder ANASCA Levinsen, 1909
Anascans are a paraphyletic grouping of primitive cheilostomes without an ascus or equivalent structure. They are variously related to the more advanced ascophoran grade cheilostomes.

First:  Aetea truncata (Landsborough, 1852), Lower Pliocene, Crete.
Extant  Comments: Monogeneric. Pre-Pliocene records of this lightly mineralized family are erroneous or very doubtful; the only certain fossil examples are those preserved by bioimmuration (Voigt, 1983). However, the family is often regarded as primitive among cheilostomes, suggesting that older examples may be forthcoming.
Extant
F. EUCRATEIDAE Johnston, 1838  Extant  Mar.
F. LABIOSTOMELLIDAE Silén, 1942  Extant  Mar.
First:  Biflastra savartii texturata (Reuss, 1848), PRB, Vicenza Province, Italy (Braga and Barbin, 1988).
Extant  Comments: The Membraniporidae, as here understood, are distinguished by the presence of a twinned ancestrula. As the ancestrula is seldom preserved or described in fossil material, ascertaining the range of the family is difficult. Membranipora s.s. is a lightly calcified epiphyte of algae and has no certain fossil record; most of the numerous fossil species assigned to Membranipora belong in families such as the Calloporidae.
Extant  Comments: A primitive paraphyletic family of malacostegan cheilostomes.
F. TENDRIDA Stach, 1937  Extant  Mar.
<table>
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<tr>
<th>Family</th>
<th>Genus</th>
<th>Subfamily</th>
<th>Notes</th>
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<tbody>
<tr>
<td>First:</td>
<td>Stichominaspora oceani (d’Orbigny, 1852), Lower CEN, Le Mans and Lamnay, Sarthe, France (Taylor, 1988, fig. 6d); Stichominaspora sp., lower CEN, Mülheim-Ruhr, Germany (Voigt, 1991).</td>
<td>Extant</td>
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<td>Last:</td>
<td>Poricellaria sp., upper MAA, Westmoreland Parish, Jamaica (Cheetham, 1968a).</td>
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<td>Comments:</td>
<td>Monogeneric.</td>
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<td>First:</td>
<td>Onychocellidae sp., upper MAA, Westmoreland Parish, Jamaica (Cheetham, 1968a).</td>
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<td>Comments:</td>
<td>Monogeneric.</td>
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<td>First:</td>
<td>Thalamoporella bifolia (Ziko, 1985, S. delicata Ziko, 1985, S. obtusa Ziko, 1985, Qarara Formation, Gabal Qarara, Maghagha, Egypt.</td>
<td>Extant</td>
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<td>Last:</td>
<td>Thalamoporella sp., lower CEN, Lamnay, Sarthe, France (Taylor, 1988, fig. 6c); lower CEN, Mülheim-Ruhr, Germany.</td>
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<td>Comments:</td>
<td>Monogeneric.</td>
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<td>First:</td>
<td>Acoscinopleura (?) vinocinensis (Filliozat, 1908), SAN (testudinarius Zone), Vendôme, France (Voigt, 1956).</td>
<td>Extant</td>
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<td>Last:</td>
<td>Coscinopleura digitata (Morton, 1834), Vincentown Limesand, New Jersey, USA.</td>
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<td>Comments:</td>
<td>Monogeneric.</td>
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<tr>
<td>First:</td>
<td>Macropora aqua Canu and Bassler, 1920, Bryozoan Bed at base of Aqua Formation, Upper Marlboro, Maryland, USA.</td>
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<td>Last:</td>
<td>Monogeneric.</td>
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<td>Comments:</td>
<td>Monogeneric.</td>
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Animals: Invertebrates

First: *Setosinella prolifica* Canu and Bassler, 1933, Vincentown Limesand, New Jersey, USA. 


First: *Setosellina houseauxi* (Meunier and Pergens, 1886), Calcaire de Mons, Mons, Belgium (Voigt, 1987). Extant


First: *Cothurnicella* sp., BRT, Biarritz, France (Debourle, 1975). Extant

Comments: Otherwise known as Cothurnicellidae Bassler, 1935.

F. ALYSIDIIDAE Levinsen, 1909 Extant Mar.

First: *Catenariopsis morningtoniensis* Maplestone, 1899, from the Oligocene (Balcombian) of Victoria, Australia, is now regarded as a chaperiid (D. P. Gordon, pers. comm.).


First: *Euritina eurita* (d’Orbigny, 1851), CEN, France (Voigt, 1981, table 1). Extant


First: *Eoscrupocellaria cretae* (Marsson, 1887), Lower MAA, Rügen, Germany (see Voigt, 1991). Extant

Comments: Equivalent to Scrupocellariidae Levinsen, 1909.

F. EUOPLOZOIDAE Harmer, 1926 Extant Mar.

First: *Euritina eurita* (d’Orbigny, 1851), CEN, France (Voigt, 1981, table 1). Extant


First: ‘Epistomiid? gen. and sp. indet’, YPR, DSDP Site 308, Koko Seamount, Pacific Ocean (Cheetham, 1975); *Synnotum* sp., Tuban Formation (Lower Miocene, Tertiary e5), Prupuh, East Java. Extant


First: *Calpidopora diota* Lang, 1916, Korycaner Schichten, Kaňík, Czechoslovakia.

Last: *Auchenopora guttur* Lang, 1916, Danian, Faxe, Denmark.


Last: *Auchenopora guttur* Lang, 1916, Danian, Faxe, Denmark.


Comments: Monospecific.


Last: *Auchenopora guttur* Lang, 1916, Danian, Faxe, Denmark.


First: *Calpidopora diota* Lang, 1916, Korycaner Schichten, Kaňík, Czechoslovakia.

Last: *Auchenopora guttur* Lang, 1916, Danian, Faxe, Denmark.


First: *Lagynopora pediculus* (Reuss, 1874), Ober-Planer, Strehlen, Dresden, Germany.


First: *Sandalopora gallica* Lang, 1916, Turonian, Lavardin, Loir-et-Cher, France.

Last: *Dishelopora claviceps* (Brydone, 1910), *Marsupites* Zone, England, UK.


Last: *Dishelopora claviceps* (Brydone, 1910), *Marsupites* Zone, England, UK.


First: *Taractopora confusa* Lang, 1916, cortestudinarium Zone, southern England, UK.

Last: *T. ernsti* Voigt and Schneemilch, 1986, lower CMP, Lägerdorf, Germany.


First: *Taractopora confusa* Lang, 1916, cortestudinarium Zone, southern England, UK.

Last: *T. ernsti* Voigt and Schneemilch, 1986, lower CMP, Lägerdorf, Germany.

F. DISHELOPORIDAE Lang, 1916 K. (CON–SAN) Mar. (see Fig. 24.2)


Last: *Dishelopora claviceps* (Brydone, 1910), *Marsupites* Zone, England, UK.


Last: Geisopora protecta Lang, 1916, MAA, Rügen, Germany.

F. CRIBRILINIDAE Hincks, 1880

First: Mumiella mumia (d’Orbigny, 1851), SAN, Sainte-Colombe, Manche, France. Extant

Comments: The relationship between the extant Cribrilinidae and the various Cretaceous/Palaeocene families of cribrimorphs listed above (Otoporidae to Rhacheoporidae) is unclear and awaits further study. In the meantime, the fossil families are retained as they reflect the high species diversity undoubtedly attained by cribrimorphs in the Late Cretaceous.

Suborder ASCOPHORA Levinsen, 1909

Ascophorans are generally regarded as a polyphyletic, grade grouping of cheilostomes with calcified frontal shields covering a space (ascus or equivalent structure) into which sea-water enters as part of the hydrodynamic mechanism of tentacle protrusion. Although progress in distinguishing separate groups within the Ascophora is beginning to be made (e.g. Voigt, 1991; Gordon, 1989), the relationships between these groups and their anascan sister groups are still poorly understood. Therefore, the Ascophora are retained as a taxonomic entity for the present. Families are arranged according to the scheme adopted by Gordon (1989 and pers. comm., 1990), except that the cribrimorphs s.s. are retained within the Anasca.

As most ascophorans are relatively heavily calcified, they have a good preservation potential. However, some taxa have aragonitic skeletons prone to diagenetic dissolution, while others inhabit the deep sea and are seldom or never found fossil.

F. EUTHYROIDIDAE Levinsen, 1909 Extant Mar.
Monogeneric for Euthyroides Harmer, 1903.

F. PLATYGLENIDAE Mersson, 1887

First: Platyglena culveriana (Brydone, 1930), Chalk (planus Zone), Isle of Wight, England, UK; P. altonensis (Brydone,
Animals: Invertebrates

472

1930), Chalk (planus Zone), Hampshire, England, UK (see Voigt, 1991).

**Last:** *P. ocellata* Marsson, 1887, DAN, Germany.


**First:** *Bifaxaria* sp. 1’, *Bifaxaria* sp. 2’, Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975; see also Gordon, 1988).

**Extant**


**First:** *Vittaticellid new genus*, Upper Palaeocene, DSDP Site 117, Rockall, North Atlantic (Cheetham and Håkansson, 1972).

**Extant**


**First:** *Ditaxiporina labiatum* Canu, 1910, Auversian, Biarritz, France.

**Last:** *D. bifenestrata* Cheetham, 1963, Vicksburgian, Chicksawhay Limestone, St Stephens, Alabama, USA.


**First:** ?Savignyella? sp., Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975). Extant


**First:** *Eurystomella foraminigera* (Hincks, 1883), Mangapanian, Waipukurau, Hawkes Bay, New Zealand (Brown, 1952, p. 286). Extant

Comments: Monogeneric for *Eurystomella* Levinsen, 1909.


**First:** *Petalostegus tenuis* (Mapleston, 1899), *Chelidozoum vespertilio* (MacGillivray, 1895), Balcombian, Muddy Creek, Victoria, Australia (Gordon and d’Hondt, 1991).

**Extant**


**First:** *Boreasina nowickii* Voigt, 1991, CON, St Christophe, Indre et Loire, France (see Voigt, 1991).

**Extant**


**First:** *Tremoschizodon porcellarioides* (Hope, 1863), Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975).

**Extant**


**First:** *Celleporaria granulosa* (Canu and Bassler, 1920), Claibornian, Cook Mountain Formation, Caldwell Co., Texas, USA.

**Extant**


**First:** *Metrarabdotos micropora* (Gabb and Horn, 1862), Upper Eocene, Shubuta Clay, Clarke Co., Mississippi, USA (Cheetham, 1968b).

**Extant**


**First:** *Staurosteginopora irregularis* (d’Orbigny, 1852), Santonian, Villedieu, Loir et Cher, France (Voigt, 1991).

**Extant**


**First:** *Exechonella? sp. 1’,* *Exechonella? sp. 2’,* Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975); *Exechonella* sp., Selsey Formation (Upper Bracklesham Beds), Sussex, England, UK (Cheetham, 1966).

**Extant**


**First:** *Actisecidae? n. gen. 1n. sp.’, *‘Actisecidae? n. gen. 2n. sp.’, Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975).

**Extant**

Comments: Monogeneric for *Actisecos* Canu and Bassler, 1927.


**First:** *Bitecipsa lineata* MacGillivray, 1895, Janjkian, Gellibrand, Victoria, Australia. Last: *Bitecipsa lineata* MacGillivray, 1895, Bairnsdalian, Bairnsdale, Victoria, Australia.


**First:** *Cryptostomella-like forms*, SAN, ?locality (Voigt, 1991).

**Extant**

**F. UMBONULIDAE** Canu, 1904 T. (LUT)—Rec. Mar.

**First:** *Umbonula leda* (d’Orbigny, 1851), LUT, Parnes, France (Canu, 1907–10). Extant

Comments: The slightly older *U. calcariformis* Gregory, 1893, from the British YPR, is probably not an umbonulid.

**Extant**


**First:** *Cellopapar graminola* (Canu and Bassler, 1920), Claibornian, Cook Mountain Formation, Caldwell Co., Texas, USA.

**Extant**


**First:** *Metrarabdotos micropora* (Gabb and Horn, 1862), Upper Eocene, Shubuta Clay, Clarke Co., Mississippi, USA (Cheetham, 1968b).

**Extant**


**Extant**

Comments: An Upper Oligocene–Lower Miocene species, described as *Porella operculata* Canu and Bassler, 1935, from Victoria, Australia, may perhaps belong to this family (Winston, 1983).

**Extant**


**First:** *Celleporaria granulosa* (Canu and Bassler, 1920), Claibornian, Cook Mountain Formation, Caldwell Co., Texas, USA.
**F. HINCKSIPORIDAE** Powell, 1968  
**Extant**  
**Mar.**

*Comments:* Monospecific for *Hincksipora spinulifera* (Hincks, 1889).

**F. PSEUDOLEPRAILIIDAE** Silén, 1942  
**Extant**  
**Mar.**

*Comments:* Monospecific for *Pseudolepralia ellisinae* Silén, 1942.

**F. ADEONIDAE** Jullien, 1903  
T. (YPR)-Rec.  
**Mar.**

*Extant*

**F. CHLIDONIOPSIDAE** Harmer, 1957  
**Extant**  
**Mar.**

*Comments:* Monogeneric for *Chidoniopsis* Harmer, 1957.

**F. EUTHYRISELLIDAE** Bassler, 1953  
T. (?RUPI?CHT)-Rec.  
**Mar.**

*First:* *Quadriscutella burlingtoniensis* (Waters, 1882), *Q. punctata* Bock and Cook, in press, Oligocene, Victoria, Australia.  
*Extant*

**F. PORINIDAE** d’Orhigny, 1852  
K. (CMP)-Rec.  
**Mar.**

*First:* *Porina aftonensis* Brydone, 1930, quadratus Zone Chalk, Hampshire, England, UK.  
*Extant*

**F. NEPHROPORIDAE** Marsson, 1887  
K. (MAA)  
**Mar.**

*First and Last:* *Nephropora elegans* Marsson, 1887, MAA, Rügen, Germany.  
*Extant*

**F. STOMACHETOSELLIDAE** Canu and Bassler, 1917  
K. (MAA)  
**Rec. Mar.**

*First:* *Taenioporella articulata* (Voigt, 1930), lower MAA, Rügen, Germany (Voigt, 1987, p. 90).  
*Extant*

**F. GIGANTOPORIDAE** Bassler, 1935  
T. (DAN)  
**Rec. Mar.**

*First:* *Tessaradoma rossica* Favorskaja, 1970, DAN, Crimea, former USSR.  
*Extant*

**F. CHEILOPORINIDAE** Bassler, 1936  
T. (DAN)  
**Rec. Mar.**

*First:* *Cianotremella gigantea* Canu, 1911, Roca Formation, Argentina (Voigt, 1985, p. 334).  
*Extant*

**F. SCHIZOPORELLIDAE** Jullien, 1883  
T. (YPR)-Rec.  
**Mar.**

*First:* ‘Schizoporellidae gen. et sp. indet.’, Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975).  
*Extant*

*Comments:* *Schizoporella carinata* Hagenow from the Campanian is a hippothoid of the genus *Boreasina* (Voigt and Hillmer, 1984), and *Systenostoma* Marsson from the CMP-MAA is not a schizoporellid, according to Voigt (1985).

**F. LACERNIDAE** Jullien, 1888  
T. (PRB)-Rec.  
**Mar.**

*Extant*

**F. SMITTINIDAE** Levinsen, 1909  
T. (YPR)-Rec.  
**Mar.**

*First:* ‘Smittinid n. gen.? n. sp.’, Ypresian, DSDP Site 308, Koko Seamount, Pacific (Cheetham, 1975); *Porella* sp., ‘Smittinid n. gen.? aff. Smittinid n. gen.? n. sp. Cheetham’, ‘Smittinidae n. gen.? n. sp.’, DSDP Site 246, Indian Ocean (Labracherie, 1975).

**F. PETRALIELLIDAE** Harmer, 1957  
T. (YPR)-Rec.  
**Mar.**

*Extant*

**F. MARGARETTIDAE** Harmer, 1957  
T. (YPR)-Rec.  
**Mar.**

*First:* *Tubucella contorta* (Canu, 1910), Lower Eocene, North Aquitaine, France; *Tubucella n. sp. 1’, *Tubucella n. sp. 2’, YPR, DSDP Site 308, Koko Seamount, Pacific (Cheetham, 1975); *Margaretta* sp., Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975).

**F. TETRAPLARIIDAE** Harmer, 1957  
T. (LUT)-Rec.  
**Mar.**

*First:* *Tetraplaria turgesi* Tewari and Srivastava, 1967, Kirthar Stage, Sché, Kutch, India.  
*Extant*

*Comments:* Monogeneric.

**F. CYCLICOPORIDAE** Hincks, 1884  
T. (BRT)-Rec.  
**Mar.**

*First:* *Cyclicopora fissurata* Canu and Bassler, 1920, *C. laticella* Canu and Bassler, 1920, Castle Hayne Limestone, Wilmington, North Carolina, USA.  
*Extant*

*Comments:* *Taenioporina arachnoides* (Goldfuss, 1826) from the MAA, tentatively assigned to this family by Larwood et al. (1967), is not a cyclicoporid (Voigt, 1985, p. 334) but is currently unplaced.

**F. HIPPOPODINIDAE** Levinsen, 1909  
T. (YPR)-Rec.  
**Mar.**

*First:* *Hippoporina* sp., Lower Eocene, DSDP Site 246, Indian Ocean (Labracherie, 1975).  
*Extant*

**F. CHEILOHORNEROPSIDAE** Annoscia, Braga and Finotti, 1984  
T. (PRB)  
**Mar.**

*First and Last:* *Cheilohorneropsis roveretana* Annoscia et al. 1984, PRB, Valle di Gresta, Italy.  
*Extant*

*Comments:* Monospecific. Contrary to the original family description, *Semihaswellia* Canu and Bassler, 1917, and *Tremotoichos* Canu and Bassler, 1917, appear not to belong in this family (D. P. Gordon, pers. comm.).
**Fig. 24.3**

**F. MYRIAPORIDAE** Gray, 1849


**First:** *Myriopora* sp., Upper Eocene, San Marino (Annoscia, 1968). **Extant**

**F. SIPHONICYTARIDAE** Harmer, 1957


**First:** *Tubitrabeucularia clypeata* (Waters, 1881), Upper Eocene, Eua, Tonga (Cheetham, 1972). **Extant**

**F. CREPIDACANTHIDAE** Levinsen, 1909


**First:** *Schizobathysella semilunata* Canu and Bassler, 1920, *S. sacrifera* Canu and Bassler, 1920, Jacksonian, Wilmington, North Carolina, USA. **Extant**

**F. INVERSIULIDAE** Vigneaux, 1949


**First:** *Inversiula airensis* Maplestone, 1910, *I. quadricornis* Maplestone, 1910, ‘Aire Coastal Beds’, Victoria, Australia. **Extant**

**Comments:** Monogeneric for *Inversiula* Julien, 1888.

**F. MICROPORELLIDAE** Hincks, 1879


**First:** *Microporella hyadesi* (Julien, 1888), Bryozoan Bed (Otaian) overlying Takaka Limestone, Tarakohe Quarry, Nelson, New Zealand (Brown, 1952), (the specific identity of this *Microporella* has been questioned by Gordon, 1984, p. 102). **Extant**

**F. CRYPTOSULIDAE** Vigneaux, 1949


**First:** *Cryptosula pallasiana* (Moll, 1803), Tortonian, Europe (Ghiurca, 1975). **Extant**

**F. WATERSIPORIDAE** Vigneaux, 1949


**First:** *Watersipora (?)* sp., Messinian, Algeria (Moissette, 1988). **Extant**

**Comments:** Possible earlier records of this family are either doubtful or require confirmation.
Fig. 24.3

F. LANCEOPORIDAE Harmer, 1957
First: Lanceopora flabellata (Livingstone, 1902), [probably Jemmys Point Formation, Kalimnan Stage], Jemmys Point, Reeves River, Victoria, Australia.
Comments: According to Voigt (1985, p. 334), Bathystomella Strand from the MAA is not related to Formularia (=Lanceopora).

F. PETRALIIDAE Levinsen, 1909 Extant Mar.
Comments: Monogeneric for Petralia MacGillivray, 1869.


F. EMINOOECIIDAE Hayward and Thorpe, 1988 Extant Mar.

F. CALWELLIIDAE MacGillivray, 1887 Extant Mar.


**First:** Didymosella sp., Middle Eocene, North Aquitaine, France (Labracherie, 1971).

**Extant**

F. PROSTOMARIIDAE MacGillivray, 1895

T. (LAN) Mar. (see Fig. 24.3)

**First and Last:** Prostomaria gibbericollis MacGillivray, 1895, Balcombian, Victoria, Australia (Gordon, 1990).

F. URCEOLIPORIDAE Bassler, 1936 **Extant** Mar.


**First:** Dysnoetopora demissa (White, 1879), 'Mesaverde' Formation and Lewis Shale, Wyoming; Pierre Shale, Colorado, USA (Toots and Cutler, 1962).

**Exament** Mar.

**Last:** *Dysnoetopora celleeporoides* Canu and Bassler, 1926, Ripley Formation, Tennessee, USA.

**Comments:** Monogeneric.

F. CELLEPORIDAE Busk, 1852


**First:** 'Cellepora' agglomerata von Hagenow in Geinitz, 1846, Lower MAA Chalk, Baltic and England, UK (Voigt, 1985).

**Extant**

F. PHIDOLOPORIDAE Gabb and Horn, 1862


**First:** *Psilosecos angustidens* (Levinsen, 1925), Upper Danish, Denmark (Berthesis, 1962); or *Reteporellina?* sp., Upper Eocene, Eua, Tonga (Cheetham, 1972).

**Extant** Comments: Otherwise known as Reteporidae Smitt, 1868, or Sertellidae Jullien and Calvet, 1903. Unlike typical members of this family, which have branches with autozooidal apertures opening on one side only, *Psilosecos* has apertures opening on both sides of the branches. Therefore, assignment to the Phidoloporidae is somewhat tentative (Voigt, 1985, p. 334). If *Psilosecos* is not a phidolopid, the earliest known representative of this family may be from the Upper Eocene (PRB).

F. KLEIDIONELLIDAE Vigneaux, 1949


**First:** Hoplocheilina osculifera (Reuss, 1872), Vincentown Limesand, New Jersey and Delaware, USA (Voigt, 1985, p. 335).

**Extant**

**First:** Kleidionella verrucosa Canu and Bassler, 1920, Marianna Limestone, Alabama, USA.

F. HIPPOPORIDRIDAE Vigneaux, 1949


**First:** Hippoporidae edax (Busk, 1859), BUR, France.

**Extant**

F. ORBITULIPORIDAE Canu and Bassler, 1923


**First:** Atactoporida globata Labracherie, 1961, Lower Eocene, Marcheprime, Gironde, France; *Batopora stoliczkai* Reuss, 1867, Lower Eocene, Bordeaux, France (Labracherie, 1971).

**Extant**

F. CONESCHARELLINIDAE Levinsen, 1909


**First:** Conescharellinopsis vineaous Labracherie, 1975, Lower Eocene, Baloze, Aquitaine, France.

**Extant**

F. LEKYTHOPORIDAE Levinsen, 1909


**First:** Lekythopora hystric MacGillivray, 1883, Janjukian, Victoria, Australia.

**Extant**

**Order** CYCLOSTOMATA Busk, 1852

This exclusively marine order of stenolaemate bryozoans is probably paraphyletic. However, there is an acute need for systematic revision, not only to establish the status of the order and its relationship with other orders of stenolaemates, but also to define more regorously its constituent families. Many of the families listed below are of highly dubious value, and their ranges are very tentative.

Replacement of the ordinal name by Tubuliporata Johnston, 1847, to avoid homonymy with the fish order Cyclostoma Duméril, 1806, as in the revised Treatise (Boardman et al., 1983), is considered to be unnecessary and potentially misleading. Such a change is not obligatory under the Rules of Zoological Nomenclature and could lead to confusion with the suborder Tubuliporina. Furthermore, the name Cyclostoma has fallen into disuse among vertebrate systematists.

F. CINCTIPORIDAE Boardman, McKinney and SpandeI, 1992

**Extant**

**First:** Wolinella baltica Dzik, 1981, Middle Volkho Stage, Baltic (Dzik, 1981).

**Extant**

**Last:** Corynotrypa voigtiana (King, 1850), Middle Magnesian Limestone, Sunderland, England, UK and Zechstein, Pössneck, Germany (Taylor, 1985); Lagenosypho permianus Spandel, 1898, Zechstein, Germany (Langer, 1980).

**Comments:** There exist uncertainties about the age of the Zechstein deposits containing the youngest coryntrypids.

F. SAGENELLIDAE Brood, 1975

O. (?CRD)—S. (?LUD) Mar.

**First:** Sagenella minnesotensis (Ulrich, 1886), Black River, St Paul, Minnesota, USA.

**Extant**

**Last:** Sagenella sp. A, Hamra Beds, Vamlingbo, Gotland, Sweden (Brood, 1975).

**Comments:** Ranges of this family are highly tentative, pending detailed investigations of Palaeozoic cyclostomes.

F. CROWNPORIDAE Ross, 1967

O. (LLN—ASH) Mar.

**First:** Kukersella borealis (Bassler, 1911), Orthoceras Lime­stone, Port Kunda, Estonia, former USSR.

**Extant**

**Last:** K. borealis (Bassler, 1911), Slade and Redhill Beds (Upper Rawtheyan), Dyfed, Wales, UK (Buttler, 1989).

**Comments:** Homonymous with Kukersellidae Brood, 1975.

F. STOMATOPORIDAE Pergens and Meunier, 1886

Tr. (CRN)—Rec. Mar.

**First:** Stomatopora sp., S. Cassiano Formation, Eastern Dolomites, Italy (Bizzarini and Braga, 1981).

**Extant**

**Comments:** Palaeozoic records of supposed Stomatopora need re-examination; at least some are coryntrypids or crownporids.


Comments: The small size of the zooids in Cinctipora sp. from the South African Cretaceous call into question its assignment to this family, which is otherwise characterized by gigantic zooids and is endemic to New Zealand (Boardman et al., 1992).

F. ONSOCOEIDAE Canu, 1918

J. (?SIN)–Rec. Mar.


Comments: Carnian forms, described by Bizzarini and Braga (1985) as belonging to the Diastoporidae and Oncousoeciidae, may represent earlier records of this family. Heterohaplooecia monticulifera, 1821 is included in the Tubuliporidae (e.g. Brood, 1972), family range is extended down into the Aalenian.

First: Dunraven Bay, Glamorgan, Wales, UK (P. D. Taylor, unpublished). Extant

Comments: The generic composition and range of this family are highly uncertain. The range given here is based on the oldest species belonging to the type genus of the family. Heterohaplooecia monticulifera, 1821 is included in the Tubuliporidae (e.g. Brood, 1972), family range is extended down into the Aalenian.

F. TUBULIPORIDAE Johnston, 1838

Tr. (RHT)–K. (CMP) Mar.

First: Tubulipora suberecta Brood, 1972, lower CMP, Illfö, Sweden. Extant

Comments: The generic composition and range of this family are highly uncertain. The range given here is based on the oldest species belonging to the type genus of the family. If ldmonoe Lamouroux, 1821 is included in the Tubuliporidae (e.g. Brood, 1972), family range is extended down into the Aalenian.

F. MULTISPARSIDAE Bassler, 1935


First: Reptomultisparsa hybensis (Frantl, 1938), Hybe Beds, Hybe, Czechoslovakia (Taylor and Michalík, 1991).


F. CELLULIPORIDAE Buge and Voigt, 1972


First: Cellulipora ornata d’Orbigny, 1850, Upper Greensand, Devon, England, UK.

Last: Cellulipora (?) rugosa (d’Orbigny, 1853), CON, Villedieu, Loir-et-Cher, France.

Comments: Monogeneric. Contrary to Buge and Voigt (1972), Berenicea spissa Gregory, 1899, is not regarded as belonging to this family, but is a plagioeciid, Mesonopora spissa (see Pitt and Taylor, 1990).

F. PLAGIOECIIDAE Canu, 1918


First: Mesenteripora wrighti Haine, 1854, Middle Lias Marlstone (spinatum Zone), King’s Sutton, Northamptonshire, England, UK (Walter and Powell, 1973). Extant

Comments: Synonymous with the Diastoporidae Busk, 1859 of some authors (e.g. Brood, 1972; Hayward and Ryland, 1985). The name Diastoporidae is best avoided because of its common usage for tubuliporines lacking brooding zooids (e.g. Bassler, 1953).

F. TREVIIIDAE Canu and Bassler, 1920


First: Lagonoea lamellifera Canu and Bassler, 1920, Bashi Formation, Woods Bluff, Alabama, USA. Extant

F. SPIPORIDAE Voigt, 1968


First: Spiropora elegans Lamouroux, 1821, BTH, Normandy, France.

Last: S. verticillata (Goldfuss, 1826), THA, Pont Labou, Pau, France (Voigt and Flor, 1970).

Comments: Monogeneric.

F. ONCPOSOECIIDAE Canu, 1918

J. (?SIN)–Rec. Mar.

First: Fasciculipora waltoni Haine, 1854, upper BTH, Bath, England, UK. Extant

Comments: As here understood, this family includes also the Fasciculiporidae Walter, 1970.

F. THEONOIDAE Busk, 1859

J. (AAL)–Rec. Mar.

First: Thesea diplopora (Branco, 1879), Lower Inferior Oolite, Gloucestershire, England, UK. Extant

F. SIPHONIOTYPHIDAE Voigt, 1967


First: Siphoniotypillus tenuis (von Hagenow, 1840), Clinopora cenomanensis Hillmer, 1971, Lower Cenomanian, Hannover, Germany (see Hillmer, 1971).

Last: Clinopora lineata (Beissel, 1865), upper MAA (mayaroensis Zone), Limhamn, Sweden (Brood, 1972, p. 268).

F. MELICRITEIDAE d’Orbigny, 1852


First: Melicerites semiclausus (Michelin, 1846) sensu Walter et al. 1975, lower BRM, Fontaine-Grailière Marls, South-Vercors, France.

Last: Meliceritella steenstrupi (Pergens and Meunier, 1887), M. armata (Levinsen, 1912), DAN, Baltic.

Comments: Homonymous with Melicerititidae Pergens, 1890, eleids are a well-defined, monophyletic family. The characteristic operculate zooids are absent in a supposed eleid from the Bathonian, Cyclocites primogenitum Canu and Bassler, 1922.

F. SEMICEIDAE Buge, 1952


First: Poriceata ardescensis Walter, 1983, upper HAU or lower BRM, Vaulion, Switzerland.

Last: Filicea danica Viskova, 1968, DAN, Crimea, Inkerman, former USSR.

Comments: Cinctipora elegens Hutton, 1873, a Recent species sometimes assigned to Filicea, has been reassigned to the Cinctiporidae.

F. CRISIDAE Johnston, 1847


Comments: The diagnostic articulated colony form has still to be established in the material described by Voigt and Walter (1991).
**F. CRISULIPORIDAE** Buge, 1979  

**First:** *Crisulipora prominens* Canu and Bassler, 1920, C. rugosodorsalis Canu and Bassler, 1920, C. flabellata Canu and Bassler, 1920, C. grandipora Canu and Bassler, 1920, Marianna Limestone. Alabama, USA. **Extant**

**F. HORNERIDAE** Smith, 1867  

**First:** *Siphodictyum gracile* Lonsdale, 1849, lower BRM, Fontaine-Grallière Marls, South-Vercors and Crupies, France (Walter et al., 1975).

**F. STIGMATOECHIDAE** Brood, 1972  

**First:** *Stigmatoechos punctatus* Masson, 1887, upper ?CMP, Denmark and Sweden (Brood, 1972, p. 370). **Extant**

**Comments:** Putative Recent examples (e.g. *S. violacea* (Sars)) require confirmation.

**F. PETALOPORIDAE** Gregory, 1899  

**First:** *Petalopora rugosa* (d’Orbigny, 1853), lower VLG, Arzier, Jura, France (see Walter, 1972). **Extant**

**Comments:** Although often regarded as extinct, the Recent *Calvetia dissimilis* Borg, 1944 (for which Borg created a new family, the Calvetiidae) is probably a petaloporid.

**F. CRISINIDAE** d’Orhigny, 1853  

**First:** *Crisidmonea tripora* (Canu and Bassler, 1926), Ripley Formation, Coon Creek, Tennessee, USA. **Extant**

**Comments:** There is considerable confusion about this family arising from the existence of numerous taxa with superficially similar colony forms, but for which the details of the brooding zooids, crucial to ascertaining true affinities, have yet to be described; and problems concerning the type species of the type genus which, as figured by Voigt (1989, pl. 6, fig. 6) may be the earliest known. *Crisidmonea tripora* may be the oldest species with cancellate brooding zooids matching the concept of the Crisinidae as here understood.

**F. CRASSODISCOPORIDAE** Brood, 1972  

**First and Last:** *Crassodiscopora alcicornis* (Levinsen, 1925), upper MAA (mayaroensis Zone)–DAN (vexillifera Zone), Denmark and Sweden (Brood, 1972, p. 391).

**Comments:** Monospecific.

**F. CYTIDIDAE** d’Orhigny, 1854  

**First:** *Charoctys compressa* Canu and Bassler, 1926, Voigtictys campicheana (d’Orbigny, 1853), Lower VLG, SE France. **Extant**

**Comments:** The definition, composition and stratigraphical range of this family are problematic.

**F. CERIOPORIDAE** Busk, 1859  
J. (TOA)–Rec. Mar.  

**First:** *Heteropora tipperi* Henderson and Perry, 1981, lower TOA, north-central British Columbia, Canada. **Extant**

**Comments:** Synonymous with *Heteroporidae* Waters, 1880. Pending systematic revision, Tretocycloeciidae Canu, 1919, Leiosoecciidae Canu and Bassler, 1920, Canuellididae Borg, 1944, and *Densioporididae* Borg, 1944 are here included within the *Cerioporididae*. Putative cerioporids from the Triassic are calcified demosponges (Engeser and Taylor, 1989).

**F. CAVIDAE** d’Orbigny, 1854  

**First:** *Ceriocava corymbosa* (Lamouroux, 1821), Lower Inferior Oolite, Gloucestershire, England, UK. **Last:** *Ceriocava incrusta* (Roemer, 1840), SAN, Germany. **Comments:** Possibly polyphyletic.

**F. BORDEAUXIDAE** Canu, 1917  

**First:** *Bordeauporella compressa* Voigt, 1974, *Bordeaupora* affinis (Klamann, 1943), SAN, Germany. **Extant**

**Comments:** Taken to include the *Bordeaupeoriae* of Klamann, 1943.

**F. CERAMOPORIDAE** Smitt, 1866  

**First:** *Ceriocavatrica inquisitor* (d’Orbigny, 1853), lower VLG, Marnes a la Sénelle, France. **Extant**

**Comments:** Includes the *Ceriocavatrica inquisitor* of d’Orbigny, 1853, and also over the exact boundary with the *Ceramoporidae*.

**Order CYSTOPORATA** Astrova, 1964

This order was created for some Palaeozoic stenolaemates previously included (e.g. Bassler, 1953) in the *Cyclostomata*. The bulk of the *Cystoporata* are likely to constitute a monophyletic grouping which is characterized by the presence of lunaria and/or vesiculose calcification between the zooids. However, there are doubts about the cystoporate affinities of certain genera, and also over the exact boundary with the *Trepostomata*. The order was revised by Utgaard (in Boardman et al., 1983) for the *Treatise*, whose classification is employed here.

**F. REVALOTRYPIDAE** Goryunova, 1986  

**First:** *Revalotrypae eugeniae* Goryunova, 1988, Latorpskiy Horizon, Estonia, former USSR. **Last:** *Metelipora monstrata* Trizna, 1950, Sterlitamak Horizon (late SAK), Ural, former USSR.

**F. CERAMOPORIDAE** Ulrich, 1882  

**First:** *Ceramopora sp.* Chazyan, Day Point Limestone, New York State, USA (Ross, 1984, fig. 2). **Last:** *Ceramopora perforata* Hennig, 1908, Hamra-Sundre Beds, Gotland, Sweden. **Comments:** The large diameter of the ‘zooids’ in *Ceramopora unapensis*, described by Ross (1966) from the Arenig Kindblade Formation of Oklahoma, throws doubt on the affinities of this potential early ceramoporid. The
systematic position of *Ganiella* Yaroshinskaya, in Astrova and Yaroshinskaya, 1968, a possible Lower Devonian ceramoporida is highly doubtful.

**F. ANOLOTICHIIDAE** Utgaard, 1968

*O. (ARG)–D. (GIV) Mar.*

**First:** Prostilulipora arctica Astrova, 1965, Nelidov Stage, Novaya Zemlya, former USSR (Nekhorosheva, 1974).

**Last:** Altishedata belgetasakensis (Nekhorosheva, 1948), GIV, Altai Mts, former USSR (Utgaard, in Boardman et al., 1983, p. 370).

**F. XENOTRYPIDAE** Utgaard, 1983


**First:** Xenotrypa primaeva (Bassler, 1911), Volkov Stage, Estonia, former USSR.

**Last:** Hennigopora florida (Hall, 1852), Rochester Shale, New York State, USA.

**F. CONSTELLARIIDAE** Ulrich, 1896

*O. (LLO)–S. (LLY) Mar.*

**First:** Constellaria islesis Ross, 1963, Chazy Formation, Vermont and New York State, USA.

**Last:** Constellaria sp., *lower Silurian of Siberia* (Ross, 1963, p. 53).

**F. FISTULIPORIDAE** Ulrich, 1882

*O. (ASH)–Tr. (CRN) Mar.*

**First:** Fistulipora sp., Slade and Redhill Beds, upper Rawtheyan, Whitland, Dyfed, Wales, UK (Buttlar, 1991).

**Last:** Cystitrypa cassiana Schäfer and Fois, 1987, southern Cassiano Formation, Cortina d’Ampezzo, Dolomites, Italy.

**F. RHINOPORIDAE** Miller, 1889


**First:** Lichenalia cf. concentrica Hall, 1852, Slade and Redhill Beds, upper Rawtheyan, Whitland, Dyfed, Wales, UK (Buttlar, 1991).

**Last:** Lichenalia concentrica Hall, 1852, Rochester Shale, New York State, USA.

**F. BOTRYLLOPORIDAE** Miller, 1889

*D. (GIV) Mar.*

**First and Last:** Botryllopora socialis Nicholson, 1874, Hamilton Group, Ontario, Canada; New York State and Michigan, USA.

**Comments:** Monospecific.

**F. ACTINOTRYPIDAE** Simpson, 1897

*C. (CHD)–P. (KAZ) Mar.*

**First:** Actinotrypa peculiaris (Rominger, 1866), Keokuk Group, Missouri and Illinois, USA (Horowitz, 1968).

**Last:** Epiactinotrypa flosculosa Kiseleva, 1973, E. incongnita Kiseleva, 1982, Chandlezy Suite, Parafusulina stricta Zone, Primor’e, former USSR (Kiseleva, 1982).

**F. HEXAGONELLIDAE** Crockford, 1947

*D. (GIV)–P. (KAZ) Mar.*

**First:** Prismopora triquetra Hall and Simpson, 1887, Hamilton Group, Indiana, USA.

**Last:** Hexagonella ramosa Waagen and Wentzel, 1886, Murgabian, Colaniella parva Zone, Primor’e, former USSR (Kiseleva, 1982).

**F. CYSTODICTYONIDAE** Ulrich, 1884

*D. (GIV)–P. (SAK) Mar.*

**First:** Acrogenia prolifera Hall, 1883, Pitlocella parallela (Hall and Simpson, 1887), Semiopora bistigmata Hall, 1883, Stictocella sinusosa (Hall, 1883), Taeniopora exigua Nicholson, 1874, T. occidentalis Ulrich, 1890, T. millichalmilformis Nicholson, 1874, T. rexulans (Hall and Simpson, 1887), T. subcarinata (Hall, 1883), Thamnotrypa divaricata (Hall, 1883), Hamilton Group, north-eastern USA and Ontario, Canada.

**Last:** Filiramopora kretaphila Fry and Cuffey, 1976, Wreford Limestone, Kansas, USA.

**F. ETHERELLIDAE** Crockford, 1957

*P. (ART–KAZ) Mar.*


**Last:** Etherella crassa Kiseleva, 1973, Chandlezy Suite, Parafusulina stricta Zone, Primor’e, former USSR (Kiseleva, 1982).

**F. GONIOCLADIIDAE** Waagen and Pichl, 1885

*C. (TOU)–P. (KAZ) Mar.*

**First:** Goniocladia kasakhstancica Nekhorosheva, 1953, TOU, Kazakhstan, former USSR.

**Last:** Goniocladia timorensis Bassler, 1929, Chandlezy Suite, Parafusulina stricta Zone, Primor’e, former USSR (Kiseleva, 1982).

**Order** TREPPOSTOMATA Ulrich, 1882 (see Fig. 24.4)

This predominantly Palaeozoic stenolaemate order has no certain autapomorphies and is likely to be paraphyletic, although some major subgroups within the order (e.g. Suborder Halloporoidea) are undoubtedly monophyletic. R. S. Boardman is currently revising the trepostomes for the Treatise. Pending this publication, the family-level classification used here is largely derived from the work of Astrova (1978).

The oldest known bryozoans are two Tremadocian trepostome genera from the Yangtze Valley, China which will be described in a forthcoming publication by Hu and Spjeldnaes. Their family assignment is currently unknown.

**F. ESTHONIOPORIDAE** Vinassa de Regny, 1921

*O. (ARG–CRD) Mar.*

**First:** Esthoniopora lessnikovae (Modzalevskaya, 1953), BI, Leningrad Oblast’, former USSR.

**Last:** Esthoniopora subsphaerica (Bassler, 1911), E, Estonia, former USSR.

**F. ORBIPORIDAE** Astrova, 1978

*O. (ARG)–D. (GIV) Mar.*

**First:** Orbipora sp. of Taylor and Cope (1987), Ogof Hên Formation, Bolahaul Member, Llangynog, Wales, UK.

**Last:** Chondraulus densus Duncan, 1939, C. granosus Duncan, 1939, and C. petoskeyensis Duncan, 1939, Traverse Group, Michigan, USA.

**F. DITTOPORIDAE** Vinassa de Regny, 1921

*O. (ARG–ASH) Mar.*

**First:** Dittopora annulata (Eichwald, 1860), D. sokolovi Modzalevskaya, 1953, D. ramosa Modzalevskaya, 1953, and D. clavaeformis Dybowsky, 1877, BII, Estonia, former USSR.
### Animals: Invertebrates

#### F. HETEROTRYPIDAE Ulrich, 1890

**O. (LLN–TR. (CRN)) Mar.**

**First:** *Stigmatella indenta* (Bassler, 1911), *S. infecta* Bassler, 1911, and *Liolema spinosa* (Bassler, 1911), BIII, Estonia, former USSR.

**Last:** *Zozariella stellata* Schäfer and Fois, 1987, Zozar Formation, Zanskar Region, West Himalaya, North India.

**Comments:** *Z. stellata* is assigned to this family with reservation by Schäfer and Fois (1987). The next youngest species is *Phragmotrypa ordinata* Schäfer and Fois (1987) from the lower to middle ANS of Nevada, USA.

**Last:** *Hemiphragma imperfectum* (Ulrich, 1890), and *H. whitfieldi* (James, 1875), Cincinnatian, USA.

**F. BIMUROPORIDAE Key, 1990 O. (LLN–CRD) Mar.**

**First:** *Champlainopora chazyensis* (Ross, 1963), Chazy, Day Point Limestone, New York State, USA.

**Last:** *Bimuropora winchelli* (Ulrich, 1886), Trenton, Guttenberg Formation, Iowa, USA.

**F. HALLOPORIDAE Bassler, 1911**

**O. (?ARGI?LLN) Mar.**

**First:** *Diplotrypa pusilla* Astrova, 1965, top of Lower–base of Middle Ordovician, Vaigach Island, Circumpolar Urals, former USSR.

**Last:** *Diplotrypa franklini* Bolton, 1966, LUD, Canadian Arctic Islands; *Hallopora elegantula* (Hall, 1852), LUD, Welsh

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Fig. 24.4
F. TREMATOPORIDAE Miller, 1889

First: Nicholsonella nelidovi Nekhorosheva, 1965, Nelidovo Horizon, Novaya Zemlya, former USSR; N. genuina Astrova, 1965, O. (L), Novaya Zemlya, former USSR.

Last: Neotrematopora tabulata (Nekhoroshév, 1956), TOU, Kazakhstan, former USSR.

F. MONTICULIPORIDAE Nicholson, 1881

First: Homotrypa instabilis Ulrich, 1886, Cl, Estonia, former USSR.

Last: Prasopora gotlandica Hennig, 1908, Hemse Beds, Gotland, Sweden.

F. MESOTRYPIDAE Astrova, 1965

First: Mesotrypa bystrovii Modzalevskaya, 1953, Cl, Estonia, former USSR; M. torosa, Modzalevskaya, 1953, Cl, Leningrad Oblast, former USSR.

Last: Mesotrypa suprasilurica Hennig, 1908, Hökglint Beds (b), Visby, Gotland, Sweden.

F. AMPLEXOPORIDAE Miller, 1889

First: Monotrypa helenae Modzalevskaya, 1953, BII, Leningrad Oblast, former USSR.

Last: Monotrypa hsui Yang, 1950, Hsiu Kiang Shan Formation, Central Hunan, China (Yang et al., 1988).

F. ATACTOTOECHIDAE Duncan, 1939
O. (ARG)–P. (KAZ) Mar.

First: Cyphotrypa antiqua (Modzalevskaya, 1953), BII, Leningrad Oblast, former USSR.

Last: Permopora kapitaii Romanchuk, 1967, Upper Permian, Khabarovsk region, former USSR; Neeriostrypella pulchra Morozova, 1970, KAZ, Russian Platform, former USSR.

F. STEREOTOECHIDAE Yang, Hu and Xia, 1988

First: Eostenopora peculiaris (Bassler, 1906), Rochester Shale, New York State, USA.

Last: E. tumida (Girty, 1911), Chesterian, Arkansas, USA.

F. ANISOTRYPIDAE Dunaeva and Morozova, 1967
S. (LUD)–P. (KAZ) Mar.

First: Anisotrypa praecox Astrova, 1970, S2, Skalsk Horizon, Podolia, former USSR.

Last: Anisotrypella borealis Morozova, 1967, Lower Kazanian Substage, Russian Platform, former USSR.

F. CRUSTOPORIDAE Dunaeva and Morozova, 1967

First: Callocladia kaugatumensis Astrova, 1970, Upper Silurian, Kaugatumas Horizon, Estonia, former USSR.

Last: Tabuliporella permiana Baranova, 1960, SAK, northern Ural, former USSR.

F. DYSCRITELLIDAE Dunaeva and Morozova, 1967
D. (GIV)–Tr. (NOR) Mar.

First: Dyscritella devonica Volkova, 1968, GIV, Gornyi Altai, former USSR.

Last: Dyscritella agischevi Nekhoroshev, 1949, NOR, Khabarovsk region, former USSR; Pseudobatostomella morbosa Morozova, 1969, NOR, Pamir, former USSR; P. maorica (Wilckens, 1927), Wairoa, Nelson, New Zealand; Paralioclema formosum Morozova, 1969, NOR, Caucasus, former USSR.

F. AISENVERGIIDAE Dunaeva, 1964

First: Polycylindricus aspinctus Boardman, 1960, P. clausius Boardman, 1960, P. devonicus (Ulrich, 1890), Hamilton Group, USA.

Last: Aisenvergella ciliata Dunaeva, 1964, Volnovachia distincta Dunaeva, 1964, Hastarian, Donbas, former USSR.

F. STENOPORIDAE Waagen and Wentzel, 1886

First: Dyoidophragma typicale Duncan, 1939, D. serratum Duncan, 1939, D. polymorphum Boardman, 1960, Traverse and Hamilton Groups, USA.

Last: Stenopora sp., Changxing Formation, South China (Yang and Lu, 1981).

F. NIPPOSTENOPORIDAE Xia, 1987

First: Nippostenopora tabulata Dunaeva, 1963, Steshevesky Horizon, early SPK, Donbas, former USSR.

Last: Nippostenopora elegantula Sakagami, 1960, Millerella Zone (late SPK or early BSH in age), Fukui, Hida Massif, Japan.

Comments: The exact age of species from China assigned to the upper Lower Carboniferous by Xia (1987) is not clear.

F. ULRICHOTRYPELLIDAE Romanchuk, 1968

First: Petalotrypa compressa Ulrich, 1890, P. delicata Ulrich, 1890, Hamilton Group, USA.


F. ARAXOPORIDAE Morozova, 1970

First: Araxopora varians (Yang, 1958), Chihsia Formation (lower Lower Permian), Yangtze region, China (Yang and Lu, 1979).


Comments: Monogenic.

F. HELENOPORIDAE Ross, 1988
C. (SPK) Mar.

First and Last: Helenopora duncanae Ross, 1988, upper Mississippian, western interior of the USA.

Comments: Monospecific.

F. ASTRALOCOMIDAE Ross, 1988
C. (SPK) Mar.
**Order** CRYPTOSTOMATA Vine, 1883

This Palaeozoic stenolaemate order comprises bryozoans with restricted linear or planar loci of zooidal budding (Blake, 1980). Following removal of the Fenestrata as a separate order, three suborders of cryptostomes are recognized: Ptilodictyina Astrovà and Morozova, 1956 (so-called 'bifoliate cryptostomes'), Rhabdomesina Astrovà and Morozova, 1956, and Timanodictyina Morozova, 1966. The first two suborders have been revised for the Treatise (Boardman et al., 1983) by Karklins and Blake respectively; the timanodictyines are a small, poorly known suborder. The phylogenetic relationships and exact taxonomic status of the three suborders have yet to be worked out.

**Suborder** PTILODICTYINA Astrovà and Morozova, 1956

Family classification follows Karklins (in Boardman et al., 1983). It should be noted that Karklins left several genera unassigned to families; these genera are therefore not taken into account in the range data that follow.

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**Family** CRYPTOZOOIDAE

Family classification follows Karklins and Bassler (1900) and Blake (1980). Following removal of the Fenestrata as a separate order, three suborders of cryptostomes are recognized: Ptilodictyina Astrovà and Morozova, 1956 (so-called 'bifoliate cryptostomes'), Rhabdomesina Astrovà and Morozova, 1956, and Timanodictyina Morozova, 1966. The first two suborders have been revised for the Treatise (Boardman et al., 1983) by Karklins and Blake respectively; the timanodictyines are a small, poorly known suborder. The phylogenetic relationships and exact taxonomic status of the three suborders have yet to be worked out.

**Suborder** PTILODICTYINA Astrovà and Morozova, 1956

Family classification follows Karklins (in Boardman et al., 1983). It should be noted that Karklins left several genera unassigned to families; these genera are therefore not taken into account in the range data that follow.

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Suborder TIMANODICTYINA Morozova, 1966

This exclusively Upper Palaeozoic suborder is characterized by dendroid or bifoliate branches with thick exozonal walls containing small styles (‘capillaries’ of Russian workers). Although regarded as cryptostomes, timanodictyines were not treated in the cryptostome section of the bryozoan Treatise (Boardman et al., 1983).

F. TIMANODICTYIDAe Morozova, 1966

First: Timanodictya dichotoma (Stuckenbg, 1895), SAK, northern Timan and Malozemelsk Tundra, Urals, former USSR; Ellesmere Island, Canada.
Last: Timanotrypa borealis Morozova, 1970, KAZ, Pinega River, Arkhangelsk Oblast’, former USSR.

F. GIRTYOPORIDAE Morozova, 1966

First: Morozovapora akiyoshienis Sakagami and Sugimura, 1978, Nagatophyllum satio Zone of the Akiyoshi Limestone, Mizuta, Japan.
Last: Girtyopora crassa Morozova, 1970, ‘Lyudyanza (?) Horizon’, basin of the Khuanikhezda River, Primor’e Region, former USSR.

Order FENESTRATA Elias and Condra, 1957

This order of Palaeozoic stenolaemates was created for taxa previously assigned to the Cryptostomata (e.g. Bassler, 1953). Fenestrates are likely to be a monophyletic group closely related to cryptostomes (e.g. Blake, 1980), but possessing the apomorphic character of apertures opening along one side of the branches only. Many fenestrates have planar colonies with a net-like or pinnate form. The order is currently being revised by F. K. McKinney for the Treatise. Family-level classification adopted here is after Lavrentjeva (1985) and Morozova (1987).

F. ENALLOPORIDAE Miller, 1889

First: Alwynopora orodamnus Taylor and Curry, 1985, Tourmakeady Limestone, County Mayo, Republic of Ireland.
Last: Pushkinella acanthoporidae (Pushkin, 1976), LLY, Byelorussia, former USSR.

F. RALFINIDAE Lavrentjeva, 1985
O. (CRD) Mar.

First and Last: Ralfina aluverensis (Männ, 1958), Ralfinella plana (Männ, 1958), CRD, Estonia, former USSR.

F. PHYLLOPORINIDAE Ulrich, 1890

First: Phylopora punctata (Bekker, 1921), P. fragilis Lavrentjeva, 1985, Pseudohornera bifida (Eichwald, 1855), LLO, former USSR.
Last: Pseudohornera diffusa (Hall, 1852), Rochester Shale, New York State, USA, and Ontario, Canada.

F. SARDESINIDAE Lavrentjeva, 1985

First: Sardesinina maxima (Toots, 1952), Kuckers Shale, Estonia, former USSR.
Last: Sardesinina corticosa (Ulrich, 1886), Black River, Minnesota, USA.

Comments: Monogeneric.
### Fig. 24.5

**F. CHAINODICTYONIDAE** Nickles and Bassler, 1900  

- **First:** *Chainodictyon aktasicum* Plamenskaja, 1964, Kazakhstan, former USSR.  
  *C. undata* (M'Coy, 1844), Carboniferous Limestone, Republic of Ireland.
- **Last:** *Chainodictyon lucidum* Goryunova, 1970, ART, Pamirs, former USSR.

**F. CHASMATOPORIDAE** Schulga-Nesterenko, 1955  

- **First:** *Esthonioporina quadrata* (Bekker, 1921), LLO, Estonia, former USSR.  

**F. SEMICOSCINIUMIDAE** Morozova, 1988  

- **First:** *Eosemiccoscinium* sp., Upper Ordovician (see Morozova, 1987, p. 82).
- **Last:** *'Neoreteporina'* sp., Namurian A, American Shelf (Ross, 1981, text-fig. 4).

**F. SEPTOPORIDAE** Morozova, 1962  

- **First:** *Septopora* sp., Lower Carboniferous (Morozova, 1987, fig. 5).
- **Last:** *Synocladiia rigida* Morozova, 1965, Dzhul'fa Gorge, Transcaucasia, former USSR.

**F. FENESTELLIDAE** King, 1850  
**Key for both diagrams**

1. Goldfussitrypidae
2. Maychellinidae
3. Maychellidae
4. Arthrostylidae
5. Rhabdomesidae
6. Rhomboporidae
7. Bactroporidae
8. Nikiforovellidae
9. Nudymiellidae
10. Pseudoascoporidae
11. Hyphasporoporidae
12. Timanodictyidae
13. Griptoporidae
14. Enalloporidae
15. Ralfinidae
16. Phylloporinidae
17. Sardesoninidae
18. Chainodictyonidae
19. Chasmatoporidae
20. Semicosciniumidae
21. Septoporidae
22. Fenestrellidae
23. Fenestrallidae
24. Septatoporidae
25. Acanthocladiidae
26. Vinellidae
27. Ascodictyidae
28. Phaceloporidae
29. Hederellidae
30. Reptariidae
31. Cuverillieridae

**Fig. 24.5**

First: *Moorephyllopora typica* Bassler, 1952, Edinburg Formation, Virginia, USA.

Last: *Fenestella sinopermiana* Yang and Lu, upper Changhsing Limestone, South China (Zhao et al., 1981).

Comments: Supposed Triassic records of fenestellids are probably erroneous.

**F. FENESTRALLIDAE** Morozova, 1963

First: *Fenestralia* sp., ? locality (Morozova, 1987, fig. 5).


**F. SEPTATPORIDAE** Engel, 1975


Last: *Septatopora* sp., KAZ, Australia (Ross, 1978, p. 351).

Comments: This monogeneric family is retained with reservation for fenestellid-like forms with septate apertures.

**F. ACANTHOCLADIIDAE** Zittel, 1880

First: *Polyporella intermedia* (Shrubsole, 1880), Wenlock Limestone, Dudley, England, UK.

Last: *Polypora* sp., Changxing Formation, South China (Yang and Lu, 1981).

Comments: 'Induan' sediments containing acanthocladiids were formerly regarded as early Triassic in age, but are now thought to be late Permian (Rostovtsev and Azaryan, 1973).

**INCERTAE SEDIS**

The following families, except for the Cuvillieridae, were included in the bryozoan *Treatise* by Bassler (1953), but are either of unknown affinities within the phylum, or do not belong to the Bryozoa.

**F. VINELLIDAE** Ulrich and Bassler, 1904

First: *Polypora* sp., Changxing Formation, South China (Yang and Lu, 1981).
First: Marcusodictyon priscum (Bassler, 1911), Ungulite Sandstone, Estonia, former USSR (see Taylor, 1984).
Last: Condranema parvula (Condra and Elias, 1944), C. magna (Condra and Elias, 1944), Lower Permian, USA.
Comments: A heterogeneous grouping of thread-like encrusters, assigned traditionally to the soft-bodied order Cysterostomata with little justification. Most, if not all, are bryozoans. At least some Mesozoic vinellids are foraminifera, but the bulk of the family are Palaeozoic species of problematic affinity (e.g. Taylor, 1984).

F. ASCODICTYIDAE Miller, 1889

Last: A. nebraskensis Condra and Elias, 1944, Big Blue Series, Nebraska, USA.
Comments: As with the Vinellidae, these encrusting, thread-like, supposed ctenostomes are unlikely to be bryozoans.

F. PHACELOPORIDAE Miller, 1889

First: Phaceolopora pertenuis Ulrich, 1890, Trenton, Kentucky, USA.
Last: Phaceolopora sp., Öjlemyrflint, Sylt, Germany (Hillmer and Schallreuter, 1987).
Comments: A monogenic family, generally regarded as belonging to the Cyclostomata but in need of re-evaluation.

F. HEDERELLIDAE Kiepura, 1973

Last: H. carbonaria Condra and Elias, 1944, Missouri Series, Dewey Limestone, Oklahoma, USA.
Comments: Together with the Reptariidae, this family forms the Suborder Hederelloidea Bassler, 1939, which has been generally assigned to the Order Cyclostomata (cf. Dzik, 1981, who tentatively assigns them to the Phylactolaemata). However, the hederelloids, in great need of revision, are thought by some not to be bryozoans, but more closely related to auloporid tabulate corals.

F. REPTARIIDAE Simpson, 1897

First: Reptaria steiningeri (Barrande, 1868), Budnany Beds, Bohemia, Czechoslovakia (Prantl, 1938).
Last: R. clouldi Bassler, 1939, Tully Limestone, West Brook Member, New York State, USA.

F. CUVERILLIERIDAE Annosica, 1965

First and Last: Cuvilliera egyptiense Pfender, 1934, upper LUT, Egypt.
Comments: This monospecific family was assigned to the anascan cheilostomes by Annosica (1965), but the bryozoan affinities of C. egyptiense are dubious.

REFERENCES


Davis, A. G. (1934) English Lutetian Polyzoa.


Prantl, F. (1938) Revision of the Bohemian Paleozoic Reptariidae. (Bryoza). Skrmkn Nidnndho Muses v Praze, 1B (6), Geologia et Paleontologia No. 73–84.


ECHINODERMATA

M. J. Simms, A. S. Gale, P. Gilliland, E. P. F. Rose and G. D. Sevastopulo

The overall classification of echinoderms used in this compilation is that of Smith (1984a) and Paul and Smith (1984). Details of the classification schemes used for particular groups are found at the start of the relevant sections. An understanding of the phylogeny of many echinoderm groups is far from clear. Of the five extant classes, echinoids are perhaps the best documented, both in terms of their representation in the fossil record and also how recently their phylogeny has been interpreted using cladistic methodology. Both asteroids and holothuroids have also been the subject of recent phylogenetic analyses. However, knowledge of the stratigraphical distribution of both groups has been hindered by their poor fossil record and, particularly in the case of the holothurians, problems inherent in identifying disarticulated material. Ophiuroids also have a rather poor fossil record, a problem further compounded by the inadequacy of the few classification schemes currently available. Crinoids represent another major area of uncertainty in echinoderm phylogenetics. Although they have a comparatively good fossil record, current classification schemes in no way can be considered to reflect their phylogeny on even the coarsest scale, and it is probable that only a minority of taxa below the level of order will, on further investigation, prove to be monophyletic.

Our understanding of the various extinct Palaeozoic echinoderm groups has benefited in particular from recent work by Andrew Smith and Chris Paul, although considerable areas of uncertainty still exist. The blastoids are one such group, which, although having been the subject of recent revision (Breimer and Macurda, 1972; Macurda, 1983; Horowitz et al., 1986) are still essentially classified in terms of ‘grade groups’.

It is evident from the following compilation that, although a great deal of recent work has been undertaken to elucidate echinoderm phylogenies, much still remains to be done and, in many cases, the data on first and last occurrences, compiled below, should not be considered to approximate in any way to real instances of origination or extinction. Perhaps the most valuable aspect of this exercise, therefore, is to highlight those areas most in need of further work. Some families of characteristically deep-water echinoids have been noted as such.

Sections are attributable to the contributors as follows: M. J. Simms – cystoids, blastoids (with GDS), crinoids (excluding disparids), edrioasteroids, ophiocistioids, ophiuroids, miscellaneous Lower Palaeozoic plesions; A. S. Gale – asteroids; P. Gilliland – holothurians (excluding ophiocistioids); E. P. F. Rose – echinoids; G. D. Sevastopulo – blastoids (with MJS), disparid crinoids.

Acknowledgements – We thank Hans Hagdorn, Clare Milsom, Chris Paul and Andrew B. Smith for assistance with certain sections.

Phylum ECHINODERMATA Bruguier, 1791

Plesion (F.) HELICOPLACIDAE Durham, 1963


Plesion (Genus) CAMPTOSTROMA Ruedemann, 1933

First and Last: Camptostroma roddyi Ruedemann, 1933, Kinzer Formation, Pennsylvania, USA.

Comment: Paul and Smith (1984) regard Camptostroma as the latest common ancestor of pelmatozoans and eleutherozoans.

Subphylum PELMATOZOA Leuckart, 1848

Plesion (F.) LEPIDOCYSTIDAE Durham, 1967

First and Last: Lepidocystis wanneri Foerste, 1938 and Kinzerocystis durhami Sprinkle, 1973, Olenellus Zone, Kinzer Formation, Pennsylvania, USA.

Comment: Paul and Smith consider the lepidocystids to lie close to the common ancestry of both crinoids and cystoids.
Fig. 25.1
Echinodermata

**Plesion** (Superclass) CYSTOIDEA Von Buch, 1846


**Plesion** (Genus) GOGIA Walcott, 1917

- **C.** (CRF—STD) Mar.

First: Gogia (Alaniscystis) andalusiense Ubaghs and Vizcaino, 1990, upper part of Marianian Stage, Sierra Morena Oriental, Andalusia, Spain.

Last: Gogia gondi Ubaghs, 1987, upper Middle Cambrian, Paradoxides mediterraneus Zone, Montagne Noire, France.

Comment: Paul (1988) considers Gogia to represent the latest common ancestor of the main cystoid groups.

**Order** EDRIOBLASTOIDA Fay, 1962

**Plesion** (F.) ASTROCYSTITIDAE Bassler, 1938

- **O.** (ARG1—LLO) Mar.

First: Cambroblastos expansus Smith and Jell, 1990, Median Upper Cambrian (Franconian), Chatsworth Limestone, western Queensland, Australia.


Comment: The relationship of edrioblastoids to other cystoid remains obscure (Paul, 1988).

**Plesion** (F.) BLASTOCYSTIDAE Jaekel, 1918

- **O.** (Parablastoids) Mar.

First: Blastoidocrinus antecedens Paul and Cope, 1982, Bolahaull Member, Ogof Hen Formation, Llangynog, southern Wales, UK.

Last: Blastoidocrinus archariaeden Billings, 1859, Aylmer Formation, Montreal, Quebec, Canada and Valcour Limestone, New York, USA.

**Order** UNNAMED HIGHER TAXON COMPRISING CRYPTOCRINOIDS, PARACRINOIDS, CORONATES AND BLASTOIDS

Paul (1988) considers each of these groups to be monophyletic and to belong to a larger monophyletic group with *Bockia* as its latest common ancestor.

**Plesion** (Genus) BOCKIA Gekker, 1938

- **O.** (ARG2?/LNN—L. CRD) Mar.


Last: Bockia neglecta Gekker, 1938, lower Caradoc, eastern Baltic.

'Superfamily' CRYPTOCRINIDA' Bassler, 1938

There has been little recent work on this 'superfamily'.

**F. CRYPTOCRINITIDAE** Bassler, 1938

- **O.** (ARG2?/LNN/LLO—CRD) Mar.

First: Cryptocrinites ? similis Bockelie, 1981, Asaphus expansus Shale, Vækerø Farm, Oslo, Sweden. The earliest definite record is Cryptocrinites laevis (Pander, 1830), from the *Echinopharaerites* Limestone Pulkova, near Leningrad, former USSR.

Last: Foerstycystis obliqua Bassler, 1950, upper Llandeilo/lower Caradoc, Tennessee, USA.

**F. COLUMBOCYSTIDAE** Bassler, 1950


First and Last: Columbocysta typica Bassler, 1950 and *Springercystis longicollis* Bassler, 1950, upper Llandeilo/lower Caradoc, Benbolt Formation, Tennessee, USA.

**F. PALAEOCYSTITIDAE** Ubaghs, 1968


First: Palaeocystites tenuiradiatus (Hall, 1847) and P. dawsoni Billings, 1858, Llandeilo, New York, USA and Canada.

Last: Bromidocystis sinclairi Sprinkle, 1982, Pooleville Member, Bromide Formation, Oklahoma, USA.

**F. SCHUCHERTOCYSTIDAE** Bassler, 1950

- **O.** (LNN/LLO) Mar.

First and Last: Schuchertocystis radiata Bassler, 1950, Middle Ordovician, Tennessee, USA.

'Superfamily' PARACRINOIDA' Regnells, 1945

**F. COMAROCYSTITIDAE** Bather, 1899


First: Sinclairocystis praedicta Bassler, 1950, Bromidocystis Bed, Bromide Formation, Oklahoma, USA.


**F. AMYGDALOCYSTIDAE** Jaekel, 1900


First: Oklahamocystis birachiatius Parsley, 1982 and O. tribachiatius (Bassler, 1943), Upper Echinoderm Zone, Bromide Formation, Oklahoma, USA.

Last: Achradocystites greeningii Von Volborth, 1870, Upper Ordovician, Estonia, former USSR.

**F. PLATYCYSTITIDAE** Parsley and Mintz, 1975


First: Platyocystites levatus Bassler, 1943, Lower Echinoderm Zone, Bromide Formation, Oklahoma, USA.

Last: Platyocystites cristatus Bassler, 1943, Upper Echinoderm Zone, Bromide Formation, Oklahoma, USA.

**F. MALOCYSTITIDAE** Bather, 1899


First: Malocystites murchisoni Billings, 1857, Canadocystis barrandeii Billings, 1858 and C. emmonsii Hudson, 1905, LLO of USA and Canada.

Last: Wellerocystis kimmswickensis Foerster, 1920, Upper LLO/Lower CRD, Missouri, USA.

**F. BISTOMIACYSTIDAE** Sprinkle and Parsley, 1982


First: Bistomiacystis globosa Sprinkle and Parsley, 1982, Lower Echinoderm Zone, Bromide Formation, Oklahoma, USA.

**Order** UNNAMED HIGHER TAXON COMPRISING CRYPTOCRINOIDS, PARACRINOIDS, CORONATES AND BLASTOIDS

Paul (1988) considers each of these groups to be monophyletic and to belong to a larger monophyletic group with *Bockia* as its latest common ancestor.

**Plesion** (Genus) BOCKIA Gekker, 1938

- **O.** (ARG2?/LNN—L. CRD) Mar.


Last: Bockia neglecta Gekker, 1938, lower Caradoc, eastern Baltic.

'Superfamily' CRYPTOCRINIDA' Bassler, 1938

There has been little recent work on this 'superfamily'.

**F. CRYPTOCRINITIDAE** Bassler, 1938

- **O.** (ARG2?/LNN/LLO—CRD) Mar.

First: Cryptocrinites ? similis Bockelie, 1981, Asaphus expansus Shale, Vækerø Farm, Oslo, Sweden. The earliest definite record is Cryptocrinites laevis (Pander, 1830), from the *Echinopharaerites* Limestone Pulkova, near Leningrad, former USSR.

Last: Foerstycystis obliqua Bassler, 1950, upper Llandeilo/lower Caradoc, Tennessee, USA.

The Coronata have been reviewed recently by Donovan et al. (1983).

**F. MESPILOCYSTINA’** Barrande, 1887

- **O.** (F. MESPILOCYSTIDAE) Mar.

First: Mespilocystites barrandeii (Barrande, 1887), Kopanina Formation, Trubsko, Czechoslovakia.

Last: Stephanoblastus mirus (Barrande, 1887), Kopanina Formation, Lodenice, Czechoslovakia.
Comment: Material identical to Stephanoblastus angulatus Conrad, 1842 has been described from the Ludlovian of Kashmir, but this record (Gupta and Webster, 1971) is now considered unreliable.

Class BLASTOIDEA Say, 1825

F. UNNAMED O. (CRD?) Mar.

First and Last: Macuradoblastus uniplicatus Broadhead, 1984, Caradoc, Ben Bolt Formation, Tennessee, USA.

Comment: Poor preservation of this material precludes ordinal or familial assignment of this species.

Order FISSICULATA Jaekel, 1918

The fissiculate blastoids have been comprehensively reviewed by Breimer and Macurda (1972) and by Macurda (1983). Their classification scheme is adopted here. However, since the spiracular blastoids are considered to have had a polyphyletic origin from several different fissiculate ancestors, then the fissiculate families in question must necessarily be paraphyletic. Hence the current classification of blastoids cannot be considered to reflect their phylogeny.

Many blastoids were described from Timor, Indonesia, particularly from the Basleo Beds, Sonnebait ‘Series’. Although the Basleo faunas have been regarded as Upper Permian in age, recent information (Webster, 1987, 1990) strongly suggests that they are of Artinskian or even Sakmarian age.

F. PHAENOSCHISMATIDAE Etheridge and Carpenter, 1886 S. (WEN)–C. (VRK?) Mar.

First: Decaschisma pulchellum (Miller and Dyer, 1878), Waldron Shale, Indiana.

Last: Undescribed phaenoschismatids A and B, Gene Autry Formation, Oklahoma, USA.

F. OROPHOCRINIDAE Jaekel, 1918

D. (EMS)–P. (SAK) Mar.


Last: Anthoblastus stelliformis Wanner, 1924, Basleo Beds, Timor, Indonesia.

F. NYPHAEOBLASTIDAE Wanner, 1940

D. (EMS)–P. (ROT) Mar.

First: Pachyblastus dicki Breimer and Macurda, 1972, Bokkeveld Beds, South Africa and Belen Formation, Bolivia.


F. ASTROCRINIDAE Austin and Austin, 1843


First: Astrocrinus sp., Meenymore Formation, Republic of Ireland (Waters and Sevastopulo, 1984).

Last: Astrocrinus tetragonus (Austin and Austin, 1843), Charlestown Main Limestone, Scotland, and other formations of the same age in England, UK and the Republic of Ireland.

F. NEOCHISMATIDAE Wanner, 1940


First: Hadroblastus blairi (Miller and Gurley, 1895), Chouteau Limestone, Missouri, USA.

Last: Fragmentary neoschismatid, Oxtrack Formation, Bowen Basin, Queensland, Australia (Breimer and Macurda, 1972).

F. CODASTERIDAE Etheridge and Carpenter, 1886


First: Codaster acutus M'Coy, 1849, Middle Limestone, Yorkshire, and other formations in England, UK and the Republic of Ireland.


F. CERATOBLASTIDAE Breimer and Macurda, 1972

P. (ART) Mar.

First and Last: Ceratoblastus nanus Wanner, 1940, Basleo Beds, Timor, Indonesia.

Order SPIRACULATA Jaekel, 1918

The spiraculates are no longer considered a natural taxon, and may have had a polyphyletic origin from at least seven fissiculate ancestors (Horowitz et al., 1986). The classification adopted here is essentially that used in the Treatise on Invertebrate Paleontology, with modifications based on Horowitz et al. (1986).

F. TROOSTICRINIDAE Bather, 1899

S. (WEN)–P. (ART) Mar.

First: Troosticrinus reinwardti (Troost, 1835), Laurel Limestone, Indiana, USA.


F. HYPEROBLASTIDAE Fay, 1964


First: Conuloblastus mallalai (Etheridge and Carpenter, 1893), Santa Lucia Formation, Spain.

Last: Petaloblastus ovalis (Goldfuss, 1821), Übergangskalke, Ratingen, Germany, or Petaloblastus boletus (Schmidt, 1930), Isenburg, Germany.

F. PENTREMITIDAE d’Orbigny, 1851

C. (HAS–CHE/MEL?) Mar.


Last: Pentremites rusticus Hambach, 1903, Boyd Formation, Arkansas, and equivalent formations in Oklahoma, USA.

F. AMBOLOSTOMATIDAE Horowitz et al., 1986

C. (ARU) Mar.

First: Ambolostoma baileyi Peck, 1930, Brazor Formation, Great Blue Limestone, Utah, USA.

UNNAMED FAMILY Horowitz et al., 1986

C. (HAS) Mar.

First and Last: ‘Pentremoblastus’ subovalis Fay and Koenig, 1963, McCraney Limestone, Missouri, USA.

The remaining five families of spiracular blastoid have yet to be revised and reinterpreted, hence their validity as natural taxonomic groups remains uncertain. The classification used below is that of Fay (1967) as in the Treatise on Invertebrate Paleontology.
F. DIPLOBLASTIDAE Fay, 1964  
First: *Diploblastus kirkwoodensis* (Shumard, 1863), St Louis Limestone, Missouri, USA.  
Last: *Nodoblastus librovitchi* (Yakovlev, 1941), Namurian, Daibar Mountain, Aktyubinsk Province, Kazakhstan, former USSR.  
Comment: *Diploblastus* is found as early as the Arenig in Estonia, former USSR.  

F. GRANATOCRINIDAE Fay, 1961  
First: *Tanaoblastus roemeri* (Shumard, 1855) and *Poroblastus chouteaunensis* (Peck, 1930), Chouteau Limestone, Missouri, USA.  

F. SCHIZOBLASTIDAE Etheridge and Carpenter, 1886  
First: *Schizoblastus aplatus* (Rowley and Hare, 1891), lower Burlington Limestone, USA.  
Last: *Deltoblastus elongatus* (Wanner, 1940) and other species of *Deltoblastus*, Basleo and Amarissi Beds, Timor, Indonesia.  

F. NUCLEOCRINIDAE Bather, 1899  
First: *Elaeocrinus verneuli* Roemer, 1851 and *E. venustus* (Miller and Gurley, 1895), Onondaga Limestone and equivalents, east and mid-west USA.  
Last: *Nucleocrinus elegans* Conrad, 1842, Tully Limestone, New York, USA.  

F. ORBITREMITIDAE Bather, 1899  
First: *Doryblastus melonianus* (Schmidt, 1930), Velbert, Germany.  

DIPOLOPORIC CYSTIDS  
Paul and Smith (1984) and Paul (1988) consider the diplopore cystids to be paraphyletic or even polyphyletic. The relationship of the stemless sphaeronitid diplopores to other cystoids is reasonably well understood, but the phylogenetic position of all other diplopores, which encompass both stemmed and stemless forms, remains unknown. They are grouped together here solely for convenience.  

**Class** DIPLOPORITA Müller, 1854  

**Superfamily** SPHAERONITIDAE Neumayr, 1889  

*Plesion* (Genus) LICHENOIDES Barrande, 1887  
First and Last: *Lichenoides priscus* Barrande, 1887, upper Middle Cambrian, Jince Formation, Czechoslovakia.  
Comment: Paul (1988) considers *Lichenoideos* to be sister group to all sphaeronitids.  

F. SPHAERONITIDAE Neumayr, 1889  
Last: *Eucystis flavus* (Barrande, 1887), Azzel Mathi, central Sahara, Morocco. Other representatives of this genus are found in equivalent strata in France, Algeria and Czechoslovakia.  

**Superfamily** PROTOCRINITIDAE Bather, 1899  

F. PROTOCRINITIDAE Bather, 1899  
First: *Protocrinites fragum* (Eichwald, 1840), Duboviki Formation, Pulkowa and Zarskoje Selo, former USSR.  
Last: *Eumorphocystis multiporata* Branson and Peck, 1940, lower Echinoderm Zone, Bromide Formation, Oklahoma, USA.  

F. GOMPHEOCYSTITIDAE Miller, 1889  
First: *Pyrocystites pirum* Barrande, 1887, Wosek, Bohemia, Czechoslovakia.  
Last: *Gompheocystites hurnockeri* Foerster, 1920, Cedarville Dolomite, Ohio, USA.  

F. DACTYLCYSTIDAE Jaekel, 1899  
First: *Dactylocystis schmidti* Jaekel, 1899, and *Estonocystis antropoffi* Jaekel, 1918, *Hemicosmites* Beds, Reval, Estonia, former USSR.  
Last: *Revalocystis mickwitzi* Jaekel, 1899, lower Echinoderm Zone, Bromide Formation, Oklahoma, USA.  

**Superfamily** ASTEROBLASTIDAE Bather, 1900  

F. ASTEROBLASTIDAE Bather, 1900  
First: *Asteroblastus sublaevis* Jaekel, 1899, Walchow Formation, Pulkowa, former USSR.  
Last: *Metasterocystis microelta* Jaekel, 1918, lower LLN, Kunda Formation, Estonia and rest of former USSR.  

F. MESOCYSTIDAE Bather, 1899  
O. (ARG/LLN1) Mar.  
First and Last: *Mesocystis pusirefskii* (Hoffman, 1866), Walchow or Kunda Formation, Leningrad, former USSR.  

**Superfamily** ARISTOCYSTITIDAE Neumayr, 1889  

F. ARISTOCYSTITIDAE Neumayr, 1889  
First: Calix dorecki Sdzuy, 1955, Leimitz-Schiefern, Frankenwald, Germany.
Last: ‘Holocystites’ gyrinus Miller and Gurley, Racine Dolomite, Wisconsin, USA.

Class RHOMBIFERA Zittel, 1879
Paul and Smith (1984) and Paul (1988) regard and in fistuliporite rhombiferans evolved independently, and hence these two groups are not closely related. The relationship of hemicosmitid rhombiferans to other cystoids remains even less clear. The Order Rhombifera, as recognized in the Treatise, clearly is polyphyletic, but is retained here for the sake of convenience.

Order FISTULIPORITA Paul, 1968

Plesion (Genus) NOLICHUCKIA Sprinkle, 1973
C. (MER) Mar.
First and Last: Nolichuckia casteri Sprinkle, 1973, Dresbachian, Cedaria Zone, Nolichucky Formation, Virginia and Tennessee, USA.

F. ECHINOSPHAERITIDAE Neumayr, 1889
First: Echinopsphaerites aurantium Gyllenhaal, 1772, Kunda Formation, Reval, Estonia, former USSR. Bockelie (1981) reports that E. aurantium may also occur in the Upper Arenig of Estonia, former USSR.

F. CARYOCYSTITIDAE Jaekel, 1918
First: Helicocrinites echinoides Leuchtenberg, Walchow Formation, Pulkowa and Zarskoje Selo, former USSR. The precise age of this record is uncertain. The first definite record is Helicocrinites araneus (von Schlotheim) and H. balticus (Eichwald) from the Kunda Formation, Reval, Estonia, former USSR.

F. STICHOCYSTIDAE Jaekel, 1918
First: Stichocystis sp., Shihtzepu Shale, Kweichou, China (Sun, 1936).
Last: Stichocystis geometria (Angelin, 1878), Kullsb erg Limestone, Dalarna, Sweden.

Order DICHOPORITA Jaekel, 1899

Superfamily GLYPTOCYSTITIDA Bather, 1899

Plesion (Genus) AKADOCRINUS Sprinkle, 1973
Comment: Paul (1988) considers Akadocrinus to be derived from Gogia and to be primitive sister group to all Glyptocystitida.

F. GLYPTOCYSTITIDAE Bather, 1899
Last: Glyptocystites multipora Billings, 1854, lower Trenton, Kirkfield Formation, central Ontario, Canada.

F. CYSTOBLASTIDAE Jaekel, 1899
First: Cystoblastus leuchtenbergi Volborth, 1867, Echinopsphaeritidae Limestone, Pavlosk, former USSR.
Last: Cystoblastus kokeni Jaekel, 1899, Kuckers Shale, Kuckers, Estonia, former USSR.

F. RHOMBIFERIDAE Kesling, 1962
O. (CRD) Mar.
First and Last: Rhombifera bohemia Barrande, 1887, CRD, Wraz, Bohemia, Czechoslovakia.

F. CHEIROCRINIDAE Jaekel, 1899
O. (TRE)–S. (GLE/GOR) Mar. (see Fig. 25.2)
First: Cheirocrinites antiqua Paul, 1972, upper TRE, Fillmore Limestone, Utah, USA.
Last: Cheirocrinus tertius Barrande, 1887, upper WEN/lower LUD, Lodenitz and Sedlitz, Bohemia, Czechoslovakia.
Comment: Paul (1968) has described an isolated pectinirhomb plate, possibly a cheirocrinid, from the uppermost Cambrian, Whipple Cave Formation, of Sawmill Canyon, Nevada, USA.

F. ECHINOENCRIPTITIDAE Bather, 1899
First: Echinoencriptites angulosus (Pander, 1830), upper ARG, Walchow Formation, Leningrad, former USSR.

F. PLEUROCYSTITIDAE Neumayr, 1889
First: Two undescribed species, Ninemile Shale, Nevada, and Fillmore Formation, Utah, USA (Sprinkle, 1990).

F. CALLOCYSTITIDAE Bernard, 1895
First: Lepadocystis moorei (Meek, 1871), Elkhorn Formation, Indiana and Ohio, USA.
Last: Strobilocystis schucherti Thomas, 1924, Shell Rock Formation, Nora Springs, Iowa, USA.

F. MACROCYSTELLIDAE Bather, 1899
First: Macrocyrtences cf. mariae Callaway, 1877, Dictyonema flabelliforme Zone, Moel Llyfnant, Gwynedd, Wales, UK (Paul, 1984).
Last: Mimocystites bohemicus Barrande, 1887, Letna Beds, Bohemia, Czechoslovakia.
Comment: Paul (1988) considers Macrocyrtences to be primitive sister group to all glyptocystitids with pectinirhombs. The earliest representative of the Macrocyrtences–glypto-
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| 1. Cheirocrinidae |
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| 3. Pleurocystitidae |
| 4. Calloccystitidae |
| 5. Macrocestellidae |
| 6. Rhipidocystitidae |
| 7. Asocostryitidae |
| 8. Hemicosmitidae |
| 9. Caryocrinitidae |
| 10. Heterocystitidae |
| 11. Thomacystitidae |
| 12. Echmatocrineae |
| 13. Zygodiplobathrina |
| 14. Endiplobathrina |
| 15. Compsocrinina |
| 16. Glyptocrinina |
| 17. Homocrinidae |
| 18. Calceocrinidae |
| 19. Pisocrinidae |
| 20. Allagecrinidae |
| 21. Catillocrinidae |

| 22. Acolocrinidae |
| 23. Anamesocrinidae |
| 24. Haplocrinidae |
| 25. Tunguskocrinidae |
| 26. Cincinnaticrinidae |
| 27. Myelodactyloidae |
| 28. Iocrinidae |
| 29. Eustenocrinidae |
| 30. Ramseyocrinidae |
| 31. Tornatiocrinidae |
| 32. Anomalocrinidae |
| 33. Blemnocrinidae |
| 34. Holynocrinidae |
| 35. Pygmaeocrinidae |
| 36. Sybathocrinidae |
| 37. Zopiacrinidae |
| 38. Peritocrinidae |
| 39. Paradoxocrinidae |
| 40. Dendocrininae |
| 41. Cystitidae |
| 42. Taxocrinidae |
| 43. Sagenocrinida |
| 44. Articulata |
| 45. Enocrinidae |
| 46. Dadocrinidae |

| 497 |
cystitid clade is *Cambrocrinus regularis* Orlowski, 1968, from the Upper Cambrian, Dresbachian, *Olenus* Beds, Holy Cross Mountains, Poland.

F. Rhipidocystidae Jaekel, 1901


First: *Lingulocrinus boliviensis* Sprinkle, 1973b, Sella Mendez Province, south Bolivia.


Comment: Paul (1988) considers the rhipidocystids to represent one of two monophyletic clades, which together constitute the sister group to the *Cambrocrinus*–glyptocystitid clade.

F. Ascocystitidae Ubaghs, 1967


First: *Paracrinus ljuhozovi* Yakovlev, 1956, upper Middle Cambrian or lower Upper Cambrian, east Siberia, former USSR.

Last: *Asccystites drabowensis* Barrande, 1887, MIDDLE Ordovician, Bohemia, Czechoslovakia.

Comment: The Ascocystitidae represent the second of the two monophyletic clades mentioned above and are sister group to the Rhipidocystidae.

**Superfamily** Hemicosmitida Jaekel, 1918

The relationship of hemicosmitids to other cystoids is unclear, although Paul (1988) suggests that their origin may lie among the Coronata.

F. Hemicosmitidae Jaekel, 1918


Last: *Hemicosmites sculptus* Bockelie, 1979, ‘Stage’ 5b ‘reef’ limestone, Ringerike, Oslo, Norway.

F. Caryocrinitidae Bernard, 1895


Last: *Striablocystites elongatus* Rowley, 1900, Bailey Limestone, Montana, USA.

F. Heterocystitidae Jaekel, 1918

S. (WEN) — Mar.

First and Last: *Heterocystites arnatus* Hall, 1851, Shelby Dolomite, Lockport, New York, USA.

F. Thomacystitidae Paul, 1969

O. (RAW) — Mar.

First and Last: *Thomacystis tuberculata* Paul, 1969, Rhiwlas Limestone, Bala, Gwynedd, Wales, UK.

**Class** Crinoidea Miller, 1821

The most recent classification of the Crinoidea, as used in the *Treatise on Invertebrate Paleontology*, is far from satisfactory, and cannot be considered to reflect the phylogeny of the group on even the coarsest scale. Of the five presently accepted subclasses, the Echmatocrinea cannot even be regarded with any certainty as crinoids, while the Inadunata is an obviously paraphyletic taxon incorporating the stem groups of several major crinoid clades. The Flexibilia and Articulata appear to represent monophyletic clades, whose origins lie among the ‘inadunates’, while the Camerata may represent another monophyletic clade perhaps sharing a common ancestry with one of the early ‘inadunates’, or else derived from them.

**Subclass** Echmatocrinea Sprinkle and Moore, 1978

**Order** Echmatocrinida Sprinkle and Moore, 1978

F. Echmatocrinidae Sprinkle, 1973

€. (STD) — Mar.


Comment: The phylogenetic position of this species remains uncertain and it is questionable whether it should even be referred to the Echinodermata.

**Subclass** Camerata Wachsmuth and Springer, 1885

Within the Camerata, it has been assumed that the orders Monobathrida and Diplobathrida are monophyletic, although monophyly is far less probable at subordinal level and below. Camerate suborders are differentiated primarily on the basis of the arrangement of plates in the cup, features which may well have arisen more than once through convergence, rather than on the presence of particular autapomorphies. Hence they are unlikely to represent natural taxa. At still lower taxonomic levels, it is probable that a few, highly distinctive, families represent monophyletic clades but the validity of many others as natural groupings is highly questionable. In consequence of this, the compilation below has been taken only to subordinal level.

**Order** Diplobathrida Moore and Laudon, 1943

**Suborder** Zygodiplobathrida Ubaghs, 1953


First: *Cleioocrinus bromides* Kolata, 1982, lower Echinoderm Zone, Bromide Formation, Oklahoma, USA.

Last: *Spyridocrinus cheuxi* (Oehlert, 1889), Limestone with *Spirifer paradoxus*, Angers, France.

**Suborder** Eudiplobathrida Ubaghs, 1953


First: *Proexenocrinus inyoensis* Strimple and McGinnis, 1972, Al Rose Formation, California, USA.

Last: *Rhodocrinus baccatus* Wright, 1939, Lower Limestone Group, Scotland, UK.

**Order** Monobathrida Moore and Laudon, 1943

**Suborder** Compsocrinrida Ubaghs, 1978


First: *Celtocrinus ubaghisi* Donovan and Cope, 1989, Brunel Beds, middle Arenig, Dyfed, South Wales, UK.

Last: *Neoamptocrinus sp.* nov., Liveringa Formation, Hardman Member, Canning Basin, Western Australia (Webster, 1990).

**Suborder** Glyptocrinida Moore, 1952

First: Abludoglyptocrinus laticostatus Kolata, 1982, upper Pooleville Member, Bromide Formation, Oklahoma, USA.

Last: Plesiocrinus pyriformis Wanner, 1937, Eutelecrinus paciliformis Wanner, 1916 and various species of Platy­

crinidae, Neoplatyocrinitidae and Pleurocrinus. All from Basleo Beds, Timor.

Comment: A late Permian age for the Basleo Beds is now considered uncertain and they are probably of Artinskian

or even Sakmarian age (Webster, 1987, 1990).

'Subclass' INADUNATA Wachsmuth and Springer, 1885

The 'subclass' Inadunata is the least clearly resolved of all Palaeozoic crinoid groups. It includes three orders, of which two, the Disparida and Hybocrinida, may be mono­

phyletic. The emended classification of the Disparida used here has enabled stratigraphical ranges of this group to

be compiled down to family level, but this has proven impossible for the Hybocrinida, which probably have been subdivided unnecessarily, and the Cladida. Instead these are listed at ordinal level. The Cladida include stem-group representatives of the Articulata and Flexibilia, and hence are demonstrably paraphyletic. At subordinal level, it is also clear that the Dendrocrinina and Poteriocrinina represent grades of development rather than natural groupings, such that the former are paraphyletic and the latter probably polyphyletic. The situation is even worse at lower taxonomic levels. Investigation of the articulate stem group (Simms and Sevastopulo, 1993) has shown that various genera, which cladistic analysis shows to lie close to the common ancestry of post-Palaeozoic crinoids, have been distributed in at least four disparate superfamilies. Furthermore, re-examination of those cladid families which lie close to the articulate stem group (e.g. Ampelocrinidae, Cymbiocrinidae) reveals that fewer than 25% of the constituent genera can justifiably be retained in these families, the remainder being uninterpretable on the data available or, in at least 25% of cases, wrongly assigned altogether. It is evident from even a cursory examination of the relevant part of the Treatise, that this problem is not confined to the articulate stem group, but pervades almost the entire classification of Palaeozoic crinoids. Consequently, it is impossible to justify listing the first and last occurrence of cladid crinoids at a taxonomic level any lower than suborder.

Order DISPARIDA Moore and Laudon, 1943

The subdivision of the Disparida follows the Treatise on Invertebrate Paleontology, with a few additions and modifications. However, the reader should be aware that this classification leaves a good deal to be desired. The superfamilies recognized in the Treatise each either contain only one family or probably are not monophyletic and are, therefore, not used in this compilation. The age of the many crinoids described from the Basleo Beds of Timor raises problems in assessing the ranges of several families of disparids. The Basleo fauna is regarded here as being of Sakmarian or Artinskian age rather than the late Permian age usually assigned to it (see comments under Blastoididae). However, because the Basleo fauna is from widely scattered localities it is possible that it contains some Upper Permian forms. Families based entirely on stem material are not listed.

F. HOMOCRINIDAE Kirk, 1914


First: Iheocrinus lepton Lane, 1970, Kanash Shale, Utah, USA.

Last: Homocrinus parus Kirk, 1914, Rochester Shale, New York, USA.

F. CALCEOCRINIDAE Meek and Worthen, 1869


First: Paracameocrinus laticardinalis Brower, 1977, Mountain Lake Member, Bromide Formation, Oklahoma, USA.

Last: Epialyssiocrinus tuberculatus (Yakovlev, 1927), Boetzky Suite, Urals, former USSR.

F. PISOCRINIDAE Angelin, 1878


Last: Triarctinus granulatus Münster, 1839, and T. pyriformis Münster, 1839, both FAM, Thuringia, Germany.

F. ALLAGECRINIDAE Carpenter and Etheridge, 1881


First: Allagecrinus americanus Weller, 1930, Louisiana Limestone, Missouri, USA.

Last: Metallagecrinus palermoensis Strimple and Sevastopulo, 1982, Sosio Limestone, Sicily, or possibly one of several species of Metallagecrinus or Wrightocrinus from Timor (?Upper Permian).

F. CATILLOCRINIDAE Wachsmuth and Springer, 1886


First: Myococrinus boletus Schultz, 1866, Myococrinus conicus Springer, 1923, or Myococrinus granulatus Jaekel, 1895, all EIF, Germany.

Last: Notiocalloctonus cephalus (Willink, 1978), Wandrawandian Siltstone, New South Wales, Australia, or possibly species of Isoctillocrinus, Neoctillocrinus, Paracatillocrinus or Xenocatillocrinus, all from Basleo Beds, Timor.

Comment: Acolocrinus Kesling and Paul, 1971, and Agostocrinus Kesling and Paul, 1971, placed in this family in the Treatise, are now assigned to the Acolocrinidae (see below).

F. ACOLOCRINIDAE Brett, 1980


First: Acolocrinus sp. (Sprinkle, 1982), ? early CRD, Tulip Creek or McLish Formations, Oklahoma, USA, or Acolocrinus hydraulicus Kesling and Paul, 1971, Benbolt Formation, Tennessee, and Virginia, USA.

Last: Paracolocrinus paradoxus Brett, 1980, Rochester Shale, New York, USA.

F. ANAMESOCRINIDAE Goldring, 1923


First and Last: Anamesocrinus lutheri Goldring, 1923, Laona Sandstone, New York, USA.

F. HAPLOCRINITIDAE Bassler, 1938


Last: Haplocrinetes boitardi (Rouault, 1847), Pineres Formation, Cantabrian Mountains, Spain.

Comment: Records of Silurian and Carboniferous haplocrinid families are regarded as erroneous.

F. TUNGUSKOCRINIDAE Arendt, 1963

First and Last: Tunguskocrinus iowanovae Arendt, 1963, ‘Middle’ Ordovician, Mangazeyan Stage, Stolbovaya Suite, former USSR.

First: Cincinnaticrinus pentagonus (Ulrich, 1882), Bull Fork Formation, Ohio, USA.

Last: Cincinnaticrinus ventricosus (Lane, 1970), Kanosh Shale, Utah, USA.

Comment: Warn and Strimple (1977) introduced the family Cincinnaticrinidae to replace Heterocrinidae Zittel, 1879, which was recognized in the Treatise. This family probably has been assigned incorrectly to the Disparida.

F. MYELODACTYLIDAE S. A. Miller, 1883

First: Myelodactylus canaliculatus (Goldfuss, 1826), Kerbelec Formation, Brittany, France, and Skaly Beds, Poland.

Last: Myelodactylus sculptus Ulrich, 1882, Bull Fork Formation, Iowa, USA.

F. EUSTENOCRINIDAE Ulrich, 1925

First: Eustenocrinus antiquus (Wachsmuth and Springer, 1877), both from upper EMS, Trebotov Limestone, Czechoslovakia.

Last: Two undescribed species of Eustenocrinus, upper EMS, Trebotov Limestone, Czechoslovakia (Prokop, 1987).

Comment: This family is not known.

F. SYNBATHOCRINIDAE S. A. Miller, 1889

First: Synbathocrinus campanulatus (Wanner, 1916), Callythara Formation, Western Australia. Wanner described these taxa from the Basleo Beds of Timor, which were considered to be late Permian in age, but Webster (1987) has described the same species from the Basleo Beds of Timor, which were considered to be late Permian in age, but Webster (1987) has described the same species from strata of undoubted ART or SAK age in Australia.

Comment: This family is not recognized in this compilation.

F. ZOPHOCRINIDAE S. A. Miller, 1892

First: Zophocrinus howardi S. A. Miller, 1892, Laurel Limestone, Indiana, USA.

Last: Zophocrinus quadrifons Schultzze, 1866, EIF, Germany.

F. BELEMNOCRINIDAE S. A. Miller, 1883

First: Belemnocrinus sampsoni S. A. Miller, 1891, Chouteau Formation, Missouri, USA. More probably B. whitei Meek and Worthen, 1866, or B. pourtalesi Wachsmuth and Springer, 1877, both from lower Burlington Limestone, Iowa, USA.

Last: Belemnocrinus typus White, 1865, or Whiteocrinus florifer (Wachsmuth and Springer, 1877), both from upper Burlington Limestone, Iowa, USA.

F. PERISSOCRINIDAE Strimple, 1963
Invalid.

McIntosh (1979) has shown that this family was based on abnormal cladid crinoids. The systematic position of the one (monotypic) genus of disparid crinoids has been shown to be incorrect.

F. HOLYNOCRINIDAE Bouska, 1948
D. (EMS) Mar.

First: Holynocrinus moorei Bouska, 1948, and H. spinifer Bouska, 1948, both upper EMS, Trebotov Limestone, Czechoslovakia.

Comment: Bouska (1947) refers, without details, to other species of Haplocrinus from the Silurian, while Prokop (1987) cites the first occurrence of the genus as Lochkovian (= Gedinnian).

F. SYNTHOCRINIDAE S. A. Miller, 1889

First: Synthocrinus antiquus Strimple, 1952, Henryhouse Formation, Oklahoma, USA.

Last: Synhoplocrinus campanulatus (Wanner, 1916), Callythara Formation, Western Australia. Wanner described these taxa from the Basleo Beds of Timor, which were considered to be late Permian in age, but Webster (1987) has described the same species from strata of undoubted ART or SAK age in Australia.

Comment: This family is not recognized in this compilation.
F. PARADOXOCRINIDAE Moore and Laudon, 1943
P. (SAK/ART or ZEC) Mar.


Comment: This family is unlikely to have been assigned correctly to the Disparida.

Order HYBOCRINIDAE Jaekel, 1918

First: Undescribed hybocrinid, lower Arenig, Fillmore Formation, Utah, USA (Guensberg and Sprinkle, 1990).

Last: Cornucrinus longicornis Regnell, 1948, basal Silurian, Dalmanitina Beds, Dalarna, Sweden.

Order CLADIDA Moore and Laudon, 1943

Three suborders are recognized in the Treatise within the Cladida; the Dendrocrinina, Poteriocrinina and the Cyathocrinina. The Cyathocrinina probably represent a monophyletic taxon but the Dendrocrinina and Poteriocrinina are clearly grade groups, representing primitive and derived taxa respectively within a continuum, and hence have no natural basis.

Suborders DENDROCRININA Bather, 1899, and POTERIOCRININA Jaekel, 1918

First: Aethocrinus moorei Ubaghs, 1969, Schistes de St Chinnian, Hérault, France.

Last: Notocrinus ornatus (Etheridge, 1892), Gerringong Volcanics, New South Wales, Australia.

Comment: Since the Articulata represent, in effect, the crown group of the Cladida, the apparent gap between the last cladids and the first articulates is entirely an artefact of collecting and/or documentation. Crinoids occur in some species from the Basleo Beds of Timor. These strata are now considered to be ART or SAK in age (Webster, 1987) rather than Upper Permian. The latest undoubted cyathocrinid is Gissocrinus ? sp., from the KUN, Catherine Sandstone, central Queensland, Australia.

Suborder CYATHOCRININA Bather, 1899
O. (LL03/CRD)–P. (KUN/2ZEC) Mar.

First: Palaeocrinus hudsoni Sprinkle, 1982, and Cerobocrinus treadwelli Sinclair, 1945, lower Echinoderm Zone, Bromide Formation, Oklahoma, USA.

Last: Numerous genera and species are listed in the Treatise as from the Basleo Beds of Timor. These strata are now considered to be ART or SAK in age (Webster, 1987) rather than Upper Permian. The latest undoubted cyathocrinid is Gissocrinus ? sp., from the KUN, Catherine Sandstone, central Queensland, Australia.

Subclass FLEXIBILIA Zittel, 1895

Order TAXOCRINIDAE Springer, 1913
O. (LLN1)–P. (SAK) Mar.

First: Archaeocrinus burfordi Lewis, 1981, Oil Creek Formation, southern Oklahoma, and A. lanei Lewis, 1981, Kanosh Shale, Utah, USA. These two species are referred tentatively to the Taxocrinida by Lewis (1981), but may well be ancestral to both Taxocrinida and Sagencocrinida.

Last: Nevadacrinus geniculatus Lane and Webster, 1966, Bird Spring Formation, Battleship Wash, Nevada, USA.

Order SAGENOCRINIDAE Springer, 1913

First: Proanisocrinus oswegoensis (Miller and Gurley, 1894), Maquoketa Group, Oswego, Illinois, USA.

Last: Trimalicrinus tunisiensis Lane, 1979, and Strobocrinus brachiatus Lane, 1979, Guadalupian, Djebal Tebaga, Tunisia.

Subclass ARTICULATA Miller, 1821

The classification scheme adopted here for the Articulata is based largely upon that of Simms (1988), but has been modified in the light of more recent work. Several major clades (Encrinidae, Isocrinina, Pentacrinitidae with Comatulidia) can be identified within the Articulata, but at lower taxonomic levels the classification used here cannot be considered to reflect relationships between these groups, and in need of considerable revision. Conflicting classification schemes exist for some groups within the Articulata, but it is not possible to take account of these here.

F. HOLOCRINIDAE Jaekel, 1918
Tr. (SPA–CRN) Mar.

First: Holocrinus smithi (Clark, 1915), Mid-Spathian, Thaynes Limestone, Idaho, and equivalent strata in adjacent states, USA.

Last: Holocrinus lunatus (Kristen-Tollmann, 1975), lower CRN, Hallstätter Kalk, Taurus Mountains, Turkey.

Comment: The Holocrinidae is a paraphyletic taxon which includes stem members of the encrinids, isocrinids and pentacrinitids. It is retained here, pending further data concerning the precise relationships of these three derived groups.

F. ENCRINIDAE Dujardin and Hupé, 1862
Tr. (ANS–CRN) Mar.

First: Encrinus terebratularum Schmid, 1876, lower ANS, Lower Muschelkalk, Gogolin Beds, Silesia, Poland.

Last: Traumatocrinus caudex (Dittmar, 1868), middle CRN, lowermost Raibl Beds, Italy.

F. DADOCRINIDAE Lowenstam, 1942
Tr. (SPA–ANS) Mar.

First: Dadocrinus kunischi (Wachsmuth and Springer, 1887), upper Spathian, Röt, Silesia, Poland.

Last: Dadocrinus sp., middle ANS, lower Muschelkalk, Terebratula Beds, Silesia, Poland.

Order ISOCRINIDAE Simms, 1988
Tr. (LAD)–Rec. Mar.

The Order Isocrinina comprises four families, of which two, the Isocrinidae and Cainocrinidae, are demonstrably paraphyletic, the Proisocrinidae is monotypic and has no fossil record, and only the Isselicrinidae is monophyletic. Hence they have not been subdivided here.

First: Isocrinus laevigatus (Münster, 1841), Laevigatocrinus ? venustus (Klipstein, 1845), Tyroleocrinus subcrenatus (Münster, 1841), and ‘Isocrinus’ propinquus (Münster, 1841), upper LAD, Pachycardia Beds, Italy.

Extant

Order COMATULIDINA Clark, 1908

The present classification of the comatulids, as outlined in the Treatise, is unsatisfactory and is considered unlikely to reflect phylogenetic relationships within the group. Furthermore, most fossil comatulid material is undiagnostic at higher taxonomic levels and hence stratigraphical range...
can be ascertained with confidence for only a few distinctive comatulid groups. The classification used here is essentially that of the *Treatise*, with minor revisions where appropriate.

**F. PENTACRINITIDAE** Gray, 1842
Tr. (NOR/RHT)–J. (OXF) Mar.


*Last*: Pentacrinites sp., upper Oxfordian, Oolithe Corallienne, France.

*Comment*: The pentacrinitids are primitive sister group to the comatulids.

**Superfamily** PARACOMATULACEA Hess, 1951

**F. EOCOMATULIDAE** Simms, 1988
Tr. (NOR)–J. (PLF)

*First*: Eocomatula sp. nov. Simms, in press. Chambara Formation, Shalypayco, central Peru.

*Last*: Eocomatula interbrachiatus (Blake, 1876), upper Pliensbachian, *margaritatus* Zone, Deddington, Oxfordshire, England, UK.

**F. PARACOMATULIDAE** Hess, 1951
Tr. (NOR)–K. (I.) Mar.

*First*: Paracomatula sp. nov. Hagdorn, in press, NOR, New Caledonia.

Infra-order COMATULIDIA Clark, 1908

F. ATELECRINIDAE Bather, 1899
First: Jaekelometra gisleni Rasmussen, 1961, Upper Chalk, Båstad, Sweden. Extant

Superfamily SOLANOCRINITacea Jaekel, 1918

F. SOLANOCRINITIDAE Jaekel, 1918
First: Palaeocomaster styricus Kristan-Tollmann, 1988, Allgäu Beds, lower part of Lias alpha, Salzkammergut, Austria.
Last: Comatulina janenschi (Sieverts-Doreck, 1958), Middle Chalk, Halberstadt, Germany.

F. DECAMERIDAE Rasmussen, 1978
First: Coelometra campichei (de Loriol, 1879), VLG, Switzerland and France.
Last: Decameros wortheimi Peck and Watkins, 1972, Glen Rose Limestone, Texas, USA.

F. THIOLLIERICRINIDAE Clark, 1908
Last: Heberticrinus algarbiensis (de Loriol, 1888), HAU, Algarve, Portugal.
Comment: Klikushin (1987a) considers the Bathonian material not to be attributable to the Thiolliericrinidae. Morphologically and stratigraphically there is little to separate the latest thiolliericrinid from the earliest bourgueticrinid. If a direct relationship between these two groups is proven, which seems highly probable, then the Thiolliericrinidae are a paraphyletic group.

F. BOURGUETICRINIDAE de Loriol, 1882
First: Bourgueticrinus sp., upper lower TUR, Belbeck Valley, Crimea, former USSR (Klikushin, 1982). Extant

Superfamily COMASTERACEA A. H. Clark, 1908

F. COMASTERIDAE A. H. Clark, 1908
First: Comaster formae Noelli, 1901, Miocene, Piemonte, Italy.
Last: MARSUPITIDAE d'Orhigny, 1852
K. (SAN) Mar.
First: Uintacrinus socialis Grinnel, 1876, lower part of testudinarius Zone, England, UK.
Last: Uintacrinus anglicus Rasmussen, 1961, top of testudinarius Zone, England, UK.

Comment: Cladistic analysis indicates that marsupitids were derived from the comasterids, despite the earliest record of a typical comasterid being from the Neogene. This discrepancy is attributable almost certainly to the poorly diagnostic nature of disarticulated material from non-marsupitid comasterids.

Superfamily MARIAMETRACEA A. H. Clark, 1909

F. MARIAMETRIDAE A. H. Clark, 1909
Extant Mar.

F. ZYGOMETRIDAE A. H. Clark, 1908
Extant Mar.

F. EUDIOCRINIDAE A. H. Clark, 1907
Extant Mar.

F. HIMEROMETRIDAE A. H. Clark, 1908
First: Hinerometra bassleri Gislen, 1934, Eocene, South Carolina and Louisiana, USA. Extant

F. COLOBOMETRIDAE A. H. Clark, 1909
Extant Mar.

Superfamily TROPIOMETRACEA A. H. Clark, 1908

F. TROPIOMETRIDAE A. H. Clark, 1908
Extant Mar.

F. PTEROCOMIDAE Rasmussen, 1978
First: Pterocoma pennata von Schlotheim, 1813, Solnhofen Limestone, Bavaria, Germany.
Last: Placometra laticirra (Carpenter, 1880), upper DAN, Hvaløsø, Denmark.

F. CONOMETRIDAE Gislen, 1924
First: Undescribed radials, brachials and cirrals, Pliocene, Indonesia (Sieverts, 1933). Extant

F. PTILOMETRIDAE A. H. Clark, 1914
Extant Mar.

F. ASTEROMETRIDAE Gislen, 1924
First: Undescribed radials, brachials and cirrals, Pliocene, Indonesia (Sieverts, 1933). Extant

F. THALASSOMETRIDAE A. H. Clark, 1908
First: Stenometra pellati de Loriol, 1897, Lower Miocene, France.
Last: Cypelometra iheringi de Loriol, 1902, Miocene, Argentina, South America.

F. CHARITOMETRIDAE A. H. Clark, 1909
Extant Mar.

Superfamily NOTOCRINACEA Mortensen, 1918

F. NOTOCRINIDAE J. (BTH)—Rec. Mar.
First: Seminometra abnormis Carpenter, 1880, Bradford Clay, Cirencester, England, UK. Extant
Three families are included within the Roveacrinida, although their relationships to each other and to other articulate groups remain unclear. Extant articulate groups remain unclear, although their relationships to each other and to other

First: *Roiometra* columbiana A. H. Clark, 1944, middle ALB, middle Villeta Formation, Cundinamarca, Colombia, South

America. Extant

Last: Undescribed roveacrinid, Meerssen Member, Maastricht Formation, upper Maastrichtian, Maastricht,

Basin, France.

First and Last: *'Entrochus* silesiacus Beyrich, 1857, upper ANS, middle Muschelkalk, *Diplopora* Dolomite, Silesia,

Poland. Extant

Comment: This species is based on columnals which bear a striking resemblance to those of certain Jurassic millericrinids. They are only tentatively assigned here to the Millericrinida.

F. UNNAMED Tr. (ANS) Mar.

First and Last: *'Entrochus* silesiacus Beyrich, 1857, upper ANS, middle Muschelkalk, *Diplopora* Dolomite, Silesia,

Poland. Extant

Comment: This species is based on columnals which bear a striking resemblance to those of certain Jurassic millericrinids. They are only tentatively assigned here to the Millericrinida.

Suborder MILLERICRINIDA Sieverts-Doreck, 1952

Infra-order MILLERICRINIDIA Sieverts-Doreck, 1952

F. MILLERICRINIDAE Jaekel, 1918

First: *Hemicerinus tithonicus* Pisera and Dzik, 1979, Red

Rogoznik coquina, lower or middle TTH, Rogoznik, Poland.

Last: *Hemicrinus tithonicus* Pisera and Dzik, 1979, Red

Rogoznik coquina, lower or middle TTH, Rogoznik, Poland.

Extant

First: *Capsocrinus sotii* Deloog and Nicosia, 1984, lower
PLB (or lowermost part of upper PLB), western Anatolia, Turkey.

**Last:** *Eugeniacrinites geveyesi* (Loriot, 1897), HAU, St Pierre de Cherenne, France.

**F. PHYLLOCRINIDAE** Jaekel, 1907

**First:** *Phyllocrinus clapsensis* Loriot, 1882, BTH, Bouches-du-Rhône, France.

**Last:** *Phyllocrinus malbosianus* d’Orbigny, 1850 and several other species of *Phyllocrinus*, Neocomian of France, Switzerland, Romania, Spain, Austria, Italy and southern Germany.

**Infra-order** HOLOPODINIDIA Arendt, 1974

**F. EUDESICRINIDAE** Bather, 1899

**First:** *Eudesicrinus cf. maysalis* (Deslongchamps, 1858), lower Lias, *davoei* Zone, Rottorf, southern Lower Saxony, Germany.

**Last:** *Eudesicrinus* sp., upper Lias Junction Bed, bifrons Zone, Ilminster, Somerset, England, UK.

**F. HEMIBRACHIocrinIDAE** Arendt, 1968

**First:** *Hemibrachiocrinus manesterensis* Arendt, 1974, middle Lias, *quenstedti* Zone, Wiirttemberg, Germany. Extant

**Comment:** Pisera and Dzik (1979) consider that there is little justification in separating the Jurassic genus *Hemibrachiocrinus* from the Cretaceous to Recent Cyathidium. This view is maintained here, although the possibility that the holopodid morphology arose more than once, through convergence, cannot be dismissed. *Hemibrachiocrinus* from the Cretaceous to Recent Cyathidium. This view is maintained here, although the possibility that the holopodid morphology arose more than once, through convergence, cannot be dismissed. *Hemibrachiocrinus* sp., lower Middle Cambrian, *davoei* Zone, Ilminster, Somerset, England, UK.

**F. HOLOPODIDAE** Zittel, 1879

**First:** *Cotyledera lineati* Quenstedt, 1852, middle Lias, Württemberg, Germany.

**Comment:** Pisera and Dzik (1979) consider that there is little justification in separating the Jurassic genus *Cotyledera* from the Cretaceous to Recent Cyathidium. This view is maintained here, although the possibility that the holopodid morphology arose more than once, through convergence, cannot be dismissed. *Cotyledera* sp., upper Lias Junction Bed, bifrons Zone, Ilminster, Somerset, England, UK.

**Subphylum** ELEUHEROZOA Bell, 1891

**Plesion** (Genus) STROMATOCYSTITES Pompeckj, 1896 E. (CRF–STD) Mar.

**First:** *Stromatocystites pentangularis* Pompeckj, 1896, and *S. walcotti* Schuchert, 1919, *Olemellus* Beds, Taconian, upper Lower Cambrian, Bonne Bay, Newfoundland.

**Last:** *Stromatocystites* sp., median Middle Cambrian, Eucarpadoxides oelandicus Zone, Sweden (Smith, 1988).

**Plesion** (Class) EDRIOSTEROIDEA Billings, 1858

The classification of edrioasteroids, including *Stromatocystites*, adopted here is that of Smith (1983, 1985).

**Plesion** (Genus) ARKARUA Gehling, 1987

**First and Last:** *Arkarua adami* Gehling, 1987, Ediacaran Member, Flinders Range, South Australia.

**Comment:** This problematic fossil is considered by Gehling to represent the earliest known echinoderm, allied to edro asteroids, a view tentatively accepted by Smith and Jell (1990).

**Order** EDROIasterida Bell, 1976

**F. TOTIGLOBIDAE** Bell and Sprinkle, 1978

**First and Last:** *Tetiglobus nimius* Bell and Sprinkle, 1978, lower Middle Cambrian, Glossopleura Zone, Chisholm Shale, Nevada, USA.

**F. EDRIOSTEROIDEA** Bather, 1898 E. (STD)–O. (SOU/LON) Mar.


**Last:** *Edrioaster bigskyi* (Billings, 1857), *E. priscus* (Miller and Gurley, 1894), *Edriophus levius* (Bather, 1914) and *E. ? saratogensis* (Ruedemann, 1912), Trenton Limestone, Ontario, Canada, and Michigan, USA.

**Order** ISOROPHIDA Bell, 1976

**Plesion** (Genus) CAMBRASTER Cabibet al., 1958 E. (STD) Mar.

**First:** *Cambraster* sp., lower Middle Cambrian, Coonigan Formation, Australia (Jell et al., 1985).

**Last:** *Cambraster canna* (Miquel, 1894), upper Middle Cambrian, *Paradoxides mediterraneus* Zone, Montagne Noire, southern France.

**Plesion** (Genus) EDRIODISCUS Jell et al., 1985 E. (STD) Mar.

**First and Last:** *Edriodiscus primotica* (Henderson and Shergold, 1971), lower Middle Cambrian, upper Ordian, Yelvertoft Beds, west Queensland, Australia.

**F. CYCLOCYSTOIDIDAE** Miller, 1882

**First:** *Paradoxides mediterraneus* O. (ARG)–C. (BRI) Mar.


**Last:** Undescribed ossicles, Meenymore Formation, Sligo, Republic of Ireland (G. D. Sevastopulo, pers. comm., 1989).

**F. AGELACRINITIDAE** Chapman, 1860

**First:** *Isorophusella incondita* (Raymond, 1915), Blackriveran, Decorah Formation, *Phyllioporina* Bed, Minnesota, USA.

**Last:** Unnamed material (Discocystis cf. kaskakiensis) (Hall, 1858), Virgilian Series, upper part of Madera Formation, Guadalupe Canyon, New Mexico (Bell, 1976).

**Order** CYATHOCYSTIDA Bockelie and Paul, 1983

**F. PYRGOCYSTIDAE** Kesling, 1967

**First:** *Pyrgocystites sardesoni* Bather, 1915, Stictopora Bed, Decorah Formation, St Paul, Minnesota, USA.

**Last:** *Rhenopyrgus whitei* Holloway and Jell, 1983, Humevale Formation, Kinglake West, central Victoria, Australia.
Fig. 25.4

F. CYATHOCYSTIDAE Bather, 1898

First: Cyathotheca corallum, Kunda Formation, Leningrad, former USSR.
Last: Cyathotheca suecica Jaekel, 1927, ?Boda Limestone, Dalarna, Sweden. The precise age of this unique specimen is uncertain, and it may be from the lowermost Silurian (Regnell, 1945).

\[\checkmark\] Class ASTEROIDEA de Blainville, 1830

The Class Asteroidea is comparatively poorly represented in the fossil record, and although most material is highly fragmentary, published descriptions have been based largely on intact specimens. The classification of post-Palaeozoic asteroids has been the subject of recent revision by Gale (1987) and by Blake (1987), with the former being adopted here. The relationships of Palaeozoic taxa are still rather poorly understood and the compilation below identifies only plesions considered to be monophyletic.

Plesion UNNAMED

First: Schuchertia stellata (Billings, 1857), Trenton Limestone, Ottawa, Canada.
Last: Palastericus devonicus Sturtz, Hünsrückschiefer, Bundenbach, Germany.


First: Uranaster ramseyensis Hick, Ogof Hên Formation, Movidunian, Ramsey Island, Dyfed, Wales, UK
### Echinodermata

#### TAT
- ELEUTHEROZOA
  - 1. Stromatocystites
  - 2. Arkarua
  - 3. Totiglobidae
  - 4. Edrioasteridae
  - 5. Cambraster
  - 6. Edriodiscus
  - 7. Cyclocystoididae
  - 8. Agelacrinitidae
  - 9. Pyrgocystidae
  - 10. Cyathocystidae
  - 11. Unnamed
  - 12. Unnamed
  - 13. Edrioasteridae
  - 14. Uractinina
  - 15. Pustulosina
  - 16. Monaster
  - 17. Calliasterella
  - 18. Permaster
  - 19. Astrocystidae
  - 20. Luidiidae
  - 21. Goniopectinidae
  - 22. Porcellanasteridae
  - 23. Benthopsectinidae
  - 24. Echinasteridae
  - 25. Gonasteridae
  - 26. Ophiasteridae
  - 27. Astropseidae
  - 28. Sphaerasteridae
  - 29. Arhasteridae
  - 30. Staurasteridae
  - 31. Pycnistidae
  - 32. Poranidae
  - 33. Asterinidae
  - 34. Chaetasteridae
  - 35. Archasteridae
  - 36. Odontasteridae

#### I I

#### KAZ
- ELEUTHEROZOA
  - 1. Stromatocystites
  - 2. Arkarua
  - 3. Totiglobidae
  - 4. Edrioasteridae
  - 5. Cambraster
  - 6. Edriodiscus
  - 7. Cyclocystoididae
  - 8. Agelacrinitidae
  - 9. Pyrgocystidae
  - 10. Cyathocystidae
  - 11. Unnamed
  - 12. Unnamed
  - 13. Edrioasteridae
  - 14. Uractinina
  - 15. Pustulosina
  - 16. Monaster
  - 17. Calliasterella
  - 18. Permaster
  - 19. Astrocystidae
  - 20. Luidiidae
  - 21. Goniopectinidae
  - 22. Porcellanasteridae
  - 23. Benthopsectinidae
  - 24. Echinasteridae
  - 25. Gonasteridae
  - 26. Ophiasteridae
  - 27. Astropseidae
  - 28. Sphaerasteridae
  - 29. Arhasteridae
  - 30. Staurasteridae
  - 31. Pycnistidae
  - 32. Poranidae
  - 33. Asterinidae
  - 34. Chaetasteridae
  - 35. Archasteridae
  - 36. Odontasteridae

#### 1 I

#### ELEUTHEROZOA
- 37. Tropasteridae
- 38. Solasteridae
- 39. Zoroasteridae
- 40. Asteridae
- 41. Brisingidae
- 42. Bothriocidaridae
- 43. Volchoviidae
- 44. Eucladidae
- 45. Sollasinidae
- 46. Rotasaccidae
- 47. Incertae sedis

#### HOLOTHUROIDEA
- 48. Palaeocucumariidae
- 49. Ypsilothuriidae
- 50. Calcclamnidae
- 51. Exlinellidae
- 52. Heterothyoniidae

Fig. 25.4.

**Plesion** (Genus) **MONASTER** Schuchert, 1915

- **P. Mar.**

**First and Last:** *Monaster wandageensis* Kesling, and *M. canarvonensis* Kesling, Wandagee Formation, Wandagee, Western Australia.

**Plesion** (Genus) **CALLIASTERELLA** Schuchert, 1914

- **C. (MOS–KAS) Mar.**

**First:** *Calliasterella mira* (Traustchold), Mosquensis Limestone, Mjatschkowa, Moscow, former USSR.

**Last:** *Calliasterella americana* Kesling and Strimple, 1966, LaSalle Limestone, Missourian, Livingston Co., Illinois, USA.

**Plesion** (Genus) **PERMASTER** Kesling, 1969

- **P. Mar.**

**First and Last:** *Permaster grandis* Kesling, 1969, Wandagee Formation, Wandagee, Carnarvon Basin, Western Australia.

**Subclass** NEOASTEROIDEA Gale, 1987

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**Last:** *Petraster speciosus* (Miller and Dyer, 1878), Richmond Formation, Preble County, Ohio, USA.

**Plesion** (Genus) **CNEMIDACTIS** Spencer, 1918

- **O. (RAW) Mar.**

**First and Last:** *Cnemidactis girvanensis* (Schuchert, 1914), Ladyburn Starfish Bed, Drummond Group, Girvan, Scotland, UK.

**Plesion** **URACTININA** Spencer and Wright, 1966

- **O. (LLO–C. (MOS) Mar.**

**First:** *Urasterella huxleyi* (Billings, 1865), Chazyan, Bed 1, Point Rich, Newfoundland, Canada.

**Last:** *Urasterella montana* (Sturowsky, 1874), Mosquensis Limestone, Moscow, former USSR.

**Plesion** **PUSTULOSINA** Spencer, 1951

- **O. (CRD–D. (EIF) Mar.**

**First:** *Hudsonaster narrawayi* (Hudson, 1912), Black River Formation, Ottawa, Canada.

**Last:** *Xenaster margaritatus* (Simonovitsch, 1871), Obere Koblenzschichten, Neiderlahnstein, Germany.
Order PAXILLOSIDA Perrier, 1884
F. ASTROPECTINIDAE Gray, 1840
First: Tethyaster jurassicus Blake, 1986, middle Bajocian, Carmel Formation, Teasdale and St George, Utah, USA.
Extant
F. LUIDIIDAE Verrill, 1889
First: Luidia sp., Miocene, California (Blake, 1973).
Extant
F. GONIOPECTINIDAE Verrill, 1889
First: ’Nymphaster’ radiatus Spencer, 1907, Middle Albian, Kent, England, UK.
Extant
F. CTENODISCIDAE Sladen, 1889 Extant Mar.
F. PORCELLANASTERIDAE Sladen, 1883
First: Palaeoctenodiscus campaniurnis Blake, 1988, CMP, Baja California, USA.
Extant
Order NOTOMYOTIDA Ludwig, 1910
F. BENTHOPECTINIDAE Verrill, 1894
First: Plesiastropecten hallovensis Blake, upper HET, Hallau, Switzerland.
Extant
Order SPINULOSIDA Perrier, 1884
F. ECHINASTERIDAE Verrill, 1867
First: Echinaster jacobseni Rasmussen, upper THA, Fur Formation, Jutland, Denmark.
Extant
F. GANERIIDAE Sladen, 1889 Extant Mar.
F. CHAETASTERIDAE Sladen, 1889
?First: Chaetasterina gracilis Hess, 1970, upper HAU, St Blaise, Neuchatel, Switzerland.
Extant
F. ARCHASTERIDAE Viguier, 1878
?First: Archaster patersoni Spencer, 1915, Miocene, Port Elizabeth, South Africa.
Extant
F. ODONTASTERIDAE Verrill, 1889
Extant
Order VALVATIDA Perrier, 1884
F. GONIASTERIDAE Forbes, 1841
First: Tylasteria berlandi (Wright), upper BAJ, upper Hautptrogenstein, Schinznach-Dorf, Switzerland.
Extant
F. OPHIDIASTERIDAE Verrill, 1867
First: Sladenia fourteauxi de Loriol, 1904, and Chariaaster elegans de Loriol, 1909, SAN, Abou-Roach, Egypt. Extant
F. OREASTERIDAE Fisher, 1911 Extant Mar.
First: Diclidaster geveryi de Loriol, 1897, HET, Ardèche, France.
Extant
F. SPHAERASTERIDAE Schondorf, 1906
First: Sphaeraster annulosus (Quenstedt), Malm alpha, southern Germany.
Extant
F. ARTHRASTERIDAE Spencer, 1918
First: Arthraster dixoni Forbes, 1848, Middle Chalk, T. lata Zone, Amberley, Sussex, England, UK.
Last: Arthraster cristatus Spencer, 1913, White Chalk, Rugen, northern Germany.
F. STAURANDERASTERIDAE Spencer, 1913
First: Aspidaster delgadai de Loriol, 1884, ? CLV, Porcas Valley, near Cinta, Portugal.
Last: Staauranderaster speculum Brunnnich-Nielsen, 1943, upper DAN, Rejstrup, Denmark.
F. ACANTHASTERIDAE Perrier, 1894
F. MITHRODIIDAE Viguier, 1879 Extant Mar.
F. ASTERODISCIDIDAE Rowe Extant Mar.
F. PYCINASTERIDAE Spencer and Wright, 1966
?Last: Pycinaster peyroti Valette, 1925, Stampian, Aquitaine, France.
F. PORANIIDAE Perrier, 1894
F. GANERIIDAE Sladen, 1889 Extant Mar.
F. CHAETASTERIDAE Sladen, 1889
?First: Chaetasterina gracilis Hess, 1970, upper HAU, St Blaise, Neuchatel, Switzerland.
Extant
F. ARCHASTERIDAE Viguier, 1878
?First: Archaster patersoni Spencer, 1915, Miocene, Port Elizabeth, South Africa.
Extant
F. ODONTASTERIDAE Verrill, 1889
Extant
Order VELATIDA Perrier, 1891
F. TROPASTERIDAE Wright, 1880
J. (PLB) Mar.
F. KORETHRASTERIDAE Danielsson and Koren, 1884 Extant Mar.
F. PTERASTERIDAE Perrier, 1884 Extant Mar.
F. SOLASTERIDAE Perrier, 1884
First: Solaster murchisoni (Williamson, 1884), lower PLB, Lower Staithe Formation, davoei Zone, Robin Hood’s Bay, Yorkshire, England, UK.
The fossil record of holothurians consists largely of dissociated sclerites, together with rare occurrences of calcareous ring and/or body fossil material. Most fossil families have been defined on sclerite morphotypes, i.e. as parafamilies. The classification here follows that of Gilliland (1992), Blue Lias Formation, Lodgopele Limestone, Madison Group, Montana, USA. This species could equally be referred to the Paracucumidae (Order Dendrochirotida). The oldest unequivocal species is Palaeocucumaria hunsrückiana (Gutschick et al., 1967), Lodgopele Limestone, Madison Group, Montana, USA. The wheel Microantyx permiana Kornicker and Imbrie, 1958, is found associated with these goniodonts but, although characteristic of ophiocistioids, this morphotype is not restricted to this group and hence these remains cannot be considered conspecific.

**Order** ARTHROCHIROTIDA Seilacher, 1961

**Parafamily** CALCLAMNIDAE Frizzell and Exline, 1966 D. (Lok/Pra) Mar.

*First and Last:* *Palaeocucumaria* hunsrückiana Lehmann, 1958, Hunsrückschiefere, Rhineland, Germany.

**Order** DACTYLOCHIROTIDA Pawson and Fell, 1965

*First:* *Crinothuria* sp., upper Burdigalian, Chita Peninsula, Russia. *Extant* Mar.


The fossil record of holothurians consists largely of dissociated sclerites, together with rare occurrences of calcareous ring and/or body fossil material. Most fossil families have been defined on sclerite morphotypes, i.e. as parafamilies. The classification here follows that of Gilliland (1992) in which, where possible, fossil species are referred to the Recent holothurians, i.e. families (F.), and extinct parafamilies synonymous with the level of 'biological family' (P.[F]) below. Many species, however, cannot be assigned satisfactorily and these are discussed under their respective parafamilies (P.).

**Plesion** (Order) *OPHIOSTICIODIDA* Sollas, 1899

The Ophiocistioida, globose echinozoa with plated tube feet, a lantern apparatus and 'goniodonts', are included here as probable stem-group holothurians.

**F. VOLCHOVIIDAE** Hekker, 1938

*O. (Arg–LLN1)* Mar.


*First* and *Last:* *Eucladia johnsoni* Woodward, 1869, lower Ludlow Shales, Dudley, England, UK.

**F. SOLLASINIDAE** Fedotov, 1926

S. (Gle)–D. (ElF) Mar.

*First* and *Last:* *Rotasacus dentifer* Haude and Langenstrassen, 1976, upper Wiedenester Schichten, Drolshagen, Überbergisches Land, Germany.

**F. INCERTAE SEDIS** (Order) BOTHRIOCIDAROIDA Klem, 1904

This systematic position of the three known bothriocidarid genera remains unclear. They have been widely held as primitive echinoids, while Smith (1984b) interpreted them as stem Holothuroidea. They are classified here as a separate plesion allied to the stem group of both echinoids and holothurians.

**F. BOTHRIOCIDARIDAE** Klem, 1904


*First:* *Unibothriocidaris bromadiensis* Kier, 1982, and *Bothriocidaris kolatai* Kier, 1982, Pooleville Member, Bromide Formation, Oklahoma, and *B. soleni* Kolata, 1975, and *Neobothriocidaris* sp., Platteville Formation, Illinois, USA.


**Class** HOLOTHUROIDEA de Blainville, 1834

The fossil record of holothurians consists largely of dissociated sclerites, together with rare occurrences of calcareous ring and/or body fossil material. Most fossil families have been defined on sclerite morphotypes, i.e. as parafamilies. The classification here follows that of Gilliland (1992) in which, where possible, fossil species are referred to the taxonomy of Recent holothurians, i.e. families (F.), and extend parafamilies synonymous with the level of 'biological family' (P.[F]) below. Many species, however, cannot be assigned satisfactorily and these are discussed under their respective parafamilies (P.).

**Plesion** (Order) *OPHIOSTICIODIDA* Sollas, 1899

The Ophiocistioida, globose echinozoa with plated tube feet, a lantern apparatus and 'goniodonts', are included here as probable stem-group holothurians.

**F. VOLCHOVIIDAE** Hekker, 1938

*O. (ARG–LLN1)* Mar.
Comment: These three parafamilies include 'basket-like' sclerites similar to those found in several families of the Dendrochirotida.

F. HETEROTHYONIDAE Pawson, 1970  
Tr. (LAD)–Rec. Mar.  
First: Strobilothyone rogente Smith and Gallemi, 1991, La Riba Reef Formation, Catalonia, Spain (known from many body fossils).  
Extant

F. PSOLIDAE Perrier, 1902  
Tr. (LAD)–Rec. Mar. (see Fig. 25.5)  
First: Monilipsolus mirabile Smith and Gallemi, 1991, La Riba Reef Formation, Catalonia, Spain (known from many body fossils).  
Extant

F. PARACUCUMIDAE Pawson and Fell, 1965  
C. (?HAS)–Rec. Mar.  
First: Clavallus spicaudina (Gutschick et al., 1967), Lodgepole Limestone, Madison Group, Montana, USA (see comments on Ypsilothuriidae above).  
Extant

Order ASPIDOCHIROTIDA Grube, 1840  
Early records of the order include two taxa, known from body fossils, whose familial position is uncertain: Bathysynactites viai Cherbonnier, 1978, tentatively referred to the Aspidochirotida, from the Muschelkalk of Catalonia, Spain (ANS/LAD), and Collbatothuria danieli Smith and Gallemi, 1991, from the La Riba Reef Formation, Catalonia, Spain (LAD).
null
**First: Staurocumites bartensteini** Deflandre-Rigaud, 1952, Hallstätt facies, Eastern Alps, Germany. 'Staurocumites-type' table are only questionably referred to the Molpadiidae. *Priscopedatus* sp. 5 Speckmann, 1968, a 'Priscolongatus-type' table (Gilliland, 1992a), recorded from the same strata, is also questionably referred to the Molpadiidae. The next oldest record is calcareous ring Type 1 Gilliland (1992a), from the Blue Lias Formation (HET), Warwickshire, England, UK; the sclerite morphospecies from the same 'biological' species as this calcareous ring is interpreted to be *S. bartensteini*. The next unequivocal sclerites of the Molpadiidae are several taxa, including *Calcancorella spectabilis* Deflandre-Rigaud, 1959, from the Middle Oligocene, Schleswig-Holstein, Germany. 

**Extant**

Comment: Sclerites of the *Punctatitidae* might also be referred to the Molpadiidae.

**F. CAUDINIDAE** Heding, 1931


**First:** Pedatopriscus pinguis (Deflandre-Rigaud, 1946), Oxford Clay, Normandy, France. 

**Extant**

Comment: Tables of the *Priscopedatidae* may be referred to the Caudinidae (see above). The record here is based on a morphotype which can be restricted to the family.

**Order APODIDA** Brandt, 1835

Two early apodid wheel morphospecies cannot be restricted to a particular family (wheels occur in all families except the Achistidae).

*Theelia? hexacneme* Summerson and Campbell, 1958, is recorded from the upper Breathith (upper Pottsville) Formation, Kentucky, USA (BSH). Wheels from the Waulsortian (TOU) of the Republic of Ireland (MacCarthy, pers. comm.) are similar to this species but also resemble ophiocistioid wheels, and hence are not included here. *T. hexacneme* is reported from the Mississippian (PND/ARN) of Slovakia (Kozur et al., 1976), but there are no supporting descriptions or figures.

*Thallatocanthus consonus* Carini, 1962, occurs in the Wewoka Formation, Oklahoma, USA (MYA). Wheels referred to this species by Gutschick et al. (1967) from the Carboniferous (HAS) are referred instead to the Paleochiridotidae.

**F.(P.) PALEOCIRIDOTIDAE** Frizzell and Exline, 1955


**First:** Rota martini Langenheim and Epis, 1957, Escabrosa Limestone, Arizona, USA.

**Last:** Paleochiridota plummerae Croneis, 1932, Keechi Creek Shale, Mineral Wells Formation, Texas, USA.

**F.(P.) ACHISTRIDAE** Frizzell and Exline, 1955


**First:** Porachistrum multitertata Beckmann, 1965, Scutellum-Schichten, Westfalen, Germany.

**Last:** Achistrum isleri Croneis, Palaeocene, Kutch, India. This record (Soodan, 1972) is unaccompanied by either a figure or description. The next youngest species is *Achistrum monochordata* Hodson et al. (1956), Speeton Clay (BRM), Yorkshire, England, UK.

**F. MYRIOTROCHIDAE** Østergren, 1907


**First:** Theelia praecacuta Mostler and Rahimi-Yazd, 1976, Ali Bashi Formation, Ali Bashi Mountains, northern Iran. 

**F. CHIRIDOTIDAE** Østergren, 1898


**First:** Protheelia geinitziana (Spandel, 1898), Zechstein, Thüringen, Germany. 

**F. SYNAPTIDAE** Burmeister, 1837

Tr. (LAD/CRN?)—Rec. Mar.

**First:** Theelia liptovskaeensis Gazdzicki et al., 1978, Korytnica Limestones, Carpathians, Czechoslovakia. This species may belong to the Chiridotidae. The next oldest species is *Theelia synapsa* Gilliland (1992), from the Blue Lias Formation (HET) of Dorset and Warwickshire, England, UK.

**Extant**

### NON-ALIGNED HOLOTHURIAN PARAFAMILIES

**Parafamily** CALCLAMNIDAE Frizzell and Exline, 1955

This parafamily includes fossil plate morphotypes many of which are not holothurian; those that can be referred to the class are included in the relevant families below.

An equivocally included plate taxon which should be noted, because it may prove to be the oldest recorded holothurian, is *Mercedescaudina tripherforata* Schallreuter, 1968, from erratics of the Brick Limestone (Middle Ordovician), Island of Hiddensee, Baltic Sea.

The oldest unequivocal (crown group) holothurian is an undescribed body fossil, complete with calcareous ring and dermal sclerites (Smith and Jell, pers. comm.) from the Upper Silurian (PRD) of Australia. The sclerites, if found isolated, would be assigned to the Calclamnidae.

**Parafamily** PRISCOPEDATIDAE Frizzell and Exline, 1955


**First:** Clavallus spicaudina Gutschick et al., 1967, a spired plate morphotype (see Ypsilothuriidae below). The oldest recorded table, the main morphotype in the Priscopedatidae, is *Priscopedus* sp. nov. Kozur et al., 1976, from the Carboniferous (PND/ARN?) of Slovakia, Czechoslovakia. This record is not accompanied by either a figure or a description and must be considered tentative.

The next oldest (table) species is *Priscopedatus quinquespinosus* Mostler and Rahimi-Yazd, 1976, from the Permian (TAT), *Arexilevis* Zone Limestones, Ali Bashi Mountains, northern Iran. 

**Extant**

Comment: An important parafamily of many fossil species of table and spired plate morphotypes which probably includes taxa from four of the six extant orders. A number of different 'groups' can be recognized, some of which can be assigned, with varying degrees of certainty, to biological families (e.g. *Priscopedus triassicus*-type tables to the Synallactidae). The earliest recorded table species could be accepted questionably as the oldest record of several families of the Dendrochirotida (but not the Heterothyridae, Paracucumidae or Psolidae), the Aspidochirotida or the Caudinidae (Molpadida). 

**Parafamily** PUNCTATITIDAE Mostler and Rahimi-Yazd, 1976

Last: *Punctatites tripexus* Mostler, 1972, 'thin-bedded red-brown limestone', Tyrol, Austria.  
Comment: The rod-shaped sclerites of this parafamily can be referred to either of the orders Dendrochirotida or Molpadiida (Molpadiidae).

**Parafamily** (F.) **KOZURELLIDAE** Mostler, 1972  
Tr. (NOR) Mar.

First and Last: *Kozurella formosa* Mostler, 1972, Hallstätt Limestone, Northern Calcareous Alps, Austria.

**Class** ECHINOIDEA Leske, 1778

Except where indicated, the taxonomic framework adopted here is that of Smith (1984b); authorship and generic plus stratigraphical assignments of species follow Lambert and Thiery (1909–1925) and Kier and Lawson (1978), with some modification of assignment to genera after Mortensen (1928–1951); generic assignments to Palaeozoic families (Subclass Perischoechinoidea) follow Smith (1984b, table 7.1); generic assignments to post-Palaeozoic families (subclasses Cidaroida, Euechinoidea) follow Durham *et al.* (1966) or Kier and Lawson (1978) for subsequent ascriptions. Amendments to these assignments are noted only where they affect the recorded family range.

The important and wide-ranging syntheses cited above only partially correct errors and omissions in the extensive earlier (often nineteenth century) literature, and inevitably introduce a few of their own. Taxonomic and stratigraphical details for species cited below are also based largely on the available literature. Consequently, they are not uniformly consistent in concept, and should be interpreted accordingly. For a consistent attempt to distinguish monophyletic from other echinoid families extinct in post-Palaeozoic time, see Smith and Patterson (1988).

For brevity, references cited for years prior to 1967 are not listed in the bibliography where they may be found in Weisbord's (1971) compendium; more recent references are listed only where absent from the key publications of Kier and Lawson (1978) and Smith (1984b). References additional to authorship of taxonomic names are given only where they add significant taxonomic or stratigraphical data; citations and references deemed insignificant by the editors have been excluded.

**Class** ECHINOIDEA Leske, 1778

**Subclass** PERISCHOECHINOIDEA M'Coy, 1849

**Unnamed stem group**  

Intervening: None.  
Comment: The four genera *Eothuria*, *Aulechinus*, *Ectenechinus* and *Aptilechinus*, although not a monophyletic group, comprise the most primitive true echinoids and include the earliest known echinoid species.

**Subclass** UNNAMED PARAPHYLETIC GROUP  
Order ECHINOCYSTITOIDA Jackson, 1912  
F. ECHINOCYSTITIDAE Gregory, 1897  

Last: *Xenechinus parvus* Kier, 1958, Niel Ranch Formation (Wolfcampian), west Texas, USA.  
Intervening: D1 and C1, known only from single specimens.

**Paraphyletic group** 'PALAEECHINOIDEA' Haackel, 1866

The two monospecific Silurian genera *Myriastiches* and *Koninckocellaris* are placed incertae sedis within this group by Smith (1984b). Their eventual family ascription may necessitate increase in the number of families here recognized in the group, or an extension to the stratigraphical range of at least one family.

**Suborder** PALAEODISCOIDA Smith, 1984

**Unnamed stem group** (= F. PALAEODISCIDAE)  
Gregory, 1897  
S. (GOR) Mar.

First and Last: *Palaeodiscus ferox* Salter, 1857, lower Ludlow, Leintwardine, England. The imperfectly known *P. gothicus* Wyville Thomson, 1861, is from the same locality 'and probably identical with *P. ferox*’ (Mortensen, 1928–1951).

**F. LEPIDOCENTRIDAE** Loven, 1874  
D. (EMS?)—P. (TAT?) Mar.

First: *Lepidocentrus lennaeaus* Wolburg, 1933, *cultrijugatus* Zone (probably Lower Devonian), Lenné, near Schmallenberg, Germany, and Middle Devonian species of *Lepidocentrus* are poorly known. *Lepidocinmodoidea* Hunti Cooper, 1931, Skaneateles Formation, Hamilton Group (Middle Devonian), Ithaca, New York, USA, is the earliest well-documented lepidocentrid.  
Last: * Pronoechinus anatolienis* Kier, 1965, Gomaniubrik Formation, Dijabarkir Province, Turkey (?Dzulfian *fide* Philip, in Harland (1967)).  
Intervening: D3, C.

**F. PALAEECHINOIDEA** M'Coy, 1849  
D. (LOK/EMS?)—C. (HLK?) Mar.

First: *Poreanus porosus* Dehm, 1961, Bundebacher Schiefer, Bundenbach, near Kiri (Nahe), Germany.  
Last: *Melonechinus wielaporus* (Norwood and Owen, 1846), St Louis Limestone, St Louis, Missouri, USA; other species of similar date are more poorly known.  
Intervening: All other known palaechinids are early Carboniferous in age (Kier, 1965).

**Paraphyletic group** 'ARCHAEOECIDAROIDA' Smith, 1984

**Unnamed stem group**  
D. (FRS?) Mar.

First and Last: *Nortonechinus welleri* Thomas, 1920, Lime Creek Shale, Portland, Iowa, USA (Kier, 1968). Other supposed early archaeocidaroids are known only from spines and isolated plates, so their true ascription remains uncertain. The earliest of these is *Silurocidaridus clavata* Regnêl, 1956 from the Upper Silurian, lower Ludlow: Gotland, Sweden.
F. HYATTECHINIDAE Smith, 1984
C. (HAS/IVO–CHD/ARU?) Mar.

First: Hyattechinus elegans Jackson, 1929, TOU, Belgium; H. dixoni Hawkins, 1935, H. toreumaticus Hawkins, 1935, just above Lower Limestone Shales, Z1 Zone, Pembroke, South Wales, UK, are also TOU.

Last: Perischodomus fraiponti Jackson, 1929, lower VIS. Belgium.

Intervening: All representatives of this family have been recorded only from the Lower Carboniferous (lower Mississippian), but precise age relationships are not known.

F. ARCHAEOCIDARIDAE M'Coy, 1849

(Family name on ICZN Official List: Direction 41).

First: Archaeocidaris nerei (Münster, 1839), TOU, Tournai, Belgium (Jackson, 1929); based on fragmentary material, as are other of the earliest Carboniferous archaeocidaroids. Lepidocidaris squamosa anglica Hawkins, 1935, Carboniferous Limestone (?C Zone), Preston, Lancashire, England, UK is ?upper Tournaisian.

Last: Archaeocidaris immanensis Kier, 1958, Dewey Limestone, Oklahoma, USA is the only well-preserved Upper Carboniferous archaeocidarid; other Upper Carboniferous archaeocidaroids are known only from disassociated test elements. Although Lambert and Thiéry (1909–1925) and Kier and Lawson (1978) together list six supposed archaeocidaroid species from the Permian, Kier (1965) notes that no Permian cidarids with more than two plate columns in each intercalabrum have been found. These species may all be miocidarids.

Intervening: C. (I., u.).

Subclass CIDAROIDEA Claus, 1880
Order CIDAROIDA Claus, 1880

Smith and Wright (1989), in a revised classification and phylogenetic interpretation of this order, recognize only two families (Rhabdocidariae Tr.?–Rec. and Cidariae J. (BAJ)–Rec.) additional to the miocidarids, and only 39 assigned genera/subgenera. The less-satisfactory classification of Durham et al. (1966) is, however, maintained here, pending assignment of the additional taxa of low species diversity which they recognize but which are excluded from the Smith and Wright revision.

F. MIOCIDARIDAE Durham and Melville, 1957

First: Miocidaris connorsi Kier, 1965, Bell Canyon Formation, Texas, USA; M. keyserlingi (Geinitz, 1848), Permian, Hungary, and Ford Formation, Zechstein Cycle 1, Sunderland, England, UK; the only two confidently ascribed species of miocidarids reliably recorded from the Palaeozoic (Kier, 1965). M. cannoni Jackson, 1912, arguably from the Lower Carboniferous of Colorado, USA, is based on a poorly preserved internal mould of uncertain family and generic ascription.

Last: Pachycidaris thieryi Collignon and Lambert, 1928, Upper Jurassic, Europe. (Miocidaris itself is known from several Lower Jurassic species).

Intervening: SCY, LAD–RHT.

Comment: A paraphyletic stem group: ‘Only those miocidarids with a perignathic girdle of apophyses definitely belong to this clade, the others being advanced stem group echinoids, primitive stem group cidaroids or primitive stem group euechinoids’ (Smith and Wright, 1989).

F. Cidaridae Gray, 1825
Tr. (CRN)–Rec. Mar.

First: Leucocidaris montanaro (Zardi, 1973), St Cassian Beds, northern Italy, a true cidarid with apophyses but a species and genus difficult to assign to any family with certainty ‘because nothing is known of its spines, pedicellariae or peristomial plates’ (Kier, 1977). Polycidaris regularis (Münster, 1841) is known only from the holotype, whose Triassic origin is doubted by Kier (1977). Mikrocidaris pentagona (Münster, 1841), referred to the Cidaridae by Kier (1977) rather than to the Miocidaridae as by Durham et al. (1966), is shown to lack apophyses and therefore excluded from the cidaroids by Kier (1984b). Four unnamed species with cidaroid apophyses are, however, known from fragments of the St Cassian Beds. Extant

Intervening: Very few gaps between Tr(u.) and Rec.

F. Psychocidaridae Ikeda, 1936
J. (BAJ)–Rec. Mar.

First: Merocidaris honorinae (Cotteau, 1880), Caenocidaris cucumifera (L. Agassiz, 1840), (Cotteau, 1875–80), Anisocidaris bajocensis (Cotteau, 1880), all Middle Jurassic (BAJ) of Europe and probably referable to genus Balanocidaris sensu Smith and Wright (1989). Levicidaris zardinia Kier, 1977, Megaporocidaris mariana Kier, 1977, both from the St Cassian Beds, northern Italy, were ascribed to the Psychocidaridae by Kier (1977) but later excluded from the cidaroids by Kier (1984b), who observed that they lacked lantern supports (apophyses). Extant


F. Diplocidaridae Gregory, 1900

First: Diplocidaris menchikoffi Lambert, 1937, Lias (upper Domerian), Morocco.

Last: Diplocidaris bicarinata Weber, 1934, Hauterivian, Crimea, former USSR.

Intervening: TOA, J.(m., u.), VLG. The family is clearly polyphyletic, according to Smith and Patterson (1988).

Subclass Euechinoidea Bromm, 1860
Infraclass ECHINOHURIOIDEA Claus, 1880
Coehort ECHINOHURIOACEA Jensen, 1981
Order ECHINOHURIOIDEA Claus, 1880

F. Echinotheriidae Thomson, 1872

First: Echinotheria floris Woodward, 1863, M. corangium Zone, Upper Chalk, Kent, England, UK. Araonosa (?) bruennichi Ravn, 1928, Asthenosoma (?) striatissimum Ravn, 1928 also occur in the Chalk (upper Senonian) of Denmark, but are known only from spines. Such distinctively ‘hoofed’ spines are a feature of Recent echinotheriids; Mortensen (1928–1951) notes that ‘it is likely that one or other of the spines belongs to E. floris’. Extant

Intervening: DAN, PLI.

F. PHORMOSOMATIDAE Mortensen, 1934
Extant Mar.
F. PELANECHINIDAE Groom, 1887
  Last: Pelanechinus corallinus (Wright, 1856), Coralline Oolite, Malton, Yorkshire, and Calne, Wiltshire, England, UK.

Infraclass ACROECHINOIDEA Smith, 1981
Cohort DIADEMACEA Duan, 1889
Order DIADEMATOIDA Duncan, 1889
F. DIADEMATIDAE Gray, 1855
  J. (HET?)–Rec. Mar.
  First: 'Eodiadema' collenoti (Cotteau, 1882), lower Lias, La Verune, near Joyeuse (Arrèche), Semur, and Saulieu, France (Smith, 1990); probably a diadematoid (Smith and Wright 1990, p. 113) although the Lower Jurassic genus, Eodiadema, itself was removed from the Diadematidae sensu Durham et al. (1966) to the new family Eodiadematidae by Smith (1984b). The only unquestionable fossil diadematoid known from more than isolated spines is Centrosthenus fragilis (Wiltshire, in Wright, 1882), Upper Chalk (SAN–CMP), England, UK and France (Smith and Wright, 1990).
  Extant
  Intervening: There are few Cretaceous and Tertiary records.

F. ASPIDODIADEMATIDAE Duncan, 1889
  First: Eosalenia varusense (Cotteau, 1881), Lias, France; referred to genus Eosalenia together with E. miranda Lambert, 1905, Middle Jurassic (BTH), France, and Pedinothuria barottei Lambert and Thiery, 1911, upper BTH, Vesaignes, Haute-Marne, France; new material of Eosalenia with spines shows this to be a true aspidodiadematid (Smith, pers. comm.).
  Extant
  Intervening: There are few Cretaceous and Tertiary records.

F. LISSODIADEMATIDAE Fell, 1966 Extant Mar.
  Order MICROPYGOIDAE Jensen, 1981
  F. MICROPYGIDAE Mortensen, 1904
    J. (OXF?)–Rec. Mar.
    First: Pedinothuria cidaroides Gregory, 1897, Weisser Jura, Upper Jurassic (OXF?), Germany, is possibly an early micropygid (Smith and Wright, 1990). Otherwise this monogeneric family is exclusively Recent, and of deep-water habitat.
    Extant

Order PEDINOIDAEA Mortensen, 1939
  F. PEDINIDAE Pomel, 1883 Tr. (CRN)–Rec. Mar.
  First: Hemipedinia(l)nicipiens Bather, 1990, based on a fragment from the Raibilian (upper CRN) of Bakony, Hungary, is considered by Kier (1977) to be intermediate between the cidaroids and the pedinoids. The earliest certain pedinoid is Hemipedinia hudsoni Kier, 1977, Elphinstone Group (probably Sumra Formation) (NOR), Oman, Arabia.
  Extant
  Intervening: A near-continuous record from early Jurassic to Recent.

Cohort ECHINACEA Claus, 1876
F. PSEUDODIADEMATIDAE Pomel, 1883
  Tr. (RHT)–K. (CMP?) Mar.
  First: Pseudodiadema silbinense Stefanini, 1923, Upper Triassic, Selvena, near Sienna, Italy, 'the only Triassic echinoid that with some certainty belongs to the . . . Echinacea' (Kier, 1977).
  Last: Heterodiadema libycum (Desor, 1846), widely distributed in CEN of North Africa, Middle East, and elsewhere; possibly TUR, arguably CMP. Cainozoic records of this family are of uncertain or originally incorrect assignment.
  Intervening: Good stratigraphical record throughout the Jurassic, early Cretaceous, and especially CEN.
  Comment: Heterodiadema was transferred from the Hemicidaridae by Smith and Patterson (1988).

Superorder STIRODONATA Jackson, 1912
  F. HEMICIDARIDAE Wright, 1857
    J. (HET)–K. (APT) Mar.
    First: Pseudodiadema primaevum Lambert, 1904 = Hessotiara minor Lambert, 1904, lower Lias, Le Simon-la-Vineuse (Vendée), France, although taxonomic position uncertain. The supposed hemicidarid Plesiocidaris florida (Merian, 1855), lower Lias, Gürbefall, Bernese Alps, Switzerland (Desor and de Lorioi, 1868–1872) is a cidarid (Smith, 1990).
    Last: Hemicidaris prestensis (Cotteau, 1863), APT. 'CEN records of Hemicidarids and Pseudocidarids are fragmentary or based on spines and thus inadequate (although they may prove eventually to be correct)' (Smith and Patterson, 1988).

Order CALYCINA Gregory, 1900
  (Synonym of SALENIOIDAE Delage and Hérouard, 1903, fide Smith and Wright (1990).)
    F. ACROSALENIIDAE Gregory, 1900
      J. (HET?)–K. (CMP/MAA?) (p) Mar.
      First: ?Acrosalenia chartroni Lambert, 1904, lower Lias, Revrac, Vendée, France. Kier (1977) does not confirm Lambert and Thiery’s (1909–1925) tentative assignment of A. balsami (Stoppani, 1860) (Tr., RHT) to Acrosalenia, or pre-HET origins of the family. Smith and Patterson (1988) note that pre-AAL species of supposed acrosalenidi are poorly preserved and of dubious taxonomic assignment. The earliest undoubted acrosalenid is probably A. lycetti Wright, 1851, Crickley Oncolite Member, (AAL), Inferior Oolite Group (Smith, 1984b).
      Intervening: Good stratigraphical record through the middle to late Jurassic and early Cretaceous.
      Comment: Recognized as a paraphyletic group by Smith and Patterson (1988); the restricted monophyletic grouping of Smith and Wright (1990) indicates an earlier last appearance.

F. SALENIIIDAE L. Agassiz, 1838
    J. (OXF)–Rec. Mar.
First: Salenia taurica Weber, 1934, Upper Jurassic (Sequanian), Crimea, former USSR. Poropeltaris sculptopunctata Quenstedt, 1875, middle OXF, Natheim, Germany, is ascribed (as a subgenus) to Hyposalenia by Smith and Wright (1990). Extant

Intervening: TTH, NEO (HAU)?; thereafter numerous species provide a near-continuous record for the family.

Order PHYMOSOMATOIDEA Mortensen, 1904

F. PHYMOSOMATIDAE Pomel, 1883
J. (TOA?)–T. (RUP/CHT?) Mar.

First: ?Jaquertiaria minuta Mortensen and Mercier, 1939, Lias, France. Lepthechinus jutieri (Cotteau, 1883), Lias (Charmouthian), Mazenay, France, a supposed earlier phymosomatid, is a cidaroid (Smith, pers. comm.).

Last: Thylechinus sethuramae (Cotteau, 1890). Extant

Porosoma (1981) removed the single genus Glyptocidaris to a new family of its own; hitherto the type species G. heteroporus, 1853 had been regarded as the only known Recent phymosomatid.

Intervening: Diverse through the Cretaceous, Palaeocene and Eocene.

F. GLYPTOCIDARIDAE Jensen, 1981

First: Glyptocidaris heteroporus (Lambert, 1897), Eocene, Aude, France. Lambert and Thiéry (1909–1925) described two species from the Eocene of Alicante, Spain, to a synonym of Glyptocidaris: Heteractis illoreae (Cotteau, 1890). H. vilanovaensis (Cotteau, 1890).

Intervening: Eoc./Oli., PLI.

F. STOMECHINIDAE Pomel, 1883

First: Jeannetia mortensi Mercier, 1937, lower Lias, France; Diplechinus hebbiensis Lambert, 1931, middle Lias (Domerian), (PLB), Morocco, is more commonly regarded as the earliest stomechinid (Mortensen, 1928–1951).

Last: Phymotaxis mansfieldi Cooke, 1941, Suwannee Limestone (Upper Oligocene), Florida, USA.

Intervening: Good stratigraphical record through the Jurassic and Cretaceous.

F. STOMOPNEUSTIDAE Mortensen, 1903


First: Atopechinus cellensis Thiéry, 1928, BTH, Celles, Ardèche; also Acrosaster michaleti Lambert, in Lambert and Thiéry, 1914, also from France.

Intervening: Moderately complete record from Jurassic to Recent.

Superorder CAMARODONTA Jackson, 1912

F. GLYPOCHYPIDAE Duncan, 1889
J. ?(PLB)/K. (HAU)–T. (LUT?) Mar.

First: ?Glyptodiadema cauclaxense (Cotteau, 1878), Lias (Charmouthian), Caylus, France, but too poorly known for certain description (Smith and Patterson, 1988). Hemidiadema neocomiense (Cotteau, 1882), Calcaire à Spatangues, Auxerre (Yonne), France, is the earliest definite record of the family.

Last: Glyphocyphus (Rhabdopleurus) ataxensis Cotteau, 1886, Middle Eocene, France. (Several other Middle Eocene glyphocyphids are known.)


Order TEMNOPLEUROIDA Mortensen, 1941

F. TEMNOPLEUROIDAE A. Agassiz, 1872

First: Glyptechinus montmolini (Desor, 1858), Marnes d’Hauterive, Villers-le-Lac (Doubs), France (Cotteau, 1862–1868).

Intervening: APT–TUR, Eoc., Mio./PLI.

Comment: Jensen (1981), on the basis of differences in tooth microstructure, indicated that this family might be divided into two or perhaps three families.

Order ECHINOIDA Claus, 1876

F. ECHINIDAE Gray, 1825

First: Echinus algirus Pomel, 1885, Pliocene, Algeria.

Extant

Intervening: PLE.

Comment: Jensen (1981) restricts this family to the single genus Echinus; other formerly ascribed genera are included within the Parechiniidae.

F. ECHINOMETRIDAE Gray, 1825

First: ‘Echinometra’ prisca Cotteau, 1875, although the characteristic plates of the apical disc are not preserved. Echinometra thomsoni Haime, 1853, Baluchistan, Pakistan (dated as ?middle Eocene by Philip, in Harland (1967) is shown by Smith (1988b) to be an imperfectly preserved phymosomatoid. The oldest undoubted Echinometra is E. micenica de Loriol, 1902 from the Upper Miocene (TOR) of France (1988) = E. mathaiei (Blainville, 1825), and from the Lower Miocene (BUR) according to Negretti et al. (1990).

Intervening: Mio., PLI, PLE.


First: Psammochinus bernouillensis Valette, 1908, VLG, Yonne, France and some 10 other Cretaceous species have been ascribed to Psammochinus (Lambert and Thiéry, 1909–1925; Kier and Lawson, 1978) plus Eocene species (e.g. P. biarritzensis Cotteau), but true generic ascription is unknown (Mortensen, 1928–1951). Most may be of Spaniochyxus, whose family ascription is uncertain (Durham et al., 1966). True echinids seemingly begin in the Miocene, with many circum-Mediterranean species ascribed to Psammochinus or Stirechinus, and the South American Hypochinus pagatonensis (d’Orbigny, 1842) and Isechinus praecursor (Ortmann, 1904), both from Patagonia. Smith (1988b) accepts ‘Toxopneustes’ bouryi Cotteau, 1883, Upper Miocene, France, as a Paracentrotus and probable early parechinid.

Extant

Intervening: ?Mio., ?PLI.

Comment: Jensen (1981, p. 22, 84) includes, within this family, genera formerly ascribed to the Echinidae, except for the genus Echinus itself.
Suborder HOLECTYPINA Duncan, 1899

F. HOLECTYPIDAE Lambert, 1899

First: Holectypus hians Lambert, 1933, Lias (lower Domerian), Algeria. H. congoensis de Cortazar, 1875, Lias (TOA), Cuenza, Spain, is the only other Lower Jurassic species known.

Last: Caenoholocidum baluchistanense (Noetling, 1897), Upper Cretaceous (MAA), Mari Hills, Baluchistan; C. nachtigali (Krumbeek, 1906), Jebel Tar, Tripolitania, Libya; Caenoholocidum is also known from the Shiranish Marls of Kurdistan.

Intervening: TOA, BAJ–OXF, THI, VLG–CMP.

F. ANORTHOPYGIDAE Wagnor and Durham, 1966

K. (ALB)–(TUR) Mar.

First: Anorthopygus texanus Cooke, 1946, Washita Group, Texas, USA.


Intervening: CEN.

F. DISCOIDIDAE Lambert, 1899


First: Discoidocidum guebhardi Lambert, 1920, Lower Cretaceous, southern France; both species and genus of uncertain assignment (Rose and Olver, 1985). Discoideus rhabbergensis Jeannet, 1933, Austria, and D. karakaschi (Rennergarten, 1926), former southern USSR, have also been dated as HAU.

Last: Metholectypus trechmanni Hawkins, 1923, Cretaceous, Jamaica; genus of uncertain stratigraphical (CMP/MAA), but probable discoidoid assignment (Rose and Olver, 1985). Lanieriæ lanieriæ (Cotteau, 1881), uppermost Cretaceous, Cuba and Mexico, L. ursulana Cooke, 1953, Texas, USA, and possibly Discoideus menchikoffi Lambert, 1937, Morocco, are of at least CMP date.

Intervening: APT–TUR.

Suborder ECHINONEINA H. L. Clark, 1925


First and Last: ?Amblypygus (Paramblypygus) houphouetii Roman, 1973, Palaeocene (THA), Fresco, Ivory Coast, West Africa; a species of uncertain taxonomic ascription. Extant

Intervening: Echinoneus itself has a well-defined stratigraphical record from Oligocene to Recent.

Comment: Amblypygus, placed ‘Family uncertain’ by Durham et al. (1966), is considered to be a true echinoneid by Rose (1982); its earliest species is A. dilatatus L. Agassiz and Desor, 1847, for although typically middle Eocene in age like most Amblypygus species, it ranges from the early Eocene (YPR). The supposed Mesozoic echinoneid Paleochineus (type P. hannai Grant and Hertlein, 1938) is based on an imperfect misidentified specimen of the globatorid Globator.

F. CONULIDAE Lambert, 1911

K. (HUA)–(MAA) Mar. (see Fig. 25.6)
First: *Conulus soubellinsis* Gauthier, 1876, Lower Cretaceous (Neocomian), Algeria; one APT, four ALB species ascribed to the genus by Lambert and Thiéry (1909–1925), Kier and Lawson (1978).

Last: *Conulus chiesai* Airaghi, 1939, *C. sanfilippoi* Checchia-Rispoli, 1930, both Upper Cretaceous (MAA), Libya.

Intervening: APT–CMP.

Comment: Of the four genera assigned by Durham *et al.* (1966) to this family, *Galeraster* is a holasteroid, and *Pygopyrina* and *Globator* should be ascribed to the Globatoridae, leaving only the type genus.

F. GLOBATORIDAE Lambert, 1911

J. (?CLV?)/K. (BRM?–(MAA))/T. (LUT?) Mar.

First: *Pygopyrina icaunensis* (Cotteau, 1855), Upper Jurassic (OXF), Yonne, France, ranging from CLV to KIM according to Lambert and Thiéry (1909–1925), but probably a cassiduloid according to Smith and Patterson, 1988; the few other species ascriptions to *Pygopyrina* are also controversial (Mortensen, 1928–1951).

Last: *Globator ilarionensis* (Dames, 1877), northern Italy, *G. obsoleta* (Bittner, 1880), southern Alps, Austria; both Eocene, but possibly neoglobatorids. Uppermost Cretaceous species include *G. dainellii* Checchia-Rispoli, 1932, Libya, and *G. minuta* (Smiser, 1935), Belgium, both MAA.

Intervening: Mostly Upper Cretaceous, a few Lower Cretaceous.


F. GALERITIDAE Gray, 1825


First: *Galerites ernsti* Schultz, 1985, Upper Cretaceous Chalk, Lägerdorf, Germany. *Galerites globosus* Roemer, 1841, Upper Cretaceous (CON), north-west Europe, is probably referable to *Echinogalerus* and to a separate lineage (Schultz, 1985).

Last: *Galerites stadensis* (Lambert, 1911), Maastrichtian Chalk of north Germany and Denmark.

F. NEOGLOBATORIDAE Endelman, 1980

T. (DAN)–(LUT?) Mar.
First: Neoglobator danicus Endelman, 1980, lower DAN, former USSR. Neoglobator ovalis (Smiser, 1935), Upper Cretaceous (MAA), Belgium is recorded only as DAN by van der Ham (1988), and N. houzei (Cotteau, 1875) occurs below it in the Guelhem chalk (DAN) at Maastricht, The Netherlands.

Last: Neoglobator akkajensis Endelman, 1980, Eocene, former southern USSR. Eocene species currently ascribed to Globator should possibly be reascribed to Neoglobator.

Intervening: THA, YPR.

Superorder MICROSTOMATA Smith, 1984

F. MENOPYGIDAE Lambert, 1911
J. (BAJ?)–(TTH) Mar.

First: Menopogon baugieri (Cotteau, 1873), BAJ–BTH?, France: a poorly known species.

Last: Infraclypeus thalebensis Gauthier, 1875, TTH, Algeria (Devriés, 1960b).

Comment: This family was redefined by Rose and Olver (1988) as a plesion of stem Microstomata which span the whole time range BAJ–TTH.

Series NEOGNATHOSTOMATA Smith, 1981

F. GALEROPYGIDAE Lambert, 1911
J. (PLB)–(OXF) Mar.

First: Galeropygus lacroixi Lambert, 1925, Lias (Domerian), Gémenos, France.

Last: Laticlypus giganteus Szörény, 1966, OXF, Hungary. Stegopolygus langeensensis Devriés and Alcaydé, 1966, CEN, France, is probably referable to the cassiduloid genus Ochetes (Smith, pers. comm.).

Intervening: BAJ, BTH, OXF.

Order CASSIDULOIDA Claus, 1880

F. CASSIDULIDAE L. Agassiz and Desor, 1847

First: Ochetes morrisii (Forbes, 1849), Upper Greensand (ALB), Blackdown, Devon (Kier, 1962b).

Extant: Good stratigraphical record through the Cretaceous and Cenozoic.

F. ARCHIACIDAE Cotteau and Triger, 1869
K. (APT)–(TUR?) Mar.


Last: Claviaster costatus Pomel, 1883, TUR?, Algeria; otherwise Gentilía chouberti Lambert, 1937, upper CEN, Morocco.

Intervening: ALB–CEN.

F. CLYPEIDAE Lambert, 1898

First: Clypeus michelini Wright, 1854, murchisonae Zone, Crickley Limestone Member, Inferior Oolite Group, Cotswolds, England, UK (Smith, 1984b).

Last: Pygurus lampassiformis Tzankov, 1934, Upper Cretaceous (SAN), Bulgaria.

Intervening: Good stratigraphical record through most of the Jurassic and Cretaceous into the Cenomanian.

F. CLYPEOLAMPADIDAE Kier, 1962
K. (CEN)–(MAA) Mar.

First: Vologesia rhotamogesnis (d’Orbigny, 1856), CEN, France, Belgium and England, UK.

Last: Clypeolampas ovatus (Lamarck, 1816), France; also C. vishnui Noëlting, 1897, Vologesia helios (Noëlting, 1897), and other MAA species.

Intervening: CMP.

F. CONOCLYPIDAE Zittel, 1879
T. (THA)–(LUT?) Mar.

First: Conoclypus sindensis (Duncan and Sladen, 1882), Ranikut Series, Petiani, Pakistan (C. sanctispiritus Sánchez Roig, 1949, Cretaceous, Cuba, is of uncertain ascription). C. leymerei is of confirmed late THA age in the northern Pyreenees of France and Spain (Plaziat et al., 1974).

Last: Conoclypus rostratus (Duncan and Sladen, 1884), Khirtlar Series, hills east of Trak, western Sind, Pakistan. (C. westraliensis Crespin, 1944, Middle Miocene, Australia, is a misidentified Echinolampas (Hypsoclypus), like other Miocene records of this family (Roman, 1965).)

Intervening: Eoc.

F. ECHINOLAMPADIDAE Gray, 1851


Extant: TUR–SAN, DAN–PLE.

Comment: The genus Arnaudaster is known from only one species, and that from a single specimen (Kier, 1962b).

F. FAUJASIIDAE Lambert, 1905

First: Faujasia araripensis Beurlen, 1956, Brazil, and F. rancherina Cooke, 1955, Colombia, are both cited from the Lower Cretaceous (ALB), although Kier (1962b) and Durham et al. (1966) do not record the genus before MAA and family before CEN. Petalobrissus inflatus (Thomas and Gauthier, 1889), P. daglenis (Thomas and Gauthier, 1889), both CEN, Tunisia, are of confirmed ascription and age. Stigmatopygus malheirio de Loril, 1888, CEN, Angola, lacks recent description.

Last: Australanthus longianus (Gregory, 1890), Upper Eocene, Australia.

Intervening: CEN–MAA, Eoc.

F. NUCLEOLITIDAE L. Agassiz and Desor, 1847
J. (BAJ)–Rec. Mar.

First: Nucleolites latiporus (Duncan and Sladen, 1884), both Inferior Oolite (parkinsoni Zone upwards) England, UK and France, Nucleolites terquemi L. Agassiz and Desor, 1846, BAF, France.


F. PLIOLAMPADIDAE Kier, 1962

First: Gitolampas tunetana (Gauthier, 1889), CMP, Midès, Tunisia; possibly Zuffardia sanfilippoi (Checchia-Rispoli, 1914), Senonian, Tripoli, Libya. The earlier Breyella (= Pliolampas) baixadoleitensis Maury, 1934, TUR?, Rio Grande do Norte, Brazil, is of uncertain ascription. Several species of Gitolampas, e.g. G. lamberti Checchia-Rispoli, 1921, G. zuffardii Checchia-Rispoli, 1921, are of undivided Senonian age, and so may be slightly earlier than CMP.
Intervening: Good record from the late Cretaceous through the Tertiary to the Recent.

**Order Oligopygoidea Kier, 1967**

F. **OLIGOPYGOIDAE** Duncan, 1889

T. **(LUT?–PRB?)** Mar.

First: ?Oligopygus phelani Kier, 1967, Inglis Limestone Formation, Florida, USA. (Most species of Haimea, and several of Oligopygus, have been recorded from supposed Middle Eocene strata, including many from the Yellow Limestone of Jamaica, so the true first occurrence is likely to be one of these species.)

Last: O. wetherbyi de Loril, 1888, O. haldemani (Conrad, 1850); Crystal River Formation, near Ocala, Florida, USA.

**Comment:** Kier (1967) restricted this family to Oligopygus and Haimea (including Bonaireaster in synonymy), with 12 valid (plus 10 inadequately known) species and 13 valid (plus six inadequately known) species respectively. The age of most of the species relative to each other is unknown. Some are reported from the Middle Eocene, others from the Upper Eocene, but these age determinations are too unreliable to be used. Of all the species, there are only three whose stratigraphical relationships are certain (Kier, 1967, p. 47).

**Order Clypeasteroida A. Agassiz, 1872**

**Unnamed stem group?** T. **(THA?)** Mar.

**First and Last:** Togocymus seefriedi (Oppenheim, 1915), Ekekoro Formation, 55 km NW of Lagos, Nigeria; T. allocyrenei Roman and Gorodiski, 1959, Senegal; both Palaeocene, of West Africa.

**Comment:** The genus Togocymus, known from only two species and classified as a fibularid by Durham et al. (1966), has been reinterpreted both as the most primitive clypeasteroid yet known (Smith, 1984b) and as the sole representative of an entirely extinct sister group to Order Clypeasteroida (Mooi, 1990).

**Suborder Clypeasterina A. Agassiz, 1872**

F. **CLYPEASTERIDAE** L. Agassiz, 1835


First: Clypeaster marbellensis (Boussac, 1911), Auversian, Biarritz, France. Reguant et al. (1970) also record Clypeaster nov. sp. in the Middle Eocene (upper Biarritzian) of Vic (Barcelona), Spain.

**Intervening:** Excellent stratigraphical record from late Eocene to Recent.

F. **ARACHNODIDAE** Duncan, 1889

T. **(CHT?)**–Rec.

First: Fellaster zelandiae (Gray, 1855), the type and then the only known species was given an Oligocene–Recent range by Durham et al. (1966).

**Intervening:** Known from a few Recent and Neogene taxa.

F. **FOSSULASTERIDAE** Philip and Foster, 1971

T. **(CHT?–Mio.)** Mar.

First: Fossulaster halli Lambert and Thiéry, 1925, and Willungaster scutellaris Philip and Foster, 1971, grouped by Philip and Foster (1971) within the new family Fossulasteridae: a taxon overlooked by Smith (1984b); both Upper Oligocene or Lower Miocene (Jankukian or Longfordian), South Australia.

**Last:** Scutellinoides patella (Tate, 1891), Morgan Limestone, Murray River Cliffs, South Australia (Foster and Philip, 1971).

**Intervening:** Mio.

**Suborder Scutellina Haeckel, 1896**

**Infraorder Fibulariina Smith, 1984**

F. **FIBULARIIDAE** Gray, 1825

T. **(YPR)–Rec.** Mar.

First: Fibularia jeanneti (Lambert, 1931), Egypt; F. planus (Lambert, 1933), Madagascar, off East Africa; both dated as early Eocene. F. cyphostomus (Lambert, in Lambert and Jacquet, 1936), Senegal, West Africa, has been redated as middle Eocene (LUT). Records of supposed fibulariids, Echinocyamus placenta (Goldfuss, 1826) and Fibularia subglobosus (Goldfuss, 1826), from the Upper Chalk of St Pieters, Holland (K., MAA) conditionally accepted by Durham (in Durham et al., 1966) and by Philip (in Harland, 1967) lack confirmation; E. kamrupensis Das Gupta, 1929, upper Senonian, India, is of doubtful taxonomic assignment. Numerous species variously ascribed to Echinocyamus and Fibularia have an imprecisely known Eocene range, and several may extend back to at least the early Eocene. Porpitella paleocenica, (upper THA), northern Pyrenees (France and Spain), is certainly Palaeocene, but Porpitella is excluded from the Fibulariidae by Mooi (1989). **Extant Intervening:** Good stratigraphical record through the Eocene to the Recent.

**Infraorder Laganina Mortensen, 1948**

**Superfamily Laganidae A. Agassiz, 1873**

F. **LAGANIDAE** Desor, 1858

T. **(YPR)–Rec.** Mar. (Family name on ICZN Official List: Opinion 608.)

First: Sismondia barabirensis Lambert, 1931, Lower Eocene, Egypt; many of the 30 species ascribed to Sismondia are of imprecise Eocene date. The oldest known Laganum is L. sorigneti Cotteau, 1890, Eocene, France. **Extant Intervening:** Good stratigraphical record from Eocene to Recent.

F. **ROTULIDAE** Gray, 1855

T. **(BUR)–Rec.** Mar.

First: Rotuloida vieirai Dartevelle, 1953, upper Burdigalian, Angola, south-west Africa. **Extant Intervening:** Mio., PLI.

F. **Neolaganidae** Durham, 1954


First: Durhamella ocalanum (Cooke, 1942), Lake City Formation (Middle Eocene), Georgia, USA.

Last: Neorumphia elegans (Sanchez Roig, 1949), Upper Oligocene, Cuba. **Intervening:** Eoc., Oli.

**Superfamily Scutellidea Smith, 1984**

F. **Scutellidae Gray, 1825**

T. **(RUP?–TOR)** Mar.

First: Scutella isseti Airaghi, 1901, S. lamberti Airaghi, 1901, S. marianii Airaghi, 1901, all from northern Italy, and three other species of Scutella are accepted by Lambert and Thiéry (1909–1925) as of Tongrian (early Oligocene) date, although...
generic ascription should perhaps be to Parascutella or Parmulechinus (sensu Durham, 1953). S. camaguyana Weisbord, 1934, S. cubae Weisbord, 1934, both late Eocene, Cuba, and other ‘New World species are unlikely to be Scutella’ (Mooi, 1989).

Last: Scutella vindobonensis Laube secunda Schaffer, 1962, middle to upper Tortonian, Austria.

Intervening: Oli.–Mio.

F. ASTRICLYPEIDAE Stefanini, 1911


First: Echinodiscus duffii (Gregory, 1911), Lower Oligocene, Cyrenaica, Libya (Checchia–Rispoli, 1913). E. ginaeensis Clegg, 1933, Lower Tertiary, Persian Gulf, and E. chikuzenensis Nagao, 1928, Palaeogene, Japan, are less precisely dated.

Extant

Intervening: Mio.

Comment: Echinodiscus tiliensis Wang, 1984, attributed to the Tachien Sandstone, Lower Eocene or Upper Palaeocene, Taiwan, on the appearance of its sandstone matrix, is known only from the holotype, found in a museum collection at the National Taiwan University. The age attribution is inconsistent with present views of the origin not only of Scutellidae but the entire Clypeasteroida (Mooi, 1989) .

F. DENDRASTERIDAE Lambert, 1889


First: Merriamaster lamberti (Grant and Hertlein, 1938), California, USA is accepted as of middle Miocene age by Kier and Lawson (1978), although Mooi (1989) gives the earliest record for the genus as ?late Miocene, and Durham (1978) excludes both lamberti and Miocene records from the genus.

Extant

Intervening: Mio., PLI.

F. ECHINARACHNIIDAE Lambert, 1914


First: Kewia sp., Upper Eocene, Oregon, USA (Linder et al., 1988). K. marquamensis Linder, Durham and Orr, 1988, Scotts Mills Formation, Oregon, USA is the best documented of the earliest (Upper Oligocene) named species.

Extant

Intervening: Mio., PLI.

F. MELLITIDAE Stefanini, 1911


First: Encope kugleri Jeannet, 1928, E. vonderschmitti Jeannet, 1928, and E. wiedenmayeri Jeannet, 1928, all Serie de Capadare, Venezuela, are cited as Middle Miocene by Kier and Lawson (1978). Durham et al. (1966) cite the early Miocene as the time of first occurrence for the family.

Extant

Intervening: PLI.

F. EOSCUTELLIDAE Durham, 1955

T. (PRB?)–Mar.


Comment: This monogenic family (Durham et al., 1966) is not adopted by Smith (1984b, p. 172) in his classifica-

F. MONOPHORASTERIDAE Lahille, 1896

T. (YPR?–BUR?) Mar.

First: Iheringiella patagoniensis (Desor, 1847), from the Lower Miocene of Argentina according to Durham (1955), but Larrain (1984) extends this range into Chile and from the Lower (Middle ?) Eocene to the Miocene (?) according to Mooi (1989).

Last: Karlaster pirabensis Marchesini Santos, 1958, Miocene, Brazil. Monophoraster darwini (Desor, 1847), and the two other species ascribed to Monophoraster, from Argentina and Chile, are also of imprecise Miocene age, so none of these species may extend beyond the range of Iheringiella patagoniensis.

F. PROTOSCUTELLIDAE Durham, 1955


First: Protoscutella mississippiensis (Twitchell, 1915), Winona Sand Member of Lisbon Formation, Mississippi, and Mount Selman Formation, Texas, USA. Four other species of Protoscutella are also known from the Middle Eocene and south-east USA.

Last: Periarchus (Mortonella) quinquefaria (Say, 1825), Sandersville Limestone Member of Barnwell Formation, Georgia, USA; a few other species of Protoscutella, Mortonella, and Periarchus are also known from the Upper Eocene of the south-east USA.

Order NEOLAMPADOIDA Philip, 1963

F. NEOLAMPADIDAE Lambert, 1918


First: Pisolampas concinna Philip, 1963, Tortachilla Limestone (lower Upper Eocene), Aldinga, St Vincent Basin, South Australia.

Extant

Intervening: LMI.

Series ATELOSTOMATA Zittel, 1879

Order DISASTEROIDA Mintz, 1968

F. DISASTERIDAE Gras, 1848


First: Tithonia sarthacensis (Cotteau, 1860), BTH, Sarthe, France; known only from the holotype.

Last: Collyropsis moussoni (Desor, 1858), Gault (ALB), Swiss Alps and Savoy. Possibly also Corthyla ambuyraci Lambert, 1924; cited plausibly as Cretaceous (ALB) by Lambert and Thiéry (1909–1925), but probably incorrectly as late Eocene in age (BRT) by Kier and Lawson (1978).

Intervening: Moderately good late Jurassic (CLV) through early Cretaceous fossil record.

F. COLLYRITIDAE d’Orbigny, 1853

J. (BAJ)–K. (VLG) Mar.

First: Cycolampas kiliani Lambert, 1909, upper BAJ, Chalet de l’Alpe de Villard d’Arcine (Massif des Ecrins-Isère), France; arguably one ammonite zone older than Orbignyana ebraei Cotteau, 1873 (Jablonski and Böttcher, 1990). Pygomaus prior (Desor, 1858), lower Lias, Aargau, Switzerland, and upper Lias, Ardèche, France, a rare, poorly known species, supposedly an earlier collyritid, is now recognized as only an imperfect C. bicordata from the upper OXF.
Fig. 25.7

**Last:** Cardiopelta oblonga (d’Orbigny, 1853), Neocomian, Jura, France.

**Intervening:** J. (m., from BAJ, u.), BER.

**Order** HOLASTEROIDA Durham and Melville, 1957

**First:** H. grasanus d’Orbigny, 1853, Neocomian, Fontanil, Isère, France; Holaster valanginensis Lambert, 1917, Switzerland; H. cordatus Dubois, 1836, former USSR; all recorded from the Lower Cretaceous (VLG).

**Last:** Toxopatagus italicus (Manzoni, 1878), Schlier, Bologna, Italy.

**Intervening:** ALB–Eoc., CHT.

**F. CORYSTIDAE** Foster and Philip, 1978

**First:** Cardabia bullaresis Foster and Philip, 1978, Cardabia Group, Carnavon Basin, Western Australia (Middle or Upper Palaeocene).

**Extant**

**Intervening:** PRB–LMI.

**Comment:** Adopted by David (1988), although not by Smith (1984b).

**F. CALYMNIDAE** Mortensen, 1907 **Extant** Mar.

**F. SOMALIASTERIDAE** Wagner and Durham, 1966

**First:** Iraniaster morgani Cotteau and Gauthier, 1895, Upper Cretaceous (Senonian) of Iran; also I. douvillei Cotteau and Gauthier, 1895, I. nodulosus Gauthier, 1902, of similar origin. Somaliaster magniventer Hawkins, 1935, and S. magniventer var. chechti Maccagno, 1941, both from East Africa, are of imprecise Cretaceous date.
### Echinodermata

#### Key for both diagrams

<table>
<thead>
<tr>
<th>TR.</th>
<th>Key for both diagrams</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANS</td>
<td>1. Pourtalesiidae</td>
</tr>
<tr>
<td>SCY</td>
<td>10. Pericosmiidae</td>
</tr>
<tr>
<td>TAT</td>
<td>19. Eophiuridae</td>
</tr>
<tr>
<td>KAZ</td>
<td>20. Palaeuridae</td>
</tr>
<tr>
<td>UFI</td>
<td>21. Stenasteridae</td>
</tr>
<tr>
<td>KUN</td>
<td>22. Antiquasteridae</td>
</tr>
<tr>
<td>ART</td>
<td>23. Encrinasiteridae</td>
</tr>
<tr>
<td>SAK</td>
<td>24. Protasteridae</td>
</tr>
<tr>
<td>ASS</td>
<td>25. Lapworthuridae</td>
</tr>
<tr>
<td>GZE</td>
<td>26. Furcasteridae</td>
</tr>
<tr>
<td>KAS</td>
<td>27. Eospondylidae</td>
</tr>
<tr>
<td>MOS</td>
<td>28. Oncychasteridae</td>
</tr>
<tr>
<td>BSH</td>
<td>29. Asteronychidae</td>
</tr>
<tr>
<td>SPK</td>
<td>30. Incertae sedis</td>
</tr>
<tr>
<td>VIS</td>
<td>31. Ophiuridae</td>
</tr>
<tr>
<td>TOU</td>
<td>32. Ophiocomaidae</td>
</tr>
<tr>
<td>FAM</td>
<td>33. Ophiacanthinae</td>
</tr>
<tr>
<td>FRS</td>
<td>34. Ophiuroidea</td>
</tr>
<tr>
<td>GIV</td>
<td>35. Ophiidiidae</td>
</tr>
<tr>
<td>EIF</td>
<td>36. Ophiurididae</td>
</tr>
<tr>
<td>EMS</td>
<td>37. Amphiochidae</td>
</tr>
<tr>
<td>PRA</td>
<td>38. Ophiothricidae</td>
</tr>
</tbody>
</table>

#### F. STENONASTERIDAE Lambert, 1922

**K. (CON–SAN?) Mar.**

**First and Last:** *Stenonaster tuberculata* (Defrance, 1816), from Italy, Algeria, Turkey and Tunisia (Zaghbib-Turki, 1987). *S. morgani* Gauthier, 1902, Iran, and *S. duculitei* Lambert, 1928, France, the only other species ascribed to this monogenic family, are both from imprecisely known (but presumably Upper Cretaceous) stratigraphical horizons.

#### F. URECHINIDAE Duncan, 1889

**T. (PRB?)—Rec. Mar.**

**First:** *Sanchezaster habanensis* Lambert, in Sanchez Roig, 1924, Eocene (Upper Eocene), Habana Province, Cuba (Kier, 1984a).

**Extant**

**Intervening:** Eoe., Mio.

---

#### F. POURTALESIIDAE A. Agassiz, 1881

**T. (LAN/SRV)—Rec. Mar.** (see Fig. 25.7)

**First:** *Pourtalesia* sp., Tatsukuroiso Mudstone, (Middle Miocene), Honshu, Japan (Kikuchi and Nikaido, 1985).

**Extant**

**Intervening:** No other fossil representatives of this family have been recorded.

#### Order SPATANGOIDA Claus, 1876

**F. TOXASTERIDAE Lambert, 1920**

**K. (BER)—Rec. Mar.**

**First:** *Toxaster laffittei* Devriès, 1960, Lower Cretaceous (BER), Bel Kheir (Aures), Algeria (although not truly a *Toxaster* according to Fischer, in Durham et al. (1966), but a taxon intermediate between *Toxaster* and the earlier disasteroid *Collyrites*). *T. rochi* Lambert, 1933, *T. africenus* (Coquand, 1875) also BER, in Tunisia. Several other Lower Cretaceous (VLG–HAU) species ascribed to *Toxaster* are...
known, mostly from Europe and North Africa. (Both Mortensen (1928–1951) and Kier and Lawson (1978) erroneously list Heteraster musandamensis Lees, 1928 from the Upper Jurassic rather than the Upper Cretaceous.)

**Intervening:** K, DAN, Eoc., Oli.

**Suborder** MICRASTERINA Fischer, 1966

F. MICRASTERIDAE Lambert, 1920


**First:** Micraster borchardi Hagenow, 1853, Chalk, Germany (I. lamarcki and I. vancouversensis Zones) and England, UK (H. planus Zone) is the first true Micraster sensu Stokes (1975) and therefore first macrasterid sensu Durham et al. (1966). M. antiquus Cotteau, 1887 is of CMP age rather than CEN as listed by Lambert and Thiery (1909–1925). M. corbois Forbes, 1850, although also H. planus Zone, is interpreted as a lineage separate from true Micraster by Stokes (1975). Epiaster michelini (L. Agassiz, 1847), (upper CEN–TUR of northern Europe) is considered to be ancestral to Micraster by Stokes (1975). If genus Epiaster, placed in synonymy with the toxasterid Heteraster by Durham et al. (1966), is considered to be ancestral to Micraster by Stokes (1975). If genus Epiaster, placed in synonymy with the toxasterid Heteraster by Durham et al. (1966), is considered to be ancestral to Micraster by Stokes (1975). If genus Epiaster, placed in synonymy with the toxasterid Heteraster by Durham et al. (1966), is considered to be ancestral to Micraster by Stokes (1975). If genus Epiaster, placed in synonymy with the toxasterid Heteraster by Durham et al. (1966), is considered to be ancestral to Micraster by Stokes (1975).

**Last:** Isopneustes subquadratus (Desor, 1857), Eocene, Italy.

**Intervening:** Micraster species are numerous and well known throughout the Upper Cretaceous (Stokes, 1975); a few less-common species, notably of Brissopneustes, extend the record of the family through the Palaeocene and early Eocene.


**First:** Diplodetus recklinghausenensis Schlüter, 1900, Chalk, Germany. (The genus Plesiaster, type species Plesiaster peini (Coquand, 1862), SAN, Algeria and Tunisia, although classified as a brissid by Durham et al. (1966) is considered to be a synonym of Micraster by Stokes (1975).

**Intervening:** Late Cretaceous (mainly CMP); otherwise confined to the Cainozoic (especially post-Palaeocene), with a near-complete stratigraphical record.


**First:** Several Eocene species of Lovenia are known, notably L. carinata (Cotteau, 1889), Alicante, Spain, L. gregoryi (Clark, 1915), USA, L. lorioli (Lambert, 1902), Barcelona, Spain, and L. suessi Bittner, 1880, Southern Alps, Austria, but precise stratigraphical horizons lack confirmation.

**Intervening:** Good stratigraphical record through the Cainozoic, especially Palaeocene and Middle Miocene.


(Family name on ICZN Official List: Opinion 608.)

**First:** Spatangus cosini (Sorignet, 1850) France; Atelospatangus magnus Szövényi, 1963, Hungary; both Middle Eocene. S. (Granopatagus) lonchophorus Meneghini, in Desor, 1858, Vincentin, Italy, and Laevipatagus bigibbus (Beyrich, 1848) have less-precise ascription within the Eocene. (The record of Spatangus baixadoleitensis Maury, 1934, Upper Cretaceous (TUR?), Brazil, accepted by Kier and Lawson (1978) is anomalous; the species is referred to Hemister by Smith and Bengtson, 1991.)

**Intervening:** Good stratigraphical record through the Cainozoic from the late Eocene.

**Suborder** HEMIASTERINA Fischer, 1966


**First:** Washiaster barremicus Tanaka and Okubu, 1954, (BRM), Japan; possibly W. (?) macroholcus Nisiyama, 1950, Neocomian, Japan.

**Intervening:** Very numerous through the Cretaceous (APT–MAA), with a good stratigraphical record through the Cainozoic.


**First:** Leioaster bosi Smiser, 1936, Comanchean, Texas, USA.

**Intervening:** Upper Cretaceous, Eoc.

**F. AEROPSIDAE** Lambert, 1896 Extant Mar.


**First:** Linthia dainelli Stefanini, 1928, Karakorum, Mongolia; Periaster maugerii Checchia-Rispoli, 1936, Sicily, central Mediterranean; Proraster dali Clark, 1915, USA; all CEN.

**Intervening:** Mostly confined to the Cainozoic.


**First:** Pericosmus gregoryi Currie, 1927, upper Auradu Series (Lower Eocene), Somalia, East Africa. If Mundaaster, known only from the type species M. tentugalensis Soares and Devriès, 1967, upper CEN to lower TUR, Portugal, is included in the family (as by Kier and Lawson, 1978), the range is extended back into the Upper Cretaceous.

**Intervening:** Good fossil record from Eocene to Recent.

**Suborder** UNKNOWN


**First:** Asterostoma dickersoni Sanchez Roig, 1949, Cuba, dated as Middle Eocene by Brodermann (1949), although this precise date is not confirmed by Kier (1984a); possibly Pygospatagus salvae Cotteau, 1889, Alicante, Spain. These species, and a few attributed to Antillaster and Moronaster, are of imprecise Eocene age.

**Intervening:** Good late Eocene to Recent stratigraphical record.

**Comment:** 'Probably a polyphyletic grouping of aberrant members of the Hemisterina and Micrasterina, which have reduced petals or fascioles or both ... a taxonomic convenience or necessity rather than a biologically meaningful unit' (Fell, in Durham et al., 1966).

**UNPLACED REGULAR ECHINOID GROUPS**

**Order** PLESIOCIDAROIDA Duncan, 1889

Subclass uncertain. Considered to be ancestral to the...
arbacioids by some authors, but referable to the cidaroids by others (Kier, 1977).

**F. TIARECHINIDAE** Gregory, 1896

Tr. (CRN) Mar.

**First and Last:** Tiarechinus princeps Neumayr, 1881, St Cassian Beds, northern Italy (Kier, 1977, 1984b).

**Comment:** Kier (1977) excludes Lysechinus from this family: known only from the holotype of L. incongruenis Gregory, 1896, it is probably a misidentified mollusc. The family is therefore confined to the monospecific Tiarechium, northern Italy (Kier, 1977, 1984b).

**Orthopsida Mortensen, 1942**

Cohort uncertain: Diadematacea or Echinacea

**F. ORTHOPSIDA** Duncan, 1889


**First:** Dubarechinus despugnalis Lambert, 1937 and D. termieri Lambert, 1937, both Lias (upper Domerian), Morocco.

Orthopsis parvituberculata (Bohm, 1884), Verona, Italy is dated as Triassic (RHT) by Lambert and Thit~ry (1909–1925), but as Jurassic (BAJ) by Smith (1990); it is excluded from his review of Triassic echinoids by Kier (1977).

**Last:** Orthopsis sanfilippani Checcchia-Rispoli, 1933, Tripolitania, Libya; Orthopsis perlatia Noetling, 1897, Mari Hills, Baluchistan, Pakistan; both MAA.

**Intervening:** BTH–CMP.

**Order UNCERTAIN**

F. HETEROCIDARIDAE Mortensen, 1934

J. (PLB)–O(XF) Mar.

**First:** Heterocidaris bruni Lambert, in Lambert and Thiery, 1925, Lias (Domerian and Toarcian), near Géménos, France. Also Cidaris taylorensis. W. B. Clark, 1893, Hard grave Sandstone (Lower Jurassic), California, USA, reascribed to Heterocidaris by Lambert and Thiery (1909–1925).

**Last:** Heterocidaris dumortieri Cotteau, 1871, OXF, Ardèche, France.

**Intervening:** BAJ.

**Comment:** This monogeneric family is not adopted by Smith (1984b), although Heterocidaris is cited as of uncertain order (1984b, p. 20). Durham et al. (1966) maintain the family, noting 'The general aspect of the test recalls the Diadematoida, but the cidaroid character of the spines is opposed to such affinity, pointing rather to the Hemicidaroida or even Cidaroidea; no precise relationships can be suggested until the lantern structure is known.'

**Class OPHIURIDEA** Gray, 1840

Current classifications of the ophiuroids are highly unsatisfactory, being based upon grades of organization rather than phylogenetic relationships. It is probable that most taxa above the level of genus are paraphyletic or even polyphylectic. This is particularly true of Palaeozoic groups, and it is likely that few, if any, represent natural groupings. Furthermore, some of the 'primitive' Lower Palaeozoic ophiuroids almost certainly will be found, upon further investigation, to represent parts of the stem group of both ophiuroids and echinoids. Hence the Ophiuroidea, as currently understood, is a paraphyletic taxon. The situation perhaps is somewhat better for post-Palaeozoic taxa and it is possible that some of these families may represent monophyletic clades. The classification adopted here is largely that of Spencer and Wright (1966), in the Treatise on Invertebrate Paleontology, but the monophyly of any particular group within the Ophiuroidea must be regarded as highly uncertain, or indeed improbable, until some attempt has been made to investigate ophiuroid relationships using phylogenetic methods.

**Order STENURIDA** Spencer, 1951

**Suborder PROTURINA** Spencer and Wright, 1966

F. PRADESURIDAE Spencer, 1951


**First:** Pradesura jaci (Thoral, 1935), Schistes de St Chinian, basal Arenig, Hérault, France.

**Last:** Sturtzaster spinosissima (Roemer, 1863), Bundenbach Slates, Germany.

F. PHRAGMACITYNIDAE Spencer, 1951

O. (RAW) Mar.

**First and Last:** Phragmaticus grayae Spencer, 1951, Starfish Bed, Girvan, Scotland, UK.

F. RHOPALOCOMIDAE Spencer and Wright, 1966


**First:** Rhopalocoma pyrotechnica Salter, 1857, Lower LUD, Leintwardine, Hereford, and Lake District, England, UK.

**Last:** Pitlonaster proueps Hall, 1868, Ithaca Beds, New York, USA.

F. BDELLACOMIDAE Spencer and Wright, 1966

S. (GOR) Mar.

**First and Last:** Bdellacoma vermiciformis Salter, 1857, Lower LUD, Leintwardine, Hereford, England, UK.

**Suborder PAROPHIURINA** Jaekel, 1923

F. EOPHURIURIDA Schoudorf, 1910

O. (ARG) Mar.

**First and Last:** Eophiura bohemica Schuchert, 1914, upper ARG, Czechoslovakia.

F. PALAEOURIDA Spencer, 1951


**First:** Palaearca neglecta Schuchert, 1914, upper ARG, Czechoslovakia.

**Last:** Medusaster rhenanus Stürtz, 1890, Dachsiefern, Germany.

F. STENASTERIDAE Schuchert, 1914


**First:** Stenaster obtusus (Forbes, 1848), Black River Limestone, Kentucky and Vermont, USA, Ontario and Ottawa, Canada.

**Last:** Stenaster obtusus (Forbes, 1848), Starfish Bed, Girvan, Scotland, UK.

F. ANTIQUASTERIDAE Kesling, 1971


**First and Last:** Antiquaster magrumi Kesling, 1971, Silica Formation, north-western Ohio, USA.

**Order OEGOPHIURIDA** Matsumoto, 1915

**Suborder LYSOPHIURINA** Gregory, 1896

F. ENCRINASTERIDAE Schuchert, 1914

O. (RAW)–C. (u) Mar.

**First:** Encraster grayae Spencer, 1914, Starfish Bed,
Girvan, Scotland, UK.

**Last:** *Armathyaster paradoxis* Harper and Morris, 1978, Brush Creek Shale, Glenshaw Formation, Conemaugh Group, Punxsutawney, Pennsylvania, USA.

F. **PROTASTERIDAE** S. A. Miller, 1889
  **First:** *Protaster salteri* (Salter, 1857), Bala Beds, North Wales, and Spy Wood Grit Shropshire, England, UK.
  **Last:** *Drepanaster scabrosus* (Whidborne, 1896), Pilton Shales, Cleistopora Zone, Devon, England, UK.

**Suborder** ZEU GOPHIURINA Matsumoto, 1929
  F. **LAPWORTHURIDAE** Gregory, 1897
  **First:** *Hallaster* sp., upper Arenig, Czechoslovakia.
  Extant

F. **FURCASTERIDAE** Stürtz, 1900
  **First:** *Furcaster trepidans* Spencer, 1925, Starfish Bed, Girvan, Scotland, UK.
  Extant

F. **EURYALINA** Lamarck, 1816
  F. **EOSPONDYLIDAE** Spencer and Wright, 1966
  **First and Last:** *Eospondylus primigenius* (Stürtz, 1886) and *Kontrospondylus decadactylus* Lehmann, 1957, Hünsrückschiefer, Rhineland, Germany.

F. **ONYCHASTERIDAE** S. A. Miller, 1889
  C. (TOU) Mar.
  **First and Last:** *Onychaster barrisi* (Hall, 1861), Lower Carboniferous, Braunton Down, Devon, England, UK, and *O. flexilis* Meek and Worthen, 1868, Lower Carboniferous, Indiana, USA.

F. **ASTERONYCHIDAE** Miller and Troschel, 1842
  **First:** *Asteronyx ornatus* Rasmussen, upper Maastrichtian, Upper Chalk, Denmark.
  Extant

F. **ASTERO SCHEMATIDAE** Verrill, 1899
  Extant Mar.

F. **GORGONOCEPHALIDAE** Ljungman, 1867
  **First:** Undescribed genus, Oligocene of New Zealand (cited by Spencer and Wright, 1966).
  Extant

F. **EURYALIDAE** Gray, 1840 Extant Mar.
  **Order** OPHIU RIDA Müller and Troschel, 1840
  **Suborder** CHILOPHIURINA Matsumoto, 1915
  F. **OPHIURIDAE** Gregory, 1897
  **First:** *Argentinaster bodenbenderi* Ruedemann, 1916, Silurian, Argentina.
  **Last:** *Silesaster longivertebralis* Schwarzbach and Zimmermann, 1936, Tournaisian, Germany.
  **F. OPHIU RIDAE** Lyman, 1865
  **First:** *Aeganaster gregarius* (Meek and Worthen, 1869), Keokuk Group, Crawfordsville, Indiana, USA.
  Extant
  F. **OPHIOLEUCIDAE** Matsumoto, 1915 Extant Mar.
  F. **OPHIOCOMIDAE** Ljungman, 1867
  **First:** *Ophiocoma nereida* (Wright, 1880), Sandsfoot Grit, upper Oxfordian, Weymouth, Dorset, England, UK.
  Extant
  F. **OPHIONERIDIDAE** Ljungman, 1867 Extant Mar.
  F. **OPHIODERMATIDAE** Ljungman, 1867
  **First:** *Palaeocoma escheri* (Heer, 1865), Insect Marl, laqueus Subzone, Schambelen, Switzerland.
  Extant

**REFERENCES**


BASAL DEUTEROSTOMES (CHAETOGNATHS, HEMICHORDATES, CALCICHOORDATES, CEPHALOCHORDATES AND TUNICATES)

M. J. Benton

The taxa included in this chapter are all apparently related to graptolites (see Chapter 27), echinoderms (see Chapter 25), and chordates (see Chapters 30–41). Many of these have been called calcichordates, carpoids or stylophorans, and include such forms as the cinctans (homosteleans), solutes (homoioosteleans), cornutes and mitrates. The calcichordates are treated here as a paraphyletic group.

The family-level documentation has been compiled from the publications of Jefferies (1969, 1986, 1990, and MS) and others, with the classification based broadly on the cladistic analyses by Jefferies (1986) and Cripps (1991). Note that this is a recent, cladistically-based classification, which is regarded as controversial by many workers on calcichordates and on modern basal chordates and echinoderms. Basic information on the older taxa is presented in Ubaghs (1967a,b) and Caster (1967). There have been problems in defining ‘family-level’ groupings: problems typical to all groups, but especially here because of the rate of new discoveries, and because of the fluid nature of the phylogenetic trees. This chapter provides a measure of present, patchy knowledge, and may be tested usefully against future discoveries, and against known earlier times of origin based on cladistic branching points.

Paraphyletic groups are marked with a ‘p’ in parentheses.

Acknowledgements – I am deeply grateful to Dick Jefferies for his help with this chapter, both in letting me draw from his unpublished MS on the subject, and for checking the details, even though the result does not really reflect his views on the possibility of producing such a taxon list from a cladistic phylogeny. I thank Derek Briggs, Paul Daley and Quentin Bone for other assistance.

Superphylum DEUTEROSTOMIA Grobben, 1908

Phylum CHAETOGNATHA Leuckart, 1854

F. UNNAMED €. (STD) Mar.

First: Undescribed specimens, Middle Cambrian, Stephen Formation, Glossopiera Zone, Mount Stephen, British Columbia, Canada (Briggs and Conway Morris, 1986).

Comments: Amiskwia Walcott, 1911, from the Burgess Shale, was described as a chaetognath, although this interpretation was rejected by Conway Morris (1977; see also discussion in Briggs and Conway Morris, 1986). The only other soft-bodied fossil of a chaetognath is Paucijaculum samamithion, described by Schram (1973) from the Mazon Creek fauna (Carbondale Formation, Francis Creek Shale (MOS), Peabody Coal Co. Pit 11, Will, Grundy and Kankakee Counties, Illinois, USA). Bieri (1991) asserts that this material contains three species in three genera, but the details are unpublished.

The other matter requiring discussion is the possibility that, if the protoconodonts are not phylogenetically linked via the paraconodonts to the euconodonts, then they may not be chordates. In that case, the striking similarities between protoconodont elements and the grasping spines of chaetognaths (e.g. Szaniawski, 1982) may indicate a relationship (see Chapter 29).

Phylum HEMICHORDATA Bateson, 1885

Details of hemichordate classification and fossil record are taken from Bulman (1970).

Class ENTEROPNEUSTA Gegenbaur, 1870

(see Fig. 26.1)

F. UNCERTAIN J. (SIN)–Rec. Mar.

First: Megaderaion sinemuriense Arduini et al., 1981, SIN, Lombardy, Italy (Arduini et al., 1981). Extant

Intervening: K. (u.).

Comment: Enteropneusts have a very limited fossil record, with this being one of the few definite fossil examples. Upper Cretaceous examples were noted by Wetzel (1972). So-called enteropneust burrows were described from the Muschelkalk of the Holy Cross Mountains, Poland (see Bulman, 1970, p. V13 for details).

Class PTEROBANCHIA Lankester, 1877

Animals: Invertebrates

<table>
<thead>
<tr>
<th>QU.</th>
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<th>21. Cothurnocystidae</th>
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</thead>
<tbody>
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<td>CHAETOGNATHA</td>
<td>22. Scotiaecystidae</td>
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<td>26. Plesion Domfrontia pissotensis</td>
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<td>4. Eocephalodiscidae</td>
<td>27. Plesion Prokopiyicystis mergli</td>
<td></td>
</tr>
<tr>
<td>LMI</td>
<td>5. Cephalodiscidae</td>
<td>‘CEPHALOCHORDATA’</td>
<td></td>
</tr>
<tr>
<td>RUP</td>
<td>‘ECHINIDERMATA’</td>
<td>29. Plesion Pikaia gracilis</td>
<td></td>
</tr>
<tr>
<td>PRB</td>
<td>7. Trochozystidae</td>
<td>30. Uncertain</td>
<td></td>
</tr>
<tr>
<td>BRT</td>
<td>8. Gyrozystidae</td>
<td>‘TUNICATA’</td>
<td></td>
</tr>
<tr>
<td>YPR</td>
<td>9. Ctenocystidae</td>
<td>31. Peltocystidae</td>
<td></td>
</tr>
<tr>
<td>THA</td>
<td>SOLUTA</td>
<td>32. Jakklocarpidae</td>
<td></td>
</tr>
<tr>
<td>DAN</td>
<td>10. Plesion Castericystis vali</td>
<td>33. Kirkocystidae</td>
<td></td>
</tr>
<tr>
<td>MAA</td>
<td>11. Minervaceystidae</td>
<td>34. Uncertain</td>
<td></td>
</tr>
<tr>
<td>CMP</td>
<td>12. Dendrocystidae</td>
<td>35. Unnamed</td>
<td></td>
</tr>
<tr>
<td>CON</td>
<td>14. Rutozycystidae</td>
<td>37. Plesion Chinianocarpus thorali</td>
<td></td>
</tr>
<tr>
<td>TUR</td>
<td>15. Syringocrinidae</td>
<td>38. Plesion Chauvelia discoidalis</td>
<td></td>
</tr>
<tr>
<td>ALB</td>
<td>17. Certocystidae</td>
<td>40. Plesion Mitrocystites mitra</td>
<td></td>
</tr>
<tr>
<td>APT</td>
<td>18. Plesion Protocystites menevensis</td>
<td>41. Plesion Mitrocystites barrantei</td>
<td></td>
</tr>
<tr>
<td>BRM</td>
<td>19. Plesion Nevadaceystis americana</td>
<td>42. Plesion Mitrocystites incipiens</td>
<td></td>
</tr>
<tr>
<td>HAU</td>
<td>20. Plesion ‘Cothurnocystis’ primaevae</td>
<td>43. Anomalocystidae</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 26.1

**Order** Rhabdopleurida Fowler, 1892

F. Rhabdopleuridae Harmer, 1905

*C. (STD)–Rec. Mar.*

First: *Rhabdotubus johannsoni* Bengtson and Urbanek, 1986, *Eccaratadoxides pinus* Zone, Middle Cambrian, Sweden (Bengtson and Urbanek, 1986). **Extant**

Comment: There are several examples of rhabdopleurids scattered through the fossil record, including some from the Jurassic of Poland, and *Rhabdopleura eoceenica* Dighton Thomas and Davis, 1949, from the London Clay (YPR) of southern England, UK.

**Order** Cephalodiscida Fowler, 1892

F. Eocephalodiscidae Kozlowski, 1949


First and Last: *Eocephalodiscus polonicus* Kozlowski, 1949, Glauconitic Sandstone, Wysoczki, Poland.

**Order** Cephalodiscidae Harmer, 1905


First: *Pterobranchites antiquus* Kozlowski, 1967, glacial boulder, Lower Ordovician, Poland. **Extant**

Intervening: LUT/BRT.

**Order** Stolonodendridae Bulman, 1955

F. Stolonodendridae Bulman, 1955


First and Last: *Stolonodendrum uniramosum* Kozlowski, 1949, TRE, Poland.

Comment: This group has often been assigned to

**Class** PLANCTOSPHAEROIDEA van der Horst, 1936

This group has no known fossil record.

**Class** GRAPTOLITHINA Bronn, 1846

See Chapter 27.

**Subsuperphylum** DEXIOTHETICA Jefferies, 1979

**STEM-GROUP ECHINODERMS**

**Order** CINCTA Jaekel, 1901

**F. TROCHOCYSTITIDAE** Jaekel, 1901

First and Last: *Trochocystites bohemicus* Barrande, 1887, Middle Cambrian, Bohemia, Czechoslovakia, and ?Bavaria, Germany; *Trochocystoides parvus* Jaekel, 1918, Middle Cambrian, Bohemia, Czechoslovakia (Ubaghs, 1967a).

**F. GYROCYSTITIDAE** Jaekel, 1918

First and Last: *Gyrocystis barrandei* (Munier-Chalmas and Bergeron, 1889), Middle Cambrian, Morocco; *Decacystis hispanica* Gislen, 1927, Middle Cambrian, Spain.

**Class** CTENOCYSTOIDEA Robison and Sprinkle, 1969

F. CTENOCYSTIDAE Robison and Sprinkle, 1969


Last: *Ctenocystis smithi* Ubaghs, 1987, upper Middle Cambrian, Montagne Noire, France (Ubaghs, 1987).

**Phylum** ECHINODERMATA de Bruguière, 1791

(Fleming, 1828)

See Chapter 25.

**Grade** SOLUTA Jaekel, 1901 (p)
The solutes are a paraphyletic group, apparently falling on the cladogram between the branch for echinoderms and the branch for chordates. The solute–cornute transition occurs, by tradition, between the Iowacystidae and the Ceratocystidae. The oldest solute known is an unnamed form from the Lower Cambrian Kinzers Formation of Pennsylvania, USA (shown in Paul and Smith, 1984, Fig. 3). It is likely that all known solutes are stem-group chordates.

**Plesion** Castericystis vali Ubaghs and Robison, 1985


**First and Last:** Castericystis vali Ubaghs and Robison, 1985, Marjum Formation, Utah, USA (Ubaghs and Robison, 1985).


**First:** ?Minervaecystis, Trempealeauan, Upper Cambrian, Nevada, USA (Ubaghs, 1969).

**Last:** Minervaecystis vidali (Thoral, 1935), TRE, France.


**First:** Dendrocystites sedgwicki (Barrande, ’867), LLN, Bohemia, Czechoslovakia; Heckericystis kuckersianus (Hecker, 1940), Middle Ordovician, Estonia, former USSR.

**Last:** Dendrocystites globulus (Dehm, 1934), Bundenbach Shale (Hunsrückian), Rhine region, Germany.

**Intervening:** LLO, ASH.

**Comment:** This may well be a paraphyletic assemblage, with Dehmicystis probably not a dendrocystitid (P. Daley, pers. comm., 1992).


**First:** Girvanicystis casteri Daley, 1992, Sholeshook Limestone (Cautleyan), Pembroke, South Wales, UK (Daley, 1992b).

**Last:** Girvanicystis batheri Caster, 1967, Starfish Bed (upper Rawtheyan), Girvan, Ayrshire, Scotland, UK (Daley, 1992b).


**First and Last:** Rutroclypeus junori Withers, 1933, R. quinseris Gill and Caster, 1960, and R. victoriae Gill and Caster, 1960, all Lower Devonian, Victoria, Australia.


**First:** Svingricrinus paradoxicus (Billings, 1859), Sherman Falls Beds, Middle Trenton Group, Quebec, Canada.

**Last:** Svingricrinus sinclairi Parsley and Caster, 1965, Upper Trenton Group, Chateau Richer, Quebec, Canada (Parsley and Caster, 1965).


**First:** Scalencystites strimplei Kolata, 1973, Dunleith Formation, Champlainian Series, Minnesota, USA, Belemnocystites wetherbyi Miller and Gurley, 1894, Curdsville Limestone, Champlainian Series, Kentucky, USA, Myeincystites natus Strimple, 1953, Bromide Formation, Champlainian Series, Oklahoma, USA and M. crossmanni Kolata et al., 1977, Dunleith Formation, Champlainian Series, Illinois, USA.

**Last:** Iowacystis sagittaria Thomas and Ladd, 1926, Fort Atkinson Formation, Cincinnati Series, Iowa, USA.

**Comment:** Includes the F. Belemnocystitidae Parsley, 1967 (Kolata et al., 1977).

**Grade** CORNUTAJaekel, 1900 (P)


**First and Last:** Ceratocyctis perneri jaekel, 1900, Skryje Shale, Skryje, Bohemia, Czechoslovakia and C. vizcainoi Ubaghs, 1987, Middle Cambrian, Montagne Noire, France (Ubaghs, 1987).

**Plesion** Protoctystites menevensis Hicks, 1872 E. (STD) Mar.

**First and Last:** Protoctystites menevensis Hicks, 1872, Hypagnostus parvifrons Zone, Menevian, Dyfed, South Wales, UK (Jefferies et al., 1987).

**Plesion** Nevadaceystis americana (Ubaghs, 1963) E. (MER) Mar.

**First and Last:** Nevadaceystis americana (Ubaghs, 1963), Trempealeauan, Nevada, USA.


**First and Last:** ‘Cothurnocyctis’ primaeva Thoral, 1935, Lower Ordovician, Montagne Noire, France.


**First:** Cothurnocyctis fellinensis Ubaghs, 1969 and C. courtesselei Ubaghs, 1969, both Lower Ordovician, Montagne Noire, France (Ubaghs, 1969).

**Last:** Cothurnocyctis eliae Bather, 1913, Starfish Bed, Girvan, Ayrshire, Scotland, UK.

**Intervening:** None.


**First:** ‘Cothurnocyctis’ bifida Ubaghs, 1988, Wheeler Formation, western Utah, USA (Ubaghs, 1988).

**Last:** Scotiaecystis curvata (Bather, 1913), Starfish Bed, Girvan, Ayrshire, Scotland, UK.

**Intervening:** ARG, LLO.


**Last:** Milonicystis kerjorriei Chauvel, 1966, Traveusot Formation, Morocco and Phyllocylcystis salaria Dubatolova, in Rozova et al., 1985, Chupino Formation, Salaire, former USSR (Chauvel, 1966; Dubatolova, in Rozova et al., 1985).

**Intervening:** ARG, LLO.


**First:** Galliacystis lignieresii Ubaghs, 1969 and Propagaliacystis ubaghsi Cripps, 1989, both basal Ordovician, Montagne Noire, France.

**Last:** Hanusia prilepensis Cripps, 1989, Dobrotiá Forma-
Basal Deuterostomes

**Phylum CHORDATA Bateson, 1886**

(see Chapters 30–41)

**STEM-GROUP CEPHALOCHORDATES**

*F. LAGYNOCYSTIDAE Jaekel, 1918 (p)*

**First and Last:** *Lagynocystis pyramidalis* (Barrande, 1887), Sarka Shales, Bohemia, Czechoslovakia.

**Last:** *Lagynocystis pyramidalis* (Barrande, 1887), Traveusot Formation, Normandy, France (Chauvel and Nion, 1977).

**Subphyllum TUNICATA Lamarck, 1816**

(UROCHORDATA Bateson, 1885)

Tunicate fossils are rare. They include spicules from the Eocene of France (?Didemnidae) and the problematic *Palaeobotryllus taylori* Müller, 1977 from the Upper Cambrian of Nevada, USA (Jefferies, 1986, pp. 316–17).

**Class ASCIDIACEA Blainville, 1824**

F. **UNCERTAIN** O. (STD) Mar.

**First and Last:** *Pikaia gracilens* Walcott, 1911, Burgess Shale, British Columbia, Canada.

**Comment:** The phylogenetic position of *Pikaia* is uncertain. It may fall here, or in the stem group of the craniates. It is described (Conway Morris, 1979) as amphioxus-like, and may well be a chordate. If it is a chordate, it may be located in the cladogram as indicated in this listing, or it may be a close sister group of the crown-group craniates (Jefferies, MS). Butterfield (1990) doubts the chordate affinities of *Pikaia*.

**Subphyllum CEPHALOCHORDATA Owen, 1846**

F. **UNCERTAIN** P. (ROT) Mar.

**First and Last:** *Chinianocarpos thorali* Ubaghs, 1961, lower Zechstein, Sosio-kalk, Palazzo Adriano, Sosio, Sicily, Italy.

**Class THALIACEA van der Hoeven, 1850**

No known fossil record (see Hoiland et al., 1967, p. 607).

**Class APPENDICULARIA Lahille, 1890**

Limited fossil record (see Holland et al., 1967, p. 607), other than the appendicularians reported by Zhang (1987) from the Cambrian of China.

**Subphyllum CRANIATA**

**Order UROCHORDATA Incertae sedis**

F. **UNCERTAIN** S. (LLY) Mar.

**First and Last:** *Appendicularians*, Lower Cambrian, China (1987).

**Order Mitrata Jaekel, 1918 (p)**

The mitrates usually include the stem-group cephalochordates and tunicates noted above, as well as the stem-group craniates noted here.

**Phylum CORDATA Bateson, 1886**

(see Chapters 30–41)

**STEM-GROUP TUNICATES**

*Suborder PELTOCYSTIDA Jefferies, 1973*

**First and Last:** *Peltecarpus hamatotergum* Whitehill Formation, Ecca Group (Lower Permian), South Africa (Oelofson and Loock, 1981).

**Comments:** This find is unconfirmed. Other supposed fossil cephalochordates have been discounted (Holland et al., 1967, p. 608).

**F. JAEKLOCARPIDAE Kolata et al. 1991**

C. (BSH) Mar.

**First and Last:** *Jaekelocarpus oklahomensis* Kolata et al., 1991, Golf Course Formation, Morrowan, Johnston County, Oklahoma, USA (Kolata et al., 1991).

**F. KIRKOCYSTIDAE Caster, 1952**


**First:** *Guichenocarpos* sp., Shineton Shales, Shropshire, England, UK.

**Last:** *Guichenocarpos nioni*, Traveusot Formation, Normandy, France.

**Subphyllum TUNICATA Lamarck, 1816**

(UROCHORDATA Bateson, 1885)

Tunicate fossils are rare. They include spicules from the Eocene of France (?Didemnidae) and the problematic *Palaeobotryllus taylori* Müller, 1977 from the Upper Cambrian of Nevada, USA (Jefferies, 1986, pp. 316–17).

**Class ASCIDIACEA Blainville, 1824**

F. **UNCERTAIN** P. (UFI) Mar.

**First:** *Permosoma tunicatum* Jaekel, 1918, lower Zechstein, Sosio-kalk, Palazzo Adriano, Sosio, Sicily, Italy.

**Class THALIACEA van der Hoeven, 1850**

No known fossil record (see Hoiland et al., 1967, p. 607).

**Class APPENDICULARIA Lahille, 1890**

Limited fossil record (see Holland et al., 1967, p. 607), other than the appendicularians reported by Zhang (1987) from the Cambrian of China.
tion, lower CRD, Bohemia, Czechoslovakia (Ubaghs, 1979).

Last: *Paracyctis petrii* Caster, 1954, Ponta Grossa Shale, Lower Devonian, Paranhé, Brazil.

**Intervening:** None.

**Plesion** Mitrocytistes mitra Barrande, 1887
  O. (LLN) Mar.

**First and Last:** Mitrocytistes mitra Barrande, 1887, Sárka Shales, Bohemia, Czechoslovakia.

Plesion Mitrocytystella barrandei Jaekel, 1901
  O. (LLN) Mar.

**First and Last:** Mitrocytystella barrandei Jaekel, 1901, Sárka Shales, Bohemia, Czechoslovakia.

**Plesion** Mitrocytystella incipiens (Barrande, 1887)
  O. (LLO) Mar.

**First and Last:** Mitrocytystella barrandei Jaekel, 1901, Dobrotiivá Beds, Bohemia, Czechoslovakia, and Formation de Traveusot, Redon, Bretagne, France.

**F. ANOMALOCYSTIDAE** Bassler, 1938

**First:** Barrandecarpus jaekeli Ubaghs, 1979, Letná Formation, Bohemia, Czechoslovakia.

**Last:** Australocystis langei Caster, 1954, Ponta Grossa Shale, Paraná Basin, Brazil.

**Intervening:** Ash, LUD–GED, EMS, EIF.

**REFERENCES**


Formation (Middle Cambrian) of western Utah. *University of Kansas Paleontological Contributions*, 120, 1–17.


The classification of graptolites is currently in a state of flux after many decades of reasonable stability, and the classification adopted here is that of Palmer and Rickards (1991), which broadly hinges on the classification of Fortey and Cooper (1986) and of Mitchell (1987, 1990) with respect to diplograptids. However, I am not entirely convinced by the argument used by Fortey and Cooper in terms of placing the family Anisograptidae in the graptoloids, and hence I retain it in the dendroids, following the Bulman (1970) Treatise decision: either decision is arbitrary and accepts the intermediate nature of the family.

Further, I am unable to accept Mitchell’s (1987) redefinition of the family Monograptidae to include biserial graptolites occurring as early as the Arenig. By raising to family level some of his constituent subfamilies of the Monograptidae (namely Monograptinae, Dimorphograptinae, Glyptograptinae and Eoglyptograptinae), I feel there is less danger of obscuring one of the most spectacular events in graptoloid evolution, namely the development of the uniserial scandent colony. This is especially the case in a volume of this kind which purports to record the true occurrence of major grades and clades. The first edition also recorded the occurrence in time of, for example, the dimorphograptids (partially uniserially scandent) and direct comparison is thus possible of any changes in the record during the past quarter of a century. In this work, I separate the Monograptidae from Mitchell’s subfamilies Eoglyptograptinae, Glyptograptinae and Retiolitinae, which I maintain as family-level taxa, as with his Monograptinae and Dimorphograptinae. The Retiolitidae of Bulman (1970) and others are, therefore, split between the Orthograptidae and Abrograptidae (the Ordovician forms) and the Retiolitidae (the Silurian forms; related to the Glyptograptidae), following the views of Mitchell (1987), Bates (1990), and others. Obut and Zaslavskaya (1986), on the other hand, retain all ‘retiolitids’ in a single group, and recognize numerous families.

Finally, I am in agreement with the work of Mierzejewski (1986) which casts serious doubt on the graptolite affinities of several orders: thus the Stolonoidea are regarded as Pterobranchia, and the orders Dithecoidea and Archaeodendrida are removed from the Hemichordata (see Chapter 26). The families Inocaulidae and Chaunograptidae I provisionally remove to the hydroids (Coelenterata, see Chapter 6), and am in agreement with Mierzejewski (1986) on this.

Acknowledgements – I am extremely grateful to Henry Williams who helped with several areas made problematic as a result of recent reclassifications.

Phylum HEMICHORDATA Bateson, 1885
  Class ENTEROPNEUSTA Gegenbaur, 1870
  See Chapter 26.

Class PTEROBRANCHIA Lankester, 1877
  See Chapter 26.

Class GRAPTOLEITHINA Bronn, 1846

Order DENDROIDEA Nicholson, 1872 (see Fig. 27.1)

First: Callograptus antiquus Ruedemann, 1947, and Dendrograptus edwardsi major Ruedemann, 1947, and D. hallianus moneymakeri Ruedemann, 1947, Nolichucky Shale, Tennessee, USA (Ruedemann, 1947); other approximately coeval species of Dictyonema, Callograptus, Dendrograptus and Aspidograptus from Upper Wilberns Formation, Texas, USA; Deadwood Formation, South Dakota, USA; Trempeleau Formation, Gaspé (Eau Claire), Quebec, Canada (Ruedemann, 1947); and Potsdam Formation, New York, USA. A dendroid graptolite, undescribed, but possibly Dendrograptus, has been obtained from the Middle Cambrian P. davidis Zone, Comley, England, UK. A Dictyonema sp. (Quilty, 1971) probably upper part of Upper Cambrian.

Last: Dictyonema sp., E2 Zone, Yorkshire, England, UK (undescribed, but examined by author).
F. ANISOGRAPTIDAE Bulman, 1950
Last: *Calyxdendrum graptoloides* Kozlowski, 1960, LLO to lower CRD, Poznan and Warsaw, Poland.

F. ACANTHOGRAPTIDAE Bulman, 1938
First: *Acanthograptus priscus* Ruedemann, 1947, Trempealeauan Stage, Jordan Sandstone, Afton, Minnesota and Arbuckle Limestone, Oklahoma, USA (Ruedemann, 1947). *Thallograptus* sp. and *Palaeodicytota* sp. have recently been recorded from the Upper Cambrian by Rickards *et al.* (1990).
Last: *Palaeodicytota rotundatum* Bouček, 1957, *P. textorium* (Počta, 1894), and *P. undulatum* (Počta, 1894), *hercynicus* Zone, Lochkov Limestone, Kasor, Czechoslovakia (Bouček, 1957).

F. PTILOGRAPTIDAE Hopkinson, 1875
First: Several species of *Ptilograptus* Hall, 1865 from Deepkill Shale and equivalents, North America (Ruedemann, 1947). from San Remo, Australia (Thomas, 1960) and from St David's, Pembrokeshire, Wales, UK.
Order TUBOIDEA Kozłowski, 1938

F. TUBIDENDRIDAEE Kozłowski, 1949

First: Tubidendrum bulmani Kozłowski, 1949, Poland (Kozłowski, 1949).
Last: Reticulograptus thorsteinsonii Bulman and Rickards, 1966, Cornwallis Island, Canadian Arctic.

Constituent genera: Tubidendrum Kozłowski, 1949 and Reticulograptus Wiman, 1901 (= Multitubus Skevington, 1963). Several LUD species placed in Reticulograptus (see Bouček, 1957) must now be referred to this genus with reserve, and are not included above.

F. IDIOTUBIDAE Kozłowski, 1949

First: Idiotubus typicalis Kozłowski, 1949, and several other Idiotubus species, Calyctocutus infundibulatus Kozłowski, 1949, Poland (Kozłowski, 1949).
Last: Cyclograptus rotadentatus Spencer, 1883, Niagara Formation, Ontario, Canada (Ruedemann, 1947), and C. multithecatous Bouček, 1957, Cyrtograptus radians Zone, Czechoslovakia (Bouček, 1957).


F. PARVITUBIDAE Skevington, 1963
O. (ARG) Mar.
First and Last: Parvitubus oelandicus (Bulman, 1936), Öland, Sweden (Skevington, 1963).


Order CAMAROIDEA Kozłowski, 1938

F. BITHECAMARIDAE Bulman, 1955
First and Last: Bithecocamara gladiator Kozłowski, 1949, Poland (Kozłowski, 1949).


F. CYSTICAMARIDAE Bulman, 1955


Order CRUSTOIDEA Kozłowski, 1962

F. WIMANICRUSTIDAE Bulman, 1970

Comment: All the known crustoids have been obtained from erratic boulders, not all of which have been dated with certainty.

Order GRAPTOLOIDEA Lapworth, 1875

Suborder DICHOGRAPTINA Lapworth, 1873

F. DICHOGRAPTIDAE Lapworth, 1873
O. (?TRE—CRD) Mar.
First: Didymograptus novus Berry, 1960, D. primigenius Bulman, 1950a, ?D. sp. Bulman, 1954, D.? stoermeri Erdtmann, 1965, D. pritchardi Hall, 1899, D. taylori Hall, 1899, D. norvegicus Monsen, 1925, D. klotichichini Obut, 1961. With the recognition of bithecae on D. kiaeri Monsen, 1925, further doubt has been cast on the true graptoloid nature of the Tremadoc ‘didymograptids’. In the lowest beds of the Arenig, however, there are several species of Tetragraptus and Didymograptus (Monsen, 1937; Thomas, 1960), and it is probable that true graptoloids do occur in the Tremadoc.

Last: Didymograptus superistes Lapworth, 1880 and D. serratulus Hall, 1858, gracilis Zone, Glenkiln Shale, Scotland, UK (Elles and Wood, 1901—1918).

F. ABROGRAPTIDAE Mu, 1958
First: Dinemagraptus warkei Kozłowski, 1952, ?hirundo Zone, erratic block of Baltic limestone.
Last: Abrograptus formosus Mu, 1958, and other genera and species, gracilis Zone, Hulo Shale, China. The recently described genus Metabrograptus Strachan, 1990 is probably also from the gracilis Zone of Scotland, UK (Strachan, 1990).

Comment: The family includes some ‘retiolite’ genera such as Retegraptus Hall, 1859 (Bates, 1990).

F. SINOGRAPTIDAE Mu, 1957
First: Holmograptus leptograptoides (Monsen, 1937), bifidus Biozone, mid ARG, North America, Scandinavia, and elsewhere.
Last: Holmograptus, Tylograptus, Nicholsonograptus, Sinograptus and others; numerous species, uppermost tentaculatus Zone or decoratus Zone, middle LLN. NB Holmograptus and Tylograptus may be congeneric, with Tylograptus the junior name.

F. SIGMAGRAPTIDAE Cooper and Fortey, 1982
First: Kiaeograptus (?) cf. pritchardi (T. S. Hall, 1914), Adeograptus antiquus Subzone, upper TRE, Peel River, Yukon Territory, Canada.
Last: Gonigraptus spp. Cosmopolitan.

F. ISOGRAPTIDAE Harris, 1933
First: Isograptus primulus Harris, 1933, Chewtonian 1, New Zealand.
Last: Isograptus caducus spinifer Keble and Benson, 1929; I. ovatus (T. S. Hall, 1914), and I. ovatus davidis Skevington and Jackson, 1976, Australasia and Wales, UK.
Note: I. primulus was separated by Fortey and Cooper (1986) as a new family, but not named; for the present, the species is left in the Isograptidae.

First and Last: Pseudotrigonoportus ensiformis Cooper and Forney, 1982 and P. minor Cooper and Forney, 1982, hirundo Zone, numerous localities in Spitsbergen, China, North America, and others (Cooper and Forney, 1982).

Main genera: Only Pseudotrigonoportus Cooper and Forney, 1982: Trigonograptus itself is invalid, and Tristichograptus Jackson and Bulman, 1970, is a junior synonym of Pseudotrigonoportus.


Last: Cryptograptus insectiformis Ruedemann, 1908, top of pygaeus Zone, Oklahoma, USA; C. tricornis (Carruthers, 1859), clingani Zone, Scotland, UK (Elles and Wood, 1908), Australia, and elsewhere.


First: Corynoides calicularis Nicholson, 1867, gracilis Zone, cosmopolitan.

Last: Corynoides curtus Lapworth, 1876, clingani Zone, cosmopolitan (Strachan, 1949).

Comment: Corynites Kozlowski, 1956, the other genus in the family, is known only from erratic boulders, but is probably also CRD.


First: Pseudisograptus hastatus (Harris, 1933), Castlemainian, maximus Zone, middle ARG.

Last: P. jiangxiensis (Yu and Fang, 1981) and P. dumosus (Harris, 1933), upper Darrwillian, lower LLN, North America, China and Scandinavia.


First: Dicellograptus moffatensis Carruthers, 1858, bifidus Zone, Wales, UK.


First: Phyllograptus ilicifolius Hall, 1858 and P. typus Hall, 1858, Bendigonian, lower ARG, North America, Australia, Eurasia.

Last: Phyllograptus anna Hall, 1858, Isograptus Zone, or bifidus Zone, Quebec, Canada and elsewhere.


First: Hustedograptus uplandicus (Wiman, 1895), widespread.

Last: Orthograptus abbreviatus Elles and Wood, 1901–1918, anceps Biozone, widespread; Orthoretiograptus denticulatus Wang et al., 1987, anceps Zone, UK and China.

Comment: Several records of O. truncatus and allies from the earliest Silurian are treated sceptically by most graptolithologists, because the proximal-end development is unlike the Ordovician species. The subfamily includes a number of retiolite genera (Bates, 1990).


Comment: Family monotypic; probably derived from Diplograptidae by modification of mode of development. Restricted to Canada.


First: Hallograptus inutilis (Hall, 1865), hirundo (3b e) Zone, Lower Didymograptus Shale, Norway (Spjeldnaes, 1953). NB This is a suspiciously early occurrence.


Comment: Family probably derived by excessive thecal differentiation from early Diplograptidae of austrodentatus group (Bulman, 1970).


First: Pseudoamplexograptus confertus (Nicholson, 1868), just above the base of the artus Biozone in the UK), widespread. NB Probably several other forms in the same horizon.

Last: Pseudoamplexograptus spp., high CRD, various, widespread.


Subfamily CLIMACOGRAPTINAE Frech, 1897 O. (ARG–ASH) Mar.

First: Climacograptus sp., top of Cowhead Group, upper ARG, Newfoundland, Canada; possibly other forms elsewhere.

Last: Climacograptus tubuliferus Lapworth, 1876 and Pseudoclimacograptus spp., widespread.

griestoniensis
Clinoclimacograptus
Comment: Rare biserial specimens from the Ludlow and Devonian are here regarded as insufficiently studied to enable a decision on their evolutionary position, or even their generic attribution.

Main genera:
First:
Pseudoclimacograptus (Metaclimacograptus)
1968, Metaclimacograptus
Boucek, 1952; all
(Rickards and Hutt, 1970)

Last:
Plectograptus macilentus
Czechoslovakia, the latter also from England, UK; and

Undulograptus
Zone, Birkhill Shale, Scotland, UK.

REFERENCES


A significant number of fossils cannot be placed within existing phyla with any degree of confidence, and are therefore regarded as ‘Problematica’. This may be either because the gross body form or ‘Bauplan’ of the fossil is not known from a recognized phylum (usually in cases where preservation is good), or because material is open to ambiguous interpretation (in which case, assignment to more than one phylum may be possible). Many such forms arise from sites of exceptional preservation (‘Konservat-Lagerstätten’), and most of the taxa listed here date from the early Palaeozoic. The Middle Cambrian Burgess Shale of British Columbia provides many of the most celebrated examples, first discussed extensively in a series of monographs by Walcott (e.g. 1908, 1911, 1912, 1918). Faunas of comparable significance have been described more recently at Chenjiang, in the Yunnan Province of China (Jiang, 1980, 1982; Zhang, 1987; Hou, 1987a–c; Hou and Sun, 1988), and in Peary Land, Greenland (Conway Morris et al., 1987).

The response of the taxonomist to such material has been varied. In some cases (e.g. Seilacher, 1984; Gould, 1989), authors postulate the existence of new phyla, often to accommodate single representatives. At the other extreme (e.g. Walcott 1911, 1912, 1918), Problematica can be forced into known phyla, either by compromising the definition of the group, or by biasing an interpretation of the fossil evidence. These assignments are at least partially influenced by the worker’s phylum concept per se. Few definitions are explicit, and there is certainly no general consensus as to how many ‘units of morphological difference’ are needed to merit phylum status.

Many hundreds of problematical taxa have been described from the fossil record. This chapter is not a complete listing of all named problematical genera. Only selected taxa erected as families or with particularly distinct or well-described characters are included. An excellent introduction to Problematica in general is given by Bengtson (1986), and to Burgess Problematica in particular by Briggs and Conway Morris (1986).

The chapter is organized into four sections for ease of reference, covering Problematica for which the highest bona fide taxonomic assignments are at the class, order, family and genus levels respectively.

Acknowledgements – Sepkoski acknowledges partial support for his research from the National Aeronautics and Space Administration (USA), under grant NAGW-1693. Wills thanks Dr D. E. G. Briggs for practical assistance with source material. His research was undertaken during the tenure of a University of Bristol Postgraduate Scholarship.

1. PROBLEMATICATA ASSIGNED TO UNRELATED CLASSES

Class TRILOBZOZA Fedonkin, 1983

Vendian and Lower Cambrian taxa with unique triradiate symmetry. Included groups are from Fedonkin (1985), with the questionable addition of the small calcareous anabaritids, as tentatively suggested by Fedonkin (1986).

F. ALBUMARESIDAE Fedonkin, 1976 V. (u.) Mar. (see Fig. 28.1)


Comment: Valkov and Sysoiev (1970) consider the Angustiochreidae to be synonymous.

F. UNNAMED, 1959 V. (u.) Mar.


Class DIPLEUROZOA Harrington and Moore, 1956


First and Last: Dickinsonia costata Sprigg, 1947, and Dickinsonia lissa Wade, 1972, Pound Quartzite, upper Adelaide Series, Ediacara Hills, South Australia, and Vendian of the White Sea region. Palaeoplota segmentata Fedonkin, 1979, Vendian of the White Sea region, former USSR.

Comment: Dickinsonia has been variously placed with the polychaetes and the platyhelminthes. Seilacher (1989) treats it as a ‘bipolar Vendozoan’, thus allying it with the ‘Petalonamae’ (see Chapter 6, Coelenterata).

Class VENDIAMORPHA Fedonkin, 1985 V. (POU) Mar.

Includes Ediacaran taxa sometimes assigned to the Arthropoda. Seilacher’s (1989) treatment as ‘Vendozoa’ would ally these taxa with the ‘Petalonamae’ (see Chapter 6, Coelenterata).


Class PARATRILOBITA Fedonkin, 1985

Includes Ediacaran taxa variously assigned to the Annelida and Arthropoda. Seilacher’s (1989) treatment as ‘Vendozoa’ would ally these taxa with the ‘Petalonamae’ (see Chapter 6, Coelenterata).
First and Last: Bomakeilia kelleri Fedonkin, 1985, Ust-Pinega Formation, White Sea region, former USSR.

Comment: Glaessner (1976) places Sprigginia within the Tomopteridae (Phyllodocemorpha, Polychaeta), (see Chapter 15, Annelida).

Class COELOSCLERITOPHORA Bengtson and Missarzhevsky, 1981

Order SACHITIDA He, 1980


First: Siphogonuchites triangularis Qian, 1977, Meischucunian Stage, Zone 1, Shizhonggou, southwestern Shaanxi, China.
Last: Trapezochites huqiuensis Xiao and Zhou, 1984, Yutaishan Formation (?Botomian), Anhui, China.

First: Wiwaxia corrugata (Matthew, 1899), Middle Cambrian Spence Shale, Cataract Canyon, Wellsville Mountains and nearby localities, Brigham City, Utah, USA (Conway Morris, 1989).
Last: Wiwaxia corrugata (Matthew, 1899), Phyllopod Bed, Walcott Quarry, Middle Cambrian Burgess Shale and Oyyopsis Shale, British Columbia, Canada (Conway Morris, 1985).
Comment: Butterfield (1990) argues that Wiwaxia is a polychaete worm, and assigns it to the order Phyllodocida, near the extant Chrysopetalidae and Aphroditidae.

Order CHANCELLORIIIDA Walcott, 1920
Last: Chancelloria sp., lower Dresbachian Crepicephalus Zone of Texas and Montana, lower Upper Cambrian, USA (Lochman, 1940); Chancelloria iranica Mostler and Mosleh-Yadzi, 1976, Upper Cambrian Mila Formation, Elburz Mountains, Iran.

Class TOMMOTIIDAE Missarzhevsky, 1970

Order MITROSAGOPHORA Bengtson, 1977

First and Last: Kennardia reticulata Laurie, 1986, Todd River Dolomite, Amadeus Basin, central Australia.

First: Micrina etheridei (Tate, 1892), Todd River Dolomite, Amadeus Basin, central Australia (Laurie, 1986).
Last: Tannuolina multifora Fonin and Smirnova, 1967, Shangan Suite, upper reaches of Shivelig-Khem River, Tuva, eastern Tan-u-Ola Range, southern Siberia, former USSR.

Last: Tommotia plana (Missarzhevsky, 1966), Toyonian Stage, Siberian Platform, former USSR.

Order UNNAMED
First: Kelanella altaica Missarzhevsky, 1966, Kameshki Horizon, Atabanian, Isha River, Shilovka, Altaj, southwestern Siberia, former USSR.
Last: Sonella rostriformis Missarzhevsky and Grigor’yeva, 1981, lower Aamginian, Kazakhstan, former USSR.
Comment: Landing (1984) includes the genera of this family within the Lapworthellidae.

This class was erected to accommodate a number of calcareous microfossils from the Lower Cambrian of the former USSR, originally assigned to the Phylum Archaeocyatha. All are oblong or isometric, one- or twowalled cups, up to 5 mm long and 1.5 mm wide, although most are smaller (Hill, 1972).

**Order CONOIDOCYATHIDA Vologdin, 1964**
Commonly conical cups, with a single wall of peripterate structure.

**F. CONOIDOCYATHIDAE Vologdin, 1964**


**Order CRIBRICYATHIDA Vologdin, 1964**
Classification is predominantly taken from Hill (1972). Cribricyathids are all double-walled cups, with a peripterate inner, and striate outer wall.

**F. CRIBRICYATHIDAE Vologdin, 1964**


**F. CAPILLICYATHIDAE Yankauskas, 1969**

*Capillicyathus fimbriatus* Vologdin, 1964, Botomian Stage, River Kyzas, west Sayan, former USSR.

**F. CRIBRICYATHIDAE Vologdin, 1964**

*Capillicyathus fimbriatus* Vologdin, 1964, Botomian Stage, River Kyzas, west Sayan, former USSR.

**F. PYXIDOCYATHIDAE Vologdin, 1964**

*Apocyathus ovalis* Vologdin, 1964, Botomian Stage, River Abakan, west Sayan; *Lagenicyathus lamellifer* Vologdin, 1964, Botomian Stage, River Abakan, west Sayan; *Thecocyathus tetragonus* Vologdin, 1964, Botomian Stage, River Kyzas, west Sayan, former USSR.

**F. LEIBAELLIDAE Yankauskas, 1969**


**F. MANACYATHIDAE Yankauskas, 1969**


**F. VOLOGDINOPHYLLIDAE Radugin, 1964**


**F. UNNAMED V. (POU)–E. (TOM) Mar.**

*First: Sinotubulites baimatuoensis* Chen et al., 1981, Upper Sinian of Yichang, Hubei Province, China.

**F. STENOTHECOIDA Yochelson, 1958**

*Order CAMBRIDIJOIDEA Horny, 1958*
**F. CAMBRIDIIDAE** Horný, 1957

**First:** *Stenothecoides* sp., *Dokidocanthus leniacus* Zone, Salanygol, Mongolia (Brasier, 1989).
**Last:** *Stenothecoides elongata* (Walcott, 1884), Mount Whyte Formation, Mount Stephen, British Columbia, Canada.

**Class** MACHAERIDIA Withers, 1926

Classification follows Dzik (1986a) except that the Sachitida and Tommotiida have been removed.

**Order** HERCOLEPADIDAE Dzik, 1986

- **F. HERCOLEPADIDAE** Dzik, 1986

**First:** *Hercolepas signata* (Aurivillus, 1892), Middle Silurian Visby Beds of Gotland, Sweden (Aurivillus, 1892).
**Last:** *Protobalanus hamiltonensis* Hall and Clarke, 1888, Marcellus Shale, Avon, New York, USA (Van Name, 1926).

**Order** TURRILEPADIDAE Pilsbry, 1916

- **F. LEPIDOCOELIDAE** Withers, 1926

**First:** *Placoleus robustus* Dzik, 1986, *E. reclinatus* Zone, Mojca Limestone, Holy Cross Mountains, Poland, and Baltic area.
**Last:** *Aulakolepos* sp., Middle Devonian (Pope, 1975).

- **F. PLUMULITIDAE** Jell, 1979

**First:** *Plumulites bohematicus* Barrande, 1872, Wosek and Sta Benigna, Bohemia, Czechoslovakia (Jell, 1979).
**Last:** Unidentified specimens, Tournaisian, Wierzchowe area, northern Poland, Illustrated by Korejwo (1979) and referred to this family by Dzik (1986a).

- **F. TURRILEPADIDAE** Clarke, 1896

**First:** *Mojezalepis multilamellosa* Dzik, 1986a, Arenig and Llanvirn of the Baltic area, Europe (Dzik, 1986a).
**Last:** *Turriolepis whitersi* Elias, 1958, and *Clarkeolepis clarkei* Elias, 1958, both upper Mississippian Redoak Hollow Formation, southern Oklahoma, USA.

**Class** CAMBROCLAVIDA Conway Morris and Chen, 1991

- **F. ZHIJINITIDAE** Qian, 1978

**First:** *Zhijinites longistriatus* Qian, 1978, middle Meishucunian Stage, Yunnan, China.
**Last:** *Cambroclavus fangxianensis* Qian and Zhang, 1983, Damao Group (Ordian), Damaodong section, Yaxian County, Hainan Island, China.

**Comment:** The family Cambroclavitidae Mambetov, 1979, is considered to be synonymous (Mambetov and Repina, 1979).

### 2. PROBLEMATICA ASSIGNED TO UNRELATED ORDERS

**Order** HYOLITHELMINTHES Fisher, 1962

- **F. HYOLITHELLIDAE** Walcott, 1886

**First:** *Hyolithellus* sp., Rovno Horizon, Russian Platform former USSR; *Mobergella holsti* (Moberg, 1892), *M. radiolata* Bengtson, 1968, and *M. turgida* Bengtson, 1968, boulders of Lower Cambrian conglomerate from Venenäs, on the Skärgåns Peninsula, Baltic region, Norway and Sweden.
**Last:** *Hyolithellus cuyanus* and *H. mendozanim* Rusconi, 1951, Isidreana Formation (Villavicence Horizon), Mendoza, Argentina.

- **F. TORELLIDAE** Holm, 1893
  - C. (TOM)–P. (SAX) Mar.

**First:** *Torelleta curvata* Missarzhevsky, 1966, lower Pestrotsvet Formation, *sunnaginicus* Zone, Dvortsy, Aldan River, Yakutia, Siberia, former USSR.
**Last:** *Phosphannulus* spp. Müller, Nagami and Lenz, 1974, Hughes Creek Shale Member, Foraker Limestone (Lower Permian, Wolfcampian), road cutting on Interstate 70, Wabaunsee County, Kansas, USA (Welch, 1976).

**F. UNNAMED** C. (STD)–O. (CRD) Mar.

**First:** *Byronia annulata* Matthew, 1889, Stephen Formation, Mount Stephen, British Columbia, Canada.
**Last:** *Byronia naumovi* Kozłowski, 1967, middle Carbonian erratic boulder, Wyszgrod, Poland (Mierzejewski, 1986).

**Comment:** Scrutton (1979) and Mierzejewski (1986) consider this to be a scyphozoan.

**Order** SABELLIDITIDA Sokolov, 1965

- **F. SABELLIDITIDAE** Sokolov, 1965

**First:** *Calyptrina partita* Sokolov, 1965, *Yudoma Horizon*, uppermost Vendian, River Kotui basin in the north-west of the Anabar uplift (Sokolov, 1968).
**Last:** *Calyptrina partita* Sokolov, 1965, basal Cambrian, northern former USSR. *Saarina tenera* Sokolov, 1965, lower part of the Baltic Stage, Russian Platform, former USSR (Sokolov, 1968).

**F. SABELLIDITIDAE** Sokolov, 1965

- **V. (POU)–C. (AB) Mar.

**First:** *Paleolina evenkiana* Sokolov, 1965, lower part of Platonovka Suite, Upper Vendian, Turukhansk region, Siberian Platform, former USSR (Sokolov, 1968); *Sabellitides* sp., uppermost Vendian, southern Siberia, former USSR.
**Last:** *Parasabellitides yanachekskyi* Sokolov, 1967, Baltic Stage of Lower Cambrian, Siberian Platform, former USSR (Sokolov, 1968).

**Order** COLEOLIDAE Bouček, 1964

Coleooids were assigned as molluscs under the order Hyolithellida by Sysoiev (1957) and as an order (Coleolida) under the class Tentaculita by Bouček (1964).

- **F. COLEOLIDAE** Fisher, 1962
  - C. (TOM)–C. (TOU) Mar.

**First:** *Coleoella differa* Lenzon, 1972, lower Tommotian, borehole, northern Poland (Brasier, 1989); *Coleolus trigonius* Sysoiev, 1962, and *S. bilingsi* (Sysoiev, 1962) lower Pestrotsvet Formation, *sunnaginicus* Zone, Yunikan, Aldan River, Yakutia, Siberia, former USSR.
**Last:** *Coleolus missouriensis* Howell, 1952, Chouteau Formation, Sedalia, Missouri, USA (Downie et al., 1967).
Order PAIUTIIDA Tynan, 1983
F. PAIUTITUBULITIDAE Tynan, 1983
C. (ATB) Mar.


Order VOLBORTHELLIDA Kobayashi, 1937
Yochelson (1977) regards this group as a distinct phylum, 'Agnata', while Glaessner (1976) places them within the Spiromorpha (Polychaeta).

F. SALTERELLIDAE Poulsen, 1932

First: Serpulites maccullichii Murchison, 1959, Salterella Grit, Loch Erriboll, Scottish Highlands (Yochelson, 1983); Salterella acervulosa Resser and Howell, 1938, Kinzers Formation, near Lancaster, Pennsylvania, USA.

Last: Salterella sp., Toquima Range, Nye County, Nevada, USA (Yochelson et al., 1970).

F. VOLBORTHELLIDAE Kiaer, 1916

First: Volborthella tenuis Schmidt (1888), lower Atdabanian equivalents of northern Norway and northern Poland (Brasier, 1989).

Last: Volborthella tenuis Schmidt (1888), Salterella Grit, Loch Erriboll, Scottish Highlands, UK (Yochelson, 1983).

Comment: Yochelson (1977) contends that Volborthella from the Baltic region, and Salterella may be the same organism, only affected by different diagenesis.

F. VOLOGDINELLIDAE Balashov, 1962
C. (MEN) Mar.

First and Last: Vologdinella antiquus (Vologdin, 1930), upper Middle Cambrian, Chinig Mountains, north-eastern Kazakhstan, former USSR (Tchernycheva, 1965).

Order UNNAMED
D. Collins (pers. comm.) has suggested that the Anomalocaridae, Opabinidae, Proboscaris, and Hurdia are related by sharing the apomorphic 'Peytoia' mouth. D. E. G. Briggs (pers. comm.) considers that the Opabinidae should not be included in the order, since they lack a sphincter-like arrangement of plates around the mouth.

F. ANOMALOCARIDAE Whittington and Briggs, 1985

First: Cassubia infercambriensis (Lendzion, 1975), subsurface Zawiszczy Formation of the basal Cambrian, north-east Poland.

Last: Anomalocaris nathorsti (Walcott), Marjum Formation, Ptychagnostus punctuosus Zone, House Range, Utah, USA (Briggs and Robison, 1984; Whittington and Briggs, 1985).


First and Last: Hurdia dentata Simonetta and Delle Cave, 1975, H. triangulata Walcott, 1912, and H. victoria Walcott, 1912, Walcott Quarry, mid Middle Cambrian Burgess Shale, Stephen Formation, near Field, British Columbia, Canada.


First and Last: Proboscaris agnosta Rolfe, 1962, Wheelertown Shale, Ptychagnostus atatus Zone, House Range, Utah, USA.

Order UNNAMED
Ramsköld and Hou (1991) have argued that the following taxa form a group which is probably related to the onychoporan 'lobopods'.

F. HALLUCIGENIIDAE Conway Morris, 1977
C. (MEN) Mar.

First and Last: Hallucigenia sparsa, Walcott, 1911, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

F. MICRODICTYONIDAE Chen et al., 1989

First: Microdictyon tenuiporatum Bengtson et al., 1986, Tommotian Stage, River Lena, Yakutia, Siberian Platform, former USSR.

Last: Microdictyon robisoni Bengtson et al., 1986, uppermost Swasey Limestone bed, Ptychagnostus gibbus Zone (or just below), Middle Cambrian, Topaz Mountain, Drum Mountains, Millard County, Utah, USA.


First and Last: Luolishania longicuris Hou and Chen, 1989, Chuingchusu Formation, at Maotianshan, Chengjiang, east Yunnan, China.

3. PROBLEMATICATA ASSIGNED TO UNRELATED FAMILIES

F. AMISKWIIDAE Walcott, 1911
C. (MEN) Mar.
(see Fig. 28.2)

First and Last: Amiskwia sagittiformis Walcott, 1911, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

F. ANCIENTIDAE Ross, 1967

First: Ancienta arborea, A pomerania and A. rossi Schallreuter, 1981, Middle Ordovician of Europe.

Last: Ancienta ohioensis and A. fortensis Ross, 1967, Waynesville Formation, Richmond Group, Cincinnation Series (Ashgill), Ohio, USA.


First: Cornulites flexuosus (Hall, 1847) [as Tentaculites flexuosus Hall], Trenton Limestone, Trenton Falls, New York, USA (Downie et al., 1967).

Last: Cornulitella carbonaria (Young), 'Carboniferous Limestone Group', Ravenscraig Castle, near Kirkaledy and Whitehouse, near Linlithgow, Scotland, UK (Etheridge, 1880).

Comment: Regarded as an Order in the Class Tentaculita by Boucek (1964).

F. CUPITHECIDAE Duan, 1984

First: Cupitheca manicae Duan, 1983, Xihaoping Formation (Meichucunian), Shennongjia District, Hubei, China.

### Problematica

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1. **Amiskwiidae** 21. **Unnamed**
2. **Anciientidae** 22. **Unnamed**
3. **Cornulitidae** 23. **Unnamed**
4. **Cupithecidae** 24. **Unnamed**
5. **Donomischidae** 25. **Unnamed**
6. **Eldoniidae** 26. **Unnamed**
7. **Konyriidae** 27. **Unnamed**
8. **Odontogriphidae** 28. **Unnamed**
9. **Opabinidae** 29. **Unnamed**
10. **Paracarinachitidae** 30. **Unnamed**
11. **Parvancorinidae** 31. **Unnamed**
12. **Platysolenitidae** 32. **Unnamed**
13. **Stoibostrombidae** 33. **Unnamed**
14. **Tianzhushanellidae** 34. **Unnamed**
15. **Typhloesidae** 35. **Unnamed**
16. **Utaphosphidae** 36. **Unnamed**
17. **Unnamed** 37. **Unnamed**
18. **Unnamed** 38. **Unnamed**
19. **Unnamed** 39. **Unnamed**
20. **Unnamed** 40. **Unnamed**

### Fig. 28.2

**F. DINOMISCHIDAE** Conway Morris, 1977

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<td><strong>First:</strong> Dinomischus venustus Chen <em>et al.</em>, 1989, Lower Cambrian, Nevadella Zone, Chiungchussu Formation, Yunnan, China.</td>
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<td><strong>Last:</strong> Dinomischus isolatus Conway Morris, 1977, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.</td>
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**Comment:** S. Bengtson (pers. comm.) suggests that these are hexactinellid sponges.

**F. ODONTOGRIPHIDAE** Conway Morris, 1976a

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<td><strong>First and Last:</strong> Odontogriphus omalus Conway Morris, 1976a, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada (Conway Morris, 1976a).</td>
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**F. OPABINIIDAE** Walcott, 1912

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<td><strong>First:</strong> Opabinia regalis Walcott, 1912, Walcott Quarry, mid Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.</td>
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F. PARACARINACHITIDAE Qian, 1988

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<td><strong>First:</strong> Paracarinachites sinensis Qian and Jiang, 1982, middle Meishucunian Stage, China (Luo <em>et al.</em>, 1982).</td>
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<td><strong>Last:</strong> Luyanhaochiton spinus Yu, 1984 (= P. sinensis) and Yangzichiton elongatus Yu, 1984, Dengyin Formation, Zhongyicun Member (upper Meishucunian), Jinning, Yunnan, China.</td>
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<td><strong>Comment:</strong> May be related to the cambroclaves (Qian and Bengtson, 1989; Conway Morris and Chen, 1991).</td>
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**F. PARVANCORINIDAE** Glaessner, 1979

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<td><strong>First and Last:</strong> Parvancorinae Qian and Bengtson, 1989; Conway Morris and Chen, 1991.</td>
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Fort Peña and lower Woods Hollow Formations of the Marathon area, western Texas, USA (Bergström, 1979).

**Comment:** S. Bengtson (pers. comm.) suggests that these are hexactinellid sponges.

F. **ELDONIIDAE** Walcott, 1911

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<td><strong>First:</strong> Stellostomites eumorphus Sun and Hou, 1987 and Yunnanomedusa eleganta Sun and Hou, 1987, Lower Cambrian, Nevadella Zone, Chiungchussu Formation, Yunnan, China.</td>
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<td><strong>Last:</strong> Eldonia ludwigi Walcott, 1911, middle part of Spence Shale, Antimony Canyon, Wellsville Mountain, USA, and middle of Marjum Formation, House Range, USA (Conway Morris and Robison, 1988).</td>
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F. **KONYRIIDAE** Nazarov and Popov, 1976

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<td><strong>First:</strong> Konyrum varium Nazarov and Popov, 1976, Middle Table Head Formation, north of Piccadilly, Fort au Port Peninsula, western Newfoundland, Canada (Bergström, 1979).</td>
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| **Last:** Konyrum varium Nazarov and Popov, 1976, upper
First and Last: Parvancorina minchami Glaessner, 1959, Pound Quartzite, Ediacara Hills, South Australia (Glaessner and Daily, 1959).

F. PLATYSOLENITIDAE Eichwald, 1969  

First: Platysolenites antiquissimus Eichwald, 1969, upper part of the Wodawa Formation (equivalent to the Rosno), Poland (Brazier, 1989).


Comment: Feyn and Glaessner (1979) and Loeblich and Daily, 1959).

F. STOIBOSTROMBIDAE Conway Morris and Bengtson, 1990  
C. (ATB) Mar.

First and Last: Stoibostrombus crenulatus Conway Morris and Bengtson, 1990, Ajax Limestone, Mt. Scott Range and other localities, South Australia.

F. TIANZHUSHANELLIDAE Conway Morris, 1990  

First: Tianzhushanella ovata Liu, 1979, upper Dengying Formation (Meishucunian), Yangtze Gorges, Hubei, China.


F. TYPHLOESIDAE Conway Morris, 1990  
C. (SPK) Mar.

First and Last: Typhloesus wellsli (Melton and Scott, 1973), Bear Gulch Limestone, Montana, USA (Conway Morris, 1990).

F. UTAPHOSPHIDAE Wrona, 1987  

First: Lenargyrion knappologicum Bengtson, 1977, upper part of the Atdabanian, middle reaches of the River Lena, Yakutia, Siberian Platform, former USSR.


F. UNNAMED  


Comment: Affinity of these two genera has been suggested by S. Bengtson (pers. comm.).

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F. UNNAMED  
C. (MER) Mar.

First and Last: Banffia constricta Walcott, 1911, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.


F. UNNAMED  
C. (ATB) Mar.

First and Last: Covilla reticulata Hinz, 1987, ‘Callavia Limestone’ (lower Comley Limestone), Comley Quarry, Shropshire, England, UK.

F. UNNAMED  
C. (TOM) Mar.

First and Last: Cyrtochites pinnooides Qian, 1983, Dengying Formation (middle Meishucunian), eastern Yunnan, China.

First and Last: Deuteronecanebus papillorum Schram, 1979, Bear Gulch Limestone, Montana, USA.

First and Last: Etacytis communis Nitecki and Schram, 1976, Pennsylvanian Essex fauna, Francis Creek Shale, Mazon Creek, northern Illinois, USA.

First: Fomitchella infundibuliformis, Missarzhevsky, 1969, lower half of Tommotian, north-western slope of Anbar Massif, rivers Kotui, Erichka and Fomich, south-east part of Yakutia, Maya River, Siberia; F. acinaciformis Missarzhevsky, 1969, Siberia, former USSR.

Last: Fomitchella infundibuliformis, Missarzhevsky, 1969, Dokidocyathus regularis Zone, upper Tommotian, Siberian Platform, former USSR (Brazier, 1989).

Comment: Fomitchella infundibuliformis is regarded by Dzik (1986b) to be the oldest of the true conodonts.

F. UNNAMED  
C. (MEN) Mar.

First and Last: Nectocaris pteryx Conway Morris, 1976, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada (Conway Morris, 1976b).

F. UNNAMED  
C. (MEN) Mar.

First and Last: Oesia disjuncta Walcott, 1911, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

F. UNNAMED  
C. (MER) Mar.

First and Last: Palaeobotryllus taylori Müller, 1977, Whipple Cave Formation (Trempealeauan), Sawmill Canyon, near Lund, Nevada, USA.

Comment: Müller (1977) suggested this was an ascidiacean tunicate (see Chapter 26).

F. UNNAMED  

First and Last: Pollingeria grandis Walcott, 1911, Middle Cambrian Burgess Shale, and localities on Fossil Ridge, Mount Field and Mount Stephen, near Field, British Columbia, Canada (Collins et al., 1983).

F. UNNAMED  
C. (MEN) Mar.

First and Last: Portalia mira Walcott, 1918, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

F. UNNAMED  
C. (ATB) Mar.

First and Last: Pyrgites mirabilis Yu, 1984, Dengying Formation, upper member (upper Meishucunian), Shanxi, China.

F. UNNAMED  
V. (POU) Mar.

First and Last: Redkinia spinosa Sokolov, 1976, borehole at Nepéitsino, Moscow Syncline, Redkinia Horizon, middle Vendian, former USSR.

F. UNNAMED  
C. (MEN) Mar.

First and Last: Redoubtia polyopta Walcott, 1918, Walcott Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.
REFERENCES


Animals: Invertebrates


Animals: Invertebrates


This chapter covers a diverse collection of poorly skeletonized taxa for which there is a minimal or underrepresentative fossil record. Some (e.g. Nematoda) are thought to have been widespread and abundant groups in the past, and their poor records therefore reflect a low fossilization potential. Others (e.g. Onychophora) are also relatively inconspicuous in today's biota, although this, of course, says little of their importance in the past.

Acknowledgements – I thank Drs D. E. G. Briggs and R. J. Aldridge for their guidance and assistance with source material. This chapter was researched during the tenure of a University of Bristol Postgraduate Scholarship.

Phylum CTENOPHORA
See Chapter 6, Coelenterata.

Phylum PLATYHELMINTHES (see Fig. 29.1)

F. UNNAMED V. (EDI) Mar.
First and Last: Platypholinia pholiata Fedonkin, 1985, Ust-Pinega Formation, Valdaiskoi Series, Vendian of the White Sea region, former USSR.
F. UNNAMED V. (EDI) Mar.
First and Last: Vladimissa missarzhevskii Fedonkin, 1985, Ust-Pinega Formation, Valdaiskoi Series, Vendian of the White Sea region, former USSR.

Class TURBELLARIA

Order TRICLADIDA
F. UNNAMED Q. (PLE) FW
First: Cocoons or fertilized egg capsules found widely distributed in modern lake deposits in the Canadian Arctic, East Africa, Europe, India and the USA (Gray, 1988).

Order INCERTAE SEDIS
First: Three unnamed species from three unnamed families, found in calcareous, petroliferous nodules formed in a Miocene lake, Calico Mountains, San Bernardino County, California, USA (Pierce, 1960).

Phylum NEMERTEA

First: Archisymplectes rhathon Schram, 1973, Francis Creek Shale Member, Carbondale Formation, Grundy County, Illinois, USA (Schram, 1973).

Phylum ROTIFERA ?Ehrenberg, 1838

Order MONOGONONTA ?Plate, 1891

First: ?Keratella sp., lower Middle Eocene, North Maslin Sands, near Adelaide, South Australia (Southcott and Lange, 1971). Extant

Phylum NEMATOIDA Rudolphi, 1808

The nematodes are known from a number of well-recorded examples, particularly in Tertiary ambers (Conway Morris et al., 1982). Störmer's (1963) description of Scorpiophagus in saprobiotic association with a scorpion carcass would place their earliest record in the Lower Carboniferous, although some authors (e.g. Poinar, 1983) dispute this identification. Schram's assignment of forms from the Upper Carboniferous Mazon Creek (Schram, 1973) and Carboniferous Bear Gulch Limestone (Schram, 1979a) to the group are also somewhat equivocal (Conway Morris, 1985).

Class ADENOPHOREA

Order MERMITHIDA
F. MERMITHIDAE Braun, 1883
First: Heydonius antiquus Heydon, 1862, found projecting from the anus of a beetle, (Hesthesis immortua Heydon) from the Rhine lignite, Eocene of Germany (Taylor, 1935). Extant

Intervening: A number of other genera also found in Oligocene Baltic (CHT) amber.

Order ARAEOLOAIMIDA
F. PLECTIDAE Chitwood and Chitwood, 1937
T. (CHT)–Rec. Terr.
First: Oligoplectus succini v. Duisberg, 1862, Oligocene Baltic amber, Königsberg, Germany. Extant

Class SECERNENTEA

Order ASCARIDIDA
F. OXYURIDAE Cobbold, 1864
Q. (PLE)–Rec. Terr.
**Animals: Invertebrates**

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**Key for both diagrams**

| PLATYHELMINTHES | 1. Unnamed | 20. Priapulidae |
| 22. Unnamed | 23. Unnamed |
| 24. Unnamed | 25. Barentsiidae |
| 26. Bonelliidae | 27. Echiuridae |
| 28. Unnamed | 29. Polybrachiidae |
| 30. Incertae sedis | 31. Echiuridae |
| 32. Incertae sedis | 33. Onychophora |
| 34. Bestiidae | 35. Westergaardodinidae |

**Fig. 29.1**

**First:** *Ascaris obvelata* Rudolphi, 1802, Pleistocene of Siberia, former USSR. Extant

**Order** DIPLOGASTERIDA

F. DIPLOGASTERIDAE T. (7LMI) Terr.

**First:** Genus and species unknown, Chiapas amber-bearing beds from the Simojovel area, Central Mesa region and parts of the Tabasco Coastal Plain, Mexico (Gray, 1988).

**Order** APHELENCHIDA

F. APHELENCHOIDIDAE T. (7LMI) Terr.

**First:** Genus and species unknown, Chiapas amber-bearing beds from the Simojovel area, Central Mesa region and parts of the Tabasco Coastal Plain, Mexico (Gray, 1988). Extant

**Class** INCERTAE SEDIS


**First and Last:** Genus and species undetermined, Lower Carboniferous limestone, Gower Peninsula, South Wales, UK (Wu, 1983).

**First and Last:** *Nemavermes mackeei* Schram, 1973, Essex sub-biota, Mazon Creek, NE Illinois (Schram, 1979b). Extant

F. UNNAMED C. (MOS) Terr.

**First and Last:** *Scorpiaphagus baculiformis* and *Scorpiaphagus*
**Phylum NEMATOMORPHA Vejovsky, 1886**

*Order GORDIOIDEA*

**F. GORDIIDAE May, 1919**  
*Gordius tenuifibrosus* Voigt, 1983, Eocene lignite, Geiseltale, Germany.  
*Extant*  
*Comment:* Sciacchitano (1955) suggests that this species is synonymous with the extant *G. albopunctatus*.

**Phylum PRIAPULIDA**

Conway Morris (1977) provides an excellent review of this phylum, which includes most of the families listed here. As a group, the priapulids once exceeded the annelids in both abundance and diversity, but are now restricted to marginal environments.

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**F. ANCALAGONIDAE Conway Morris, 1977**  
*G. (MEN) Mar.*  
*First and Last:* Ancalagon minor (Walcott, 1911), Burgess Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

**F. FIELDIIDAE Conway Morris, 1977**  
*G. (MEN) Mar.*  
*First and Last:* Fieldia lanceolata Walcott, 1912, Phyllopod bed of Burgess Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

**F. MISKOIIDAE Walcott, 1911**  
*G. (MEN) Mar.*  
*First and Last:* Louisiella pedunculata Walcott, 1911, Burgess Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

**F. OTTOIIDAE Walcott, 1911**  
*G. (TOM–STD) Mar.*  
*First:* Maotianshania cylindrica Sun and Hou, 1987, Chiuangchussu Formation, Mount Maotianshan, Yunnan.
Animals: Invertebrates

Provinces, China. [Maotianshania is a junior pseudonym for Ottoia.]

**First:** Ottoia prolifica Walcott, 1911, Phyllopod bed of Burgess Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

**F. PRIAPULIDAE** Gosse, 1855  C. (MOS)–Rec. Mar.

**First:** Priapulites konicenuorum (Schram, 1973), Moscovian, Francis Creek Shale, Mazon Creek, NE Illinois, USA.


**First:** Selkirkia pennsylvanica Resser and Howell, 1938, Kinzers Formation, near Lancaster, Pennsylvania (Conway Morris, 1977).

**Last:** Selkirkia columbia Walcott, 1911, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada (Conway Morris, 1977).

**F. UNNAMED** C. (ATB) Mar.

**First and Last:** Cricosomia jinningensis Hou and Sun, 1988, Chinguichusso Formation, Mount Maotianshan, Yunnan Province, China.

**F. UNNAMED** C. (MEN) Mar.

**First and Last:** Lecithioscopa simplex Walcott, 1931, Phyllopod Bed of Burgess Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada (Conway Morris, 1977).

**F. UNNAMED** C. (MEN) Mar.

**First and Last:** Scolecofurca rara Conway Morris, 1977, Raymond’s Quarry, Middle Cambrian Burgess Shale, near Field, British Columbia, Canada.

**Phylum ECHIURIDA**

The phylum today comprises about 150 species of solitary or colonial, predominantly sessile metazoans. All are marine except members of the genus Urnatella. Only one fossil representative is known.

**F. BARENTSIIDAE** J. (OXF, KIM)–Rec. Mar.

**First:** Barentsia sp., Amphitrite or bestimmerid Clay, South Ferriby, Humberside preserved as bio-immured colonies beneath the oyster Deltoideum from the Upper Jurassic of England (Todd and Taylor, 1992).

**Phylum ECHIURIDA**

Despite considerable differences between the adults of the two phyla, a number of authors (e.g. Harms, 1934; Beklemischew, 1958–1960), consider the Echiura to be secondarily reduced annelids, and therefore members of that phylum. The similarities between the two groups are discussed by Clark (1969).

**Order ECHIURIDAE** Bock, 1942


**First:** Coprinoscolex ellogimus Jones and Thompson, 1977, Moscovian, Francis Creek Shale, Mazon Creek, NE Illinois, USA.

**Phylum SIPUNCULOIDA** Sedgwick, 1898

**F. PRIAPUdae** Gosse, 1855  V. (EDI)–Rec. Mar.

**First:** Protechiurus edmonsi Gaessner, 1799, upper Vendian, Kuibis Quartzite, lower Nama Group, Namibia.


**First:** Trypanites sp., uppermost Silurian Bertie Formation, and lowest Devonian Bois Blanc Formation (Emsian), Hagersville to Port Colborne, Southern Ontario, Canada (Pemberton et al., 1980).

**Phylum POGONOPHORA** Johannson, 1937

Fossil tubes interpreted as belonging to pogonophores (e.g. Sabellitides and Saarina) are abundant in some Upper Precambrian/Lower Cambrian rocks, particularly in eastern Europe and the former USSR (Sokolov, 1972). Differences in ultrastructure between such tubes and those produced by modern Pogonophora have thrown some doubt upon the relationship, and the fossil forms listed are assigned to the phylum on the basis of gross morphology. There are five extant families, in addition to the two listed here with a fossil record.

**Order THECANEPHRIA** Ivanov, 1955


**First:** Adekunbiella durhami Adegoke, 1967, Oligocene Shales of Keasey Formation, west bank of Nehalem River, Oregon, USA.

**Order THECANEPHRIA or ATHECANEPHRIA?**


**First:** Ivanovites fundibulatus Kozlowski, 1967, Ordovician erratic rocks, Mochty province of Warsaw, and Sokolovites ponoaphorides Kozlowski, 1967, Ordovician erratic rocks, Zakroczym-Wyszogród Province, Poland.

**Last:** Tasselia sp. de Heinzelin, 1965, Lower Pliocene concretions in the Antwerp basin, Belgium (Sokolov, 1968).

**Phylum TARDIGRADA**

**F. BEORNIDAE** Cooper, 1964  K. (u.) FW?

**First and Last:** Born legi Cooper (1964), amber, Cedar Lake, Manitoba, Canada.

**Phylum UNIRAMIA** Manton, 1972

**Subphylum ONYCHOPHORA** Grube, 1853

**F. INCERTAE SEDIS**  C. (MOS)–Rec. Mar.

**First and Last:** Helenodora inopinata Thompson and Jones, 1980, Moscovian, Francis Creek Shale, Mazon Creek, NE Illinois, USA.

**Comment:** Assignment to the subphylum level is made only tentatively, since detailed preservation of the extreme anterior and posterior of the animal is lacking. Aysheaia pedunculata from the Middle Cambrian Burgess Shale, British Columbia is considered by most authors to represent a sister group to the Onychophora. True
Onychophorans possess jaws and an extension of the body beyond the posterior-most pair of appendages. Ramsköld and Hou (1991) consider Hallucigenia, Microdictyon and Luolishania to form a group which is probably related to the onychophorans. (see Chapter 28, section 2).

**Phylum ?CONODONTA Eichenberg, 1930**

**Class ?CONODONTA Eichenberg, 1930**

The true conodonts are dealt with elsewhere (see Chapter 30), where Sweet’s (1988) classification, including only the euconodonts, has been adopted. This leaves the protoconodonts and paraconodonts. Müller and Hinz (1991) considered the protoconodonts to constitute a subgroup within the Paraconodontida, as they are similar in their overall direction of growth. The classification in Clarke (1981), which recognizes only the Paraconodontida as a formal taxon, has been adopted here.

Bengtson (1983) interpreted an evolutionary sequence from proto- through para- to euconodonts. This seems quite plausible, since all sclerites are composed of an organic matrix with an inlay of apatitic crystals, and there is remarkable uniformity in the development of structures within the Phylum. There is also a temporal trend from simple to more complicated shapes, consistent with a chemical evolution from early sclerites with a high organic and low phosphatic content to forms with gradually more phosphate and decreased proportions of organic material (Müller and Hinz, 1991).

At present it is unclear whether protoconodonts should necessarily be excluded from the true conodonts (Müller and Hinz, 1991). The term ‘protoconodont’ was introduced by Bengtson (1976) for slender Cambrian elements with only basal-internal growth increments. This structure was demonstrated for the Middle Cambrian Gapparodus bisulcatus (Müller, 1959), and later for the widespread Upper Cambrian ‘Prooneotodus’ tenuis Bengtson, 1977. These forms, along with Amphigeisina danica (Poulsen, 1966) also show a three-layered wall structure with a thick, laminated middle layer, bounded on either side by thinner lamellae. Szaniawski (1982, 1983) has argued that protoconodonts are the grasping elements of chaetognaths. He made further comparisons between chaetognath teeth and paraconodont elements, suggesting a common ancestry for chaetognaths and the conodonts as a whole (Szaniawski, 1987). Protoconodonts occur from the Precambrian–Cambrian boundary to the lowermost Ordovician.

The genera Rhombocorniculum and Fomitchella are treated as Problematica not assigned to taxa above the genus level, while Lapworthella is included within the class Tommotiida (see Chapter 28, Problematica).

**Order PARACONODONTIDA Müller, 1962**

There is fairly wide acceptance that the paraconodonts are the ancestors of the true conodonts (euconodonts). Paraconodonts are known from Middle Cambrian to Middle Ordovician times, while the euconodonts appear in the basal Upper Cambrian and become extinct by the Upper Triassic.

**Superfamily AMPHIGEISINACEA Miller, 1981**

These are non-geniculate elements, distinguished by an unusual three-layered wall. The inner layer lines the basal cavity, the middle layer is thick and mostly apatite, and the outer layer covering the element is thin and mostly or entirely organic.

**F. AMPHIGEISINIDAE Miller, 1981**

C. (LEN) Mar.


**Superfamily FURNISHINACEA Miller, 1981**

Non-geniculate coniform and unusual coniform multi-cuspate elements with a two-layered wall. Outer wall is thin and mostly organic, while the inner is thick and composed mostly of apatite (Clark, 1981).

**F. FURNISHIDAE Müller and Nogami, 1971**

V. (POU)–O. (ARG) Mar.

Elements with growth lamellae discontinuous on the outside of the cusp and on the inside of the basal cavity (Clark, 1981).

**First:** Protohertzina anabaria Missarzhevsky, 1973, Uppermost Precambrian and Tommotian of Siberia and Kazakhstan, former USSR.

**Last:** Albiconus postcostatus Miller, 1980, Symphysurina Zone, Lower Ordovician, Utah, Nevada, Oklahoma, Texas, Alberta, USA; Nogamiconus spp. Miller, 1980, Asia, Australia and North America; Procodus obliquus Müller, 1959, Nevada, Utah and Wyoming, USA; Sweden and Germany (glacial erratics), China and Siberia; Problematiconites perforata Müller, 1959, Nevada, Utah and Wyoming, USA; Sweden and Germany (glacial erratics), Iran and Queensland, Australia; Phakelodus tenuis (Müller, 1959), Great Britain; Prosagittdownus dahlmani (Müller, 1959), Nevada, Utah and Wyoming, USA; Sweden and Germany (glacial erratics), China, Kazakhstan, Iran.

**F. WESTERGAARDODINIDAE Müller, 1959**


Aberrant forms with two to five unequally sized projections. The basal cavity is continuous from side to side, and growth lamellae are interrupted on either side or divided into two lateral cavities with growth lamellae round the base (Clark, 1981).

**First and Last:** Westergaardodina spp. Müller, 1959, widespread in western and SW. states of USA, glacial erratics of Sweden, Poland and Germany; also Siberia, China, Poland, Iran and Queensland, Australia (Müller, 1962).

**REFERENCES**


Walcott, C. D. (1911) Middle Cambrian annelids. Smithsonian Miscellaneous Collections, 57, 109–44.


Animals: Vertebrates

*Acanthostega gunnari* Jarvik, 1952, skull in right lateral view, from the Britta Dal Formation (Upper Devonian, Famennian) of Stensiöbjerg, Gauss Halvø, East Greenland (specimen MGUH 1300A, Geologisk Museum, Copenhagen). One of the oldest tetrapods. The skull is about 120 mm long. Photograph courtesy of S. E. Bendix-Almgreen, with the permission of the Geologisk Museum, Copenhagen, and J.A. Clack.
Before 1970, conodont classification was entirely utilitarian. Each element type was regarded as a distinct taxon, and suprageneric categories consisted of groupings of elements that showed overall morphological similarities. In the last edition of *The Fossil Record*, the utilitarian classification of Hass (1962) was used, with modifications, by Rhodes (1967), who recognized that it had no phylogenetic significance. Subsequently, classifications have been developed that take account of the multi-element nature of conodont apparatuses and are thus closer to biological reality. The most comprehensive are those of Lindström (1970), Clark (with other authors in the *Treatise on Invertebrate Paleontology*, Robison (ed.) 1981) and Sweet (1988). All of these are exploratory and have limitations (see Fähræus, 1983, 1984 for a critical discussion of the *Treatise* classification), and none has been based on well-formulated cladistic or other methodological principles.

Despite these reservations we have endeavoured to follow the most recent classification, that of Sweet (1988), as far as possible in this contribution. We have made some modifications to Sweet’s scheme and have added families to accommodate additional genera. We emphasize, however, that much of conodont suprageneric classification is still probationary.

The conodont fossil record is very good, and there are few recorded major gaps in familial ranges. At the level of precision documented here, each conodont family is represented in all intervening chronostratigraphical intervals between its recorded first and last occurrences. We have used the stage level for quoting ranges to provide uniformity with other contributions, but have endeavoured to give more precise entries for the first and last occurrences. In most cases, the range limits are quoted to biozonal or sub-biozonal level. For some Middle and Upper Ordovician taxa, published ranges have been given in terms of the graphically correlated composite standard section of Sweet (1984), and are consequently cited here in terms of conodont chronozones; where taxa of this age have not been graphically correlated, Sweet’s intervals are used as first-appearance biozones. For chronostratigraphical intervals in which more than one conodont biozonation is available, we have used the most suitable scheme for the particular record; for example, we have employed the North American Midcontinent Province and the North Atlantic Province biozonations as appropriate for Ordovician entries.

**Acknowledgements** – We appreciate information freely provided by many colleagues.

*Phylum* CHORDATA Bateson, 1886  
*Class* CONODONTA Eichenberg, 1930  
Sensu Clark, 1981  

*Order* PROCONODONTIDA Sweet, 1988  

F. CORDYLODONTIDAE Lindström, 1970  
Є. (MER)–O. (TRE) Mar. (see Fig. 30.1)  

**First:** *Eocordyloodus notchpeakensis* (Miller, 1969), San Saba Member, Wilberns Formation, Threadgill Creek–Lange Ranch section, central Texas, USA; *notchpeakensis* Sub-biozone (Miller et al., 1982).  
**Last:** *Cordyloodus angulatus* Pander, 1856, House Formation, Ibex area, Utah, USA; *angulatus* Biozone (Ethington and Clark, 1982).  

F. FRYXELLODONTIDAE Miller, 1981  
Є. (MER) and/or O. (TRE) Mar.  

**First:** *Fryxelloodontus inornatus* Miller, 1969, San Saba Member, Wilberns Formation, Threadgill Creek–Lange Ranch section, central Texas, USA; *inornatus* Sub-biozone (Miller et al., 1982).  
**Last:** *Fryxelloodontus lineatus* Miller, 1969, Lava Dam Member, Notch Peak Formation, southern House Range, Utah, USA; *elongatus* Sub-biozone (Miller et al., 1982).  

F. PROCONODONTIDAE Lindström, 1970  
Є. (MER) Mar.  

**First:** *Proconodontus tenuiserratus* Miller, 1980, Point Peak Member, Wilberns Formation, Threadgill Creek–Lange Ranch section, central Texas, USA; *tenuiserratus* Biozone (Miller et al., 1982).
Last: Procondontus muelleri Miller, 1969, San Saba Member, Wilberns Formation, Threadgill Creek–Lange Ranch section, central Texas, USA; top of minutus Sub-biozone (Miller et al., 1982).

Order BELODELLIDA Sweet, 1988

F. ANSELLIDAE Fähraeus and Hunter, 1985

In addition to the genera included by Sweet (1988), we follow Fähraeus and Hunter (1985) in including Goverdina Fähraeus and Hunter, 1985.

First: Ansellajemtlandicus(Löfgren, 1978), Brunflo area, Lake Storsjön, Jämtland, Sweden; top of flabellum Sub-biozone (Löfgren, 1978).

Last: Hamarodus europaeus(Sergi, 1967), mucronata Beds, Troutbeck Formation, Brow Gill, Cumbria, England,
UK; ordovicicus Biozone, Rawtheyan (Orchard, 1980). If Hamarodus Viira, 1975 is not included in the Ansellididae, the last is Ansellia neudenis (Ethington and Schumacher, 1969); compressa Chronozone in the composite standard section of Sweet (1984).


Last: Belodela resima (Philip, 1965), Sadler Limestone (?), Canning Basin, Western Australia (Druce, 1976).

Order PROTOPANDERODONTIDA Sweet, 1988

The Protopanderodontida contains the majority of euconodonts that have their apparatuses composed entirely of coniform elements. Although knowledge of apparatus plans has advanced substantially in recent years, the group is still poorly known in terms of evolutionary relationships.


The family composition adopted here differs from that of Sweet (1988). We refer Cornodus Fähraeus, 1966 and Scalpellodus Dzik, 1976 to the Cornuodontidae, but include Eucharodus Kennedy, 1980 (synonymized with Ulrichodina Furnish, 1938 by Sweet) in the Acanthodontidae. The family remains a particularly poorly understood group in need of further taxonomic work.

First: Acanthodus lineatus (Furnish, 1938), House Formation, Ibex area, Utah, USA; intermedius Biozone (Ethington and Clark, 1982).

Last: Parapaltodus flexuosus (Barnes and Poplawski, 1973), top of Table Cove Formation, Table Point, Newfoundland, Canada; sulcatus Sub-biozone (Stouge, 1984).


First: Granatodus ani Chen and Gong, 1986, ‘Xiaoyangqiao Lower Section’, Dayangcha, Jilin Province, China; tenuiserratus Biozone (Chen et al., 1988).


First: Cornodus longibasis (Lindström, 1955), Köpingskлин Formation, Köpingskлин, Öland, Sweden; deltifer Biozone (van Wamel, 1974, who described the species as Protopanderodus longibasis (Lindström, 1955)).

Last: Scalpellodus cavus (Webers, 1966), McGregor Member, Platteville Formation, Olmsted County, Minnesota, USA (Webers, 1966); probably tenuis Chronozone.


Last: Dapsilodus obliquostatus (Branson and Mehl, 1933), chert and shale member, Caballos Novaculite, Marathon Uplift, Texas, USA; Lower Devonian (Barrick, 1987).


We follow Bergström (in Robison, 1981) in referring Nordiaus Serpagli, 1967 and Scandodus Lindström, 1955 to this family in addition to the genera listed by Sweet (1988). Decoriconus Cooper, 1975 may well also belong here.

First: Pallodus deltifer (Lindström, 1955), Djupvik Formation, Köpingskлин, Öland, Sweden; delaBiozone (van Wamel, 1974, who described the species as Drepanoistodus inequalis (Pander, 1856)).

Last: Drepanoistodus suberectus (Branson and Mehl, 1933), top of Member 5, Ellis Bay Formation, Anticosti Island, Quebec; ensifer Biozone (McCracken and Barnes, 1981). If Decoriconus is included in the family, the last occurrence becomes: Decoriconus fragilis (Branson and Mehl, 1933), chert and shale member, Caballos Novaculite, Marathon Uplift, Texas, USA; Lower Devonian (Barrick, 1987).


To the genera included by Miller (in Robison, 1981), we add Teridontus Miller, 1980. Semiacoachtodontus Miller, 1969 is transferred to the Protopanderodontidae, and Pseudopanderodus Landing, 1979 is a junior synonym of Panderodus Ethington, 1959 (Sweet, 1988).


Last: Oneotodus costatus Ethington and Brand, 1981, Fillmore Formation, Ibex area, Utah, USA; upper part of communis Biozone (Ethington and Clark, 1982).


This is a large family group, probably containing representatives of several lineages, although a common ancestor may prove to exist in Semiacoachtodontus nogamii Miller, 1969. To the genera listed by Sweet (1988), Anodontus Stouge and Bagnoli, 1988, Juanognathus Serpagli, 1974, Parapanderodus Stouge, 1984, Scoleopodus Pander, 1856 and Ulrichodina Furnish, 1938 are added. Following Miller (in Robison, 1981), a separate family Oneotodontidae is recognized, in which we include Monocostodus, Oneotodus, Teridontus and Utahconus. Pseudoneotodus and Strachanognathus, question-
ably included in the Protopanderodontidae by Sweet (1988), are assigned to separate families.

**First**: *Semiacontiodus nogamii* Miller, 1969, Signal Mountain Limestone, Wichita Mountains, Oklahoma, USA; base of *elongatus* Sub-biozone (Miller et al., 1982).

**Last**: *Staufferella inaligerae* McCracken and Barnes, 1981, base of Member 6, Ellis Bay Formation, Anticosti Island, Quebec, Canada; *nathanii* Biozone, Ordovician/Silurian boundary beds (McCracken and Barnes, 1981).

**F. STRACHANOGNATHIDAE** Bergström, 1981

O. (ARG—ASH) *Mar.*

**First**: *Strachanognathus pervus* Rhodes, 1955, Borghamn, Östergotland, Sweden; Vokhovian (Löfgren, 1978).


**Order** PANDERODONTIDA Sweet, 1988

F. PANDERODONTIDAE Lindström, 1970

O. (ARC?/LLN)—D. (GIV) *Mar.*


**First**: *Panderodus sulcatus* (Fähræus, 1966), Jamtland, Sweden; upper part of the *gracilis* Sub-biozone (Löfgren, 1978). An unnamed species of *Panderodus* was figured by Serpagli (1974, pl. 24, figs 12, 13) from the *eva* Biozone of the San Juan Formation, Argentina.

**Last**: *Neopanderodus perlineatus* Ziegler and Lindstrom, 1971, Dunkle Kalke, Ebbesattels, Germany; *varcus* Biozone (Ziegler, 1965).

**Order** PRONIOIODONTIDA Dzik, 1976

F. BALOGNATHIDAE Hass, 1959

O. (ARC—ASH) *Mar.*


**First**: *Baltoniodus crassulus* (Lindström, 1955). Bruddesta Formation, Oland, Sweden (van Wamel, 1974), or *Baltoniodus bohemicus* Dzik, 1984, Klabava Formation, Svatostepansky rybnik, Myto, Czechoslovakia (Dzik, 1984); both *eva* Biozone.

**Last**: *Gamachignathus ensifer* McCracken et al., 1980 and *Gamachignathus hastatus* McCracken et al., 1980, base of Member 6, Ellis Bay Formation, Anticosti Island, Quebec, Canada; *ensifer* Biozone (McCracken and Barnes, 1981).

**F. CYRTONIODONTIDAE** Hass, 1959

O. (LLN—ASH) *Mar.*

**First**: *Phragmodus harrisi* Bauer, 1989, base of *harrisi* Chronozone (= *P. pre-flexuosus* Chronozone) in the composite standard section of Sweet (1984).

**Last**: *Phragmodus undatus* Branson and Mehl, 1933, Member 5, Ellis Bay Formation, Anticosti Island, Quebec, Canada; top of *ensifer* Biozone (McCracken and Barnes, 1981).

**F. DISTOMODONTIDAE** Klapper, 1981

S. (LLY—LUD/PRD) *Mar.*

**First**: *Distomodus kentuckyensis* Branson and Branson, 1947, Bronydd Formation, Llandovery, Wales, UK; *kentuckyensis* Biozone, low Rhuddanian (Aldridge and Mohamed, in Cocks et al., 1984). Specimens identified as *Distomodus aff. D. kentuckyensis* were reported from the lowermost Silurian of the Ellis Bay Formation, Anticosti Island, Quebec, Canada by McCracken and Barnes (1981).

**Last**: *Dentacodina? dubia* (Rhodes, 1953), Long Quarry Formation, Llandovery, Wales, UK (Aldridge, 1975); *eosteinhornensis* Biozone?, latest LUD or earliest PRD.

**F. ICRIODELLIDAE** Sweet, 1988

O. (LLN)—S. (WEN) *Mar.*


**First**: *Icriodella cerata* (Knüpfert, 1967)?, Rzeszów slate, Kaczawa Mountains, Sudetes, Poland; *A. variabilis* Biozone (Dzik, 1989).

**Last**: *Icriodella inconstans* Aldridge, 1972, Brinkmarsh Formation, Torkworth, Bristol, England, UK (Aldridge, 1975); *sagitta rhenana* Biozone, lower Sheinwoodian.

**F. ICRIODELLITIDAE** Müller and Müller, 1957


We include *Pedavis*, *Sannemannia* and *Streptotaxis* here, rather than follow Sweet (1988) in placing them in the Icriidellidae. *Playfordia* Glinster and Klapper, 1966 may also belong.

**First**: *Pedavis latialata* (Walliser, 1964), Alticola Kalke, Carnic Alps, Austria; *latialata* Biozone (Walliser, 1964). *Corysognathus?* sp. nov. Aldridge and Mohamed, 1982, Solvik Formation, Asker, Norway (kentuckyensis Biozone, Aeronian?) is a possible progenitor.

**Last**: *Pelekysgnathus inclinatus* Thomas, 1949, upper *praesulcata* Biozone (Sandberg and Dreesen, 1984).

**F. MULTIOISTODONTIDAE** Harris, 1964

O. (ARC—CRD) *Mar.*

Of the genera listed by Sweet (1988), *Leptochirognathus* Branson and Mehli, 1943 is transferred to Fam. nov. 3. *Trigonodus Nieper, 1969, considered a probable junior synonym of Pteracontiodus Harris and Harris, 1965 by Sweet (1988), is here accepted as a separate genus.

**First**: *Trigonodus larapintinensis* (Crespin, 1943), Horn Valley Siltstone, Amadeus Basin, Northern Territory, Australia; *eva* Biozone (Cooper, 1981).

**Last**: *Pteracontiodus alatus* (Dzik, 1976), Mountain Lake Formation, Oklahoma, USA; *gerdae* Sub-biozone (Dzik, 1983).

**F. OISTODONTIDAE** Lindström, 1970

O. (TRE—ARG) *Mar.*

Sweet (1988) divided the Oistodontidae into three subfamilies: Oistodontinae, Tripodontinae and Juanognathinae. There is no diagnostic basis for recognizing the Oistodontinae and Tripodontinae, and their constituent genera,
with the exception of *Protoprioniodus* McTavish, 1973, are here treated simply as members of the Oistodontidae. *Protoprioniodus* is transferred to the Paracordylodontidae. *Juanognathus* Serpagli, 1974, the nominate genus of the Juanognathinae, does not have a prioniodontid apparatus and is transferred, pending a review of that family, to the Protopanderodontidae. *Histiodella* Harris, 1962, also included in the Juanognathinae by Sweet (1988), remains in the Oistodontidae.

**First:** *Rossodus manitouensis* Repetski and Ethington, 1983, House Limestone, Ibex area, Utah, USA; *manitouensis* Biozone (Ethington and Clark, 1982). Repetski and Ethington (1983) also included *Utahconus tenuis* Miller, 1980 in *Rossodus*; if this is correct then the first occurrence becomes: House Limestone, Ibex area, Utah, USA; *hintzei* Sub-biozone (Miller et al., 1982).

**Last:** *Histiodella sinuosa* Graves and Ellison, 1941; *friendsvillensis* Chronozone in the composite standard section of Sweet (1984).

**F. PARACORDYLODONTIDAE** Bergström, 1981


Bergström (in Robison, 1981) erected this family for one genus, *Paracordylodus* Lindström, 1955; Sweet (1988) included neither the family nor the genus in his classification. The concept of the family is expanded here to include *Fahraeusodus* Stouge and Bagnoli, 1988 and *Protoprioniodus* McTavish, 1973, which probably form part of the same lineage.

**First:** *Paracordylodus gracilis* Lindström, 1955, Köpingsklint Formation, Oland, Sweden; *deltifer* Biozone (van Wann, 1974).

**Last:** *Fahraeusodus marathonensis* (Bradshaw, 1969), Kanosh Shale, Ibex area, Utah, USA; *sinuosa* Biozone (Ethington and Clark, 1982).

**F. PERIODONTIDAE** Lindström, 1970


**First:** *Periodon selenopsis* (Serpagli, 1974), upper part of Bed 9, Cow Head Group, Point of Head, Cow Head Peninsula, Newfoundland, Canada; *elegans* Biozone (Stouge and Bagnoli, 1988). *Periodon primus* Stouge and Bagnoli, 1988, from the base of Bed 9 (proteus Biozone) is adenticulate and, although possibly ancestral (Löfgren, 1978; Stouge and Bagnoli, 1988), should probably be referred to *Diaporododus* Kennedy, 1980 (Oistodontidae).

**Last:** *Periodon grandis* (Ethington, 1959), velicuspus Chronozone in the composite standard section of Sweet (1984).

**F. PLECTODINIDAE** Sweet, 1988

O. (LLN—ASH) Mar.

**First:** *Plectodina aff. flexa* (Rhodes, 1953), Rzeszów slates, Karzawa Mountains, Sudetes, Poland; *navis/triangularis* Biozone (Dzik, 1989).

**Last:** *Plectodina aculeatoides* Sweet, 1979, upper part of *divergens* Chronozone in the composite standard section of Sweet (1984).

**F. POLYPLACOGNATHIDAE** Bergström, 1981

O. (LLN—CRD) Mar.

We include *Prattognathus* Bergström, 1983 here in addition to the genera listed by Sweet (1988).

**First:** *Eoplacognathus zgierzensis* Dzik, 1976, –510.35 m, Ohesaare borehole, Estonia, former USSR; *A. variabilis* Biozone (Dzik, 1983).

**Last:** *Polyplacognathus ramosus* Staufer, 1935, lower part of *confuens* Chronozone in the composite standard section of Sweet (1984).

**F. PRIONIODONTIDAE** Bassler, 1925


**First:** *Protoprioniodus gilberti* Stouge and Bagnoli, 1988, uppermost Bed 8, Cow Head Group, Point of Head, Cow Head Peninsula, Newfoundland, Canada; *deltifer* Biozone (Stouge and Bagnoli, 1988).

**Last:** *Oepikodus communis* (Ethington and Clark, 1964), Wah Wah Formation, Ibex area, Utah, USA; *communis* Biozone (Ethington and Clark, 1982). A possible successor species was identified as *Oepikodus? aff. minutus* (McTavish, 1973) by Ethington and Clark (1982), from the Kanosh Shale, Ibex area, Utah, USA; *altifrons* Biozone.

**F. PTEROSPATHODONTIDAE** Cooper, 1977

S. (LLY—WEN) Mar.

Of the genera included by Sweet (1988), *Carniodus* Walliser, 1964 is transferred to Fam. niv. 6, and *Johnognathus* Mashkova, 1977, if indeed a distinct genus, probably belongs in the Dictomodontidae. The apparatus of *Aulacognathus* Mostler, 1967 resembles that of *Clenognathodus* Pander, 1856, and the genus is tentatively transferred to the Kockeellidae. The relationships of *Apsidogathus* Walliser, 1964 and *Astropentagnathus* Mostler, 1967 remain to be clarified, but they are retained at present in the Pterospathodontidae. *Pranognathus* Mannik and Aldridge, 1989 is also included here, and *Huddella* Mashkova, 1979 may belong.

**First:** *Pranognathus sil Ricus* (Pollock et al., 1971), Neaghga Shale, Niagara Falls, Ontario, Canada (Pollock et al., 1971) or *Pranognathus tenuis* (Aldridge, 1972), Solvik Formation, Oslo, Norway (Aldridge and Mohamed, 1982); both species from the upper part of the *kentuckyensis* Biozone, Aeronian.


**First:** *Pranognathus variabilis* (Pollock et al., 1971), Neaghga Shale, Niagara Falls, Ontario, Canada; *sil Ricus* Biozone, Aeronian.

**Last:** *P. (ARG)—O. (ASH)/?S. (LLY—WEN) Mar.

**Thrinocodus** Bauer, 1987 is a possible addition to the genera included by Sweet (1988). *Tasmanognathus* Burrett, 1979 shows some similarities to *Rhipidognathus* Branson et al., 1951, and may also belong.

**First:** *Bergstroemognathus extensus* (Graves and Ellison, 1941), Bed 9, Cow Head Group, Cow Head Peninsula, Newfoundland, Canada; *proteus* Biozone (Stouge and Bagnoli, 1988), or *B. hubeiensis* An, 1985, Honghuayuan Formation, Yichang, Hubei, China; *diversus* Biozone (An et al., 1985).

**Last:** *Rhipidognathus symmetricus* Branson et al., 1951, Member 1, Ellis Bay Formation, Anticosti Island, Quebec, Canada; *ensifer* Biozone (McCracken and Barnes, 1981). Possibly 'Apparatus A' Uyeno, 1981, Cape Storm Formation, Goodsir Creek, Cornwallis Island, Canadian Arctic Archipelago; *sil Ricus* Biozone (Uyeno, 1981).
Order PRIONIODINIDAE Sweet, 1988

F. BACTROGNATHIDAE Lindström, 1970
In addition to the genera listed by Sweet (1988), *Geniculatus* Hass, 1953 may belong here. *Apatella* Chauff and Klapper, 1978 has a closely similar Pa element to *Bactrognathus* Branson and Mehl, 1941 and may also belong, although the similarities have been interpreted as homeomorphic (Chauff and Klapper, 1978; Chauff, 1985).


F. CHIROGNATHIDAE Branson and Mehl, 1944

First: *Erraticodon patu* Cooper, 1981, Horn Valley Siltstone, Amadeus Basin, Northern Territory, Australia; *eva* Biozone (Cooper, 1981).


F. ELLISONIIDAE Clark, 1972
C. (BSH)–Tr. (CRN) Mar.
From the genera listed by Sweet (1988), we transfer *Merrillina* Kozur and Mock, 1974 to the Gondolellidae, following its reconstruction by Swift (1986). *Stepanovites* Kozur, 1975 belongs here, if it is a distinct genus.

First: *Ellisonia latilaminata* von Bitter and Merrill, 1983, Eagle Limestone, Mingo County, West Virginia, USA; *Morrowan* (von Bitter and Merrill, 1983).

Last: *Gladiogondolella tethydis* (Huckriede, 1958), Hallstatt Limestone, Feuerkogel, Rothelstein, Steiermark, Austria; *tethydis* Biozone (Huckriede, 1958).

F. GONDOLELLIDAE Lindström, 1970
C. (BSH)–Tr. (RHT) Mar.

First: *Neogondolella clarki* (Koike,1967), Marble Falls Limestone, San Saba County, Texas, USA; *Morrowan* (von Bitter and Merrill, 1977).

Last: *Axiothea posthernsteini* (Kozur and Mock, 1974), Kösseiner Schichten, Eiberg, Austria; *posthernsteini* Biozone (Golebiowski, 1986).

F. PRIONIODINIDAE Bassler, 1925


Last: *Idioprioniodus typus* Gunnell, 1933, Topeka Limestone, Shawnee Group, Shawnee County, Kansas, USA; *Virgilian* (von Bitter, 1972, see Merril and Merril, 1974).

Order OZARKODINIDAE Dzik, 1976

F. ANCHIGNATHODONTIDAE Clark, 1972
C. (TOU)–Tr. (DIE) Mar.

First: *Hindeodus crassidentatus* (Branson and Mehl, 1934), Bushberg Sandstone, Frenchman Creek, Missouri, USA (Branson and Mehl, 1934); *sandbergi* Biozone.

Last: *Hindeodus typicalis* (Sweet, 1970), Khunamuh Formation, Guryul Ravine, Kashmir (Sweet, 1979); *kummeli–cristagalli* Biozone.

F. CAVUSGNATHIDAE Austin and Rhodes, 1981
D. (FAM)–P. (SAK/ART?) Mar.

First: *Patrognathus ourayensis* Sandberg and Ziegler, 1979, Ouray Limestone, San Juan Mountains, Colorado, USA; *Middle*? Upper * styriacus* Biozone (Sandberg and Ziegler, 1979).


F. ELICTOGNATHIDAE Austin and Rhodes, 1981

First: *Alternognathus pseudotrigosus* (Dreesen and Dusar, 1974), Hamoir-Fairon section, near Liege, Belgium; upper * rhomboidea* Biozone (Dreesen and Dusar, 1974).

Last: *Siphonodella isosticha* (Cooper, 1939), pre-Welden Shale, Pontotoc County, Oklahoma (Cooper, 1939); *isosticha–Upper crenulata* Biozone.

F. GNATHODONTIDAE Sweet, 1988


F. IDIOGNATHODONTIDAE Harris and Hollingsworth, 1933
C. (BSH)–P. (ART) Mar.

First: *Declinognathodus noduliferus* (Ellison and Graves, 1941), Target Limestone, Springer Formation, Carter
County, Oklahoma, USA; primus Biozone, Morrowan (Lane and Straka, 1974).

**Last:** Streptognathodus elongatus Gunnell, 1933, topmost Tensleep Sandstone, Mayoworth, Wyoming, USA (Rhodes and Straka, 1963); bisselli/whitiei Biozone.

**F. KOCELELLIDAE** Klapper, 1981


In addition to the genera listed by Sweet (1988), this family includes Ctenognathodus’ Pander, 1856, and possibly Aulacognathus Mostler, 1967, and Tuxekania Savage, 1985.

**First:** ?Ctenognathodus’ pseudofossilis Lindström, 1959, Crug Limestone, Llandeilo, Wales, UK (Lindström, 1959); ?superbus/orandicus biozonal boundary, Cautleyan (Orchard, 1980). Otherwise Kockelella manitoulinensis (Pollock et al., 1971), Manitoulin Dolomite, Manitoulin Island, Ontario, Canada (Pollock et al., 1971); kentuckyensis Biozone, ?Ruddanian.

**Last:** Kockelella variabilis Walliser, 1957 from the Cardiola–Niveau beds of Cellon, Carnic Alps, Austria (Walliser, 1964); siluricus Biozone, Ludfordian.

**F. MESTOGNATHIDAE** Austin and Rhodes, 1981


**First:** Mestognathus grossensi Belka, 1983, borehole WB-64, Olkus, Poland; isosticha–Upper crenulata Biozone (Belka, 1983).


**F. PALMATOLEPIDAE** Sweet, 1988


**First:** ‘Polygnathus’ latifossatus Wirth, 1967, Quinto Real Massif, Pyrenees, Spain (Wirth, 1967); upper varcus Subbiozone.

**Last:** Palmatolepis gracilis sigmoidalis Ziegler, 1962, Wocklumeria Limestone, Oberrödinghausen, Rheinisches Schiefergebirge, Germany (Ziegler, 1962); upper praesulcata Biozone.

**F. POLYGNATHIDAE** Bassler, 1925


In addition to the genera listed by Sweet (1988), we provisionally include Rhodalepis Druce, 1969.

**First:** Polygnathus pireneae Boersma, 1974, Basibe Formation, central Pyrenees, Spain (Boersma, 1974); pireneae Biozone.

**Last:** Polygnathus bischoffi Rhodes et al., 1969, Carboniferous Limestone (C Zone), Gower, Wales, UK (Rhodes et al., 1969); homopunctatus Biozone.

**F. SPATHOGNATHODONTIDAE** Hass, 1959


**First:** ?Yaoxiangognathus? abruptus (Bergström and Sweet, 1966); undatus Chronzone in the composite standard section of Sweet (1984). Otherwise, ‘Plectodina’ tenuis (Branson and Mehl, 1933), tenuis Chronzone in the composite standard section.

**Last:** Rhachistognathus minutus declinatus Baesemann and Lane, 1985, Bird Spring Formation, Arrow Canyon, Nevada, USA; Atokan, ?lower Desmoinesian (Baesemann and Lane, 1985).

**F. SWEETOGNATHIDAE** Ritter, 1986

C. (VIS)–Tr. (GRI) Mar.

**First:** Diplognathodus spp., Ship Cove Limestone, Codroy, Newfoundland, Canada; ‘Diplognathodus’ Biozone (von Bitter and Plint-Geberl, 1982).

**Last:** Isarcicella isarcica (Huckriede, 1958), Werfen Formation, Fufelsbach, Val Gardena, northern Italy; isarcica Biozone (Huckriede, 1958).

**Order UNKNOWN**

**F. COLEODONTIDAE** Branson and Mehl, 1944


**First:** Coleodus simplex Branson and Mehl, 1933, Tyner Formation, Cherokee County, Oklahoma, USA; harrisii Biozone (Bauer, 1989).

**Last:** Coleodus delicatus Branson and Mehl, 1933, C. simplex Branson and Mehl, 1933, Neocoleodus brevicornus Branson and Mehl, 1933 and Stereocomus gracilis Branson and Mehl, 1933, upper sandstone member, Harding Sandstone, Fremont County, Colorado, USA (Sweet, 1955); undatus Biozone.

**F. FAM. NOV. 1** C. (MER)–O. (ARG) Mar.

Comprises Cambropustula Müller and Hinz, 1990, Polomodus? sensu Stouge and Bagnoli, 1988, and possibly Nericodus Lindström, 1955; the group constitutes the oldest euconodont family.

**First:** Cambropustula kinneikullenensis Müller and Hinz, 1990. Alum Shale, Kinnekulle, Västergötland, Sweden; Agnostus pisiformis trilobite Biozone (Müller and Hinz, 1991).

**Last:** ‘Polomodus’ corbatoi (Serpagli, 1974), Bed 11, Cow Head Group, Point of Head, Cow Head Peninsula, Newfoundland, Canada; evae Biozone (Stouge and Bagnoli, 1988).


Contains only Chosonodina Müller, 1964; may be in the same order as Fam. nov. 3.


**Last:** Chosonodina rigbyi Ethington and Clark, 1982, Lehman Formation, northern Egan Range, Nevada, USA (Harris et al., 1979); uppermost harrisii Biozone or friendsvillensis Biozone.


**First:** Loxodus bransoni Furnish, 1938, House Formation, Iben area, Utah, USA; manitouensis Biozone (Ethington and Clark, 1982).

**Last:** Leptochoirognathus quadratus Branson and Mehl, 1943, Tulip Creek Formation, Arbuckle Mountains, Oklahoma, USA; friendsvillensis Chronzone (Bauer, 1987).
Contains only Dischidognathus Ethington and Clark, 1982.
First: Unnamed species of Dischidognathus, Eleanor River Formation, Canadian Arctic Archipelago; communis Biozone (Nowlan, 1976).
Last: Dischidognathus primus Ethington and Clark, 1982, Antelope Limestone Formation, Martin Ridge, Monitor Range, Nevada, USA; uppermost harrisi Biozone or friendsvillensis Biozone (Harris et al., 1979).

First: ??Pseudooneotodus mitratus mitratus (Moskalenko, 1973), Table Point Formation, Table Head, Newfoundland, Canada; holodentata Biozone (Stouge, 1984, single unfigured specimen, lost prior to publication). Otherwise, P. mitratus, Gonioceras Bay Member, Kap Jackson Formation, Wulff Land, North Greenland; sweeti Biozone (Tull, 1988).


Contains only Caenodontus Behnken, 1975.
First and Last: Caenodontus serrulatus Behnken, 1975, Cherry Canyon and Bell Canyon Formations, Culberson County, Texas, USA; Guadalupian (Behnken, 1975).

REFERENCES

Branson, E. B. and Mehl, M. G. (1934) Conodonts from the Bushberg Sandstone and equivalent formations of Missouri. The University of Missouri Studies, 8, 265–99.


Sweet, W. C. (1979) Late Ordovician conodonts and biostratigraphy of the western Midcontinent Province. Brigham Young University Geology Studies, 26 (3), 45–86.


Conodonta
Animals: Vertebrates


The Agnatha are frequently divided into two groups – the armoured fossil forms and the naked living cyclostomes, the latter until 1968 without a fossil record. Stensiö (1927), however, established the close affinity between the lampreys (Petromyzontida) and cephalaspids (Osteostraci) and anaspids. His contention that the hagfish (Myxini) and pteraspids (Heterostraci) were similarly closely related has not met with such ready acceptance, although it was acknowledged that the lampreys and hags were very distantly related. The Cyclostomata were considered to be an unnatural grouping, resulting from convergent evolution. Work during the 1980s now indicates they are, after all, a natural group, and the classification used here reflects this (Schaeffer and Thomson, 1980; Yalden, 1985). Discoveries of new fossils in China, Australia, and South America in the 1970s and 1980s have added enormously to our understanding, while at the same time necessitating a re-evaluation of the classification. Details of the internal anatomy, coupled with the microstructure of the bony armour, indicate that the Agnatha belong to two distinct classes: the Diplorhina which includes the Heterostraci and Thelodonti, and the Monorhina comprising four subclasses, Osteostraci (cephalaspids), Anaspida, Galeaspida and Cyclostomata (lampreys and hagfish). Some of the new material cannot be assigned to any subclass, and one subclass, the Astraspida, can no longer be linked to either of the established agnathan classes. General references on the ranges and significance of Siluro – Devonian agnathans are Halstead (1966, 1973, 1985a,b) and Novitskaya (1983, 1986).

**Acknowledgement** The editor thanks Professor David L. Dineley for his considerable help in checking this chapter, and Mrs Jane Hawker for retyping Bev’s rather eccentric MS.

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**Superclass** AGNATHA Haeckel, 1895

**Class** DIPLORHINA Haeckel, 1895

(PTERASPIDOMORPHI Goodrich, 1909)

**Subclass** HETEROSTRACI Lankester, 1868

(PTERASPIDES) (see Fig. 31.1)

**Order** ARANDASPIDIFORMES Ritchie and Gilbert-Tomlinson, 1977

**F.** ARANDASPIDIDAE Ritchie and Gilbert-Tomlinson, 1977

First and Last: *Arandaspis prionotolepis* Ritchie and Gilbert-Tomlinson, 1977, Stairway Sandstone, Northern Territory, Australia; *Saccambaspis janvieri* Gagnier, 1987, Anzaldo Formation, Sacabamba, Bolivia, previously dated as CRD, was then placed in LLN (Gagnier, 1989), but now again in CRD (Elliott et al., 1991).

**Order** ERIPTYCHIFORMES Tarlo, 1962

**F.** ERIPTYCHIIDAE Tarlo, 1962

First and Last: *Eriptychius americanus* Walcott, 1892, Harding Sandstone, Canyon City, Colorado, USA; *Eriptychius orvigi* Denison, 1967, Bear Rocks, Bighorn Mountains, Sheridan County, Wyoming, USA.

**F.** POROPHORASPIDIDAE fam. nov.

O. (LLN) Mar.


**F.** ASERASPIDIDAE fam. nov. S. (PRD) FW

First and Last: *Aseraspis canadensis* Dineley and Loeffler, 1976, Delorme Formation, District of Mackenzie, Northwest Territories, Canada.

**F.** TESSERASPIDIDAE Berg, 1940

S. (PRD) – D. (PRA) FW

First: *Tesseraspis denisoni* Halstead Tarlo, 1965, Beaver River, south-east Yukon, Canada.


**Order** CYATHASPIDIFORMES Kier and Heintz, 1935

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*This may be one of Bev’s last papers: he died tragically, soon after submitting it. [Editor]*
Fig. 31.1

F. TOLYPELEPIDIDAE Strand, 1934
S. (WEN)–D. (LOK) Mar./FW
First: *Tolypelepis* sp. nov., Allen Bay Formation, Shellabear Creek, Cornwallis Island, North-west Territories, Canada. This material, noted by Thorsteinsson (1958), is still to be described.
Last: *Tolypelepis timanica* Kossovoi and Obruchev, 1962, Eptarmenskaya Beds, Velikaya River, Timan, former USSR.

F. CYATHASPIDIDAE Kiaer, 1932
S. (WEN)–D. (LOK) Mar./FW
Last: *Seretaspis zychi* Stensiö, 1958, Czortkow Series, Lochkovian, Podolia, Ukraine; *Steinaspis miroshnikovi* Obruchev, 1964, lower Zubova Horizon, Norilsk, Nats Okrug, Knasnoyar sky Territory, Siberia, former USSR.

F. IRREGULAREASPIDIDAE Denison, 1964
S. (PRD)–D. (LOK) Mar./FW
First: *Dikenaspis yukonensis* Denison, 1963, Limestone and graptolitic shales, Beaver River, SE Yukon, Canada; *Nahanniaspis mackenziei* Dineley and Loeffler, 1976, Delorme Formation, Mackenzie District, North-west Territories, Canada.
Last: *Irregularaspis stensioei* Zych, 1931, Czortkow Stage, Lochkovian, Podolia, Ukraine, former USSR; *I. hoelti* (Kiaer, 1932), Red Bay Series, Ben Nevis Formation, Ben Nevis, Spitsbergen.

F. PORASPIDIDAE Kiaer, 1932
S. (PRD)–D. (PRA) Mar./FW
First: *Americaspis americana* (Claypole, 1884), Landisburg Sandstone Member, Wills Creek Formation, Landisburg, Perry County, Pennsylvania, USA; *A. claypolei* Denison, 1964, Longwood Shale, Shin Hollow, Orange County, New York, USA.
Last: *Allocryptaspis elliptica* (Bryant, 1934), Beartooth Butte Formation, Beartooth Butte, Park County, Wyoming, USA; *A. laticostata* Denison, 1960, Holland Quarry, Lucas County, Ohio, USA.

Comment: This family is abundant in Lochkovian in Podolia, Ukraine, Spitsbergen, England and Wales, Canadian Arctic.

F. CTENASPIDIDAE Kiaer, 1930
S. (PRD)–D. (LOK) Mar./FW
First: *Ctenaspis* n. sp. aff. *dentatus* Thorsteinsson, 1958, Snowblind Bay Formation (Lochkovian–Pragian), Read Bay, Cornwallis Island, North-west Territories, Canada.
Last: *Ctenaspis dentata* Kiaer, 1930, Ben Nevis Formation, Red Bay Series, Ben Nevis, Spitsbergen; *Ctenaspis obruchevi* Dineley, 1976, Upper Member, Peel Sound Formation (Lochkovian), Prince of Wales Island, North-west Territories, Canada.

F. TORPEDASPIDIDAE fam. nov. S. (PRD) FW
First and Last: *Torpedaspis elongata* Broad and Dineley, 1973, Somerset Island and Peel Sound Formations (Pridolian–Lochkovian), Somerset and Prince of Wales Islands, North-west Territories, Canada.

F. CORVASPIDIDAE Dineley, 1953
S. (PRD)–D. (LOK) Mar./FW
First: *Corveolepis arctica* (Loeffler and Dineley, 1976), Peel Sound Formation (Lochkovian), Pressure Point, Somerset Island, North-west Territories, Canada.
Last: *Corvaspis graticulata* Dineley, 1953, Ben Nevis Formation, Red Bay Series, Ben Nevis, Spitsbergen.

Order PTERASPIDIFORMES Berg, 1940
Range data on pteraspidiform heterostracans is derived in part from Bliick (1984).
F. PENCYGASPIDIDAE fam. nov. D. (PRA) FW
First and Last: *Penygaspis dixoni* (White, 1938), Senni Beds Formation, Breconian, Pen-y-gau Farm, Dyfed, South Wales, UK.

F. ANCHIPTERASPIDIDAE Elliott, 1984 S. (PRD)–D. (LOK) Mar./FW
First: *Ulilitaspis aquilonia* Elliott, 1984, Somerset Island Formation (Pridolian), Somerset Island, North-west Territories, Canada.
Last: *Anchipteraspis crenulata* Elliott, 1984, Peel Sound Formation, Somerset Island, North-west Territories, Canada.

F. PTERASPIDIDAE Claypole, 1885 S. (PRD)–D. (EIF) FW
Last: *Pteraspiformis fyny and Heintz, 1943, Widje Formation, Breconian, Pen-y-gau Farm, Dyfed, South Wales, UK.

Order *PSAMMOSTEIFORMES* Berg, 1940
F. DREPSASPIDIDAE Traquair, 1899 D. (PRA–EMS) Mar./FW
Last: *Drepanaspis liperti* Gross, 1937, Kletterfischichten, Zweifelscheide, Rhineland, Germany.

Last: *Schizosteus asatkini* Obruchev, 1940, *Pycnosteus palaeformis* Zone, Arukula Horizon, Luga River, near Leningrad, former USSR. *Schizosteus perneri* (Ruzicka, 1929), Chotek Limestone, Horizon g, Holin Hlubocepy, near Prague, Czechoslovakia, is the only psammosteid of EIF age.

F. PYCNOSTEIDAE Tarlo, 1962 D. (GIV–FRS) FW
First: *Pycnolepis splendens* (Eichwald, 1844), *Schizosteus striatus* Zone, Narowa Horizon, River Slawanka, NW of former USSR.
Last: *Ganoestes stellatus* Rohon, 1901, *Pycnosteus paradoxa* Zone, Gauja Horizon, Eglin, Leningrad District, former USSR.

F. PSAMMOLEPIDIDAE Tarlo, 1962 D. (GIV–FRS) FW

F. PSAMMOSTEIDAE Traquair, 1896 D. (FRS) FW
First: *Psammosteus praecursor* Obruchev, 1947, *Psammosteus undulata* Zone, Amata Horizon, Yam-Tesov, River Oresdesch, NW Russia, former USSR; *Psammosteus markae* Halstead Tarlo, 1961, *Psammosteus undulata* Zone, Amata Horizon, Vastseliina, Latvia, former USSR.
Last: *Psammosteus falcatus* Gross, 1942, *Psammosteus falcatus* Zone, Horizon e, Jurenski, River Pededze, Latvia; Scaat Craig Beds, Upper Old Red Sandstone, Scaat Craig, Elgin, Scotland, UK.

F. OBRUCHEVIIIDAE Halstead Tarlo, 1965 D. (FRS) FW
First: *Obruchevia heckeri* (Obruchev, 1936), *Psammosteus falcatus* Zone, River Lovat, NW Russia, former
Order CARDIPELTIFORMES Tarlo, 1962

F. CARDIPELTIDAE Bryant, 1933 D. (PRA) FW


Order AMPHIASPIDIFORMES Berg, 1940

F. AMPHIASPIDIDAE Obruchev, 1939 D. (EMS) FW

First and Last: Amphiaspis argos Obruchev, 1939, Razvedochinski Horizon, left bank of River Kureyka, tributary of River Yenisei, NW Siberia, former USSR.

F. SIBERIASPIDIDAE Novitskaya, 1968 D. (PRA) FW

First: Aphataspis kiaeri Obruchev, 1964, Putoranaspis prima Obruchev, 1966, Lower Kureyka Formation, left bank of River Kureyka, NW Siberia, former USSR, Boothiaspis ovata Broad, 1973, identified by Broad (1973) as a siberiaspid, Peel Sound Formation (GIV), Prince of Wales Island, North-west Territories, Canada, is here identified as a cyathaspid.

Last: Argyriaspis tcherkesovae Novitskaya, 1971, Ust-Tareya Series, River Tareya, central Taimyr, NW Siberia, former USSR.

F. OLBIASPIDIDAE Obruchev, 1964 D. (PRA) FW

First: Kureykaspis salebrosa Novitskaya, 1968, Lower Kureyka Formation, left bank of River Kureyka, NW Siberia, former USSR. "Olbiaspididae genus indet. ’of Broad (1973), Peel Sound Formation (GIV), Somerset Island, North-west Territories, Canada, is here identified as a cyathaspid.

Last: Gerronaspis dentata (Obruchev, 1964), Middle Kureyka Formation, left bank of River Kureyka, NW Siberia: Gerronaspis elegmatractae n.sp. (Mark-Kurik, 1974), Rybnaya River Formation, River Ryasakh-Kanga, Kotelnely Island, New Siberian Islands, former USSR.

F. ANGARASPIDIDAE fam. nov. D. (PRA) FW

First and Last: Angaraspis urvantzevi Obruchev, 1964, Middle Kureyka Formation, left bank of River Kureyka, Kureyksi Horizon, NW Siberia, former USSR.

F. GABREYASPIDIDAE Novitskaya, 1968 D. (LOK–PRA) FW

First: Prosarctaspis taimyrca Novitskaya, 1968, Belokamenski sloj, Ust-Tareya Horizon (Lochkovian–Pragian), River Tareya, central Taimyr, NW Siberia, former USSR.

Last: Gabreyiaspis tarda Novitskaya, 1968 and Pelasaspis teres Novitskaya, 1971, Urum Formation, Ust-Tareyski Horizon (Lochkovian–Pragian), River Tareya, central Taimyr, NW Siberia, former USSR.

F. HIBERNASPIDIDAE Obruchev, 1939 D. (PRA) FW

First and Last: Hibernaspis macrolepis Obruchev, 1939 and Edaphaspis Novitskaya, 1968, upper Kureyksi Horizon, left bank of River Kureyka, NW Siberia, former USSR.

F. EGONASPIDIDAE Tarlo, 1962 D. (PRA–EMS) FW

First: Lecaniaspis lata Novitskaya, 1971, middle Kureyski Horizon, left bank of River Kureyka, NW Siberia, former USSR.

Last: Pelurgaspis macrorhyncha Obruchev, 1964, Razvedochinski Horizon, left bank of River Kureyka, near River Nijny, NW Siberia, former USSR.

Subclass THELODONTI (COELOLEPIDES)

Order THELODONTIDA

Range data on thelodontids is based on Turner (1976), and Turner and Dring (1981).


First: Thelodus parvus Agassiz, 1839, Petalocrinus Lime­stone (Telychian), Littlehope, Welsh Borderland, England, UK.


F. TURINIIDAE Obruchev, 1964 S. (PRD)–D. (FRS) Mar./FW


F. APALOEPIDIDAE Turner, 1976 D. (LOK–EIP) FW

First: Apalolepis obruchevi Karatajute-Talimaa, 1968, Czortkow Stage, Dittonian (Lochkovian), Podolia, Ukraine, former USSR.

Last: Skamolepis sp., Turner and Janvier, 1979, Khush­Yeilagh Formation, NE Iran.

F. NIKOLIVIIDAE Karatajute-Talimaa, 1978 D. (LOK–FRS) FW


Order PHLEBOLEPIDIFORMES Berg, 1940 (syn. KATOPORIDA)

F. PHLEBOLEPIDIDAE Berg, 1940 D. (WEN)–D. (PRA) Mar./FW

First: Phlebolepis elegans Pander, 1856, K1 Horizon, Wenlock, Oesel (Saarema), Estonia, former USSR (pre­viously considered LUD).

Last: Katoporodus grossi (Karatajute-Talimaa, 1970) and Goniiaspis alatus (Gross, 1947), Althaspis leachi Zone, Ditton Group (Lochkovian–Pragian), Cwm Mill, Abergavenny, Wales, UK.

F. LOGANELLIDAE fam. nov. S. (LLY)–D. (LOK) Mar./FW
**Fig. 31.2**

**First:** *Loganella asiaticus* (Karatajute-Talimaa, 1978), Kizilchirskie Division, Tuva, Siberia, former USSR; *Loganella scotica* (Traquair, 1898), Venusbank Formation, Hope Quarry, Shropshire, Telychian Wych Beds, Gullet Quarry, Malvern Hills, England, UK.

**Last:** *Loganella cuneata* (Gross, 1947), Beyrichienkalk erratics, Germany; *Psammosteus* Limestone Group, Ross Motorway and Gardiner’s Bank, Herefordshire, England, UK.

**Class** MONORHINA Haeckel, 1895

**Subclass** OSTEOSTRACI Lankester, 1868 (CEPHALASPIDES)

**Order** TREMATASPIDIFORMES Halstead Tarlo, 1967

F. TREMATASPIDIDAE Woodward, 1891


**First:** *Tremataspis schmidtii* Rohon, 1892, Rootsiküla Formation K₄, Horizon, Oesel (Saaremaa), Estonia, former USSR.

**Last:** *Tremataspis mammillata* Patten, 1931, *T. milleri* Patten, 1931, and *T. rohoni* Robertson, 1938, Paadla Formation, K₂ Horizon, Oesel (Saaremaa), Estonia, former USSR.

F. DARTMUTHIIDAE Robertson, 1935


**First:** *Saaremaaspis mickwitzii* (Rohon, 1892), Rootsiküla Formation, K₁ Horizon, Oesel (Saaremaa), Estonia, former USSR.

**Last:** *Dartmuthia gemmifera* Patten, 1931, Paadla Formation, K₂ Horizon, Oesel (Saaremaa), Estonia, former USSR.

F. OESELASPIDIDAE Robertson, 1935

S. (WEN–LUD) Mar. (see Fig. 31.2)
First: Oeselaspis pustulata (Patten, 1931), Rootsiküla Formation, K1 Horizon, Oesel (Saaremaa), Estonia, former USSR.

Last: Oeselaspis pustulata Patten, 1931, Paadla Formation, Oesel (Saaremaa), Estonia, former USSR.

F. DIDYMASPIDIDAE Berg, 1940
S. (PRD)–D. (LOK) Mar./FW


F. TANNUASPIDIDAE Obruchev, 1964
S. (PRD)–D. (LOK) Mar./FW
First: Tuanaspis margaritae Obruchev, 1956, Samagaltayskaya Group, Kizil, near Lake Khashin, Tuva, former USSR.

Last: Tuanaspis levenskii Obruchev, 1956, Kendeyskaya Group, Kutuk Valley, Tannu-Ola Mountains, Tuva, former USSR.

First and Last: Timanaspis kossowoi Obruchev, 1962, Eptarminskaya Group, Velchikaya River, northern Timan, former USSR.


First and Last: Osteostracan fragments showing cellular dentine (mesodentine) and cellular bone, Hardin Sandstone Formation, Canyon City, Colorado, USA (Smith, 1991).

Order SCLERODONTIFORMES
F. SCLERODONTIDAE Fowler, 1947
First and Last: Sclerodus putulliferus Agassiz, 1839, Ludlow Bridge Bed, Ludlow and Shropshire; Downton Bridge and Kington, Worcester and Herefordshire; Baggenbridge Colliery, Staffordshire, England, UK.

Order THYESTIFORMES
F. THYESTIIDAE Berg, 1940
First: Thyestes verrucosus Eichwald, 1854, Rootsiküla Formation, K1 Horizon, Oesel (Saaremaa), Estonia, former USSR; Hall Formation, Gotland, Sweden.

Last: Fieldingaspis egertonii Lankester, 1870, Lower Red Downton Formation (Lochkovian), Ledbury, England, UK.

Order ATELEASPIDIFORMES
F. ATELEASPIDIDAE Traquair, 1899
First: Atelaspis tesselata Traquair, 1899, Slot Burn, Birkenhead Burn, Lesmahagow Hills, Lanarkshire; Hagshaw Hills, Ayrshire, Scotland, UK; Witaaaspis schrenkii (Pander, 1856), Rootsiküla Formation, K1 Horizon, Oesel (Saaremaa), Estonia, former USSR.

Last: Hemicyclopis murchisoni (Egerton, 1857), Lower Red Downton Formation (Pridolian), Ledbury, Herefordshire; Baggenbridge Colliery, Staffordshire, England, UK; Atelaspis robustus (Kiaer, 1911) [Hirella gracilis (Kiaer, 1911) = immature A. robustus], ‘Downtonian’ Sandstones (?Ludlovian), Rudstangen, Ringerike, Norway.

Order CEPHALASPIDIFORMES Halstead Tarlo, 1967
F. PROCEPHALASPIDIDAE Stensiö, 1958
First: Procephalaspis oseleensis (Robertson, 1939), Paadla Formation, K2 Horizon, Oesel (Saaremaa), Estonia, former USSR.


F. CEPHALASPIDIDAE Agassiz, 1843
D. (LOK–PRA) FW
First: Cephalaspis lyelli Agassiz, 1835, Lower Old Red Sandstone, Glamis, Forfarshire, Scotland, UK.

Last: Meteoraspis mothomasi (Wangsjö, 1953) and M. semicircularis (Wangsjö, 1952), Stjordalen Division, Wood Bay Formation, Stjordalen Valley, Spitsbergen.

Order BENNEVIASPIDIFORMES
F. BENNEVIASPIDIDAE Denison, 1952
D. (LOK–PRA) FW


F. BOREASPIDIDAE Stensiö, 1958
D. (PRA) FW

Last: Dicranaspis curtirostris (Wangsjö, 1952), Lykta Division, Wood Bay Formation, Dickson Bay, Mt. Triplex, Mt. Lykta, Mt. Errol White and Spatulaspis costata (Wangsjö, 1952), Lykta Division, Wood Bay Formation, Dickson Bay, Mt. Rebbing, Mt. Lykton, Spitsbergen.

Order SCOLENASPIDIFORMES
F. SCOLENASPIDIDAE Janvier, 1985
D. (LOK–FRS) FW

Last: Alasaspis macrotuberculata Ørvig, 1957, A. rosamundae (Robertson, 1937), and Escuminaspis laticeps (Traquair, 1899), Escuminac Formation, Scauenac Bay (Miguasha Bay), Quebec, Canada.

Order KIAERASPIDIFORMES Halstead Tarlo, 1967
F. KIAERASPIDIDAE Stensiö, 1932
D. (LOK–PRA) FW
First: Kiaeraspis achenaspidoides Stensiö, 1927, Ben Nevis...
Division, Red Bay Group, Mt. Ben Nevis, Red Bay, Spitsbergen.
Last: Norselaspis glacialis Janvier, 1981, Sigurdjfelljar
Division, Wood Bay Formation, Sigurdjfelljar, Wood Bay, Spitsbergen.

F. NECTASPIDIDAE Stensiö, 1958 D. (PRA) FW
First: Acrotomaspis instabilis Wängsjö, 1953, Kapp Kjeldsen
Division, Wood Bay Series, Mt. Kronprinz, Wood Bay, Spitsbergen.
Last: Gustavaspis trinodis (Wängsjö, 1952), Stjordalen
Division, Wood Bay Formation, Mt. Scott Keltie, Wood Bay, Spitsbergen.

F. NECTASPIDIDAE Stensiö, 1958 D. (PRA) FW
First: Acrotomaspis instabilis Wängsjö, 1953, Kapp Kjeldsen
Division, Wood Bay Series, Mt. Kronprinz, Wood Bay, Spitsbergen.
Last: Gustavaspis trinodis (Wängsjö, 1952), Stjordalen
Division, Wood Bay Formation, Mt. Scott Keltie, Wood Bay, Spitsbergen.

F. AXINASPIDIDAE Janvier, 1985 D. (PRA) FW
First: Axinaspis sp. 1. (Janvier, 1981), Sigurdjfelljar
Division, Wood Bay Formation, Sigurdjfelljar, Wood Bay, Spitsbergen.
Last: Axinaspis whitei Wängsjö, 1952, Kapp Kjeldsen
Division, Wood Bay Formation, Mt. Sigurd, Bock Bay, Mt. Kronprinz, Wood Bay, Spitsbergen.

Order JAMOYTIIFORMES
F. JAMOYTIIDAE White, 1946
First: Jamesyiitus kerwoodi White, 1946, Patrick Burn Formation, Kip Burn Formation, Lesmahagow Hills, Scotland, UK.
Last: Jamoytius-like vertebrates (Janvier and Busch, 1984), Manlius Formation, Paris, New York, USA.

Order ENDEIOLEPIDIFORMES Berg, 1940
F. ENDEIOLEPIDIFORMES Stensiö, 1939 D. (FRS) FW
First and Last: Endeiolepis aneri Stensiö, 1939, Escuminac Formation, Scaumenac Bay (Miguasha Bay), Quebec, Canada.

Order BIRKENIIFORMES Berg, 1940
First: Birkenia elegans Traquair, 1899
S. (WEN)–D. (LOK) Mar./FW
First: Birkenia elegans Traquair, 1899, 'Downtonian', Lesmahagow Hills, Lanarkshire, Scotland, UK.
Last: Anaspid scales (Ball et al., 1961), Phialaspis yonmordzi Zone, Psammosteus Limestone Group, Targrove Dingle, Whitbatch, Shropshire, England, UK.

First and Last: Lasanius problematicus Traquair, 1899, Lesmahagow and Hagshaw Hills, Lanarkshire; L. armatus Traquair, 1899, Seggholm, Lanarkshire, Scotland, UK.

F. EUPHANEROPIDAE Woodward, 1900
D. (FRS) FW
First and Last: Euphanerops longaeus Woodward, 1900, Escuminac Formation, Escuminac Bay (Miguasha Bay), Quebec, Canada.

Subclass GALEASPIDA Halstead, 1982
Order EUGALEASPIDIFORMES Pan, 1983
F. EUGALEASPIDIDAE Liu, 1980
S. (WEN)–D. (LOK) FW

Order POLYBRANCHIASPIDIFORMES Liu, 1965
F. DAYONGASPIDIDAE Pan, 1985 S. (LLY) FW
First and Last: Dayongaspis hunanensis Pan, 1985, Rongxi Formation, Wentang, Hunan, China.

F. HANYANGASPIDIDAE Pan and Liu, 1975
S. (WEN) FW
First and Last: Hanyangaspis guodingshanensis Pan and Liu, 1975, Goudingshan Formation, Wuhan, Hubei and Latrocraspis chaukensens Wang et al., 1980, Fentou Formation, Xiazhucun, Anhui, China (referred to Hanyangaspis by Pan, 1986).

F. XIUSHUIASPIDIDAE Pan and Wang, 1983
S. (WEN) FW

F. POLYBRANCHIASPIDIDAE Liu, 1965
D. (LOK – EMS) FW
First: Polybranchiaspis miandiancunensis Pan and Wang, 1978 and Dongfangaspis sp., Miandiancun Formation, Qujing, Yunnan, China.
Last: Duyunolepis paoyangensis (Pan and Wang, 1978), Shujiapin Formation, Paoyang, Guizhou, China.

Order NANPANASPIDIFORMES Liu, 1965
F. NANPANASPIDIDAE Liu, 1975 D. (LOK) FW
First and Last: Nanpanaspis microclus Liu, 1965, Chifengshan Formation, Qujing, Yunnan, China.

Order HUANANASPIDIFORMES Janvier, 1975
F. HUANANASPIDIDAE Liu, 1973 D. (LOK) FW
Last: Asiaspis expansa Pan, 1975, Nagaoling Formation, Liujiang, Guangxi, China.

F. SANCHASPIDIDAE Pan and Wang, 1981
D. (LOK – PRA/EMS) FW
First: Antiquisagittaspis cornuta Liu, 1985, Nagaoling Formation, Hengxiian, Guangxi, China.
Last: Sanchaspis magalarostra Pan and Wang, 1981, Chifengshan Formation, Sancha, Qujing, Yunnan, China.

F. SANCHASPIDIDAE Pan and Wang, 1981
D. (LOK – EMS/EIF) FW
Animals: Vertebrates

Last: *Wumengshanaspis cuntianensis* Wang and Lan, 1984, Suotoushan Formation, Yiliang, Yunnan, China.

Order **QINGMENASPIDIFORMES** Pan and Wang, 1981

F. **QINGMENASPIDIDAE fam. nov.** D. (PRA-EMS) FW

First and Last: *Qingmenaspis microculus* Pan and Wang, 1981, Chifengshan Formation, Xishancun, Qujing, Yunnan, China.

F. **UNNAMED** D. (GIV) Mar.

First and Last: Undescribed remains listed by Pan and Dineley (1988), Yidade Formation, Panxi, Huaning, Yunnan, China.

Comment: Further undescribed 'galeaspid' remains listed by Pan and Dineley (1988) from the Zhongning Formation (FRS), Zingwei, Ningxia, are not here accepted as galeaspid.

Last: *Wumengshanaspis cuntianensis* Wang and Lan, 1984, Suotoushan Formation, Yiliang, Yunnan, China.

Order **PETROMYZONIFORMES** Berg, 1940

F. **HARDISTIELLIDAE fam. novo** C. (SPK) FW

First and Last: *Hardistiella montanensis* Janvier and Lund, 1983, Bear Gulch Member, Heath Formation, Montana, USA.

F. **MAYOMYZONIDAE** Bardack and Zangerl, 1971 C. (MOS) FW

First and Last: *Mayomyzon pieckoensis* Bardack and Zangerl, 1968, Francis Creek Shale, Carbondale Formation, Illinois, USA.

F. **PIPISCIIDAE fam. nov.** C. (MOS) FW

First and Last: *Pipiscius zangerli* Bardack and Richardson, 1971, Francis Creek Shale, Carbondale Formation, Illinois, USA.

F. **GILPICHTHYIDAE fam. nov.** C. (MOS) FW

First and Last: *Gilpichthys greenii* Bardack and Richardson, 1977, Francis Creek Shale, Carbondale Formation, Illinois, USA.

Comment: *Scaumenella mesacanthi* Graham-Smith, 1935, Escuminac Formation (FRS), Miguasha, Quebec, Canada, tentatively identified as a larval lamprey (Tarlo, 1960), has been shown by Bélanger and Arsenault (1985) to be the degraded remains of the acanthodian fish *Triazeugacanthus affinis* (Whiteaves, 1887).

Superorder **MYXINIDA**

Order **PETROMYZONIDAE** Berg, 1940

F. **PETROMYZONIDAE** Berg, 1940

First and Last: Undescribed remains listed by Pan and Dineley (1988), Yidade Formation, Panxi, Huaning, Yunnan, China.

Comment: Further undescribed 'galeaspid' remains listed by Pan and Dineley (1988) from the Zhongning Formation (FRS), Zingwei, Ningxia, are not here accepted as galeaspid.

Order **PETROMYZONIFORMES** Berg, 1940


Order **QINGMENASPIDIFORMES** Pan and Wang, 1981

F. **QINGMENASPIDIDAE fam. nov.** D. (PRA-EMS) FW

First and Last: *Qingmenaspis microculus* Pan and Wang, 1981, Chifengshan Formation, Xishancun, Qujing, Yunnan, China.

F. **UNNAMED** D. (GIV) Mar.

First and Last: Undescribed remains listed by Pan and Dineley (1988), Yidade Formation, Panxi, Huaning, Yunnan, China.

Comment: Further undescribed 'galeaspid' remains listed by Pan and Dineley (1988) from the Zhongning Formation (FRS), Zingwei, Ningxia, are not here accepted as galeaspid.

Order **PETYROMYZONIFORMES** Berg, 1940

F. **HARDISTIELLIDAE fam. novo** C. (SPK) FW

First and Last: *Hardistiella montanensis* Janvier and Lund, 1983, Bear Gulch Member, Heath Formation, Montana, USA.

F. **MAYOMYZONIDAE** Bardack and Zangerl, 1971 C. (MOS) FW

First and Last: *Mayomyzon pieckoensis* Bardack and Zangerl, 1968, Francis Creek Shale, Carbondale Formation, Illinois, USA.

F. **PIPISCIIDAE fam. nov.** C. (MOS) FW

First and Last: *Pipiscius zangerli* Bardack and Richardson, 1971, Francis Creek Shale, Carbondale Formation, Illinois, USA.

F. **GILPICHTHYIDAE fam. nov.** C. (MOS) FW

First and Last: *Gilpichthys greenii* Bardack and Richardson, 1977, Francis Creek Shale, Carbondale Formation, Illinois, USA.

Comment: *Scaumenella mesacanthi* Graham-Smith, 1935, Escuminac Formation (FRS), Miguasha, Quebec, Canada, tentatively identified as a larval lamprey (Tarlo, 1960), has been shown by Bélanger and Arsenault (1985) to be the degraded remains of the acanthodian fish *Triazeugacanthus affinis* (Whiteaves, 1887).

Superorder **MYXINIDA**

Order **PETROMYZONIDEA**

Order **PETROMYZONIFORMES** Berg, 1940


Last: *Tescaviaspis concentrica* Bockelie and Fortey, 1976, Valhallfonna Formation, O. (ARG-LLN), Ny Friesland, Spitsbergen, attributed to the Heterostraci (figured in Smith and Hall, 1990), has an ornamentation and microstructure unlike any known vertebrate. Its vertebrate assignation is not here accepted (see also Ørvig, 1989). *Anatolepis cf. heintzi* Repetski, 1978, Deadwood Formation, C. (MER), Crook County, Wyoming, USA (figured in Benton, 1990) is not here recognized as a vertebrate (see also Ørvig, 1989).

REFERENCES


Agnatha


PLACODERMI

B. G. Gardiner

The placoderms flourished in the Devonian and are almost entirely restricted to this period. However, antiarch remains have been recorded from the marine Upper Silurian of the Guandi Formation in the Qujing District, eastern Yunnan Province, and in western Hunan Province (Pan and Dineley, 1988), while more primitive placoderms (possibly related to palaeacanthaspids) have been recovered from marine Middle Silurian sediments of the Yulongssu Formation, Qujing (M.-M. Chang, pers. comm.). Classification mainly after Denison (1978) and Gardiner (1990).

Order STENSIOELLIDA White, 1952 (see Fig. 32.1)

F. STENSIOELLIDAE Berg, 1940


First and Last: Stensioella heintzi Broili, 1933, Hunsrück-schiefer, Germany. Stensioella is a very poorly known genus (Gröss, 1962) from a single Lower Devonian locality, and can only be associated with placoderms on phenetic grounds (Forey and Gardiner, 1986).

Order PSEUDOPETALICHTHYIDA Denison, 1975

F. PARAPLESIOBATIDAE Berg, 1940


First and Last: Pseudopetalichthys problematicus Moy-Thomas, 1939, Hunsrück-schiefer, Germany. Paraplesiobatus heinrichsi Broili, 1933, also from the Hunsrück-schiefer (Gröss, 1962) are probably both synonyms with P. problematicus.

Order PTYCTODONTIDA Gröss, 1952

F. PTYCTODONTIDAE Woodward, 1891


First: Tollodus brevispinus Mark-Kurik, 1934, shales and limestones of the Siberian Platform, Byachs-Karga and Sokolow Rivers, former USSR. Last: Chelyophorus verneuli Agassiz, 1844, Dankov-Lebedyan Beds, former USSR. (Denison, 1978). Ptyctodus calculeus Newberry and Worthen, 1866, from the Bushberg Sandstone, North America (Branson and Mehl, 1938) appears to have been derived from earlier, Devonian strata.

Comment: This order is marine except for one genus, Rhamphodopsis which occurs in fresh water, Middle Old Red Sandstone deposits of Scotland, UK.

Order GEMUENDINIDA Gröss, 1963 (= RHENANIDA Broili, 1930)

F. ASTEROSTEIDAE Woodward, 1891


First: Gemuendina stuertz Traquair, 1903, Hunsrück-schiefer, Germany (Gröss, 1963).

Last: Jagorina pandora Jaekel, 1921, Manticoceras Beds, Germany (Jaekel, 1921; Stensiö, 1925).

Order PALAEACANTHASPIDA Obruchev, 1964

F. PALAEACANTHASPIDIDAE Stensiö, 1944


Last: Breizosteus armoricensis Goujet, 1980, calcareous shales, Armorique, France (Goujet, 1980).

F. RADOTINIDAE Arambourg, 1958


F. KOLYMASPIDIDAE Bystrow, 1956

D. (EMS) Mar.

First and Last: Kolymaspis siberica Bystrow, 1956, Neliudim Formation, Siberia, former USSR (Denison, 1978).

F. WEEJASPERASPIDAE White, 1978

D. (EMS) Mar.

First and Last: Murrindalaspis wallacei Long, 1988, Buchan Group, Receptaculites Limestone and Weejasperaspis gavini White, 1978, Yarssensis Limestone, Murrumbidgee Series, Australia (Long and Young, 1988).

Order BRINDABELLASPIDA

F. BRINDABELLASPIDAE fam. nov.

D. (EMS) Mar.

First and Last: Brindabellaspis stensioi Young, 1980, Taemas Limestone (Receptaculites, Warroo and Crinoidal Limestone), Australia (Young, 1980).
### Animals: Vertebrates

**Order** PETALICHTHYIDA Jaekel, 1911

**F. MACROPETALICHTHYIDAE** Eastman, 1898  

**First:** *Diandongpetalichthys liaojiaoshanensis* Pan and Wang, 1978, Xishancun Member, Quijing, Yunnan, China, and *Xinanpetalichthys shedaowanensis* Pan and Wang, 1978, Xishancun Member, Quijing, Yunnan, China (Pan and Dineley, 1988).

**Last:** *Epipetalichthys wildungensis* Stensio, 1925, *Manticoceras* Beds, Germany (Stensiö, 1925).

**F. QUASIPETALICHTHYIDAE** Liu, 1973  

**First:** *Neopetalichthys yamenpaensis* Liu, 1973, Pingyipu Formation, Jiangyou and Sichon, China.

**Last:** *Epiptetalichthys widungensis* Stensiö, 1925, *Manticoceras* Beds, Germany (Stensiö, 1925).

**Order** PHYLLOLEPIDA Stensio, 1934  
F. PHYLLOLEPIDAE Woodward, 1891  
D. (FRS–FAM) FW

**First:** *Austrophyllolepis ritchiei* Long, 1984, Dulcie Sandstone; South Blue Range, Taggerty and Mt. Howitt; Harajica Sandstone, Australia, Victoria Land, Antarctica; *Placolepis budawangensis* Ritchie, Bairdwood, New South Wales, Australia (Young, 1988).

**Last:** *Phyllolepis Agassiz, 1844, Phyllolepis* Series and base of *Remigolepis* Series, East Greenland; Rosebrae Beds and Dura Den Beds, Scotland, UK; also occurs in England, UK, Turkey, Belgium, former USSR, Greenland, North America, Australia and Antarctica (Denison, 1978).

**Order** ANTIARCHA Cope, 1885

(Earliest (Silurian) members marine, most genera, however, are fresh water – some genera have both marine and freshwater species.)

**F. ASTEROLEPIDIDAE** Traquair, 1888  
D. (EIF–FAM) Mar./FW

**First:** *Asterolepis estonica* Gröss, 1940, Narova and Arukiila Beds, Baltic States, former USSR.

**Last:** *Remigolepis Stensiö, 1931, Remigolepis* Series, East Greenland (Jarvik, 1961). Also recorded from the Upper Devonian of Australia and North and South China (Young, 1974; Young, MS).

**F. BOTHRIOLEPIDIDAE** Cope, 1886  
D. (GIV–FAM) Mar./FW

**First:** *Bothriolepis Eichwald, 1840, Upper Mangzixia Series, Guitou Group, Kwangtung Province; Tiaomachien Series, Hunan and Yunnan Provinces, China (Denison, 1978);* *Aztec Siltstone, Antarctica (Young, 1988);* *Monarolepis verrucosa* (Young, 1988, ex Young and Gorter, 1981), Hatchery Creek Formation, New South Wales, Australia – precise age uncertain (EIF–GIV).
**Placodermi**  

### F. MICROBRACHIIDAE Gross, 1965  
**D. (GIV)** Mar./FW  
**First and Last:** Microbrachius dicki Traquair, 1885, John O’Groats Sandstone, Caithness, Eday Beds, Orkney, Scotland, UK (Denison, 1978); Hohsienolepis hsintuensis P’an, Xindu and Hexian Members, China; Hunanolepis tieni P’an and Tzeng, 1978, Dahepo, Haikou and Tiaomachin members, China; Wudinolepis weni Chang, Yunnan Province, China (Pan and Dineley, 1988).  

### F. PTERICHTHYODIDAE Cope, 1885  
**D. (EMS–FRS) Mar./FW**  
**First:** Pterichthyes Bleeker, 1859, is reported from New South Wales, Australia (Young, 1974). However, elsewhere it is restricted to the Middle Old Red Sandstone (Middle Devonian) of Scotland, UK.  
**Last:** Gerdalepis dohmi (Gröss, 1933) Assize de Masy, Belgium; Lepadolepis stensioei (Gröss, 1933), Mantioceras Beds, Germany; Stegeolepis jungata Malinovskaja, 1973, Taldysay Series, former USSR (Denison, 1978).  

### F. QUIJINOLEPIDIDAE Zhang, 1978  
**D. (LOK–PRA) Mar.**  
**First and Last:** Qujinolepis gracilis Zhang, 1978; Procondylolepis qujingensis Zhang, 1978; Zhanjilepis aspratilis Zhang, 1978, Xitun Member, Cufengshan Formation, Qujing, China.  
**Last:** Liujiangolepis suni Wang, 1987, Xiaoshan and Guangxi Members, China (Pan and Dineley, 1988).  

### F. SINOLEPIDIDAE Liu and P’an, 1958  
**D. (GIV–FAM) Mar.**  
**First:** Xichonolepis qujingensis P’an and Wang, 1978, Haikou Member, Yunnan, China (closely resembles Sinolepis).  
**Last:** Sinolepis macrocephala Liu and P’an, 1958, Wutung Series, South China (Pan and Dineley, 1988).  

### F. YUNNANOLEPIDIDAE Gross, 1965  
**D. (LOK) Mar.**  
**First and Last:** Yunnanolepis Liu, 1963, Xishancun, Nagading, Mianidiancan, Wudang and Lianhuashan Members, China; Phymolepis cuiyengshanensis Zhang, 1978, Xiang and Xitun Members, Cufengshan Formation, Qujing, China (Pan and Dineley, 1988).  

**Order** WUTTAGOONASPIDA Ritchie, 1973  
**F. WUTTAGOONASPIDADE Ritchie, 1973**  
**D. (EIF) FW**  
**First and Last:** Wuttagoonaspis fletcheri Ritchie, 1973, Mulga Downs Formation, New South Wales, Australia. This is probably a stem-group arthrodire (Denison, 1978; Forey and Gardiner, 1986).  

**Order** ARTHRODIRA Woodward, 1891  
**ACTINOLEPIDOIDS Gardiner, 1990**  

The earliest actinolepids appear in freshwater deposits.  

**F. ACTINOLEPIDIDAE Gröss, 1940**  
**D. (LOK–GIV) FW/Mar.**  
**First:** Baringaspis dineleyi Miles, 1973, Peel Sound Formation, Prince of Wales Island, Canada; Kujdanowiaspis Stensiö, 1942, Babin Sandstone, Podolia; Ditionian, Great Britain; Old Red Stage 1, Ukraine, former USSR.  

**PHLYCTAEONOID Gardiner, 1990**  
**F. ARCTASPIDIDAE Heintz, 1937**  
**D. (PRA) FW**  
**First and Last:** Arctaspis kiæeri Heintz, 1929, Dicksonosteus arcticus Goujet, 1975, Wood Bay Series, Spitsbergen (Heintz, 1929; Goujet, 1975).  

**F. ARCTOLEPIDIDAE Heintz, 1937**  
**D. (EMS–EIF) FW**  
**First:** Arctolepis decipiens (Woodward, 1891), Lykta Formation, Wood Bay Series, Spitsbergen.  
**Last:** Neophlyctaenius sherwoodi (Denison, 1950), Onteora and Katsberg Formation, USA (Denison, 1978).  

**F. WILLIAMSASPIDIDAE White, 1952**  
**D. (EMS) Mar.**  
**First and Last:** Williamsaspis bedfordi White, 1952, Murumbidgee Group, Australia (Denison, 1978). This family appears to be stem-group groenlandaspids.  

**G. GROENLANDASPIDS Gardiner, 1990**  
**F. GROENLANDASPIDIDAE Obruchev, 1964**  
**D. (PRA–FAM) Mar./FW (see Fig. 32.2)**  
**First:** Tiaraspis subtilis (Gröss, 1933), Rheinland, Germany.  
**Last:** Groenlandaspis mirabilis Heintz, 1932, Groenlandaspis Series, Greenland; Ketorcan Beds, Republic of Ireland; Astec Siltstone, Antarctica. Upper Old Red Sandstone, England, UK; Hunter Siltstone, Australia (Denison, 1978).  

**H. HOLONEMATIDS Gardiner, 1990**  
**F. HOLONEMATIDAE Obruchev, 1932**  
**D. (EIF–FRS) Mar./FW**  
**First:** Holonema Newberry, 1889, Aruküla Beds, Estonia; Narova Beds, former USSR.  
**Last:** Holonema Newberry, 1889, Afghanistan, Morocco, Turkey and Iran; Somerset Island, Canada; Redheugh, Scotland, UK; Aspidichthys Newberry, 1873, Huron and Olentangy Shale, Ohio, USA, Mantioceras Beds, Germany and Poland, Morocco; Devonema obrucevi Kulczycki, 1957, Gyroplacosteus Obruchev, 1932, Sheldon Beds, Latvia, former USSR; Oberer Plattenkalk, Germany (Denison, 1978).  

**B. BUCHANOSTEIDS Gardiner, 1990**  
**F. BUCHANOSTEIDAE White, 1952**  
**D. (PRA–EMS) Mar.**
Fig. 32.2

First: *Kweichowlepis sinensis* P’an and Wang, 1975, Wudang Member, Guiyang and Guizhou, China.

Last: *Buchanosteus conferituberculatus* (Chapman, 1916), *Spirifer yassensis* and *Receptaculites* Limestones, Buchan Group, Australia; *Arenipiscis westolli* Young, 1981a, Taeman Limestone, Australia (Young, 1981a,b).

F. BURRINJUCOSTEIDAE White, 1978
D. (EMS) Mar.

First and Last: *Burrinjucosteus asymmetricus* White, 1978, Warro Limestone, Murrumbidgee Series, Australia; *Errolosteus goodradigbeensis* Young, 1981a; *Toombsosteus denisoni* White, 1978, Taemus Limestone, Australia (Young, 1981a,b).

F. GOODRADIGBEONIDAE White, 1978
D. (EMS) Mar.


F. GEMUENDENASPIDAE Miles, 1962
D. (EMS) Mar.

First and Last: *Gemuendedaspis angusta* (Traquair, 1903), Hunsrückschiefer, Germany. Known from a single specimen which may be a stem heterostiid, homostiid or coccosteid (Denison, 1978).

HETEROSTIIDS Gardiner, 1990

F. HETEROSTEIDAE Jaekel, 1903
D. (EIF-GIV) Mar./FW


Last: *Heterosteus asussii* (Agassiz, 1845) Arukula Beds, Baltic States, former USSR; *Stingocephalus* Beds, Germany; Wijde Bay Formation, Spitsbergen; *Yinosteus major* Wang and Wang, 1984, Hakou Formation, Yunnan, China (Denison, 1978; Pan and Dineley, 1988).

HOMOSTIIDS Gardiner, 1990

F. HOMOSTIIDAE Jaekel, 1903
D. (PRA-GIV) FW

First: *Euleptaspis depressa* (Gröss, 1933), Lower Devonian, Germany; Kapp Kjeldsen Formation, Spitsbergen.


PHOLIDOSTEIDS Gardiner, 1990


COCOCOSTEOIDS Gardiner, 1990
F. COCCOSTEIDAE Traquair, 1888
D. (EIF–FAM)FW (Predom.)

First: Coccosteus Miller, 1841, Caithness flagstones, Scotland, UK; Arukūla and Burtnieki Beds, Baltic States, former USSR; Livosteus grandis (Gröss, 1933), Arukūla and Burtnieki Beds, Latvia, former USSR; Millerostus orvikui (Gröss, 1940), Narova and Luga Beds, Baltic States, former USSR. Protitanichthys fossatus Eastman, 1907, Delaware Limestone, USA (Denison, 1978).

Last: Mylostoma Newberry, 1883, Cleveland Shales, USA (Denison, 1978).

TREMATOSTEIDS Gardiner, 1990
F. TREMATOSTEIDAE Gross, 1932

First: Belosteus Jaekel, 1919; Brachyosteus Jaekel, 1927; Braunosteus Stensiö, 1959; Parabelosteus Miles, 1969; Trematosteus Jaekel, 1927; all from the Manticoceras Beds (Upper FRS), Germany.

Last: Burgarius perissus Dunkle, 1947; Paramylostoma arcuatus Dunkle and Burgart, 1945, Cleveland Shale, USA (Denison, 1978).

LEIOSTEIDS Gardiner, 1990

First and Last: Erromenosteus Jaekel, 1919, Manticoceras Beds, Germany (Denison, 1978).

HADROSTEIDS Gardiner, 1990

First and Last: Hadrostes rapax Gröss, 1932, Manticoceras Beds, Germany (Gröss, 1932).


First and Last: Selenostes brevis (Claypole, 1869); Gymnotrachelus hydei Dunkle and Burgart, 1939, Cleveland Shales, USA (Denison, 1978).

PACHYOSTEIDS Gardiner, 1990

First and Last: Enseosteus Jaekel, 1919; Microsteus Gröss; 1932; Pachyosteus bulla Jaekel, 1903, all from the Manticoceras Beds, Germany (Denison, 1978).

RHINOSTEIDS Gardiner, 1990

First and Last: Rhinosteus Jaekel, 1919, Manticoceras Beds, Germany; Melanosteus occitanus Lelièvre and Goujet, 1987, Serve Formation, France (Lelièvre et al., 1987).

BRACHYDEIRIDS Gardiner, 1990

First and Last: Brachydeirus Koenen, 1880; Oxyostes Jaekel, 1911, Synauchenia Jaekel, 1919, all from the Manticoceras Beds, Germany (Denison, 1978).


First and Last: Leptosteus Jaekel, 1911, Manticoceras Beds, Germany; Java Formation, New York, USA (Denison, 1978).

The informal higher-order terms used above (namely Brachydeirids) refer to the successive levels of organization within the arthrodires, and therefore indicate individual clades.

REFERENCES

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ACANTHODII

J. Zidek

The classification below follows Miles (1966), except for the position of the Ischnacanthiformes, which are listed first to allude to the possibility that they may be the most primitive acanthodians (Long, 1986b), and the addition of Culmacanthidae Long, 1983 (Diplacanthoidei). The most recent review of the Acanthodii is Denison (1979), who merged the Euthacanthidae (monogeneric) into the Climatiidae and recognized only one acanthodiform family, the Acanthodidae. However, there is much in favour of upholding the families suppressed by Denison (Euthacanthidae, Mesacanthidae, Cheiracanthidae). Miles and Denison may have erred in including the Diplacanthidae and Gyracanthidae in the Climatiiformes. The histology of diplacanthid scales (Valiukevičius, 1985), and the paucity of our knowledge of the gyracanthids suggest that the two should be regarded as separate orders; however, this is not the place to argue controversial issues, and Miles' arrangement is therefore maintained.

Harland et al. (1982) are followed in stage/age assignments, with the exception of the Silurian, where Llandovery, Wenlockian, Ludlovian and Pridolian are considered stages/ages rather than series/epochs (Jaeger, 1980; Chlupáč et al., 1981).

Class ACANTHODII Owen, 1846

Order ISCHNACANTHIFORMES Berg, 1940

F. ISCHNACANTHIDAE Woodward, 1891

5. (LUD)–C. (MRD) Mar. (see Fig. 33.1)

First: Gomphonchus sandelensis (Pander, 1856) and G. hoppei (Gross, 1947), both from middle LUD Paadla (K2) beds of Saaremaa, Estonia, former USSR, and the Hemse Formation of Gotland, Sweden.

Last: Marsdenius summiti Wellburn, 1902 and M. acuta Wellburn, 1902, both from the Pendleside Limestone (upper Namurian B), Yorkshire, England, UK.

Intervening: PRD–EIF, FRS.

Comment: Acanthodopsis Hancock and Atthey, 1868, from the Coal Measures of England and Scotland, is Westphalian B in age (probably VRK), but Long (1986b) has provided a convincing argument for placing this genus in the Acanthodidae.

Order CLIMATIIFORMES Berg, 1940

Suborder CLIMATIOIDEI Miles, 1966

F. CLIMATIIDAE Berg, 1940

S. (LLY)–D. (GIV)

Mar./FW

First: Onchus graptolitarum Fritsch, 1907, allegedly roughly contemporaneous with O. clintoni, in reality is PRD, as evidenced by the character of the matrix (Chlupáč et al., 1972; Zajíč, 1986). Kříž et al. (1986) found O. graptolitarum only in the upper PRD. Gross (1951) mentioned Nostolepis-like scales from either upper WEN or lower LUD of Bohemia, Czech Republic, and Denison (1979) listed these as Nostolepis sp. from the Liten Beds, which would make them WEN or possibly even LLY. However, these scales are associated with the holotype of Onchus graptolitarum and thus are of PRD age. The genera Onchus Agassiz, 1837 and Nostolepis Pander, 1856 are based on isolated spines and scales, respectively, and the noted spine–scale association is the only instance hitherto known. It would be premature to synonymize Nostolepis with Onchus on this evidence, but it does allow to transfer Onchus from Acanthodii incertae sedis (Denison, 1979) to the Climatiidae.

F. EUTHACANTHIDAE Berg, 1940

D. (PRA) FW

First and Last: Euthacanthus macnicoli Powrie, 1864, Dundee Formation, Forfarshire, Scotland, UK. This is dated as LOK according to Paton (1976).

Suborder DIPACANTHIDEOI Miles, 1966

F. DIPACANTHIDAE Woodward, 1891

D. (EIF–FRS) FW/Mar.(?)


Last: Diplacanthus horridus Woodward, 1892, Escuminac Formation, Quebec, Canada.

Intervening: GIV.

Comment: Rhadinacanthus Traquair, 1888 may be syn-
Fig. 33.1

F. CULMACANTHIDAE Long, 1983  D. (FRS) FW
First and Last: Culmacanthus stewarti Long, 1983, lower part of Avon River Group, Mt. Howitt, Victoria, Australia.

F. GYRACANTHIDAE Woodward, 1906

First: Gyracanthus? convexus Gross, 1933, Wahnbachtschichten and Taunusquarzit, Rheinisches Schiefergebirge, Germany.

Last: Gyracanthus duplicatus Dawson, 1868, Joggins Formation, Nova Scotia, Canada.

Intervening: EMS–FAM, TOU–BSH.

Comments: Mader (1986) recorded Gyracanthus sp. from the lower LOK Upper Carazo Formation, Palencia Province, northern Spain. Gyracanthus sp. from the Mecca Quarry Shale of Carbondale Formation, Kankakee County, Illinois, USA (Baird, 1978), is early Westphalian D, i.e. either the latest POD or the earliest MYA.

Order ACANTHODIFORMES Berg, 1940

F. MESACANTHIDAE Moy-Thomas, 1939
D. (PRA–FRS) FW/Lagoonal

First: Mesacanthus mitchelli (Egerton, 1861), Dundee Formation, Forfarshire, Scotland, UK (dated as LOK by Paton, 1976).

Last: Triazeugacanthus affinis (Whiteaves, 1887), Escuminac Formation, Quebec, Canada.

Intervening: EMS–GIV.

F. CHEIRACANTHIDAE Berg, 1940
D. (EMS–C. (TOU) FW/Lagoonal

First: Cheiracanthus costellatus Traquair, 1893, Atholville Beds, New Brunswick, and Battery Point Formation, Quebec, Canada.

Last: Carycinacanthus lopatini (Rohon, 1889), Nadaltaiskaja Formation, Minusinsk Depressions, former USSR; and/or Homalacanthus bergi (Obruchev, 1962), upper part of Shivelikskaja Formation, Tuva Basin, former USSR.

Anonymous with Diplacanthus Agassiz, 1844, but this remains to be ascertained. Ptychodictyon Gross, 1973 was placed in Acanthodii incertae sedis by Denison (1979), but Valiukevičius (1979, 1985) recognized its diplacanthid scale histology.

Gladiobranchus probaton Bernacsek and Dineley (1977) is a LOK species (Delorme Formation, District of Mackenzie, NWT, Canada) included by Denison (1979) in the Diplacanthidae. However, it is not clear whether this is a diplacanthid or an ischnacanthiform (Long, 1983), and it is left as incertae sedis.

All undisputed diplacanthids but D. horridus are EIF and early GIV in age. Valiukevičius (1985) did not correlate the Narva Regional Stage (Narova Beds of Denison, 1979) with the international standard scale, but he observed that the Kernavė Formation of Lithuania, former USSR, which contains conodonts of early EIF age, corresponds with the Upper Narva Regional Substage. This means that his second acanthodian assemblage, which characterizes the lower part of the Middle Narva Regional Substage and contains the first occurrence of R. balticus? and P. rimosum, must be early EIF in age and thus older than the diplacanthid occurrences in the Middle Old Red Sandstone of Scotland (upper EIF–lower GIV). Even older, earliest EIF, are Diplacanthus? sp. nov. 1, Rhadinacanthus sp. nov. 1, and Ptychodictyon sp. nov. 1 from the Pärnu and Rezekne Regional Stages of the Baltic region, listed but not described by Valiukevičius (1985).

Contrary to the generally accepted interpretation, Schultze (in Carroll et al., 1972) proposed a marine depositional environment for the Escuminac Formation.
Intervening: EIF–FAM.

Comments: The Atholville Beds/Battery Point Formation assemblage is usually regarded as early EIF, but C. costellatus is known from locality (zone) 1 at D’Aiguillon (Pageau, 1968; Carroll et al., 1972), in the lower part of the Battery Point Formation, which has produced miospores of late EMS age (McGregor, 1973). Should this occurrence prove to be lower EIF, then C. costellatus would be roughly contemporaneous with C. longicostatus Gross, 1973, C. breviceps Gross, 1973 and C. crassus Valiukevičius, 1985 from the Pärnu and Rezekne Regional Stages in the Baltic region (Valiukevičius, 1985), and probably also with *Isoden-dracanthus* *ramiformis* Valiukevičius, 1979 and *Ectopacanthus* *cristiformis* Valiukevičius, 1979 from the Grey Hoek Formation of Vestsipitsbergen.

According to Obruchev (1962), *C. lapatini* is known from the Izykchulskii Fish Horizon in the middle of Bystrianskaia Formation up into the Nadaltaiskaia Formation, and *H. berti* from Dzhangiskaia Formation and the upper part of Shiveliskaia Formation, all belonging in the TOU series. So far as can be discerned from Kotliar assemblage is usually regarded as early ElF, but contemporaneous with 1968; Carroll is known from locality (zone) 1 at D’Aiguillon (Pageau, EMS age (McGregor, 1973). Should this occurrence prove to be lower ElF, then *H. costellatus* of Vestspitsbergen.

Obruchev’s (1962) remarks, the Nadaltaiskaia Formation of the Minusinsk depression corresponds with the upper part of Shiveliskaia Formation in the Tuva Basin, and the two species thus can be said to be roughly contemporaneous, more likely HAS than IVO.

### REFINES


### REFERENCES


Last: *Acanthodes luedersensis* (Dalquest et al., 1988), Lueders Formation, uppermost Wichita Group (uppermost Wolfcampian), Baylor County, Texas, USA.

Intervening: TOU, VIS, KIN–ASS.

Comments: *A. luedersensis* was described as a new genus, *Rodriguezichthyes* [sic], based chiefly on misinterpretation of the scale histology (Schultze, 1990). The species is said to have been shallow-water marine. *Acanthodes* sp. from the Purcell Sandstone at the base of the Hennessey Formation in Tillman County, Oklahoma, USA (Zidek, 1975) is early Leonardian in age, i.e. early ART. The depositional environment is fresh water.

In the Saar–Pfalz region of Germany, *Acanthodes* sp. occurs as high in the Rotliegendes section as in the N4–N5 informal subdivisions of the Nahe Group (Boy, 1987), a level that is considered Saxonian by Boy (1987) and is correlated by him with the Olivétin Member of Broumov Formation in the Intra-Sudeten Basin (Bohemia, Czech Republic), the upper part of Prosečně Formation (Kalná Horizon) in the Krkonošě Piedmont Basin (Bohemia, Czech Republic), and upper Leonardian (KUN) in the USA. Although Czech authors place the named formations in the upper Autunian rather than Saxonian (Zajíc and Štamborg 1986), Boy’s (1987) correlation of the N4–N5 levels of the Nahe Group with the upper Leonardian appears to be realistic and is accepted here. The Nahe Group *Acanthodes* thus is KUN, and represents the youngest known occurrence of the family and of the entire class. The depositional environment is pond/lacustrine according to Boy (1987).
Journal of Vertebrate Paleontology, 10, 49–58.

CHONDRICHTHYES
H. Cappetta, C. Duffin and J. Zidek

The most recent comprehensive treatments of the Palaeozoic and Cainozoic elasmobranchs are respectively by Zangerl (1981) and by Cappetta (1987), whose classifications are followed.

The oldest elasmobranch teeth are Leonodus carlsi Mader, 1986 from the lower GED of northern Spain. They have been placed tentatively in the Xenacanthida. The oldest teeth of neoselachian design are Mcmurdodus whitei Turner and Young, 1987 from EMS/EIF of western Queensland, Australia. Turner and Young (1987) compared them with Mcmurdodus featherensis White, 1968 from GIV/FRS of south Victoria Land, Antarctica, and tentatively placed the genus Mcmurdodus White, 1968 in the order Hexanchida. The oldest elasmobranch scales are Elegestolepis grossi Karatajute-Talimaa, 1973 from the LDF/PRD or PRD of Tuva, former USSR. They have been likened to edestid scales, but are not allocated to any higher taxon in this review. The oldest elasmobranch(?) spine is Bulbocanthus rugosus Bryant, 1932 from the SIG of Wyoming, USA.

Some genera whose familial status is uncertain were not taken into consideration; they belong mainly to the Batomorphii and their number is insignificant compared with the number of genera included in this compilation.

The holocephalans are in desperate need of taxonomic revision. There is a considerable body of literature, based largely upon isolated tooth plates assigned to nominal species. Much synonymy probably exists, especially among Palaeozoic groups. Complete dentitions and articulated skeletons are rare, giving rise to problems with form genera (Smith and Patterson, 1988). The classification scheme for Palaeozoic groups followed here is that of Zangerl (1981), which is also the most recent. The scheme is provisional, in anticipation of the Holocephali volume of the Handbook of Palaeoichthyology (in prep.). Owing to the paucity of information, no cladistic analysis is presented here other than that already developed by Zangerl (1981).

Note that the menaspids (WEN ???, TAT; Mar.), formerly based upon Pilolepis margaritifera Thorsteinsson, 1973 (earliest Cape Phillips Formation, upper Wenlock of Cornwallis Island, Canadian Archipelago), and Menaspis armata Ewald, 1848 from the Kupferschiefer of Mansfeld, Germany, have been recently reassigned to the arthrodires (Ortlam, 1985).

Zangerl (1981) left several higher taxa (one superorder, three orders and one suborder) unnamed in the Subterbranchialia. Only a careful revision of these groups will allow the introduction of new names so, in the present contribution, these taxa remain in open nomenclature.

In the absence of clear official recommendations concerning the spelling of order-group names, and to preserve homogeneity, the order names have been altered, when necessary, to provide a standardized spelling; so, all the order names are formed with the suffix-iformes.

Age determinations from the older literature are sometimes difficult, but the standard nomenclature of Harland et al. (1982) has been adopted wherever possible. Some age assignments had to be broadened, especially in certain Carboniferous, Cretaceous and Tertiary records, e.g. Tournaisian, Viséan, Mississippian, Moscovian and Senonian, reflecting the degree of stratigraphical resolution possible from the relevant literature. In a study devoted to Jurassic fishes, Schaeffer and Patterson (1984) consider the fossiliferous localities of the Solnhofen area (Germany) to be Kimmeridgian, when in fact they are lower Tithonian (= Portlandian).

Subclass ELASMOBRANCHII Bonaparte, 1838
(see Fig. 34.1)

Cohort EUSELACHII Hay, 1902
Superfamily CTENACANTHOIDEA Zangerl, 1981

F. CTENACANTHIDAE Dean, 1909
D. (GIV)–C. (ASB) Mar./FW?
First: Ctenacanthus wrightii Newberry, 1884 and C. nodocostatus Hussakof and Bryant, 1918, both from the Hamilton Group, Erian, New York State, USA.

**Animals: Vertebrates**

### Cretaceous

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**Fig. 34.1**

**Last:** *Ctenacanthus harrisoni* St John and Worthen, 1883, *C. littoni* Newberry, 1889, and *C. pellensis* St John and Worthen, 1883, all from the St Louis Limestone (upper Meramecian) of Illinois, Missouri and Iowa (USA), respectively. *C. harrisoni* and *C. littoni* may be synonymous with *C. major* according to Maisey (1984). *Ctenacanthus denticulatus* McCoy, 1855, from Armagh and Drumlish, Northern Ireland, and Shropshire, England, is Asbian and thus correlatable with the upper part of St Louis Limestone.

**Intervening:** FRS–HAS, CHD, ARU?, HLK.

**Comment:** *Ctenacanthus amblyxiphias* Cope, 1891 is known from the Desmoinesian (= upper MOS) of Oklahoma (Zidek, 1976) and the Wolfcampian (= SAK) of Texas (Berman, 1970), but these spines may in fact belong to the petalodont *Megactenopetalus* (cf. Maisey, 1984, pp. 2, 9). Maisey (1981, 1982, 1984) reviewed and revised the genus *Ctenacanthus* and reassigned a number of its species to other genera some of which may not be ctenacanthid or even ctenacanthoid. Therefore, only the species not explicitly
removed from the genus by Maisey (1982, 1984) are considered in this section.

**F. Bandringidae** Zangerl, 1969

C. (POD/MYA, MYA) FW/Mar.

**First and Last:** Bandringa rayi Zangerl, 1969 and B. herdinae Zangerl, 1979, Essex (predominantly marine, B. rayi) as well as Braidwood (predominantly freshwater, B. herdinae) faunas of Francis Creek Shale, Carbondale Formation, lower Westphalian D, Mazon Creek, Illinois, USA. B. rayi is also known from the Kittanning Formation, middle Westphalian D, Cannelton, Pennsylvania, USA (Baird, 1978). The Cannelton deposit (upper Kittanning Coal) is fresh water.

**F. Phoebodontidae** Williams, 1985

D. (EIF)–Tr. (RHT) FW/Mar.

**First:** Phoebodus floweri Wells, 1944, East Liberty and Kiddville Bone Beds, Eifelian, Ohio and Kentucky, USA.

**Last:** Phoebodus brodiei Woodward, 1893, upper Keuper, Warwick, Warwickshire, England, UK; and P. keuperensis Seilacher, 1948, Gipskeuper, Wurttemberg, Germany. The teeth from the upper Keuper of England may be distinguished from the typical teeth of *Phoebodus* by the absence of secondary cusplets between the principal cusps.

**Intervening:** GIV–HAS, POD, KLA, NOG, SAK.

**F. Unnamed** Tr. (ANS/LAD) Mar.

**First and Last:** Acronemus tuberculatus (Bassani, 1886), Middle Triassic of the southern Alps (Grenzbittuminenzone...
of Monte San Giorgio, Tessin, Switzerland). Also in the same beds near Besano, Lombardy, Italy (Rieppel, 1982).

**Comment:** In Cappetta (1987), this genus seems to be included in the family Phoebodontidae, because the head section was accidentally omitted. In fact, *Acroneus* belongs to a quite different family. On the basis of fin spine structure, *Acroneus* must be assigned to Ctenacanthoidae; yet, the teeth look like those of *Acrodon* (Hybodontoidae), raising the problem of the exact systematic position of the numerous species of *Acrodon* founded on isolated teeth (Rieppel, 1982).

**Superfamily HYBODONTOIDEA Zangerl, 1981**
The group existed possibly as early as the late Devonian (*Ctenacanthus* vetustus Newberry 1873, late Fam, Cleveland Shale Member of Ohio Shale, Ohio, USA), but it is impossible for the moment to group the Palaeozoic forms into families because of our insufficient knowledge (Zangerl, 1981). For the post-Palaeozoic forms, the classification follows Cappetta (1987).

**F. HYBODONTIDAE Owen, 1846**
Tr. (ANS/LAD)–K. (MAA) Mar./FW

**First:** Hybodus plicatilis Agassiz, 1843, Middle Triassic, Schweuningen, Württemberg, Germany, and Lunéville, north-eastern France. Many other species have been described from the Middle Triassic. In the Fossilium Catalogus (Deecke, 1926) the genus is cited from the SCY of described from the Middle Triassic. In the Fossilium Catalogus (Deecke, 1926) the genus is cited from the SCY of... (Mont Laurel Sands) Monmouth Co., New Jersey, USA.

**Intervening:** LAD/ANS, RHT, OXFIKIM, BERIBRM, APT-CEN, CMP-MAA.

**F. ACRODONTIDAE Casier, 1959**
Tr. (SCY)–K. (MAA) Mar.

**First:** Acrodon saberi Stensiö, 1921, lowest Triassic, Mt. Congress, Spitsbergen.

**Last:** Asteracanthus aegyptiacus Stroemer, 1927, MAA, Mt. Igdaman, Niger (Cappetta, 1972). This species was founded on isolated teeth from the CEN of Gebel El Dist, Baharija Oasis, Egypt. Oral teeth from the same locality, corresponding with some doubt, in the new family Distobatidae. The new genus, *Aegyptobatus*, founded on isolated teeth from the CEN of Gebel El Dist, Baharija Oasis, Igdaman, Niger (Cappetta, 1972). This species was founded... (Mont Laurel Sands) Monmouth Co., New Jersey, USA.

**Intervening:** LAD/ANS, RHT, OXF/KIM, BER/BRM, APT–CEN, CMP–MAA.

**F. POLYACRODONTIDAE Glickman, 1964**
C. (VIS)–K. (MAA) Mar./FW

**First:** Lissodus wirszworhens Duffin, 1985, Crawder Limestones, PI subzone, Wirksworth, Derbyshire, England, UK (Duffin, 1985).

**Last:** Lissodus selachos (Estes, 1964), Lance Formation, eastern Wyoming, USA.

**Intervening:** SCY–RHT, BTH, TTH, BER–BRM, ALB–TUR, SAN.

**Order XENACANTHIFORMES Berg, 1940**

**F. DIPLODOSELACHIDAE Dick, 1981**
C. (CHD–HLK/ASB) Lagoonal

**First and Last:** Diploselache woodi Dick, 1981, from the
base of Lower Oil Shale Group (Granton Sandstones) to the Upper Oil Shale Group (Dunnet Shales), Viséan C₂ S₁ to S₂ or D, Edinburgh area, Scotland, UK (Dick, 1981).

F. XENACANTHIDAE Fritsch, 1889

D. (GIV/FRS–Tr. (RHT) FW/Lagoonal/Mar.

First: ‘Dittodus’ prisus (Eastman, 1899) and ‘D.’ striatus (Eastman, 1899), Conodont Bed of Genesee Formation, uppermost Erian/lowermost Senecan, New York State, USA.


Intervening: FAM, CHD, HLK, ASB, SPK, BSH, POD/MYA, MYA, CHV–KLA, ASS–ART, LAD–NOR.

Comments: A third ‘Dittodus’ species from the Genesee Conodont Bed, D. *grabiensis* Hussakof and Bryant, 1918, is *Phoebas* (*Phoebocondonta*, *Ctenacanthoidea*). *Anodontacanthus* *pusillus* Hussakof and Bryant, 1918, also from the Genesee Conodont Bed, is a fragmentary spine which cannot be unequivocally assigned to that genus and, at any rate, the assignment of *Anodontacanthus* to the Xenacanthidae, or even to the Xenacanthidae, is equivocal (Zidek, 1978, p. 1075).

Young (1982) described *Antarcctilamna prisca* from upper GIV/lower FRS freshwater deposits of south Victoria and New South Wales, and suggested that it is a xenacanth shark immediately related to *Xenacanthus*. However, although the teeth of *A. prisca* are diplodont, their bases appear to be phoebodont (Ctenacanthoidea) in character, the fin spines are clearly ctenacanthoid, and the scales are taxonomically inconclusive. The isolated teeth identified by Young (1982) as *Xenacanthus* sp. certainly do not belong to that genus and probably are not of xenacanth derivation.

Mader (1986) named isolated teeth from the Lower Devonian (lower LOK–PRA) of northern Spain *Leonodus carlisi*, and assigned them to *Xenacanthus incertae sedis*. Overall, these teeth are similar to *Xenacanthus*, but the basolabial articulating boss, as well as the basolingular margin, show a tendency toward splitting (Mader, 1986, pl. 5, figs 1b, 3, 4), raising the possibility that these teeth are ctenacanthoid.

Poplin and Heyler (1989) proposed a different familial arrangement, recognizing three families, the Diplodo­selidae, Orthacanthidae and Expleuracanthidae. The content of the last two corresponds with the Xenacanthidae of this compilation.

**Order CLADOSELACHIFORMES** Dean, 1909

F. CLADOSELACHIDAE Dean, 1894

D. (FAM) Mar.

First and Last: *Cladoselache fyleri* (Newberry, 1889) and *Monocladodus clarkei* Claypole, 1893, Cleveland Shale Member, Ohio Shale, upper FAM, Ohio, USA.

Comment: Mader (1986) described two types of scales, *Iberolepis aragonensis* and *Luna­lepis leonensis* from the Lower Devonian (lower LOK–PRA) of northern Spain, and tentatively assigned them to the Order Cladoselachida.

**Order CORONODONTIFORMES** Zangerl, 1981

F. CORONODONTIDAE Harris, 1950

D. (GIV/FRS–FAM) Mar./Lagoonal (?)

First: *Coronodus reimannii* Bryant, 1923, Conodont Bed of Genese Formation, uppermost Erian/lowermost Senecan, New York State, USA.

**Last:** *Diademodus hydei* Harris, 1950, Cleveland Shale Member of Ohio Shale, upper FAM, Ohio, USA.

Comment: Williams (1985) described *Diademodus?* sp. teeth from the Mecca Quarry Shale of Linton Formation (upper Westphalian C = POD), Indiana, and from the Excello Shale of Carbondale Formation (lower Westphalian D = POD/MYA), Indiana, and noted that a specimen from the Stark Shale of Dennis Formation (upper Westphalian D = MYA), Iowa, may also be assignable to *Diademodus*.

**Order SYMMORIIFORMES** Zangerl, 1981

F. SYMMORIIDAE Dean, 1909

C. (VIS–POD) Mar./Lagoonal

First: *Denaea fournieri* Pruvost, 1922, Marbres noirs de Denée, lower Viséan (CHD or ARU), Denée area, Belgium.

**Last:** *Symmorium reniforme* Cope, 1893 and *Denaea mecaensis* Williams, 1985, Excello Shale of Carbondale Formation, lower Westphalian D (= POD/MYA), Indiana, USA (Williams, 1985).

Comment: Mader and Schultz (1987) recorded *Symmorium* sp. from Viséan IIIa3 of the Rheinisches Schieferge­birge, Germany, but since this is in the lower part of the *Goniattes* Zone, it appears to be somewhat younger (HLK) than the occurrence at Denée. Unpublished symmoriid specimens are known from the Virgilian (Stephanian B = KAS–GZE) of New Mexico, USA.

**F. STETHACANTHIDAE** Lund, 1974

D. (FAM)–C. (MYA) Mar./Lagoonal

First: *Stethacanthus altonensis* (St John and Worthen, 1875), Cleveland Shale Member of Ohio Shale, Ohio, USA (Williams, 1985).

**Last:** Altamont Limestone Member of Oologah Lime­stone, Westphalian D (= upper MYA), locality unknown (old specimen, cf. Williams 1985, p. 146); the unit is recognized in south-eastern Kansas, southern Iowa, south­western Missouri, and north-eastern Oklahoma, USA.

**Intervening:** HAS, IVO, HLK–ARN, POD, MYA.

**Comment:** *Stethacanthus praecursor* Hussakof and Bryant 1918, from the Conodont Bed of the Genese Formation (GIV/FRS), New York State, USA, has been declared an ‘indeterminate lump’ (Lund, 1984, p. 283), but it may well warrant at least the generic assignment (cf. Hussakof and Bryant, 1918, pl. 54, figs 1a, 2).


**F. FALCATIDAE** Zangerl, 1990

C. (HAS–ARN) Mar./Lagoonal

First: *Falcatus falcatus* (St John and Worthen, 1875), Kinderhookian, Iowa, USA (Lund, 1985a).

**Last:** *Falcatus falcatus* (St John and Worthen, 1875) and *Damocles serratus* Lund, 1986, both Bear Gulch Limestone, upper Chesterian, Namurian E2b, Montana, USA (Lund, 1985a, 1986a, 1990).

**Intervening:** HLK/ASB.
Order EUGENEODONTIFORMES Zangerl, 1981

Superfamily CASEODONTOIDEA Zangerl, 1981

F. CASEODONTIDAE Zangerl, 1981
C. (POD)–P. (KAZ) Mar./Lagoonal

Last: Fadenia crenulata Nielsen, 1932 and Erikodus groenlandicus (Nielsen, 1932), Posidonia Shale Member, Foldvik Creek Formation, East Greenland.

Intervening: MYA.

Comment: Teeth identifiable as Campodus sp. (Caseodontoidea inc. sedis) are known from the Salem Limestone (middle Meramecian = ARU/HLK) of Missouri, USA (Zangerl, 1981, p. 85).

F. EUGENEODONTIDAE Zangerl, 1981
C. (POD–KRE) Mar./Lagoonal

Last: Bobodus schaefferi Zangerl, 1981, Queen Hill Shale of Lecompton Formation, Stephanian A, Nebraska, USA.

Intervening: POD/MYA, MYA.

Superfamily EDESTOIDEA Hay, 1930

F. AGASSIZODONTIDAE Zangerl, 1981

First: Agassizodus variabilis (Newberry and Worthen, 1870). The holotype, from Illinois, USA, is presumably early Westphalian D (= POD/MYA) in age, but a new specimen referred to this species by Zangerl (1981, pp. 75, 77), from the Queen Hill Shale of Lecompton Formation, Nebraska, USA, is Stephanian A (= KRE). Arpagodus rectangulus Trautschold, 1879, from Myachkova, USSR, is late Westphalian D or Cantabrian (= MYA), and is thus nearly contemporaneous with A. variabilis.
Last: Sarcopriion edax Nielsen, 1932, Posidonia Shale Member of Foldvik Formation, East Greenland.

Intervening: KRE, MYA, ASS/SAK, ART, KUN (incomplete, ages of many specimens uncertain).


Last: Parahecylodocus sphaerici Nielsen, 1952, Wordie Creek Formation, lower SCY, East Greenland. Helicamphodus euloni Obruchev, 1965, from Dzhul’fa on the Araks River, Armenia, former USSR, is also SCY, probably roughly contemporaneous with P. sphaerici.

Intervening: POD, MYA, ART, KUN, KAZ (incomplete, ages of many specimens uncertain).

Order ORODONTIFORMES Zangerl, 1981

F. ORODONTIDAE de Koninck, 1878
D. (FAM)–P. (SAK) Mar./Lagoonal


Intervening: HAS/IVO through ASS; with the exception of POD and MYA, stage names cannot be given due to dating and taxonomic uncertainty.

Order PETALODONTIFORMES Zangerl, 1981

F. PRISTODONTIDAE Woodward, 1889
C. (BRI)–P. (TAT) Mar./Lagoonal

First: Pristodus falcatus Davis, 1883, Brigantian, Yorkshire, England, UK.
Last: Megactenopetalus kaibabanus Davis, 1944, Dzulfian (lower TAT), China and Iran (cf. Hansen, 1978).

Intervening: PND, ARN, KRE, NOG, ASS?, KUN–KAZ.

F. JANASSIDAE Jaekel, 1899 C. (ASB)–P. (KAZ) Mar./Lagoonal

First: Janassa clavata (M’Coy 1855), Asbian, Armagh, Northern Ireland, UK.
Last: Janassa kochi Nielsen, 1932 and J. urguicula (Eastman, 1903), Posidonia Shale Member, Foldvik Creek Formation, East Greenland.

Intervening: BRI, ARN, CHE–MYA, CHV, KLA, ASS–UFI.

Comment: Zangerl (1981), following Hansen (1978), included Peripristis St John, 1870, Pristodus Davis, 1883 and Megactenopetalus David, 1944 in the Pristodontidae, and left all other petalodont genera without family affiliation. Hansen (1985) revived the family Janassidae (Jaekel’s subfamily) to include Janassa Muenerst, 1839 and Fissodus St John and Worthen, 1875, and possibly Peltoodus Newberry and Worthen, 1870 and Cholodus St John and Worthen, 1875, should they prove distinct from the former two. Lund (1986b, 1989) added four more families, the Petalodontidae (Petalodus Owen, 1840 and Polythrictodus M’Coy, 1848), Peripristidae (presumably for Peripristis St John, 1870, but generic content not specified), Pristodontidae (Pristodus Davis, 1883, Siksika Lund, 1989, Petalorhynchus Newberry and Worthen, 1866, Peripristis St John, 1870, and Megac­tenopetalus David, 1944), and Belantseidae (Belantsea Lund, 1989, Netsepoje Lund, 1989 and Ctenophtychus Agassiz, 1838). However, the content of the Petalodontidae is far from clear, the separation of the Peripristidae (Lund, 1986b) has later been retracted (Lund, 1989), and the family Belantseidae appears to be based on specimens that may prove to be a Ctenophtychus (Belantsea montana Lund, 1899) and possibly a juvenile Fissodus (Netsepoje hauwe Lund, 1899), i.e. a janassid. To clarify these issues would require a major research undertaking, which is beyond the scope and purpose of this review, and which could easily fail because of the paucity of the existing material. Therefore, only the Pristodontidae and Janassidae are recognized.

Order SQUATINACTIFORMES Zangerl, 1981

F. SQUATINACTIDAE fam. nov. C. (ARN) Mar.

First and Last: Squatinactis caudispinatus Lund and Zangerl, 1974, Bear Gulch Limestone Member, Heath Formation, Namurian E2b, Montana, USA (Lund and Zangerl, 1974).

Subcohort NEOSELACHII Compagno, 1977

Superorder SQUALOMORPHII Compagno, 1973
Order HEXANCHIFORMES Buen, 1926

Suborder CHLAMYDOSELACHIOIDEI Berg, 1958

F. CHLAMYDOSELACHIDAE Garman, 1884
First: Chlamydoselachus thomsoni Richter and Ward, 1990, Beta Member, Santa Marta Formation, Brandy Bay area, James Ross Island (Antarctic) (Richter and Ward, 1990). An undescribed species also occurs in the Campanian of Angola (Cappetta, 1987). Extant
Intervening: LUT, RUP/CHT, BUR, SRV, ZAN.

Suborder HEXANOCHIDAE Garman, 1913

F. HEXANOCHIDAE Gray, 1851
J. (SIN)–Rec. Mar.
First: Hexanchus arzoensis (Beaumont, 1960), Lotharingian, Tessin, Switzerland. Extant
Intervening: OXF, ALB, SAN–YPR, RUP–CHT, TOR, ZAN.

F. HEPTRANCHIDAE Barnard, 1925
First: Heptranchias howelli (Reed, 1946), Lower Eocene(?), Montmouth Co., New Jersey, USA. The original specimen was found in a boulder probably derived from the Shark River Formation of early Eocene age. This species also occurs in the YPR of Morocco (Cappetta, 1981).
Intervening: LUT/BRT, BUR–LAN.

F. ORTHACODONTIDAE Beaumont, 1960
First: Sphenodus helveticus Beaumont, 1960 [in part], Tessin, Switzerland. The type material is a mixture of teeth of Sphenodus and of Paroarchacodus. Extant
Intervening: OFX, ALB, SAN–YPR, RUP–CHT, TOR, ZAN.

F. HEXANCHIDAE Garman, 1884
Intervening: MAA–LUT, RUP, BUR–LAN, ZAN.

F. SQUALIDAE Bonaparte, 1834

Subfamily SQUALINAE Bonaparte, 1834

J. (TTH)–Rec. Mar.
First: Squalogaleus woodwardi Maisey, 1976, lower TTH, Solnhofen, Germany. Maisey (1976) assigned this genus to the suborder Galeoidea (Lamniformes + Charcharhiniformes sensu Compagno, 1973). Cappetta (1987), based mainly on the dental morphology, considered Squalogaleus close to the ancestral stock leading to more advanced Squaliformes. In case Squalogaleus proves not to be a squaliform, the most ancient representative of the subfamily Squalinae would be Proto squalus albertsii Thies, 1981, BRM, Braunschweig, NW Germany (Thies, 1981).
Extant
Intervening: BRM, ALB, TUR, SAN–LUT, RUP–CHT–TOR, ZAN–PLE.

Subfamily ETMOPTERINAE Fowler, 1934
First: Eoetmopterus supracretaceus Muller and Schollmann, 1989, Upper Coesfelder Schichten, Westphalia, NW Germany. A species of Eoetmopterus has been described from the MAA of Hemmoor, NW Germany (E. hemmoorensis Herman, 1982) but its dental morphology indicates that it is Eoetmopterus Muller and Schollmann, 1989.
Extant
Intervening: MAA, BUR–LAN, TOR.

Subfamily OXYNOTINAE Rafinesque, 1810
First: Protoxynotus misburgensis Herman, 1975, upper CMP, Hannover, NW Germany (Herman, 1975).
Extant
Intervening: AQT/BUR, ZAN.

Subfamily SOMNIOSINAE Jordan, 1888
First: Cretascymnus adonis (Signeux, 1950), upper SAN, Sahel Alma, Lebanon.
Extant
Intervening: CMP–MAA, CHT, SRV, ZAN, PLE.

Subfamily DALATINAE Gray, 1851
First: Isistius trituratus (Winkler, 1874), LUT, Woluwe-St-Lambert, Belgium. This species occurs as early as the THA in Morocco (Arambourg, 1952). The genus Scymnorhinus (= Dalatais) has been recorded from the Palaeocene of former USSR on the basis of a single crown from a lower file (Glickman, 1964), but this occurrence needs to be confirmed by more complete and convincing material.
Intervening: YPR–TOR, ZAN–PIA.

First and Last: Centropterus lividus Costa, 1861, APT, Naples area, Italy. The single specimen, a heavily damaged skeleton, shows a second dorsal fin with a spine. Its assignment to the Squaliidae is quite provisional.

Order PRISTIOPHORIFORMES Berg, 1958
F. PRISTIOPHORIDAE Bleeker, 1859

?Superorder SQUALOMORPHII Compagno, 1973
F. PROTOSPINACIDAE Woodward, 1919
J. (TTH) Mar.
First and Last: Protospinax annectans Woodward, 1919, lower TTH, Solnhofen, Germany. Extant Intervening: TTH, VLG, APT, CEN–MAA, THA–PRB, Hannover, Germany (Thies, 1983). S. 1854 is represented by complete specimens in the lower Intervening: AAL, TTH, VLG, APT - TUR, SAN–PRB, AQTIMES, PLE. Lower Eocene of Monte Boica, Italy. Discovery of identical teeth from the CLV of England and OXF of Germany; these two genera as valid. Thies (1983) described as a juvenile specimen of the former. Yet, on the basis of the skeletal calcification, arrangement of the tooth rows, teeth by their morphologies, particularly the root with a completely closed groove, are easily separated from Protospinax.

Superorder SQUATINOMORPHII Compagno, 1973
Order SQUATINIFORMES Buen, 1926
First: Squatina sp., upper OXF (lower bittiumatum Zone), Hannover, Germany (Thies, 1983). S. acanthoderma Fraas, 1854 is represented by complete specimens in the lower TTH, Nusplingen, southern Germany. Extant Intervening: TTH, VLG, APT, CEN–MAA, THA–PRB, LAN, ZAN.

Superorder GALEOMORPHII Compagno, 1973
Order HETERODONTIFORMES Berg, 1937
First: Heterodontus duffini Thies, 1983, upper TOA (dispansum to aelensis Zones), near Hannover, Germany. This genus is known by complete skeletons from the lower TTH, H. falcifer (Wagner, 1857), Nusplingen, southern Germany. Extant Intervening: AAL, TTH, VLG, APT–TUR, SAN–PRB, AQT/MES, PLE.

Order ORECTOLOBIFORMES Applegate, 1972
First: Mesiteia emilae Kramberger, 1885, CEN, Hakel, Lebanon. It was believed, following the original description, that the type specimen had been collected in the Lower Eocene of Monte Bolca, Italy. Discovery of identical specimens from Lebanon and studies of the microfossils from the matrix of the type specimen have demonstrated that the true source of the type was the Lower Eocene of Italy. Extant Intervening: TUR–CMP, THA–LUT.

F. ORECTOLOBIDAE Jordan and Fowler, 1903
J. (CLV)–Rec. Mar.

F. BRACHAELURIDAE Applegate, 1972
J. (TOA)–Rec. Mar.
First: Ginglystemostoma lithuanica Dalinkevicius, 1935, ALB, Sventoji River, Lithuania, former USSR. Intervening: CEN–TUR, MAA–LUT, LAN.
F. RHINCODONTIDAE Garman, 1913
First: Palaeorhincodon dartevellei (Arambourg, 1952), YPR, Oued Oussen, Ouled Abdoun Basin, Morocco. This species has been collected also in the Gargasian, upper AAL (scissum and murchisoniae Zones), Hannover, NW Germany. The same species occurs in the upper TOA (dispansum to aelensis Zones) at the same locality (Thies, 1983). Extant Intervening: AAL, BRM, LUT–BRT. Comment: In Cappetta (1987), the range of the family is erroneously listed as Barremian to Recent.

First: Carcharias striatula Dalinkevicius, 1935, ALB, Sventoji River, Lithuania, former USSR. This species has been collected also in the Gargasian, upper APT, Vaucoule, southern France (Cappetta, 1975). Intervening: ALB–PIA. Comment: The generic assignment of numerous odontaspid species has been controversial until recently (Compagno, 1984; Cappetta, 1987; Ward, 1988). All the species previously assigned to the genera Synodontaspis White, 1931 and Eucromphodus Gill, 1861, must be assigned to the genus Carcharias Rafinesque, 1810.

Chondrichthyes

F. LAMNIDAE Müller and Henle, 1838
T. (THA)—Rec. Mar. (see Fig. 34.2)
First: Isurus winkerli (Vincent, 1876), THA (Pholadomya oblitterata level), Liège Province, Belgium.
Intervening: YPR—LUT, RUP, AQT—PLE.

F. CRETOXYRHINIDAE Glickman, 1958
K. (VLG)—PRB Mar.
First: Protolamna infracretacea Leriche, 1910, upper Neocomian (VLG/HAU), Liege Province, Belgium. Also in the Qsar-el-Sagha Formation of Fayum, Egypt. (Case and Cappetta, 1990).

First: Otodus obliquus Agassiz, 1843, London Clay (YPR), Kent, England, UK. This species appears in the THA: Morocco (Arambourg, 1952), Belgium and the Paris Basin (Leriche, 1906, and Bulgaria (Datchev, 1971).
Last: Parotodus benedeni (Le Hon, 1871), Neogene, Belgium. This species persists up into the Pli: Angola (Dartevelle and Casier, 1959), Belgium (Leriche, 1926), England, UK (Woodward, 1894), Italy (Lawley, 1881; Landini, 1977) and North America (Cappetta, pers. obs.).
Intervening: YPR—LUT, RUP, AQT—TOR.

F. ALOPIDAE Bonaparte, 1838
First: Paramonotodon angustidens (Reuss, 1845), TUR, Czechoslovakia. This species appears in the CEN: England, UK (Woodward, 1911 [1912] and Lithuania, former USSR (Dalnikevicius, 1935). Paramonotodon is assigned to the Alopiidae because of the great resemblance of its teeth to those of some species of Alopias (Cappetta and Case, 1975); however, this resemblance may be the result of convergent evolution. If this genus proves not to be an alopid, the first unquestionable representative of the family will be Alopias denticulatus Cappetta, 1981, lower YPR, Ouled Abdoun Basin, Morocco.
Intervening: YPR—BRT, RUP, BUR—SRV.

First: Cetorhinus marinus Leriche, 1908, RUP, Belgium. Usually only the gill-rakers are collected and figured; the teeth generally escape attention because of their small size. The family seems to be present in the Eocene of North America (B. Welton in litteris), but this needs to be confirmed by published material.
Intervening: BUR—SER, ZAN, PLE.

First: Squalicorax australis (Chapman, 1909), Boulia, Queensland, Australia. The genus is known from the ALB of Angola (Antunes, 1972).
Last: Pseudocorax affinis (Münster, in Agassiz, 1843);

Paracorax jaekeli (Woodward, 1895); Squalicorax pristodontus (Agassiz, 1843), MAA, Maastricht, The Netherlands; Squalicorax yangaensis (Dartevelle and Casier, 1943), Senonien, Yanga Lake, Cabinda, western Africa; MAA, Morocco (Arambourg, 1952); Squalicorax bassanii (Gemmellaro, 1920), MAA, Nile Valley and Red Sea phosphate deposits, Egypt; also in the MAA of Morocco as S. kaupi (Arambourg, 1952).
Intervening: CEN—CMP.

Order CARCHARHINIFORMES Compagno, 1973

First: Galeorhinus sp. (figured as G. minutissimus (Arambourg, 1952)], Lublin, Poland (Marcinowski and Radwanski, 1983). The first described species is Paratriakis bettrechienensis Herman, 1977, TUR, Bettrechies, northern France (Herman, 1977).
Extant: TUR, VLG, ALB—TUR, SAN—YPR, BUR—TOR, ZAN.

First: Hemipristis curvatus Dames, 1883, Middle Eocene, Birket-EI-Qurun, Fayum, Egypt.
Extant: PRB, BUR—TOR, PLE.

First: New genus and species, Ouarzazate Basin, south Morocco (Cappetta et al., 1987). It is probable that Scyliorhinus africanus Arambourg, 1952 from the THA of Morocco will be reassigned to the genus Abdounia. The first named representatives of the family are: Abdounia beaugei (Arambourg, 1952), YPR, Ouled Abdoun Basin, Morocco; Eogaleus bolcensis Cappetta, 1975, YPR, Monte Bolca, Italy; Galeocerdo latidens (Agassiz, 1843), upper YPR of Morocco (Cappetta, 1987); Physogaleus secundus (Winkler, 1874), TUR, Neder-Ockerzeel, Belgium; YPR, Morocco (Arambourg, 1952; Cappetta, 1981, 1987), and Anglo-Franco-Belgian Basin (Leriche, 1905, 1906; Priem, 1908; Casiere, 1946, 1966).
Extant: YPR—RUP, AQT—SRV, ZAN, PLE.

First: Sphyra arambourgi Cappetta, 1970, Langhian, Loupian, southern France (Cappetta, 1970). The teeth from the LUT of Nigeria that White (1926) attributed to this genus Abdounia. The first named representatives of the family are: Abdounia beaugei (Arambourg, 1952), YPR, Ouled Abdoun Basin, Morocco; Eogaleus bolcensis Cappetta, 1975, YPR, Monte Bolca, Italy; Galeocerdo latidens (Agassiz, 1843), upper YPR of Morocco (Cappetta, 1987); Physogaleus secundus (Winkler, 1874), TUR, Neder-Ockerzeel, Belgium; YPR, Morocco (Arambourg, 1952; Cappetta, 1981, 1987), and Anglo-Franco-Belgian Basin (Leriche, 1905, 1906; Priem, 1908; Casiere, 1946, 1966).
Extant: YPR—RUP, AQT—SRV, ZAN, PLE.

Superorder GALEOMORPHII INCERTAE ORDINIS

First: ?Palaeospinax sp. (Thies, 1982), Dienerian, cristaglii
Fig. 34.2

Zone, Kocaeli Peninsula, between Istanbul and Izmit, western Turkey (Thies, 1982). Although incomplete, the tooth figured by Thies really seems to belong to the genus *Palaeospinax* Egerton, 1872.

**Last:** *Paraorthacodus clarkii* (Eastman, 1901), Aquia Formation, Liverpool Point, Maryland, USA; *P. eocaenus* (Leriche, 1902), THA, Erquelinnes, Belgium. These two species may be synonymous. The last species occurs at Dormaal, Belgium, where it is associated with mammalian remains of early Eocene age; therefore, the teeth of *P. eocaenus* seem to be reworked.

**Intervening:** RHT, SIN, TOA–AAL, TTH, VLG, APT–TUR, CMP–DAN.

**Superorder** BATOMORPHII Cappetta, 1980

**Order** RAJIFORMES Berg, 1940
Suborder **RHINOBATOIDEI** Fowler, 1941

F. RHYNCHOBATIDAE Garman, 1913


**First:** Undescribed species of *Rhyynchobatus*, THA, Ouarzazate Basin, south Morocco (Gheerbrant et al., 1993). The first described species is *Rhyynchobatus vincenti* Jaekel, 1894, LUT, Woluwe-St-Lambert, Belgium. *Rhyynchobatus arganiae* Arambourg, from the Maastrichtian of Morocco, has been recently reassigned to another genus which does not belong to the Rhyynchobatidae (Cappetta, 1989). Some undescribed teeth from the MAA of Imin Tanout, Morocco, could represent the most ancient occurrence of the genus *Rhyynchobatus*.

**Extant Intervening:** THA-LUT, RUP, AQT-SRV.

F. RHINOBATIDAE Muller and Henle, 1838

J. (TOA)—Rec. Mar.

**First:** *Jurobatos cappettai* Thies, 1983, upper TOA (dispansum to aalensis Zones), Hannover, northern Germany (Thies, 1983).

**Extant Intervening:** AAL, BTH, KIM—TTH, VLG, APT, CEN-TUR, SAN—MAA, THA-BRT, BUR—SRV, ZAN.

F. PLATYRHINIDAE Jordan, 1923


**First:** *Platyrhina bolcensis* Molin, 1860 and *Platyrhina egeroni* (Zigno, 1876), Monte Bolca, northern Italy. The teeth of *Platyrhina ypresiensis* Casier, 1946, from the YPR of Belgium, cannot belong to this genus because of their very different morphology.

**Extant Intervening:** None.

F. HYPSOBATIDAE Cappetta, 1992


**First:** Undescribed species of *Hypsobatis* Cappetta, 1992, CMP, Negev Desert, Israel (Cappetta, 1992). The first described species is *Hypsobatis weileri* Cappetta, 1992, lower MAA, Level VI, ‘Tranche d’essa’ near Benguerir, Gantour Basin, Morocco. This species occurs also in the lower MAA of Egypt, where it was figured as *Rhombodus* sp. (Weiler, 1930).

**Last:** *Youssoubatis ganntourensis* Cappetta, 1992, upper MAA, Youssoufia, ‘Recette 4, Sillon X’, Gantour Basin, Morocco.

**Extant Intervening:** CMP—MAA.
**Suborder RAJOIDEI** Garman, 1913


First: Rajorhina expansa, 1887, CEN, Hakel, Lebanon; Maffetia tibniensis Werner, 1889, upper CEN, Gebel Dist Member of the Baharija Formation, Baharija Oasis, Egypt (Werner, 1889).

Extant

Intervening: SAN, THA–YPR, RUP, BUR–TOR, ZAN.


First and Last: Cyclobatis oligodactylus Egerton, 1844, CEN, Hakel, Lebanon; C. major Davis, 1887, CEN, Hakel and Hadjula, Lebanon; C. tuberculatus Cappetta, 1980, CEN, Hakel, Lebanon.

**Suborder RHINOBATOIDEI or SCLORORHYNCHOIDEI**


First: Parapalaeobates pygmaeus (Quaas, 1902), MAA, Libyan Desert, Egypt. This species occurs as early as the SAN of Dordogne, south-western France (Landemaine, 1991). This author, on the basis of superficial morphological dental resemblances, attributed erroneously the genus Parapalaeobates to the family Heterodontidae. Parapalaeobates has been collected in the Cenozoic of the Sahara Desert, in the Libyan Desert, and in North Africa. It remains to be proved that the Egyptian and Moroccan species belong to the same species as suggested by Landemaine (1991).

Last: P. atlanticus Arambourg, 1952, MAA, Morocco. This species occurs in the YPR and LUT of Europe and Africa (Cappetta, 1987, 1988) and then, the genus disappears from the fossil record. Miocene records (Tortonian of Portugal: Jonet, 1968 and Rec. FW) are based on erroneous determinations (Cappetta, 1987).

Extant

Intervening: SAN–MAA.


First: Onchoprists praecursor Thurmond, 1971, Trinity Group (APT/ALB), Texas, USA (Thurmond, 1971); O. numidus (Haug, 1905), upper ALB, Djoua, Algeria.

Last: Ctenopristis nougareti Arambourg, 1940, MAA, Ouled Abdoun Basin, Morocco; Dalpiazia stromeri Chechica-Rispoli, 1933, MAA, Tripolitania, Libya; Canopristis leptodon Arambourg, 1935, MAA, Ouled Abdoun Basin, Morocco; Ischirhiza nigeriensis (Tabaste, 1963), MAA, Mont Igdaman, Niger (several other species of this last genus occur in MAA deposits); Pucapisris branisii Schaeffer, 1963, El Molino Formation (MAA), Toror-Torol, Bolivia; Schizorhiza stromeri Weiler, 1930, 'Grès de Nubie' (MAA), Egypt.

Intervening: ALB–CMP.

**Suborder PRISTIOIDEI** Cappetta, 1980


First: Peyeria libyca Weiler, 1935, lower CEN, Baharija, Egypt. It is probable that this species is not a pristid; indeed, unquestionable pristids are present only since the early Eocene: Pristis lathami Galeotti, 1837, LUT, Melsbroek, Belgium. This species occurs in the YPR of the Anglo-Franco-Belgian Basin. Rostral teeth of Anoxypristis type – i.e. teeth devoid of posterior groove – occur in the lower YPR of the Ouled Abdoun Basin, Morocco (Cappetta, pers. obs.).

Extant

Intervening: YPR–BRT, AQT, LAN.

**Order TORPEDINOFORMES** Buen, 1926

**Superfamily TORPEDINOIDEA** Compagno, 1973


First: Eotorpedo zennaroi Cappetta, 1988, Danian, Imin Tanout, P3 Level, Morocco (Cappetta, 1988). There is a long gap in the fossil record between the last Eotorpedo in the YPR and the first Torpedo in the LAN.

Intervening: THA–YPR, LAN, ZAN.

**Superfamily NARCINOIDEA** Compagno, 1973


First: Narcine molini Jaekel, 1894, YPR, El Cairo, Egypt. Isolated teeth of Narcine have been collected in the YPR and LUT of Europe and Africa (Cappetta, 1987, 1988) and then, the genus disappears from the fossil record. Miocene records (Tortonian of Portugal: Jonet, 1968 and Miocene of India: Sahni and Mehrotra, 1981) are based on erroneous determinations (Cappetta, 1987).

Extant

Intervening: SAN–MAA, BRT, RUP, AQT–SRV, ZAN.

F. POTAMOTRYGONIDAE Garman, 1913  Q. (PLE)–Rec.  FW


Extant

Comment: This family occurs only in fresh water in South America. In Africa and Asia, Dasyatoidea occur also in some rivers and lakes but they belong to the genera Dasyatis and Himantura; so the assignment, by Arambourg, of the dermal tubercles from the PLE of East Africa to Potamotrygon, remains questionable. Patterson (1967), following Arambourg (1947), assigned to this family the dermal tubercles described by Larrazet (1866) as Dynatobatis, from the Tertiary (probably Neogene) of Rio Parana (Argentina). However, these tubercles could also belong to other batoids (Dasyatidae, Rajidae, etc.), and the fossil occurrence of Potamotrygonidae thus remains to be demonstrated.


First: Urolophus crassicauda Blainville, 1818, YPR, Monte Bolca, northern Italy. Despite the close resemblance between this species and the Recent genus, it is possible, considering the marked differences in the teeth, that the fossil form belongs to a different genus, all the more so because the genus Urolophus disappears completely from the fossil record until the PLE of southern California (Fitch, 1964).

Extant

Intervening: PLE.

First: Gymnura lateralata Werner, 1989, upper CEN, Gebel Dist Member of the Baharija Formation, Baharija Oasis, Egypt (Werner, 1989).

Extant Intervening: THA–LUT, RUP, AQT–SRV, ZAN.

Superfamily MYLIOBATOIDEA Compagno, 1973

F. MYLIOBATIDAE Bonaparte, 1838


First: Brachyrhizodus wchitanaensis Romer, 1942, 'Permocarboniferous', Godwin Creek, Texas, USA. This species does not come from Palaeozoic deposits, as asserted by Romer; it is not uncommon in the lower MAA deposits of New Jersey, USA (Cappetta and Case, 1975).

Extant Intervening: THA–LUT, RUP, AQT–SRV, ZAN.

F. RHINOPTERIDAE Jordan and Evermann, 1896


First: Rhinoptera prisca Woodward, 1907, Palaeocene, Pernambuco Province, Brazil; Rhinoptera raeburni White, 1934, THA, Wurno, northern Nigeria. The occurrence of Rhinoptera in the upper CEN of Baharija, Egypt (Werner, 1989), rests on the evidence of a single heavily damaged tooth which can probably be assigned to a hybodont.

Intervening: LUT, BUR–SRV.

F. RHOMBODONTIDAE Cappetta, 1987

K. (MAA)–Mar.

First and Last: Rhombodus levis Cappetta and Case, 1975, Mount Laurel Sands (lower MAA), New Jersey, USA; R. binkhorsti Dames, 1881, MAA, Maastricht, Holland; R. microdon Arambourg, 1952, MAA, Ouled Abdoun Basin, Morocco; R. meridionalis Arambourg, 1952, MAA, Oued Erguila, Morocco. The species R. bondoni Arambourg, 1952 (Maastrichtian, Ouled Abdoun Basin, Morocco) previously assigned to the genus Rhombodus is now attributed to a new genus inc. fam. (Noubhani and Cappetta, in press). The age of R. levis, previously considered to be late CMP, is early MAA in age on the basis on new stratigraphical and micropalaeontological studies (Petters, 1976).

Superfamily MOBULOIDEA Whitley, 1936

F. MOBULIDAE Gill, 1893


Intervening: YPR–LUT, RUP, AQT–SRV.

Subclass SUBTERBRANCHIALIA Zangerl, 1979

Superorder UNNAMED

Order INIOPTERYGIFORMES Zangerl and Case, 1973

Extant

F. INIOPTERYGIDAE Zangerl and Case, 1973

C. (POD–KRE)–Rec. Mar./Lagoonal


Superorder HOLOCEPHALI Bonaparte, 1832–1841

Order HELODONTIFORMES Patterson, 1965

F. HELODONTIDAE Patterson, 1965


First: Helodus spp., Louisiana, Missouri (Branson, 1914), and H. simplex Agassiz, 1838, also from Missouri, USA (Bryant and Johnson, 1936).

Last: Helodopsis spp., Upper Productus Limestone, Salt Range, Pakistan (Waagen, 1879).

Comment: Bendix-Almgren (1975) has shown that Permian 'Helodus' teeth may well belong to the edestids;
Smith and Patterson (1988, pp. 184, 194) comment that Helodus is polyphyletic and used as a form genus for the anterior teeth of various bradyodonts.

Order BRADYODONTIFORMES Smith Woodward, 1921

Suborder UNNAMED
F. PSEPHODONTIDAE Zangerl, 1981
First: Psphodus sp., Louisiana, Missouri, USA (Branson, 1914).
Intervening: HAS–BRI.

Order CHIMAERIFORMES Berg, 1940
Suborder ECHINOCHIMAEROIDEI Lund, 1977

Suborder MENASPOIDEI Patterson, 1965
First and Last: Deltoptychius armigerus (Traquair, 1887), upper Calcareous Sandstone Group, Cementstones (C2), Glencarholme, Scotland, UK.
Last: Deltoptychius armigerus (Traquair, 1887), Flex Coal, Namurian, Midlothian, Scotland, UK.

F. COCHLIODONTIDAE Owen, 1867
First: Thoralodus cabri Leeman, 1953, Cabrières, SE Montagne Noire, France, and Sandalodus minor Bryant and Johnson, 1936, Chaffee Formation, Gribble Creek, Fremont County, Colorado, USA.
Last: Crassiodonta subcrenulata Teichert, 1943, Permian, Wandagee Station, Western Australia, and C. stuckenbergi Branson, 1916, Lower Phosphate Member, Phosphoria Formation, Wyoming, USA.
Intervening: HAS–ALP.

F. DELTODONTIDAE Zangerl, 1981
C. (HAS)–P. (?KUN) Mar.
REFERENCES


Herman, J. (1977) Les selaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d’une biostratigraphie inter-continentale. Mémoires pour servir à


Chondrichthyes


OSTEICHTHYES: BASAL ACTINOPTERYGIANS

B. G. Gardiner

The 'lower' Actinopterygii, until recently called the Chondrostei, include a number of separate lineages or groups that share various primitive actinopterygian characters as well as a variety of derived or specialized ones. Traditionally, the Chondrostei have contained numerous extinct families, assigned to the broadly inclusive Palaeonisciformes plus the living polypterids (Cladistia) and the sturgeons and paddlefishes (Acipenseriformes). It is now apparent that the palaeonisciforms represent a grade group and are hence paraphyletic. The polypterids, in spite of numerous autapomorphies, are related to the primitive palaeonisciforms, while the sturgeons and paddlefishes form a monophyletic group (for which the term Chondrostei is now employed) affiliated with the Triassic saurichthyid fishes.

A great majority of these extinct 'lower' actinopterygian genera are represented by poorly preserved usually compressed specimens, which, more often than not, yield minimal information even for critical parts of the dermal skull pattern (Gardiner, 1984). However, the design of the fins and the squamation may often prove to be diagnostic at least at the family level. The higher classification is based on the dermal skull roof patterns, in particular, the various configurations displayed by the bones on the otic branch of the infra-orbital canal.

Some 270 fossil genera have been described so far and there are six extant genera (Polypterus, Acipenser, Huso, Scaphirhynchus, Polyodon and Psephurus).

The higher actinopterygians (Neopterygii) are usually subdivided into Holostei and Teleostei (treated in Chapter 36). The teleosts are undoubtedly monophyletic, whereas the Holostei are probably paraphyletic. Accordingly, the grade Holostei is divided into the Division Ginglymodi for the gars, and the Division Halecostomi for the more teleost-like holosteans. The higher actinopterygians are characterized by such features as the elongation of the upper caudal fin-rays, premaxillae with nasal processes, a coronoid process on the mandible, a vertical suspensorium and unpaired fins in which the fin rays have equalled their supports in number. Halecostome characters include an interopercular, uncinate processes on the epibranchials, median neural spines and a mobile maxilla.

One hundred and twenty genera of 'holosteans' (Ginglymodi + Halecostomi, other than Teleostei) have been described, of which two survive to the present day (Lepisosteus, Amia).

Class OSTEICHTHYES Huxley, 1880

Subclass ACTINOPTERYGII Klein, 1885

The earliest undoubted actinopterygians are late Devonian in age, although isolated scales have been recorded from the marine Upper Silurian of China (Naxilepis) and Europe (Lophosteus, Andreolepis), and from Lower Devonian deposits of both Canada (Dialipina) and Australia (Ligulalepis) (Märss, 1986; Schultz, 1968).

F. UNNAMED S. (LUD) Mar. (see Fig. 35.1)

First and Last: Andreolepis hedei Gross, 1968, Hemse Beds, Sweden; Paalda Beds, Baltic; Velikoretskaya Formation, north Timan; Ust-Spokoinaya Formation, Severnaya Zemlya; Long Quarry Beds, South Wales, UK (Märss, 1986).

F. CHEIROLEPIDIDAE Pander, 1860

D. (EIF/GIV – FRS) FW

First: Cheirolepis trailli Agassiz, 1835, middle Old Red Sandstone, Nairnshire, Scotland, UK.

Last: Cheirolepis canadensis Whiteaves, 1881, Escuminac Bay Formation, Quebec, Canada.

Infraclass CLADISTIA Cope, 1871

F. POLYPTERIDAE Lacépède, 1803

K. (MAA)–Rec. FW


Infraclass ACTINOPTERI Cope, 1871

F. MIMIIDAE fam. nov. D. (FRS) Mar./FW

### Key for both diagrams

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<thead>
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<th>TERTIARY</th>
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<tr>
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<td>2. Cheirolepididae</td>
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<td>21. Cornuboniscidae</td>
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<td>22. Amblypteridae</td>
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<td>3. Polypetidae</td>
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<td>23. Redfieldiidae</td>
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<tr>
<td>ACTINOPTERI</td>
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<td>24. Haplolepididae</td>
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<td>4. Mimiidae</td>
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<td>25. Stryacopteridae</td>
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<td>5. Tegeolepididae</td>
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<td>26. Canobiidae</td>
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<td>6. Stegotrachelidae</td>
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<td>27. Tarrasiidae</td>
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<td>7. Osorioichthyidae</td>
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<td>28. Aeduellidae</td>
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<td>8. Kentuckiidae</td>
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<td>29. Platsorniidae</td>
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<td>9. Acrolepididae</td>
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<td>30. Amphicentridae</td>
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<td>32. Boroclepidae</td>
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<td>12. Willomorichthyidae</td>
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<td>33. Urostheniidae</td>
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<td>13. Radkinichthyidae</td>
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<td>34. Brachydegmiidae</td>
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<td>14. Phanerorhynchidae</td>
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<td>15. Holuridae</td>
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<td>36. Trisolepididae</td>
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<td>37. Commentryidae</td>
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<td>17. Dwykiidae</td>
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<td>DORYPTERIFORMES</td>
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<td>18. Carboveliidae</td>
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<td>19. Gonatodidae</td>
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</tbody>
</table>

### Fig. 35.1

**First and Last:** Mimia toombsi Gardiner and Bartram, 1977, Gogo Formation, Australia; Howqualepis rostridens Long, 1988, lacustrine shales, Mt. Howitt, Australia.

**F. TEGEOLEPIDIDAE** Romer, 1945
D. (FAM) Mar.

**First and Last:** Tegeolepis clarki (Newberry, 1888), Cleveland Shale, Ohio, USA.

**F. STEGOTRACHELIDAE** Gardiner, 1963
D. (EFR/GIV -FAM) Mar./FW

**First:** Stegotrachelus Woodward and White, 1926; Moythomasia Gross, 1950, Orvikuna Gross, 1953, middle Old Red Sandstone, Scotland, UK; Wildungun, Bergish-Gladbach, Germany, and western Estonia, former USSR.

**Last:** Moythomasia, Ohio and Genesee shales, New York State, USA (Gardiner, 1963).

**F. OSORIOICHTHYIDAE** Gardiner, 1967

**First and Last:** Osorioichthys marginis (Casier, 1952), Belgium.

**F. KENTUCKIIDAe** fam. nov. C. (TOU/VIS) Mar.

**First:** Kentuckia deani (Eastman, 1905), Waverly Shales, Kentucky, USA.

**Last:** Eionichthys robloni (Hibbert, 1835), Calciiferous Sandstone, Oil Shales, Dunnet Shale, Scotland, UK.

**F. ACROLEPIDIDAE** Aldinger, 1937
C. (TOU)–Tr. (CRN/NOR) Mar./FW
### Osteichthyes: Basal Actinopterygians

#### Permian

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<thead>
<tr>
<th>Family</th>
<th>First Species</th>
<th>Last Species</th>
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</thead>
<tbody>
<tr>
<td>PTYCHOLEPIDIDAE</td>
<td>Nematoptychius greenocki (Traquair, 1866)</td>
<td><em>Paralogoniscus lautus</em> Kazantseva, 1981, Kupferschiefer, Germany.</td>
</tr>
<tr>
<td></td>
<td><em>Calciferous Sandstone, Scotland, UK; Acrolepis</em></td>
<td><em>Neuburgella cognominis</em> Kazantseva, 1981, Jemenei Basin, Kazakhstan, former USSR.</td>
</tr>
<tr>
<td></td>
<td>Agassiz, 1833, several species, Marl Slate, UK;</td>
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<tr>
<td></td>
<td><em>Kupferschiefer, Germany.</em></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>COSMOPTYCHIIDAE</td>
<td>Watsonichthys pectinatus (Traquair, 1877)</td>
<td><em>Inichthys gorelovae</em> Kazantseva, 1979, Neuburgella</td>
</tr>
<tr>
<td></td>
<td><em>Cosmoptychius striatus</em> (Agassiz, 1835), Calciferous</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sandstone, Scotland, UK.</td>
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</tbody>
</table>

#### Carboniferous

<table>
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<th>Family</th>
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<tr>
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<td>Madagascar and Greenland.</td>
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<td></td>
<td>(F. RHABDOLEPIDIDAE Gardiner, 1963)</td>
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</table>

#### Devonian

<table>
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<tr>
<th>Family</th>
<th>First Species</th>
<th>Last Species</th>
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<tbody>
<tr>
<td></td>
<td><em>Rhabdolepis</em> macropterus (Bronn, 1829), Lower</td>
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<tr>
<td></td>
<td>Permian, Lebach, Germany; <em>Tienshaniscus</em></td>
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<tr>
<td></td>
<td>longipterus Lui and Wang, 1978 and <em>Sinoniscus</em></td>
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<tr>
<td></td>
<td>macropterus Lui and Wang, 1978 from the Upper</td>
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</tr>
<tr>
<td></td>
<td>Permian of China doubtfully belong here.</td>
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</table>

#### Sinian

<table>
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<tr>
<th>Family</th>
<th>First Species</th>
<th>Last Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>F. RHADINICHTHYIDAE Romer, 1945</td>
<td><em>Rhadinichthys</em> Traquair, 1877, <em>Cycloptychius</em> Young, 1866, Calciferous Sandstone, Scotland, UK and elsewhere.</td>
<td></td>
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</tbody>
</table>

#### Table

<table>
<thead>
<tr>
<th>Period</th>
<th>Family</th>
<th>First Species</th>
<th>Last Species</th>
<th>Reference</th>
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<tr>
<td></td>
<td></td>
<td><em>Calciferous Sandstone, Scotland, UK; Acrolepis</em></td>
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<tr>
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<td>Agassiz, 1833, several species, Marl Slate, UK;</td>
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<td></td>
<td><em>Kupferschiefer, Germany.</em></td>
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<td></td>
<td></td>
<td><em>Cosmoptychius striatus</em> (Agassiz, 1835), Calciferous</td>
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<tr>
<td></td>
<td></td>
<td>Sandstone, Scotland, UK.</td>
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</table>

### Fig. 35.1

First: *Nematoptychius greenocki* (Traquair, 1866), Calciferous Sandstone, Scotland, UK; *Acrolepis* Agassiz, 1833, several species, Marl Slate, England, UK; Kupferschiefer, Germany. 

Last: *Turseodus acutus* Leidy, 1857, Newark Group, Pennsylvania and New Jersey, USA. 

F. PTYCHOLEPIDIDAE Brough, 1939

<table>
<thead>
<tr>
<th>Tr. (SCY)–J. (TOA)</th>
<th>Mar./FW</th>
</tr>
</thead>
<tbody>
<tr>
<td>First: Boreosomus Stensiö, 1921, several species, Spitsbergen, Madagascar and Greenland.</td>
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F. COSMOPTYCHIIDAE Gardiner, 1963

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<tbody>
<tr>
<td>First: Watsonichthys pectinatus (Traquair, 1877), <em>Cosmoptychius striatus</em> (Agassiz, 1835), Calciferous Sandstone, Scotland, UK.</td>
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F. WILLOMORICHTHYIDAE Gardiner, 1969

<table>
<thead>
<tr>
<th>C. (VIS)–P. (ROT)</th>
<th>Mar./FW</th>
</tr>
</thead>
</table>

F. RHADINICHTHYIDAE Romer, 1945

<table>
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<th>C. (TOU)–P. (ROT)</th>
<th>Mar./FW</th>
</tr>
</thead>
<tbody>
<tr>
<td>First: <em>Rhadinichthys</em> Traquair, 1877, <em>Cycloptychius</em> Young, 1866, Calciferous Sandstone, Scotland, UK and elsewhere.</td>
<td></td>
</tr>
<tr>
<td>Last: <em>Inichthys cozarti</em>, <em>Nozamichthys contorta</em> Schultze</td>
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</tbody>
</table>
and Bardack, 1986, Mazon Creek, USA; Cycloptichus and Rhadinichthys also in the Upper Carboniferous; Uydenia latifrons Kazantseva, 1980 and Eigilia nielsen Kazantseva, 1981 from the Lower Permian of Kazakhstan also appear to belong to this family.

F. PHANERORHYNCHIDAE Stensiö, 1932
C. (BSK/MOS) FW
First and Last: Phanerorhynchus armatus Gill, 1923, Middle Coal Measures, Lancashire, England, UK.

First and Last: Holurus parki Traquair, 1881, Cementstone Group, Scotland, UK.


First and Last: Paramblypterus decorus (Egerton, 1850), Coal Measures, France.

Last: Amblypterus Agassiz, 1833, Amblyptera Berg, 1940, Lebach, Germany, Kargala, former USSR; Gardinerichthys tewarii Gupta et al., 1978, Lower Permian, India; Korutichthys korutensis Kazantseva, 1980, Lower Upper Permian, former USSR.

F. REDFIELDIIDAE Berg, 1940 Tr. (SCY)–J. (I.) Mar./FW

Last: Redfieldius Hay, 1902, Redfieldius beds, Newark, USA.

F. HAPLOLEPIDIDAE Westoll, 1944
C. (BSK/MOS)–P. (ASS/KUN) Mar./FW
First: Haplolepis Miller, 1892, several species, Linton, Ohio, Mazon Creek, Illinois, USA, Coal Measures, Northumberland and Staffordshire, England, UK.


F. STYRACOPTERIDAE Moy-Thomas, 1939
First: Styracopterus fulcatus Traquair, 1890, Cementstone Group, Scotland, UK; Whiteichthys Moy-Thomas, 1942, Greenland.


F. CANOBIIDAE Aldinger, 1937
First: Canobius Traquair, 1881, Mesopoma Traquair, 1890, Cementstone Group, Dumfriesshire, Scotland, UK.

Last: Tarrasiusproblematicus Traquair, 1881, Cementstone Group, Dumfriesshire, Scotland, UK.

F. TARRASIIDAE Traquair, 1881
First: Tarrasius elegantulus Gardiner, 1969, upper Witteberg Series, South Africa; Charleluxia Heyler, 1969, from the ASS of France doubtfully belongs to this family.

F. TARRASIIDAE Traquair, 1881
First: Tarrasiusproblematicus Traquair, 1881, Cementstone Group, Dumfriesshire, Scotland, UK.

Last: Palaeophichthys parvulus Eastman, 1908, Coal Measures, Mazon Creek, Illinois, USA.

F. AEDUELLIIDAE Romer, 1945
First and Last: Aduella blainvillei (Agassiz, 1833), Westollia crassus (Pohlig, 1892), Icornella, Decazella, Burbonella Heyler, 1969, Autunian of Bourbon-’l-Archambault Decazeville and Autun, France; Palaethrissum Blainville, 1818, Marl Slate, England, UK, Germany.

F. PLATYSOMIDAE Young, 1866
First: Mesolepis Young, 1866, Parmesolepis Moy-Thomas and Dryne, 1938, Wardichthys Traquair, 1875, Platysomus Agassiz, 1833, Cementstone Group, Dumfriesshire, Scotland, UK.

Last: Caruichthys ornatus Broom, 1913, South Africa;
Osteichthyes: Basal Actinopterygians

**Order** SAURICHTHYIFORMES Berg, 1937

**F. SAURICHTHYIDAE** Goodrich, 1909 (= Belonorynchidae Woodward, 1888)

Tr. (SCY)–J. (TOA) Mar.

**First:** Saurichthys Agassiz, 1834, several species, Muschelkalk, Germany; Raibl, Lombardy, Madagascar, Nepal and Spitsbergen. *Saurichthys* Liu and Wel, 1988, is said to come from the Upper Permian of China.

**Last:** Saurorhynchus brevirostris (Woodward, 1895), upper Lias, England and Germany.

**Superdivision** CHONDROSTEI Müller, 1845

**Order** ACIPENSERIFORMES Berg, 1940

**F. PEPIAOSTEIDAE** Liu and Zhou, 1965

J. (TTH) Mar.

**First and Last:** Peipiaosteus pani Liu and Zhou, 1965, Tsien-shan-tze-kou, Nanling, China.

**F. CHONDROSTEIDAE** Traquair, 1877

J. (SIN–TOA) Mar./FW

**First:** Chondrosteus acipenseroides Egerton, 1844, *Chondrosteus pachyrurus* Egerton, 1858, lower Lias, Lyme Regis and Barrow-on-Soar, Leicestershire, England, UK.

**Last:** Strongylosteus hindenburgi (Pompeckz, 1914), upper Lias Holzmaden, Germany; *Gyrosteus mirabilis* Egerton, 1858, upper Lias, Whitby, Yorkshire, England, UK. *Gyrosteus subdelloides* Stinton and Torrens, 1968, is recorded from the BTH.

**F. ACIPENSERIDAE** Bonaparte, 1831

K. (TUR/CMP)–Rec. Mar./FW.

**First:** Paleosephurus wilsoni McAlpin, 1947, Hell Creek Beds, Montana; *Acipenser Linnaeus, 1758*, Edinburgh Beds, Alberta, Canada.

**Extant**

**F. POLYDONTIDAE** Bonaparte, 1838

T. (YPR)–Rec. Mar./FW.

**First:** Crassopholis magnicaudata Cope, 1883, Green River Shales, Wyoming, USA.

**Extant**

**Superdivision** NEOPTERYGII Regan, 1925

**Order** PALAEONISCIFORMES Goodrich, 1909

**F. PALAEONISCIDAE** Vogt, 1852

C. (TOU)–J. (SIN) Mar.

**First:** Elonymichthys serratus Traquair, 1881, *E. pulcherrimus* Traquair, 1881, Calciferous Sandstone, Scotland, UK.

**Last:** Cosmolepis ornatus (Egerton, 1854), *Cosmolepis egertonii* Egerton, 1858, lower Lias, Lyme Regis, England, UK.

**F. CENTROLEPIDIDAE** Gardiner, 1960

J. (SIN) Mar.

**First and Last:** Centrolepis aspera Agassiz, 1844, lower Lias, Lyme Regis, England, UK.

**F. COCCOCEPHALICHTHYIDAE** Romer, 1945


**First:** Coccocephalichthys wilii (Watson, 1925), Coal Measures, Lancashire, England, UK.

**Last:** Coccocephalichthys tessallatus Beltan, 1981 = *Mones-deiphus depressus* Beltan, 1990, Uruguay.
### TERTIARY

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<th>TOA</th>
<th>PLB</th>
<th>SIN</th>
<th>HET</th>
<th>RHT</th>
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</table>

### TRIASSIC

| ANS | SCY | 1 | 2 | 7 | 11 | 12 | 16 | 18 | 20 | 25 | 37 | 38 | 41 |

**Fig. 35.2**

**F. COCCOLEPIDIDAE** Berg, 1940  

**First:** Coccolepis liassica Woodward, 1890, lower Lias, Lyme Regis, England, UK; Plesiococcolepis humanensia Wang, 1977, Lower Jurassic, China.  
**Last:** Sunolepis yumenensis Liu, 1957, China. Coccolepis macroptera Traquair, 1911, Ber, Belgium–Coccolepis is widely distributed and is also recorded from the K1 of Turkestan, former USSR and Australia.

**F. SCANILEPIDIDAE** Romer, 1945  
Tr. (SCY/ANS–RHT) Mar.

**First:** Evenkia eunotoptera Berg, 1941, Tunguska Basin, Siberia, former USSR.  
**Last:** Scanilepis dubia (Woodward, 1893), Sweden. Fukangichthys longidorsalis Su, 1978, China and Tanaocrossus kalliokoskii Schaeffer, 1967, Norian, New Mexico, doubtfully belong in this family.

**F. BIRGERIIDAE** Aldinger, 1937  
Tr. (SCY)–K. (NEO) Mar.

**First:** Birgeria Stensiö, 1919, several species, Europe, Spitsbergen, Madagascar and Greenland.  
**Last:** Psilichthys selwyni Hall, 1900, Victoria, Australia.

**F. ASAROTIDAE** Schaeffer, 1968  

**First and Last:** Asarotus Schaeffer, 1968, Niobrara Formation, Kansas, USA.
**Order** Pholidopleuriformes Berg, 1937

F. Pholidopleuridae Wade, 1932  
Tr. (SCY – LAD) Mar.

First: *Australosomus* Piveteau, 1930, several species, Greenland, Spitsbergen and Madagascar. *Arctosomus sibiricus* Berg, 1941, Induan/Anisian, Tunguska Basin, Siberia, former USSR.

Last: *Pholidopleurus typus* Bronn, 1858, Besano, Italy; *Macroaethes* Wade, 1932, Middle Triassic, Brookvale, Australia.

**Order** Perleidiformes Berg, 1937

F. Colobodoidae Stensiö, 1916  
Tr. (SCY/ANS – CRN/NOR) Mar.


Last: *Colobodus* Agassiz, 1844, several species, Besano, Italy, and many other European localities.

F. Aetheodontidae Brough, 1939  
Tr. (LAD) Mar.

First and Last: *Aetheodontus besanensis* Brough, 1939, Besano, Italy.

F. Cleithrolepididae Wade, 1935  
Tr. (ANS – CRN) Mar./FW


Last: *Dipteronotus cyphus* Egerton, 1854, Worcestershire and Otter Sandstone, Devon, England, UK.

**Order** Peltolepidiformes Lehman, 1966

F. Peltolepididae Brough, 1939  
Tr. (LAD) – J. (SIN) Mar.

First: *Peltolepis* Kner, 1866, Besano, Italy, and Kueichow, China; *Placocephalus* Brough, 1939, Besano, Italy; *Platysiaicum* Egerton, 1872, Besano, Italy.
First: Platyxiagum sclerocephalus Egerton, 1872, lower Lias, Lyme Regis, England, UK; Placeopleurus sp. Italy.

Order CEPHALOXENIFORMES Lehman, 1966

First: Habroichthys minimus Brough, 1939, Besano, Italy.
Last: Nannolepis elegans Griffiths, 1977, Rheingraben Schiefer, Lunz, Austria.

F. HABROICHTHYIDAE Gardiner, 1967
Tr. (LAD–CRN) Mar.

First: Habroichthys minimus Brough, 1939, Besano, Italy.
Last: Nannolepis elegans Griffiths, 1977, Rheingraben Schiefer, Lunz, Austria.

Order CEPHALOXENIFORMES Lehman, 1966

F. CEPHALOXENIDAE Brough, 1939
Tr. (LAD) Mar.

First and Last: Cephaloxenus macropterus Brough, 1939, Besano, Italy.

F. MACROSEMIIDAE Lehman, 1966


First: Callopterus Thiollière, 1858, Ionoscopy Thiollière, 1858, Cerin, France, Bavaria, Germany.
Last: Ionoscopy Thiollière, 1858, Dalmatia, former Yugoslavia, Portlandian, England, UK.

F. MACROSEMIIDAE Thiollière, 1858
Tr. (RHT)–K. (HAV) Mar.

First: Legonatus Egerton, 1854, Rhaetic, Gloucestershire, England, UK, Hallein, Austria.
Last: Enchelyolepis Woodward, 1918, Meuse, France; Wealden, England, UK.

F. UARBRICHTHYIDAE Bartram, 1977 J. (u.) FW
First and Last: Uarbrichthys Wade, 1941, Talbragar Beds, New South Wales, Australia.

Order LUGANOIFORMES Lehman, 1958

F. LUGANOIIIDAE Brough, 1939 Tr. (LAD) Mar.

First and Last: Luganoia Brough, 1939, several species, Besania micrognathus Brough, 1939, Besano, Italy.


First and Last: Thoracopterus Bronn, 1858, Gigantopterus Abel, 1904, Upper Triassic, Carinthia, Austria, and Salerno, Italy.

Division GINGLYMODYI Cope, 1871

F. LEPISOSTEIDAE Cuvier, 1825
K. (I.)–Rec. FW

First: Paralepidosteus Arambourg and Joleaud, 1943, Damergou, Niger, Africa; Lepisosteus Lacépède, 1903 ranges back into the CMP in North America and Europe and into the Eocene in India.

Extant

Division HALECOSTOMI Regan, 1923


First and Last: Acentrophorus Traquair, 1877, Magnesian Limestone, Durham and Northumberland, England, UK.

F. SEMIONOTIDAE Woodward, 1890
Tr. (ANS/LAD)–K. (MAA) Mar./FW

First: Semionotus Agassiz, 1832, Europe; North America, and Africa; Allelolepis, Apheloilepis Heller, 1953, Europe; Asialepidotus Su, 1959, China; Sinoseminotus Yuan and Koh, 1936, China; Allelolepis Frič, 1906, Europe; Paralepidotus Stolley, 1920, Europe. Pericentrophorus Jörg, 1969, Europe, possibly from the Scythian may belong here.

Last: Lepidotus Agassiz, 1832, England, France, Germany and Switzerland.

F. DAPEDIIDAE Vogt, 1852
Tr. (CRN/NOR)–J. (KIM) Mar./FW

First: Dandy White and Moy-Thomas, 1940, Hallein, Austria; ?Prohalecites Deeke, 1889, Raibl, Carinthia, Besano, Italy, Polzberg, Austria.

Last: Heterostrophus Wagner, 1860, Solnhofen, Germany.


First: Oligopleurus Thiollière, 1850, Cerin, France.
Last: Spathius Davis, 1887, Lebanon; Oskunia Wentz and Kellner, 1986, APT, Brazil, may belong here.

F. IONOSCOPIDAE Lehman, 1966

First: Callopterus Thiollière, 1858, Ionoscopy Thiollière, 1858, Cerin, France, Bavaria, Germany.
Last: Ionoscopy Thiollière, 1858, Dalmatia, former Yugoslavia, Portlandian, England, UK.

F. MACROSEMIIDAE Thiollière, 1858
Tr. (RHT)–K. (HAV) Mar.

First: Legonatus Egerton, 1854, Rhaetic, Gloucestershire, England, UK, Hallein, Austria.
Last: Enchelyolepis Woodward, 1918, Meuse, France; Wealden, England, UK.

F. UARBRICHTHYIDAE Bartram, 1977 J. (u.) FW
First and Last: Uarbrichthys Wade, 1941, Talbragar Beds, New South Wales, Australia.

Order LUGANOIFORMES Lehman, 1958

F. LUGANOIIIDAE Brough, 1939 Tr. (LAD) Mar.

First and Last: Luganoia Brough, 1939, several species, Besania micrognathus Brough, 1939, Besano, Italy.


First and Last: Thoracopterus Bronn, 1858, Gigantopterus Abel, 1904, Upper Triassic, Carinthia, Austria, and Salerno, Italy.

Division GINGLYMODYI Cope, 1871

F. LEPISOSTEIDAE Cuvier, 1825
K. (I.)–Rec. FW

First: Paralepidosteus Arambourg and Joleaud, 1943, Damergou, Niger, Africa; Lepisosteus Lacépède, 1903 ranges back into the CMP in North America and Europe and into the Eocene in India.

Extant

Division HALECOSTOMI Regan, 1923


First and Last: Acentrophorus Traquair, 1877, Magnesian Limestone, Durham and Northumberland, England, UK.

F. SEMIONOTIDAE Woodward, 1890
Tr. (ANS/LAD)–K. (MAA) Mar./FW

First: Semionotus Agassiz, 1832, Europe; North America, and Africa; Allelolepis, Apheloilepis Heller, 1953, Europe; Asialepidotus Su, 1959, China; Sinoseminotus Yuan and Koh, 1936, China; Allelolepis Frič, 1906, Europe; Paralepidotus Stolley, 1920, Europe. Pericentrophorus Jörg, 1969, Europe, possibly from the Scythian may belong here.

Last: Lepidotus Agassiz, 1832, England, France, Germany and Switzerland.

F. DAPEDIIDAE Vogt, 1852
Tr. (CRN/NOR)–J. (KIM) Mar./FW

First: Dandy White and Moy-Thomas, 1940, Hallein, Austria; ?Prohalecites Deeke, 1889, Raibl, Carinthia, Besano, Italy, Polzberg, Austria.

Last: Heterostrophus Wagner, 1860, Solnhofen, Germany.


First: Oligopleurus Thiollière, 1850, Cerin, France.
Last: Spathius Davis, 1887, Lebanon; Oskunia Wentz and Kellner, 1986, APT, Brazil, may belong here.

F. PROMECOSOMINIDAE Wade, 1941
Tr. (SCY–CRN) Mar.
First: Paracentrophorus madagascariensis Piveteau, 1941, Madagascar.
Last: Phaidrosoma lunzensis Griffith, 1977, Rheingabener Schiefer, Polzberg, Austria.

Order AMIIFORMES Huxley, 1861
F. CATURIDAE Owen, 1860 (FURIDAE Jordan, 1923) Tr. (NOR)–K. (ALB) Mar./FW
First: Heterolepidotus Egerton, 1872, Tyrol, Austria; Perledo, Lombardy, Italy.
Last: Macrepistus Cope, 1894, Kansas, USA; Lophiostomus Egerton, 1852, from the CEN of Europe may also belong here.

F. AMIIDAE Bonaparte, 1837

F. OPHIOPSIDAE Bartram, 1975
Tr. (m.)–K. (TUR) Mar./FW
First: Ophiopsis attenuata Wagner, 1859, Perledo, Como, Italy.
Last: Neorhombolepis excelsus Woodward, 1888, Wealden, Europe; Aphanepygus Bassani, 1879, Lebanon, Lesina, Lago, Italy; Dalmatia, former Yugoslavia.

REFERENCES
OSTEICHTHYES: TELEOSTEI

C. Patterson

The Teleostei, with about 22,000 living species, are by far the largest vertebrate group, accounting for more than half of the total of recognized species of living vertebrates (Nelson, 1984). They are also the vertebrate group to which cladistic analysis was first applied, and, for that reason, teleost systematics has probably progressed further down the road from traditional phenetics towards a phylogenetic system than has the classification of any other vertebrate group. The principal result of cladistic analysis is to uncover and eliminate paraphyletic groups, and therefore the general acceptance of cladistics tends to have more radical effects on the systematics of fossils than on extant taxa. The traditional phenetic method resulted in many extinct and paraphyletic ‘ancestral groups’ which dissolve under cladistic analysis, either into an assemblage of incertae sedis genera, most of them monotypic, or into a series of plesions (Patterson and Rosen, 1977), each the sister taxon of everything distal to it in the cladogram. Of course, we are still very far from a thorough analysis of fossil teleosts along these lines, and deficiencies of preservation convince me that we shall never achieve anything like it. In making this compilation, I have tried to strike a balance between simplicity of presentation and the cladist's expectation that groups shall be monophyletic. Some extinct taxa that I know or guess to be merely phenetic are included; comments on the status of nominal extinct families of teleosts are given in Smith and Patterson (1988).

In general, the arrangement of teleost families used here is that of Nelson (1984), except where subsequent revisions provide better supported classifications of particular subgroups. Nelson’s (1984) check-list of extant teleostean families included 409 names. The following list includes 494 families, of which 69 are extinct, leaving 425 extant families. Among the 69 extinct nominal families, 32 (most of them monotypic) are listed as incertae sedis at various levels in the hierarchy. About 50 more nominal extinct families are merged or synonymized with other families, living or extinct. A few extinct monotypic nominal families are not listed, because I believe that the fossils are incertae sedis at levels in the hierarchy which do not make them the earliest members of the lowest-ranked taxon to which they may be assigned (e.g. Varasichthyidae Arratia, 1981, Chongichthyidae Arratia, 1982). In addition to the 494 families, the compilation includes ten Recent genera of Percoidae which Johnson (1984) listed as incertae sedis within that suborder, and because of its importance and extensive fossil record, the family Scombridae is subdivided into nine tribes (following Johnson, 1986 and Schultz, 1987).

The difference of sixteen between Nelson's (1984) 409 extant families and the 425 extant families in this compilation implies that there has been little change (a mere 4% increase in number) in teleost familial classification over the period of about seven years, surely the most active in the history of ichthyology, between the completion of Nelson’s list and of this one. In fact, the differences between Nelson's list and this one are much more extensive, involving almost one family in five. Thirty-two families in Nelson’s compilation are synonymized or merged with others in this list (because Nelson’s book is widely used, those synonymized family names are capitalized for easy recognition), and 48 extant families in this list are absent in Nelson’s. Among the 425 extant families listed here, 181 (43%) have no fossil record. Among the 244 extant families that do have a fossil record, that record consists only of otoliths for 58 families (24%).

The notations O and S mean respectively otolith and skeletal records, where it seems necessary to distinguish the latter from otoliths in a summary of stratigraphical range. Johnson (1984), in his review of Percoidae, uses an asterisk (*) after the family name to indicate percoid families with only one extant genus. That convention is used throughout this compilation (usually following Nelson’s (1984) assessment of generic status), and may give those unfamiliar with teleosts a feel for families in which fossils outweigh Recent representatives, or in which a lack of a fossil record.
might be expected. Of the extant families 133 (31%) are monogeneric; among them, 82 (62%) have no fossil record, and of the 51 with a fossil record, 36 (70.5%) are known by skeletal fossils, and 15 (29.5%) have a fossil record only of otoliths. Monogeneric families account for 45% (81 out of 181) of the extant families without known fossils.

The higher classification used here is eclectic but not original, and parts are presented only in outline, as an asymmetrical (with more ranks towards the higher teleosts) hierarchy, principally so that taxa are available for incertae sedis fossils. Perciform classification, in particular, is in a state of flux, and I have taken some liberties in seeking to reduce the number of families left in the basal Percidei. As one example, I have taken Johnson and Fritzsche’s (1989) suggestion (based on a shared pattern of the ramus lateralis accessorius nerve) that several ‘percoid’ families might be related to the stromateoids to mean that those families should be classified with the stromateoids, and I have included them there as Stromateoidei sensu lato. Other instances are to be found. A reference placed after the name of a higher taxon means either that the classification follows that source, or that the citation contains a review of fossil members. References are generally kept to a minimum.

Three general points on stratigraphy deserve mention here. Firstly, the fish beds at Monte Bolca, Verona, Italy, provide the earliest records for a very large number of teleost higher taxa. Traditionally regarded as Lutetian, Monte Bolca is now generally treated as topmost Ypresian (e.g. Blot, 1980) following the discovery of nannoplankton which place the beds in the zone of Discocysta sublodoensis (NP 14). But according to the Harland et al. (1990) time-scale used in this volume, NP 14 is lowermost Lutetian, and Monte Bolca records are so entered here. Secondly, the fish beds in the Danatinsk Formation, Kopetdag, SW Turkmenia (former USSR), contain an extensive teleost fauna first described by Daniil’chenko (1968). He dated the fishes as late Palaeocene, and that allocation has been accepted in subsequent Russian work on the fauna (e.g. Bannikov, 1985a; Daniil’chenko, 1980) and by other palaeoichthyologists. However, Tyler and Bannikov (1992), in describing new tetraodontiforms from the fish beds, point out that in the 1975 compendium on Russian Palaeogene stratigraphy, Solun and Travina (1975) placed the fish beds (which are about 9 m thick) in the middle portion of the Danatinsk Formation, with a suite of foraminifera including Globorotalia subbotinae (now called Morozovella subbotinae), an index fossil for the lowermost Eocene (basal YPR). Solun and Travina excluded the fish beds from the lower part of the Danatinsk containing Acarina subsphaerica (now called A. mckannai), an index fossil for the top Palaeocene. In that 1975 compendium, Daniil’chenko himself (1975, p. 436) referred the fishes to the lower Eocene, although elsewhere he subsequently continued to call them Upper Palaeocene. If that Thanetian age for the Danatinsk Formation is accepted, then it marks the earliest record for some fifteen families or higher taxa of teleosts, including Clupeidae, Chanidae, Urospenididae, Serranidae, Menidae, Caristiidae, Carangidae, Acanthuroidei, Siganidae, Luviridae, Euzaphlegiidae, Scombrini and Sardini. I have decided to accept Solun and Travina’s (1975) work as authoritative, and have entered all the Danatinsk fishes as Ypresian. Finally, in translating Russian stratigraphical terms, I have followed the practice of the translators of the Paleontologicheskii Zhurnal by taking ‘svita’ (suite) as ‘Formation’.

The authorship of family-group names in teleosts is still an outstanding problem, for no trustworthy compilation exists. In general, I have followed Nolf (1985): the only modern and reasonably complete list that I know; I have commented elsewhere (Patterson, 1987) on the unjust burden thrown on Nolf, a fossil otolith specialist, in attempting to determine the authorship of all teleost family-group names. Nolf had a little help from me, mostly on higher-category names, but he traced the vast majority of the family names and I believe that he did an excellent job. However, a recent authoritative work on eels (Böhlke, 1989) showed that in that group Nolf had the author and/or date wrong for seven out of 25 families (28%). Although I have corrected those and other slips that I have found in Nolf’s authorship of families, I have added many more families, and it will not surprise me if my error rate is as high as 28%. I beg indulgence and correction from those better informed.

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Subclass TELEOSTEI Müller, 1846

F. PACHYCORMIDAE Woodward, 1895 (including Protosphyraenidae Lydekker, 1889)

J. (TOA)–K. (CMP) Mar. (see Fig. 36.1)

First: Euthynotus, Pachycormus, Prosauropsis, Sauropsis, Saurostomus all in upper Lias, UK, France, Germany.

Last: Protosphyraena spp., CMP zones, European Chalk and Demopolis Chalk, Alabama and Mississippi, USA

Intervening: CLV-MAA.

F. ASPIDORHYNCHIDAE Bleeker, 1859 (including Vinctiferidae Silva Santos, 1990)

J. (BTH)–T. (THA) Mar./FW

First: Aspidorhynchus crassus Woodward, 1890, Stonesfield Slate, Oxfordshire, England, UK.

Last: Belonostomus sp. Bryant, 1987, Tongue River Formation, Morton County, North Dakota, USA.

Intervening: CLV–MAA.

F. PLEUROPHOLIDAE Saint-Seine, 1949 (including Archaeomenidae Boulenger, 1904)

J. (KIM)–K. (APT) Mar./FW

First: Pleuropholis thiollieri Sauvage, 1883, Cerin, Ain, France.

Last: Pleuropholis decastroi Bravi, 1991, Calcari ad itilioli, Pietroaroja, Campania, Italy.

Intervening: TTH–BRM.

F. PHOLIDOPHORIDAE Woodward, 1890 (including Archaeomenidae Boulebner, 1904)

Tr. (CRN)–K. (APT) Mar./FW

First: Pholidophorotes salutus Griffith, 1977, Reingrabeiner Schiefer, Austria.


Intervening: PLB-HAU.

F. ICHTHYODECTIDAE Crook, 1892


First: Thrissops formosus Agassiz, 1833, S. subovatus Münster, 1833, Cerin, Ain, France.

Last: Gillicus, Ichthyolectes, Xiphactinus, Niobrara Formation, Kansas, USA.

Intervening: TTH–SAN.

F. SAURODONTIDAE Cope, 1871


First: Saurodon intermedius (Newton, 1878), Lower Chalk, Kent, England, UK.

Last: Surocephalus lanciformis Harlan, 1824, Navesink Formation, New Jersey, USA; Maastricht, The Netherlands; Gramame Formation, Pernambuco, Brazil (Silva Santos and de Figueiredo, 1987).

Intervening: TUR–CMP.

Supercohort OSTEOGLOSSOMORPHA

Greenwood et al., 1966

Order OSTEOGLOSSIFORMES Regan, 1909

Osteoglossiformes incertae sedis

(F. HUASHIIDAE Chang and Chou, 1977)

J. (u.)/K. (l.) FW

First and Last: Kuntulunia longipterus Liu et al., 1982, Inner Mongolia and Ningxia, China, in beds thought to be ‘somewhere near the Jurassic–Cretaceous boundary’ (Chang and Chow, 1986).

Suborder NOTOPTEROIDEI Jordan, 1923

F. HIODONTIDAE* Valenciennes, 1846 (including Lycopteridae Cockerell, 1925)

J. (u.)/K. (l.)–Rec. FW

First: Lycoptera spp. and other genera, widespread in China (Liaoning, Hebei, Jilin, Gansu, Shanxi, Shandong, Ningxia), Mongolia and south-eastern former USSR, in beds thought to be ‘somewhere near the Jurassic–Cretaceous boundary’ (Chang and Chow, 1986). Extant Intervening: K. (m.)–RUP.

?F. OSTARIOSTOMIDAE Schaeffer, 1949

K. (MAA)/T. (DAN) FW

First and Last: Ostariostoma wilseyi Schaeffer, 1949, Livingston Formation, Madison County, Montana, USA (Grande and Cavender, 1991).

F. NOTOPTERIDAE Bleeker, 1859

O T. (?DAN)–Rec. FW

First: O 'Notopteridarum' nolfi Rana, 1988, Intertrappeans between Deccan Trap Flows no. 4 and 5, Rangapur, Hyderabad, India. S ?Eoc., Notopterus notopterus (Pallas, 1810).
1769, ?including *N. primaevus* Günther, 1876), Padang, Sumatra. The Eocene age of the fish shales at Padang is still dubious.

**Intervening:** ?Eoc.  
**Extant**  
**First:** *Hyperopisus* sp., Wadi el Natrun, Egypt (Greenwood, 1974).

**Extant**  
**Intervening:** PLE.
Osteichthyes: Teleostei

F. GYMNARCHIDAE* Bleeker, 1859 Extant FW

Suborder OSTEOGLOSSOIDEI Regan, 1909

F. OSTEOGLOSSIDAE Bleeker, 1859 (including PANTODONTIDAE Peters, 1876)

T. (DAN)–Rec. Mar./FW

First: Scales assigned to Musperia, Phareoids and Osteoglossidae incertae sedis, Intertrappean beds, central India; Brychaetus caheri Taverne, 1969, Montian, Landana, Cabinda, Angola. Phareodus is also reported from the Lameta Formation (MMA) and equivalent infratrappean strata in India by Sahni and Bajpai (1988) and Prasad (1989).

F. ARAPAIMIDAE Bleeker, 1859

K. (APT)–Rec. FW

First: Laelichthys ancestralis Silva Santos, 1985, Areado Formation, Minas Gerais, Brazil. Extant

Intervening: CEN.

Supercohort ELOPOCEPHALA Patterson and Rosen, 1977

ELOPOCEPHALA incertae sedis

F. PROTOSTOMIATIDAE Arambourg, 1954


First: Protostomias marocanus Arambourg, 1954, Jebel Tseifat, Morocco; Cinto Euganeo, Padova, Italy. Last: Pronotacanthus sahelalmae (Davis, 1887), Sahel Alma, Lebanon. This family was assigned to the Stomiiformes by Arambourg (1954), and may belong there (L. Taverne, pers. comm.), but no stomiiform apomorphies are yet recorded.

Cohort ELOPOMORPHA Greenwood et al., 1966

ELOPOMORPHA incertae sedis

(including Anaethalionidae Gaudant, 1968)

J. (KIM) Mar.

First: Anathalion spp., Cerin, Ain, France. The genus also occurs in TTH and VLG.

F. ELOPIDAE* Bonaparte, 1832


Intervening: SAN, Eoc. (I.–m.), ?UMI.

F. MEGALOPIDAE* Jordan and Gilbert, 1882 (including Sedenhorstiidae Goody, 1969)


Intervening: CEN, CMP, YPR, UMI.

Order ANGUILLIFORMES Regan, 1909

Suborder ALBULOIDEI Jordan, 1923

ANGUILLIFORMES incertae sedis

(including Osmeroideidae Forey, 1973)

O K. (HAU) S K. (APT)

First: O ‘Albuloides’ ventralis Weiler, 1971, lower HAU, Engelbostel, Hannover, Germany; S Brannerion vestitum Jordan and Branner, 1908, Santana Formation, Ceara, Brazil.

F. ALBULIDAE* Bleeker, 1859


First: Lebonichthys lewisi Davis, 1887, Hakel, Lebanon. Extant

Intervening: SNT, CMP, O THA–PLI.

F. PHYLLODONTIDAE Jordan, 1923


First: Casierius heckelii (Costa, 1864), Albian of Italy, France, UK and Texas (Estes, 1969). Last: Paralbula stromeri (Weiler, 1929), Qasr-el-Sagha Formation, Egypt.


F. PTEROTHRISSIDAE* Gill, 1893


First: Hajulia multidens Woodward, 1942, Hakel and Hajula, Lebanon. Extant

Intervening: SAN, CMP, O THA–PLI.

F. HALOSAURIDAE Giinther, 1868


First: Echidnocephalus troscheli Marck, 1858, Sendenhorst, Westphalia, Germany. Extant

Intervening: UMI.

F. NOTACANTHIDAE Rafinesque, 1810 (including LIPOGENYIDAE Goode and Bean, 1894)


First: O Notacanthus sp. Nolf and Lapiere, 1979, Calcaire Grossier, Thiverval, Yvelines, France. Extant

Suborder ANGUILLINOIDEI Regan, 1909

(arrangement of extant families follows Böhle, 1989)

ANGUILLINOIDEI incertae sedis


Comment: These fishes, conventionally allocated to the (paraphyletic) extinct families Anguillavidae Hay, 1903 and Urenchelyidae Regan, 1912, are primitive eels. Robins (1989) examined specimens of Anguillavus and Urenchelys and asserted that ‘there is no basis to align them with the Anguilloides’ (i.e. they are not eels) but I believe that they are true eels (Patterson, in press). Anguilloid otoliths are recorded from the Severn Formation (MAA), Maryland, by Huddleston and Savoie (1983).

Superfamily ANGUILLOIDEA Rafinesque, 1810

ANGUILLOIDEA incertae sedis
F. ANGUILLOIDIDAE Blot, 1978

First and Last: Anguilloides branchiostegalis (Eastman, 1905), Veronanguilla ruffoi Blot, 1978, Monte Bolca, Verona, Italy.

F. MILANANGUILLIDAE Blot, 1978

First and Last: Milananguilla lehmani Blot, 1978, Monte Bolca, Verona, Italy. Comment: These two families (Anguilloididae, Milananguillidae) are said by Blot (1984) to be close to the ancestral stock of anguilloids.

F. ANGUILLIDAE* Rafinesque, 1810
T. (YPR)-Rec. Mar./FW

First: 0 Anguilla annosa Stinton, 1975, upper London Clay Formation, SE England, UK; first skeletal remains are LUT, Eoanguilla leptoptera (Agassiz, 1835), Monte Bolca, Verona, Italy. Extant

Intervening: BRT - PLI.

F. MORINGUIDAE Gill, 1890


F. CHLOPSIDAE Rafinesque, 1810 (= XENOCONGRIDAE Regan, 1912)

First: Whitapodus breviculus (Agassiz, 1839), Monte Bolca, Verona, Italy. Extant

F. PARANGUILLIDAE Blot, 1978

First and Last: Paranguilla tigrina (Agassiz, 1839), Dalpiazziella brevicauda Cadrobbi, 1962, Monte Bolca, Verona, Italy. The family is said by Blot (1984) to be close to the ancestral stock of muraenids.

F. MURAENIDAE Risso, 1826


Intervening: YPR-PLE.

F. PROTEOMYRIDAE Blot, 1980

F. PARECHELIDAE Casier, 1967

F. CONGRIDAE Kaup, 1856 (including MACROCEPHENCHELYIDAE Fowler, 1934)

First: ?Two juvenile congrid otoliths, Tupelo Tongue of the Coffee Sand Formation, Chapelville, Mississippi, USA (Nolf and Dockery, 1990). The next oldest records are otoliths of Conger, Gnathophis and Hildebrandia from the Ypresian of Aquitaine and Belgium, and of ‘Congridarum’ from the Ypresian of England, Belgium, Aquitaine, Mississippi and New Zealand. Extant

Intervening: YPR-PLE.

F. NETTASTOMATIDAE Jordan and Davis, 1891
O T (YPR)-Rec. Mar.
F. PATAVICHTHYIDAE Blot, 1980

First: Patavichthus bolcensis (Bassani, 1898), Monte Bolca, Verona, Italy.
Last: Proserrivomer mequemeni Arambourg, 1967, Elam, Luristan, Iran. This genus, previously placed in the succeeding family, was transferred to Patavichthyidae by Blot (1984).

F. SERRIVOMERIDAE Roule and Bertin, 1929 Extant Mar.

Superfamily SACCOPHARYNGOIDEA Bleeker, 1859

First and Last: Enchelion montium Hay, 1903, Hokel, Lebanon (Patterson, in press).

FF. CYEMATIDAE Regan, 1912, SACCOPHARYNGIDAE* Bleeker, 1859, EURYPHARYNGIDAE* Gill, 1883, MONOGNATHIDAE* Bertin, 1936 Extant Mar.

Cohort CLUPEOCEPHALA Patterson and Rosen, 1977
CLUPEOCEPHALA incertae sedis J. (TTH) Mar.

First: Daitingichthys tischlingeri Arratia, 1987, Malm Zeta 3, Daiting, Bavaria, Germany.

Order CROSSOGNATHIFORMES Taverne, 1989

Suborder CROSSOGNATHIDAE Taverne, 1989

First: Crossognathus sabaudianus Pictet, 1858, Voiron, Switzerland; Hilštěn, Hildesheim, Hannover, Germany.
Last: Apsopelix anglicus (Dixon, 1850), Pierre Shale, western interior USA; Fox Hills Sandstone, Colorado, USA.
Intervening: ALB–SAN.

Comment: Taverne (1989), who has revised the crossognathids, regards them as occurring first in the lower Aptian (Töck, Heligoland), but does not comment on the stratigraphy of the localities in Switzerland (Voiron) and Hannover (Hildesheim) from which Crossognathus was first recorded (Woodward, 1901). These localities are traditionally regarded as Neocomian, but the ammonites associated with the Voiron fishes imply Barremian age.

Suborder PACHYRHIZODONTIDAE Forey, 1977

First and Last: Notolops brama (Agassiz, 1841), Santana Formation, Serra do Araripe, Ceará, Brazil.


Last: Platinx macroperus (de Blainville, 1818), Monte Bolca, Verona, Italy.
Intervening: ALB–CMP, THA, YPR.

Suborder TSELFATIOIDEI Bertin and Arambourg, 1958


Last: Bananomgius spp., Moorevillia hardi Applegate, 1970, Mooreville Formation, Alabama, USA.
Intervening: CEN–SAN.

Subcohort CLUPEOMORPHA Greenwood et al., 1966 (Grande, 1985)
CLUPEOMORPHA incertae sedis K. (BRM) Mar./FW

First: ‘Clupea’ antiqua Pictet, 1858, ‘C’. voironensis Pictet, 1858, Voiron, Switzerland.
Comments: These beds, conventionally dated as Neocomian, contain a cephalopod fauna implying Barremian age. ’Diplomystus’ spp. said to be of Neocomian age include ’D’. goodi Eastman, 1912, from the middle part of the Cocobeach Series in Gabon and Rio Muni, and ’D’. primotinus Uyeno, 1979 and ’D’. kokarenais Uyeno, 1979 from the Karamiya Formation, Kitakyushu, Fukuoka, Japan. The first of these is here included in Ellimmichthys (below); the two Japanese species occur in poorly dated freshwater sediments, and there is no good reason to believe that they are earlier than Barremian. Paraclupea chetungensis Du, 1950 is from freshwater deposits in SE China dated as late Jurassic or early Cretaceous, but correlated (by Chang and Chow, 1986, using fishes) with the Cocobeach Series in West Africa and the Ilhas Formation of Brazil. Paraclupea may be an ellimmichthyid (below), but no apomorphies indicating that are recorded.

Order ELLIMMICHTHYIFORMES Grande, 1982


First: Ellimmichthys longicosstatus (Cope, 1886), Ilhas Formation, Bahia, Brazil and ’Diplomystus’ goodi Eastman, 1912 (here taken to belong in Ellimmichthys), Cocobeach Series, Rio Muni. These freshwater beds are conventionally dated as Neocomian, but could well be Barremian or even Aptian (e.g. de Klasz and Gageonnet, 1965; Brito, 1979).
Last: Diplomystus dentatus Cope, 1877, Green River
Formation, Wyoming, USA; *Diplomystus shengliensis* Zhang et al., 1985, Shahejezu Formation, Henan, China.

**Intervening:** ?APT, CEN, SAN, YPR.

**Order** CLUPEIFORMES Bleeker, 1859

**Suborder** DENTICIPITOIDEI Greenwood et al., 1966

F. DENTICIPITIDAE* Clausen, 1959

T. (Oli./Mio.)–Rec. FW

First: *Palaeodenticeps tanganikae* Greenwood, 1960, lacustrine shales, Singida, Tanzania. Extant

Suborder CLUPEOIDEI Bleeker, 1859

**Superfamily** ENGRAULOIDEA Gill, 1861

F. COILIIDAE* Jordan and Seale, 1925

Extant Mar./FW


Intervening: ?PLI, PLE.

Superfamily PRISTIGASTEROIDEA Jordan and Evermann, 1896

**Incertae sedis**

K. (MAA) Mar./FW

Extant


F. PELLONIDAE Bleeker, 1859 (ine. Palaeoesocidae Berg, 1935)

T. (THA)/(YPR)–Rec. FW


Extant

Intervening: YPR–UMI, PLE.

**Division** OSTARIOPHYLI Sagemehl, 1885

**Series** ANOTOPHYSI Rosen and Greenwood, 1970

**Order** GONORYNCHIFORMES Regan, 1909

GONORYNCHIFORMES incertae sedis K. (BER)

First: *Aethalionopsis robustus* (Traquair, 1911), Bernissart, Belgium.

F. CHANIDAE* Giinther, 1868 (including Haleeopsidae Casier, 1946)


First: *Chanos torosus* Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR; *Halecopsis insigis* Delvaux and Ortlieb, 1887, London Clay Formation, southern England, UK; Argile des Flandres, Hainaut, Belgium; Nord, France; and equivalents in NW Germany.

Intervening: YPR, LUT, Oli.


Extant

Intervening: SAN, CMP, THA–CHT.

**Series** OTOPHYLI Garstang, 1931

?OTOPHYSI incertae sedis

(including Salminopsidae Gayet, 1985) K. (CEN)


**Comment:** The status of these two genera is controversial; if they are not otophysans, the first otophysans are the MAA catfishes cited below.

**Order** CYPRINIFORMES Bleeker, 1859

F. CYPRINIDAE Cuvier, 1817

T. (THA)–Rec. Mar./FW

First: *Knightia vetusta* Grande, 1982, Tongue River Formation, Bay Horse, Montana, USA.

Intervening: YPR–PLI.

Subcohort EUTELEOSTEI Greenwood et al., 1967

EUTELEOSTEI incertae sedis K. (BER) FW


**Order** ESOCIFORMES Bleeker, 1859

F. UMBRIDAE Bleeker, 1859 (inc. Palaeoesocidae Berg, 1936) T. (THA)/(YPR)–Rec. FW


Extant

Intervening: YPR–UMI, PLE.

F. ESOCIDAE* Cuvier, 1817

K. (CMP)–Rec. FW (see Fig. 36.2)


Intervening: MAA–PLE.
Fig. 36.2

precisely. In agreement with Fink et al. (1984), I do not accept Molinichthys inopinatus Gayet, 1982, from the El Molino Formation (MAA/DAN), Bolivia, as a cyprinid or cyprinoid. Blica croydonensis White, 1931, from the THA Woolwich and Reading Formation, SE England, UK, was cited as the earliest cyprinid in the first edition of this compilation (Patterson, 1967), but there is no evidence that the single specimen is cyprinid or even otophysan. Intervening: LUT–PLE.

F. PSILORHYNCHIDAE* Hora, 1925 Extant FW
F. HOMALOPTERIDAE Bleeker, 1859 Extant FW
F. COBITIDIDAE Swainson, 1839
T. (MMI)–Rec. FW
First: Cobitis centrochir Agassiz, 1835, Ohningen, Bavaria, Germany; C. cf. taenia Linné, 1758, western Kazakhstan,
**Animals: Vertebrates**

former USSR. *Noemacheilus musceli* Paucu, 1929, RUP, Romania, is an argentinid.  

**Intervening:** UMI-.PLI.

**F. GYRINOCHIELIDAE** Boulenger, 1904  
Extant  

**F. CATOSTOMIDAE** Heckel, 1843  
T. (?DAN)–Rec.  
FW  

First: Cleithra like those of *Amyzon*, Paskapoo Formation (Tiffanian), Alberta, Canada (Wilson, 1980); the next oldest records are LUT: *Amyzon gosiutensis* Grande et al., 1982, Laney Shale member, Green River Formation, Wyoming, USA, and *A. aggregatum* Wilson, 1977, respectively from the Allenby Formation and Horsefly River Beds of British Columbia, Canada; *Amyzon zaissanieus* (Sytchevskaya, 1983) and *Catostomidae indet.*, Obailinskaya Formation (YPRILUT), River Ul’ken-Ulast’y, Kazakhstan, former USSR.  

**Intervening:** LUT-.PLE.

**Order CHARACIFORMES** Goodrich, 1909  

**CHARACIFORMES incertae sedis**

K. (MAA)(T. (DAN)  
FW

First: Teeth referred to Characidae and Erythriniidae from the El Molino Formation, Bolivia (de Muizon et al., 1983), and similar teeth from the Vilquechico Formation, Peru (pers. observation). These formations have been described as MAA but their dating is controversial (Mourier et al., 1988; Van Valen, 1988; Marshall, 1989; Cappetta, 1990). Characiformes *incertae sedis* are also known from the Palaeocene of Morocco (THA, Cappetta, 1990) and Niger (undescribed BMNH material).

**F. CITHARINIDAE** Günther, 1864  
Extant  

**F. HEMIODONTIDAE** Bleeker, 1859  
T. (LMI)–Rec.  
FW  


**F. CURIMATIDAE** Bleeker, 1859  
T. (PLE)–Rec.  
FW  

First: *Curimata mosei* Travassos and Silva Santos, 1955, Tremembé, São Paulo, Brazil.  

**F. ANOSTOMIDAE** Günther, 1864  
T. (LMI)–Rec.  
FW  


**F. ERYTHRINIDAE** Gill, 1858  
T. (LMI)–Rec.  
FW


**F. LEBIASINIDAE** Eigenmann, 1910  
Extant  

**F. GASTEROPELECIDAE** Bleeker, 1859  
Extant  

**F. CTENOLUCIDAE** Schultz, 1944  
(= *Xiphostomidae* Boulenger, 1904)  
Extant  

**F. HEPSETIDAE** Fowler, 1958  
Extant  

**F. CHARACIDAE** Bleeker, 1859  
T. (LMI)–Rec.  
FW  


**Intervening:** MML-.PLE.

**Order SILURIFORMES** Cuvier, 1817  

**Suborder SILUROIDEI** Cuvier, 1817  

**SILUROIDEI incertae sedis**

FW

First: Undetermined fin-spines (Cione, 1987), Los Alamitos Formation, Rio Negro, Argentina. Early South American siluroids also occur in the Bauru Group, Brazil (Gayet and Brito, 1989, SEN), Coli Toro Formation (lower MAA), Argentina, and in the Yacoraita Formation (Argentina), the Vilquechico Formation (Peru) and the El Molino Formation (Bolivia), which are probably correlated (Mourier et al., 1988; Van Valen, 1988), and are late MAA or DAN in age. Skulls from the El Molino have been assigned to three extinct monotypic genera, one in a monotypic F. Andinichthyidae Gayet, 1988 (Gayet, 1990). In Africa, MAA siluroids occur at In Beceten, Niger (BMNH material).

**F. DIPLOMYSTIDAE** Eigenmann, 1890  
K. (CMP)–Rec.  
FW


**F. HYSIDORIDAE** Grande, 1987  
T. (LUT)  
FW

First and Last: *Hypsidoris farsonensis* Lundberg and Case, 1970, Laney Shale Member, Green River Formation, Wyoming, USA.  

**F. ICTALURIDAE** Gill, 1861  
(= *Ameljuriidae* Günther, 1864)  
T. (THA)–Rec.  
FW

First: *?Astephus* sp. Lundberg, 1975, Polecat Bench Formation, Big Horn County, Wyoming, USA. Extant  

**Intervening:** YP-.PLE.

**F. BAGRIDAE** Bleeker, 1858  
T. (THA)–Rec.  
FW


**Intervening:** LUT-.RUP, PLI-.PLE.

**F. CRANOGLANIDIDAE*** Myers, 1931  
Extant  

**F. SILURIDAE** Cuvier, 1817  
T. (TOR)–Rec.  
FW

First: *Silurus* sp., Howenegg-im-Hegau, Baden, Germany. Extant  

**Intervening:** PLI.

**F. SCHILBEIDAE** Bleeker, 1859  
Extant  

**F. PANGASIIDAE** Bleeker, 1859  
T. (?Eoc.)–Rec.  
FW

First: *Pangasius indicus* von der Marck (1876), Padang, Sumatra. The Eocene age of the fish shales at Padang is still dubious. Extant
F. AMBLYCIPITIDAE Regan, 1911 Extant FW
F. AMPHILIDAE Regan, 1911 Extant FW
F. PARAKYSIDAE* Roberts, 1989 Extant FW
F. AKYSIDAE Günther, 1864 Extant FW
F. SISORIDAE Bleeker, 1859 (= Bagariidae Günther, 1864)
T. (PLI)–Rec. FW
First: Bagarius yarrelli (Hamilton-Buchanan, 1822), Siwallaks, Nahan, India.
F. CLARIIDAE Günther, 1864 T. (MMI)–Rec. FW
Intervening: UMI-PLE.
F. HETEROPNEUSTIDAE* Hora, 1936 Extant FW
F. CHACIDAE* Bleeker, 1859 Extant FW
F. OLYRIDAE* Hora, 1936 Extant FW
F. MALAPTERURIDAE* Bleeker, 1859 Extant FW
F. ARIIDAE Günther, 1864 K. (CMP)–Rec. Mar./FW
Intervening: MAA-PLE.
F. PLOTOSIDAE Bleeker, 1859 Extant Mar./FW
F. MOCHOKIDAE Regan, 1911 T. (LMI)–Rec. FW
First: Synodontis sp., BUR, Moghara, Egypt; LMI, Rusinga Island, Lake Victoria, Kenya.
Intervening: MMI-PLE.
F. DORADIDAE Günther, 1864 T. (Mio.)–Rec. FW
F. Auchenipteridae Eigenmann and Eigenmann, 1890 Extant FW
F. PIMELODIDAE Bleeker, 1859 T. (UMI)–Rec. FW
First: Phractocephalus hemiolopterus (Bloch and Schneider, 1801), Ururumaco Formation, Falcon State, Venezuela; Pimelodus sp., Cione, 1986, Ituzaingo Formation, Parana, Argentina.
Intervening: PLI–PLE.
FF. Ageneiosidae Bleeker, 1858, Helogenidae Regan, 1911, Cetosidae Bleeker, 1858, Hypophthalmididae* Cope, 1871
ASPREDINIDAE Bleeker, 1859,
Nematogenyidae* Günther, 1864
Trichomycteridae Bleeker, 1858
Extant FW
F. CALLICHTHYIDAE Bleeker, 1859 T. (THA)–Rec. FW
First: Corydoras revelatus Cockerell, 1925, Maiz Gordo Formation, NW Argentina.
Extant
Intervening: PLE.
F. SCOLOPLACIDAE* Bailey and Baskin, 1976 Extant FW
F. LORICARIIDAE Bonaparte, 1831 T. (Mio.)–Rec. FW
Extant
F. ASTROBLEPIDAE* Eigenmann, 1922 Extant FW

Suborder Gymnotoidei Gill, 1872
GYMNOTOIDEI incertae sedis T. (UMI) FW

FF. Sternopygidae Cope, 1871

Division Neognathi Rosen, 1973
NEOGNATHI incertae sedis (with PU1 + U1 fused) K. (?BRM) FW
First: Casieroides yamangaensis (Casier, 1961), Chardonius longicaudatus (Casier, 1961), Pseudoleptolepis minor (Casier, 1961), Couches de la Loia, Yamangi Moke, Zaire.

Order Osmeriformes
OSMERIFORMES incertae sedis O. K. (CMP) FW
First: O juvenile otoliths from Beds B and E of the Tupelo Tongue of the Coffee Sand Formation, Chapelville, Mississippi, USA (Nolf and Dockery, 1990).

Suborder Argentinoidae (Begle, 1992)
Superfamily Argentinioidea
First: O juvenile otoliths from Beds B and E of the Tupelo Tongue of the Coffee Sand Formation, Chapelville, Mississippi, USA; O undetermined argentinid otoliths, Severn Formation (MAA), Maryland, USA (Huddleston and Savoie, 1983), and Argentina extenuata Stinton, 1966, London Clay Formation (YPR), SE England, UK; S Glossanodon (Proargentina)
Animals: Vertebrates

nebulosa (Danil'chenko, 1960), Dabaxanskaya Formation (LUT/BRT), Georgia, former USSR. Extant

**F. MICROSTOMATIDAE Gill, 1861**
**O T. (SRV)–Rec. Mar.**
**First:** O Nansenia sp. Nolf and Steurbaut, 1983, Tonen der Ziegelei Sunder, Twistringen, Bremen, Germany.

**Intervening:** O TOR–PIA.

**F. BATHYLAGIDAE Gill, 1884**
(including OPISTHOPROCTIDAE Roule, 1915)
**O T (PRB)–Rec. Mar.**
**First:** O Opisthoproctus weitzmani Nolf, 1988, Marnes de Brihande, Chalosse, France.

**Intervening:** MMI–UMI, 0 PLI.

**Superfamily ALEPOCEPHALOIDEA**

**F. ALEPOCEPHALIDAE Valenciennes, 1846**
**T. (CHT)–Rec. Mar.**
**First:** Carpathichthys polonicus Jerzmanska, 1979, Zone IPM 5, Menilite Beds, Korzeniec, Carpathians, Poland.

**Intervening:** 0 MMI, PLI.

**Suborder OSMEROIDEI**

**Weitzman, 1967**

**Superfamily OSMEROIDEA Regan, 1913**

**F. OSMERIDAE Regan, 1913**
(including PLECOGLOSSIDAE Bleeker, 1859)
**T. (THA)–Rec. Mar.**
**FW**
**First:** Speirsaenigma lindoei Wilson and Williams, 1991, Paskapoo Formation, Joffre Bridge, Alberta, Canada; 0 'Osmeridarum' tricrenulatus (Stinton, 1965), Thanet Formation, Pegwell Bay, Kent, England, UK. Extant

**Intervening:** S RUP–CHT, PLE; 0 LUT–RUP, LMI, PLI–PLE.

**Superfamily GALAXIOIDEA Bonaparte, 1832**

**F. LEPIDOGALAXIIDAE* Frankenberg, 1968**
**Extant**

**F. SALANGIDAE Bleeker, 1859**
(including SUNDASALANGIDAE Roberts, 1981)
**Extant**

**F. RETROPINNIDAE McCulloch, 1927**
**Extant**

**F. GALAXIIDAE Bonaparte, 1832**
**T. (?PLI)–Rec. Mar.**
**FW**
**First:** Galaxias brevipinnis Günther, 1866, Kaikorai Valley, Dunedin, New Zealand, and G. vulgaris Stokell, Foulden Hills, Middlemarch, New Zealand, both from diatomaceous shales of ‘Taranakian (Upper Miocene) to Waitotaran (Pliocene) age’ (McDowall, 1976). Extant

**Order SALMONIFORMES Bleeker, 1859**

**SALMONIFORMES incertae sedis**
**O T. (?DAN) FW**
**First:** O ‘Salmoniformorum’ rectangulus Rana, 1988, Inter-trappes between Deccan Trap Flows no. 4 and 5, Rangapur, Hyderabad, India. According to D. Nolf (pers. comm.) the allocation of these ooliths to Salmoniformes lacks real support.

**F. SALMONIDAE Rafinesque, 1815**
**T. (LUT)–Rec. Mar./FW**
**First:** Eosalmo driftwoodensis Wison, 1977, Driftwood Creek Beds, British Columbia. Helgolandichthys schmidt Taverne, 1981, from the Aptian Töck, Heligoland, was described as a salmonid sensu lato, and would be the first if correctly placed. Extant

**Intervening:** UMI–PLE.

**F. COREGNIDAE Gill, 1892**
**T. (PIA)–Rec. Mar.**
**FW**
**First:** Prosopium pridicus Smith, 1975, Glens Ferry Formation, Idaho, USA. Extant

**Intervening:** PLE.

**Subdivision NEOTELEOSTEI Nelson, 1969**

**Order STOMIIFORMES Regan, 1909**

**F. GONOSTOMATIDAE Gill, 1893**
**T. (RUP)–Rec. Mar.**
**First:** Valenciennellus sp. Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France; S Eoc. (m), Polyipnoides levis Danil’chenko, 1962, Dabaxanskaya Formation, Georgia, former USSR. Extant

**Intervening:** MMI–PLI.

**F. STERNOPTYCHIDAE Duméril, 1806**
**O T. (YPR)–Rec. Mar.**
**First:** O Valencennellus sp. Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France; S Eoc. (m), Vinciguerria distincta Danil’chenko, 1962, Dabaxanskaya Formation, Georgia, former USSR. Extant

**Intervening:** LUT–PLI.

**F. PHOTICHTHYIDAE Weitzman, 1974**
**O T. (YPR)–Rec. Mar.**
**First:** O Pelmeme dartagnan Nolf, 1988, ‘Photichthyidarum’ sp. Nolf, 1988, Argile de Gan, Gan, Pyrénéennes-Atlantiques, France; S Eoc. (m), Vinciguerria distincta Danil’chenko, 1962, Dabaxanskaya Formation, Georgia, former USSR. Extant

**Intervening:** LUT/BRT–PLI.

**F. STOMIIDAE Bleeker, 1859**
(including Astronesthidae Gill, 1882, Chauliodontidae Bleeker, 1859, Idiacanthidae Gill, 1892, Malacosteidae Gill, 1892, Melanostomiidae Parr, 1927, following Fink, 1985) **T. (LUT/BRT)–Rec. Mar.**
**First:** Astronesthes praevius Danil’chenko, 1962, Dabaxanskaya Formation, Georgia, former USSR. Extant

**Intervening:** UMI.
Section EURYPTERYGII Rosen, 1973

EURYPTERYGII incertae sedis

F. CHEIROTHRICIDAE Woodward, 1901

First: Exocoetoides minor Davis, 1887, _Telepholis tenuis_ (Davis, 1887), Hakel, Lebanon.

Last: _Telepholis acrocephalus_ von der Marck, 1868, _Cheirothrix guestphalicus_ (Schlüter, 1858), Baumberg, Westphalia, Germany.

*Intervening:* SAN.

Order ALEPISAURIFORMES Regan, 1911


First: Rharbichthys ferox Arambourg, 1954, Jebel Tsselfat, Morocco; Cinto Euganeo, Padova, Italy.

Rosen (1973) regarded all the genera making up the following three extinct suborders (including seven extinct families) as Alepisauriformes *incerta sedis*. They are listed here much as grouped by Goody (1969).

Suborder ICHTHYOTRINGOIDEI Goody, 1969

_F._ ICHTHYOTRINGIDAE Jordan, 1905 (including Apateopholidae Goody, 1969)

First: Apateodus glyphodus (Blake, 1863), Gault, SE England, UK.

Last: _Apateodus corneti_ (Forir, 1887), Lower Maestricht Chalk, The Netherlands.

*Intervening:* TUR–CMP.

F. CIMOLICHTHYIDAE Goody, 1969

First: _Cimolichthys levesiensis_ Leidy, 1857, _H. subglobosus_ Zone, Chalk, SE England, UK.

Last: _Cimolichthys manzadiniensis_ Dartevelle and Casier, 1949, Calcaire de Manzada, Zaire.

*Intervening:* TUR–CMP.

F. DERCETIDAE Pictet, 1850 (including Stratodontidae Cope, 1872)

First: _Benthesikyme_ sp. Taverne, 1981, Töck, Heligoland, based on a single fragmentary braincase; _Dercetis_ (Benthesikyme) is otherwise unknown before TUR. If the APT Töck specimen is not a dercetid, then the first would be K. (CEN), _Rhyrhodercetis_ spp. from Lebanon, Israel, Morocco and the former Yugoslavia, and _Dercetoides venator_ Chalifa, 1989 from Israel.

Last: _Stratodus apicalis_ Cope, 1872, MAA phosphates, Morocco and Israel.

*Intervening:* TUR–CMP.

F. PRIONOLEPIDIDAE Goody, 1969
K. (CEN–?SAN) Mar.

First: _Prionolepis cataphractus_ (Pictet and Humbert, 1866), Hakel and Hajula, Lebanon.

Last: _?Leptecodon rectus_ Williston, 1899, Smoky Hill Chalk Member, Niobrara Formation, Kansas.

*Intervening:* TUR.

Suborder ENCHODONTOIDEI Berg, 1937

F. ENCHODONTIDAE Lydekker, 1889
K. (CEN)–T. (DAN) Mar.?FW

First: _Enchodus_ spp., Lower Chalk, SE England, UK; Hakel and Hajula, Lebanon; Jebel Tsselfat, Morocco; Cinto Euganeo, Padova, Italy; Woodbine Formation, Texas, USA; _Parenchodus longiperygius_ Raab and Chalifa, 1987, Kefar Shaul Formation, Israel.

Last: _Enchodus_ spp., Montian Phosphates, Morocco; _Intertrappeans_, Gitti Khadan, Madhya Pradesh, India.

*Intervening:* TUR–MAA.

F. EURYPHOLIDAE Goody, 1969

First: _Eurypholis boissieri_ Pictet, 1850, Hakel and Hajula, Lebanon; _Saurorhamphus freyeri_ Heckel, 1850, Scisti di Comeno, Comeno, NW Italy (these beds are conventionally assigned to CEN, but may range up to SEN; Medizza and Sorbini, 1980).

Last: _Eurypholis japonicus_ Uyeno and Minakawa, 1983, Izumi Group, Matsuyama, Ehime, Japan. (_Saurorhamphus freyeri_ may be younger, above).

*Intervening:* TUR.

Suborder HALECOIDEI Goody, 1969

F. HALECIDA Agassiz, 1834


Last: _Halec eupterygius_ (Dixon, 1850), _M. coranguinum_ Zone, Chalk, SE England, UK.

*Intervening:* TUR, CON.

Suborder SYNODONTOIDEI Gill, 1872

SYNODONTOIDEI incertae sedis K. (CEN?)

*First and Last:* _Volcichthys dainellii_ D’Erasmo, 1946, Volci, Comeno, NW Italy (these beds may range in age from CEN to TUR or higher, see under Eurypholidae above).

F. PSEUDOTRICHONOTIDAE* Yoshino and Araga, 1975
_Extant_ Mar.

F. SYNODONTOIDEI Gill, 1872 (including Harpadontidae McCulloch, 1929)


*Intervening:* O YPR–PRB, Mio., PLI S. UMI–PLI.

F. GIGANTURIDAE Brauer, 1906
_Extant_ Mar.

Suborder ALEPISAUROIDEI Regan, 1911

F. PARALEPIDIDAE Gill, 1872
O

First: _O Lestidiops ypresiensis_ Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France; _S LUT, Holosteus_
Animals: Vertebrates

esocinus Agassiz, 1839, Monte Bolca, Verona, Italy. A 'Holosteus'-like fish is also recorded from the THA Fur Formation (Mo Clay) of NW Denmark (Bonde, 1987).

Intervening: LUT, RUP, UMI, PLI.

F. POLYMERICHTHYIDAE Uyeno, 1967


Extant

First and Last: Polymerichthys nagurai Uyeno, 1967, Tubozawa Formation, Aichi, Japan.

F. ANOTOPTERIDAE* Fowler, 1936 Extant Mar.

F. EVERMANNELLIDAE Fowler, 1901 Extant Mar.

Comment: The Pliocene otoliths from Nice, France, reported as Evermannella by Nolf (1985) do not belong here but to the zeiform Zenion (D. Nolf, pers. comm.).

F. OMOSUDIDAE* Regan, 1911 Extant Mar.

F. ALEPISAURIDAE* Bonaparte, 1832 (T. (MMI))–Rec. Mar.

First: Alepisaurus paraonai D’Erasmo, 1924, Rosignano, Piemonte, Italy. Extant

Order AULOPIFORMES Rosen, 1973


First: Nematonotus bottae (Pictet and Humbert, 1866), Lebanon; Nematonotus longispinus Hay, 1903, Lebanon; N. ponticus (Hay, 1903), Hakel and Hajula, Lebanon. If Sardinioides is not a neoscopelid, the only fossil is an undescribed CHT otolith from Aquitaine, France (D. Nolf, pers. comm.). Extant

Intervening: TUR–CMP, O CHT.

Sept ACANTHOMORPHA Rosen, 1973

ACANTHOMORPHA incertae sedis

F. ASINEOPIDAE Cope, 1884 K. (CMP)–T. (LUT) FW

First: Nardoichthys francisci Sorbini and Bannikov, 1991, Calcare di Mellissano, Nardo, Italy; this genus is described as a percoid, but in my view is most similar to Asineops. Last: Asineops squamifrons Cope, 1870, Green River Formation, Wyoming, USA.

Intervening: THA, YPR.


First and Last: Pharmacichthys spp., Hakel, Lebanon, and Ramallah, Israel (Gayet, 1980a).

The following two nominal extinct families are conventionally placed in the Perciformes, either in the suborder Scombroidei (e.g. Danil’chenko, 1964; Blot, 1980) or the suborder Xiphioidei (e.g. Fierstine and Applegate, 1974). Johnson (1986) has shown that xiphioids (billfishes) are a subgroup of Scombridae, and has characterized Scombroidei and Scombridae by a number of apomorphies, none of which is yet demonstrated in bluchiids or palaeorhynchids. Palaeorhynchids may be scombroids; bluchiids are almost certainly unrelated to them.


First: Cylindracanthus libanicus (Woodward, 1942), Hajula, Lebanon; C. creticus (Dixon, 1850), zone of Holaster subglobosus, Chalk, Sussex, England, UK. Last: Cylindracanthus rectus (Agassiz, 1844), Barton Clays, Barton Formation, southern England, UK.

Intervening: CMP–LUT.


First: Enniskillenus radiatus Casier, 1966, London Clay Formation, Sheppey, Kent, England, UK. There may be a palaeorhynchid in the THA Fur Formation (Mo Clay) of NW Denmark (Bonde, 1987).

Last: Pseudotetrapturus luteus Danil’chenko, 1960, Abadzekhski Horizon, Maikop Series, Caucasus, former USSR.
Intervening: LUT–RUP.

Order POLYMIXIIFORMES Patterson, 1964

F. AIPICHTHYIDAE Patterson, 1964 (including Aipichthyoideae Gayet, 1980)


First and Last: Aipichthys spp., Hakel and Hajula,

Lebanon; Lower Chalk, Sussex, England, UK; Aipichthyoideae spp., Ramallah, Israel (Gayet, 1980a,b).

F. POLYMIXIIIDAEPoey, 1868 (including Berycopsidae Regan, 1911, Dalmatichthyidae Radovic, 1975, Omosomopsidae Gaudant, 1978)

Animals: Vertebrates


Intervening: TUR, SAN-CMP, O MAA, THA, PRB, Mio.

Superorder PARACANTHOPTERYGII Greenwood et al., 1966

Order PERCOPSIFORMES Berg, 1937

PERCOPSIFORMES *incertae sedis* T. (THA) FW


F. PERCOPSIDAE* Agassiz, 1846

First: *Amphiplaga brachyptera* Cope, 1877, Fossil Butte Member, Green River Formation, Wyoming, USA. Extant

Intervening: LUT.

F. APHREDODERIDAE* Bonaparte, 1832

First: *Trichophanes hians* Cope, 1872, Osino Shales, Osino, Nevada, USA (Cavender, 1986). Extant

Intervening: ?CHT.

F. AMBLYOPSIDAE Bonaparte, 1832 Extant FW

ANACANTHINI Müller, 1846

ANACANTHINI *incertae sedis*


First and Last: *Sphenocephalus fiscicauus* Agassiz, 1839, Baumberg, Westphalia, Germany.

F. MCCONICHTHYIDAE Grande, 1988 T. (DAN) FW

First and Last: *Macconnichthys longipinnis* Grande, 1988, Tullock Formation, McCon County, Montana, USA.

Order OPHIDIIFORMES Berg, 1937

OPHIDIIFORMES *incertae sedis* T. (YP) Mar.

First: *Eolamprogrammus senectus* Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR.

F. OPHIDIIDAE Rafinesque, 1810


First: O ‘Sireminor’om* bavaricus* (Koken, 1891), Senonian, Siegsofdorf, Bavaria, Germany; S Amphistus toliapicus König, 1825, London Clay Formation, SE England, UK. Extant

Intervening: O DAN/THA–PLE; S ?LUT, RUP–MMI.

F. CARAPIDAE Jordan and Fowler, 1902 (including Pyramodontidae Smith, 1955)

First: *Onuxodon kiriakoffi* Nolf, 1980, Argile de Gan, Gan, Pyrénées-Atlantiques, France. Extant

Intervening: O LUT–PLI.

F. BYTHITIDAE Gill, 1861


First: O ‘Dinematichthynorum’ crepidatus* (Voigt, 1926), erratic boulder, Cőthen, Anhalt, Germany. Extant

Intervening: O THA–PLI.

F. APHYONIDAE Jordan and Evermann, 1898 Extant Mar.

Order BATRACHOIDIFORMES Goodrich, 1909

F. BATRACHOIDIDAE Jordan and Evermann, 1898


First: O ‘Batrachoidarid’um* trapezoidalis* Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France; S *Batrachoides didactylus* Bloch and Schneider, 1801, MES, Oran, Algeria. Extant

Intervening: O RUP/CHT–PLI.

Order LOPHIIFORMES Garman, 1899

F. LOPHIIDAE Rafinesque, 1810

First: *Lophius* brachysomus Agassiz, 1835, Monte Bolca, Verona, Italy (Blot, 1980). Extant

Intervening: BRT–PLI.

F. ANTENNARIIDAE Gill, 1863

First: *Batrachoididarum* trapezoidalis* (Stinton, 1966), London Clay Formation, Sheppey, Kent, England, UK; Argile de Gan, Gan, Pyrénées-Atlantiques, France. Extant

Intervening: O LUT–PRB.

F. LOPHICHTHYIDAE* Boeseman, 1964 Extant Mar.

F. BRACHIONICHTHYIDAE* Gill, 1893

First: *Histionotophorus bassanii* (de Zigno, 1887), Monte Bolca, Verona, Italy. Extant


Intervening: O PRB, UMI.

F. OGCOCEPHALIDAE Gill, 1893

First: *Ogcocephalus cirrhosus* Stinton, 1978, Selsey Formation, Selsey, Sussex, England, UK; S an undescribed genus from Monte Bolca, Verona, Italy, is mentioned by Blot (1980). Extant

Intervening: O PRB, Mio.

FF. CAULOPHRYNIDAE Regan, 1912, CERATIIDAE Gill, 1864, GIGANTACTINIDAE Boulenger, 1904, NEOCERATIIDAE* Regan, 1926 Extant Mar.

F. LINOPHRYNIDAE Regan, 1926

First: *Acentrophryne longidens* Regan, 1926, Puente Formation, Hacienda Heights, Los Angeles County, California, USA. Extant
Osteichthyes: Teleostei


Order GADIFORMES Goodrich, 1909 (Cohen, 1989)

F. MURAENOLEPIDIDAE* Regan, 1903 Extant Mar.


First: O Melanonus ellesmerensis Schwarzhans, 1985, Eureka Sound Formation, Ellesmere Island, NWT, Canada. Extant Intervening: 0 RUP—PLI.


First: O Tripterophycis immutatus Schwarzhans, 1980, Kaiatan, McCullough’s Bridge, Canterbury, New Zealand; Aldingian, South Australia; T. elongatusimus Schwarzhans, 1985, Aldingian, South Australia. Eophycis, a genus known by skeletons in the RUP of Poland, and which is probably a morid, may also occur in the THA Fur Formation of NW Jutland, Denmark (Bonde, 1987, p. 36). Extant Intervening: O RUP—PLI.

Suborder MACROUROIDEI Garman, 1899 MACROUROIDEI incertae sedis O T. (PRB)

First: O Bathygadus mauli Nolf, 1988, Couches de Cauneille, Chalosse, France. Extant FW


First: O Nezumia lindsayi Schwarzhans, 1985, Dartmoor Formation, Mt. Gambier, South Australia. Extant Intervening: O UMI—PLI.


First: Rhinopephalus sp., Fur Formation (Mo Clay), NW Jutland, Denmark. Extant Intervening: YPR—PLI.


First: O Physic praecongatus Schwarzhans, 1977, Hückelhoven, Nordrhein-Westphalen, Germany. Extant Intervening: O CHT—PLI.


First: O Raniceps hermani Nolf, 1978, Formation de Heers, Orp-le-Grand, Marte, Belgium; S Onobromus sagus (Fedotov, 1974), CHT, Voskovogorskii Horizon, northern Caucasus, former USSR. Extant Intervening: O RUP—UMI.

F. LOTIDAE Bonaparte, 1838 T. (RUP)—Rec. Mar./FW


First: O ‘Parvicollolus’ minutulus (Gaemers, 1978), Berg Sand, Nucula Clay, Belgium, Ratum Formation, The Netherlands; Gadicus altus (Gaemers and van Hinsbergh, 1978), Brinkherune Formation, The Netherlands, Boom Clay, Belgium; S first in UMI. Extant Intervening: CHT—PLE.

Superorder ACANTHOPTERYGII Gouan, 1770

ACANTHOPTERYGII incertae sedis ??J. (BTH)

First: O ‘Acanthopterygiorum’ circularis (Stinton, 1968) and ‘Acanthopterygiorum’ dorsetensis (Stinton, 1968), otoliths from the Bradford Clay, Bradford on Avon, Wiltshire, and Fuller’s Earth Clay, Langton Herring, Dorset, UK. Originally assigned (without good reason) to pycnodonts, these otoliths are listed by Nolf (1985) under the heading given here. If they are acanthopterygian, they precede the earliest skeletal record of the group by some 60 Ma.

Series AETHERINOMORPHA Greenwood et al., 1966 (Rosen and Parenti, 1981)

Order AETHERINIFORMES Rosen, 1964

F. AETHERINIDAE Risso, 1826 O T. (YPR)—Rec. Mar./FW


F. BEDOTIIDAE Jordan and Hubbs, 1919 Extant FW
Animals: Vertebrates

F. MELANOTAENIIDAE Weber and de Beaufort, 1922  Extant  FW
F. PHALLOSTETHIDAE Regan, 1916 (including NEOSTETHIDAE Aurich, 1937)  Extant  Mar./FW
F. DENTATHERINIDAE* Patten and Ivantsoff, 1983  Extant  Mar.
F. PHALLOSTETHIDAE Regan, 1916 (including NEOSTETHIDAE Aurich, 1937)  Extant  Mar./FW


CYPRINODONTIFORMES incertae sedis

First: Cyprinodon ?primulus Cockerell, 1936 was based on isolated scales from the THA Maiz Gordo Formation, NW Argentina; Cockerell stated that the scales might be poeciliid. "Cyprinodontoideorum" ornatissimus Noif, 1988, YPR (Argile de Gan, Gan, Pyrenees-Atlantiques, France), is probably a percoid (Mene) rather than cyprinodontiform (D. Noif, pers. comm.).

Suborder APLOCHEILOIDEI Parenti, 1981
F. APLOCHEILIDAE Bleeker, 1859  Extant  FW
F. RIVULIDAE Myers, 1925  Extant  FW

Suborder CYPRINODONTOIDEI Jordan, 1923
F. PROFUNDULIDAE* Hoedeman and Bronner, 1951  Extant  FW
First: Fundulus lariversi Lugaski, 1977, Siebert Tuff, Nevada, USA. Extant
Intervening: UMI - PLE.

F. VALENCIIDAE* Parenti, 1981  Extant  FW
F. ANABLEPIDAE Bonaparte, 1837 (including JENYNSIIDAE Garman, 1895)  Extant  FW/Mar.
F. POECILIIDAE Bonaparte, 1837  T. (THA)-Rec.  FW
First: Cyprinodon ?primulus Cockerell, 1936 was based on isolated scales from the THA Maiz Gordo Formation, Santa Barbara, Jujuy, Argentina, is here treated as Cyprinodontiformes incertae sedis. Extant
Intervening: CHT - MES.

Order BELONIFORMES Berg, 1937

Suborder ADRIANICHTHYOIDEI Rosen and Parenti, 1981
First: ?Lithopoecilus brouweri de Beaufort, 1934, Gimpoe Basin, central Sulawesi. Age unknown, but presumably Neogene, and said by de Beaufort to be intermediate between Orzyas and adrianichthyids. Extant

Suborder EXOCOETOIDEI Regan, 1911
Intervening: BRT - PLI.

First: Rhamphexocoetus volans Bannikov et al., 1985, Monte Bolca, Verona, Italy. Extant
First: Scomberesox lacatæ Sauvage, 1880, Licata, Sicily, and Oran, Algeria; S. edwardsi Jordan and Gilbert, 1919, California, USA. Extant
F. BELONIDAE Bonaparte, 1837  T. (LUT/RUP)-Rec.  Mar./FW
First: ?Xiphopterus falcatus (Volta, 1796), Monte Bolca, Verona, Italy, may be a belonid (Blot, 1980); if not, the first records are RUP, Belone harmati Weiler, 1933, Eger, Hungary, B. menelitica Pauca, 1938, Tarleti, Romania. Extant
Intervening: CHT - PLI.

Series PERCOMORPHA Rosen, 1973

Order BERYCIFORMES Regan, 1909
BERYCIFORMES incertae sedis (including Digoriidae Bannikov and Danil'chenko, 1985, Dinopterygiidae Jordan, 1923, Pycnosteroideidae Patterson, 1964)
First: Pycnosteroideus levispinosus (Hay, 1903), Hajula, Lebanon. Extant

Suborder TRACHICHTHYOIDEI Moore, 1990
TRACHICHTHYOIDEI incertae sedis
(including Hoplopterygiidae Jordan, 1923, Lissoberycidae Gayet, 1980) K. (CEN)

First: Several genera, Hakel and Hajula, Lebanon, Ramallah, Israel, Lower Chalk, SE England, UK; O otoliths assigned to Trachichthyidae are recorded from CMP and MAA of USA, but they are treated here as trachichthyoids.

**Superfamily TRACHICHTHYOIDEA Parr, 1933**

F. TRACHICHTHYIDAE Bleeker, 1859


First: Several genera, Hakel and Hajula, Lebanon, Ramallah, Israel, Lower Chalk, SE England, UK; O otoliths assigned to Trachichthyidae are recorded from CMP and MAA of USA, but they are treated here as trachichthyoids.

**Intervening:** O LUT–PLI.

F. MONOCENTRIDIDAE Bleeker, 1859


First: Several genera, Hakel and Hajula, Lebanon, Ramallah, Israel, Lower Chalk, SE England, UK; O otoliths assigned to Trachichthyidae are recorded from CMP and MAA of USA, but they are treated here as trachichthyoids.

**Extant**

Intervening: O PRB–CHT.

F. ANOMALOPIDAE Gill, 1885


First: Several genera, Hakel and Hajula, Lebanon, Ramallah, Israel, Lower Chalk, SE England, UK; O otoliths assigned to Trachichthyidae are recorded from CMP and MAA of USA, but they are treated here as trachichthyoids.

**Extant**


F. DIRETMIDAE* Goode and Bean, 1896


First: Several genera, Hakel and Hajula, Lebanon, Ramallah, Israel, Lower Chalk, SE England, UK; O otoliths assigned to Trachichthyidae are recorded from CMP and MAA of USA, but they are treated here as trachichthyoids.

**Extant**

Intervening: O UMI, O RUP, UMI, PLI.

F. RONDELETIIDAE* Goode and Bean, 1892, BARBOURIsIIDAE* Parr, 1945, CETOMIMIDAE* Goode and Bean, 1892, HISPIDOBERYCIDAe* Kotlyar, 1956, EUTAENIONIIDAE* Bertelsen and Marshall, 1958, MEGALOMYCTERIDAE* Myers and Freihofer, 1966

**Extant**

Suborder BERYCOIDEI Regan, 1909

F. BERYCIDAe Gill, 1862


First: Several genera, Hakel and Hajula, Lebanon, Ramallah, Israel, Lower Chalk, SE England, UK; O otoliths assigned to Trachichthyidae are recorded from CMP and MAA of USA, but they are treated here as trachichthyoids.

**Extant**

Intervening: O THA–Oli.

Suborder HOLOCENTROIDEI new

HOLOCENTROIDEI incertae sedis (including Caproberyidae Patterson, 1967, Alloberycidae Gayet, 1982, Stichocentridae Gayet, 1982) K. (CEN)

(see Fig. 36.4)


F. HOLOCENTRIDAe Richardson, 1846


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.

F. MYRIPRISTIDAE Nelson, 1955


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.

Order LAMPRIDIFORMES Regan, 1909

LAMPRIDIFORMES incertae sedis

T. (LUT) Mar. (see Fig. 36.4)


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.

F. LOPHOTIDAE* Goode and Bean, 1859


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.

F. ATELEOPODIDAE Kaup, 1858


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.

F. LOPOGONIDAE* Goode and Bean, 1859


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.

F. VELIFERIDAE* Goode and Bean, 1859


**Extant**

Intervening: O LUT, MMI–PLI., S PLI.
### Order ZEIFORMES Regan, 1909

**F. PARAZENIDAE** Greenwood et al., 1966  
**Extant**  
**Mar.**

**F. MACRUROCYTIIDAE** Myers, 1960  
**Extant**  
**Mar.**

**F. ZENIONTIDAE** Myers, 1960  
**Extant**  
**T. (ZAN)–Rec.**  
**Mar.**

**F. ZEIDAE** Bonaparte, 1831  
**Extant**  
**T. (THA)–Rec.**  
**Mar.**

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**First:**  
**O Zenion hololepis** Goode and Bean, 1896, Zandian, SE France.  
**Extant**

**Intervening:**  
**O**  
**PLI.**

**Order ZEIFORMES Regan, 1909**

**F. PARAZENIDAE** Greenwood et al., 1966  
**Extant**  
**Mar.**

**F. MACRUROCYTIIDAE** Myers, 1960  
**Extant**  
**Mar.**

**F. ZENIONTIDAE** Myers, 1960  
**Extant**  
**T. (ZAN)–Rec.**  
**Mar.**

**F. ZEIDAE** Bonaparte, 1831  
**Extant**  
**T. (THA)–Rec.**  
**Mar.**

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**First:**  
**Undescribed ?zeid, Fur Formation (Mo Clay), NW Jutland, Denmark.**  
**Palaeocyttus princeps** Gaudant, 1978, K. (CEN), Laveiras, Portugal, was described as a zeid, but differs substantially from other members of the family; it may be a zeiform *incertae sedis.*  
**Extant**  
**Intervening:**  
**Oli., UMI.**

**F. OREOSOMATIDAE** Bleeker, 1859  
**Extant**  
**Mar.**

**F. GRAMMICOLEPIDIDAE** Poey, 1873  
**Extant**  
**Mar.**

**F. CAPROIDAE** Lowe, 1844  
**T. (YPR)–Rec.**  
**Mar.**

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**First:**  
**Antigonia sp.** Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France;  
**S Antigonia veronensis** Sorbini, 1983, Monte Bolca (LUT), Verona, Italy.  
**Microrops libanicus** Gayet, 1980, K. (CEN), Hajula, Lebanon, was described as a caproid, but no features relating it to this
group are cited. An undescribed THA ‘Antigonia’ from the Fur Formation, Denmark, is illustrated by Bonde and Christensen (1991).

**Intervening:** Oli., Mio.

**Order** GASTEROSTEIFORMES Goodrich, 1909

(Pietsch, 1978)

GASTEROSTEIFORMES incertae sedis


**First:** Gasterorhamphus zuppichinii Sorbini, 1981, Calcare di Mellissano, Nardo, Italy.

**Suborder** GASTEROSTEOIDEI Goodrich, 1909

F. HYPOPTYCHIDAE* Jordan, 1923 Extant Mar.

F. AULORHYNCHIDAE Gill, 1861 (? including Protosyngnathidae Boullenger, 1902) ?T. (Eoc.)–Rec. Mar./FW

**First:** Protosyngnathus sumatrensis von der Marck, 1876, Padang, Sumatra. The Eocene age of the fish shales at Padang is still dubious. If Protosyngnathus is not an aulorhynchid, the family has no fossil record, since Protaulopsis bolcensis Woodward, 1901, from Monte Boica, Verona, Italy (LUT) - the only other fossil assigned to the family – belongs elsewhere according to Blot (1980).

**Extant**

F. GASTEROSTEIDAE Bonaparte, 1832

T. (UMI)–Rec. Mar./FW

**First:** Gasterosteus aculeatus Linne, 1758, Monterey Formation, Lompoc, California, USA; Pungitius hexacanthus (Schtylko, 1934), Pavlodarskaya Formation, western Siberia, former USSR.

**Intervening:** PLI, PLE.

**Superfamily** PEGASOIDEA Bonaparte, 1832

F. INDOSTOMATIDAE* Prasad and Mukerji, 1929 Extant FW

F. PEGASIDAE* Bonaparte, 1832 Extant Mar.


**First:** Ramphosus rosenkrantzi Nielsen, 1960, Fur Formation (Mo Clay), NW Jutland, Denmark.

**Last:** R. spp. (Blot, 1980), Monte Bolca, Verona, Italy.

**Superfamily** SYNGNATHOIDEA Regan, 1909

F. SOLENOSTOMATIDAE Pegasoidea Bonaparte, 1832

**Extant**

**Intervening:** RUP–PLI.

**Superfamily** MACRORHAMPHOSOIDEA Bleeker, 1859

**F.** MACRORHAMPHOSIDAE Bleeker, 1859

**Extant** Mar.

Two monotypic fossil genera, Gasterorhamphus, K. (CMP), Calcare di Mellissano, Nardo, Italy, and Protorhamphus, T. (YPR), Danatinsk Formation, Turkmenia, former USSR, have been placed in this family, but they are here treated as Gasterosteiformes incertae sedis.


**First:** Three genera (Blot, 1980), Monte Bolca, Verona, Italy. Extant

**Intervening:** RUP–LMI, PLI.

**Superfamily** AULOSTOMOIDEA Regan, 1909


**First:** Urosphenopsis sagitta Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR.

**Last:** Urosphen dubia (de Blainville, 1818), Monte Bolca, Verona, Italy.


**First:** Four genera (Blot, 1980), Monte Bolca, Verona, Italy.

**Intervening:** RUP.


**First:** Fistularioides veronensis Blot, 1980, F. phyllolepis Blot, 1980, Parasynarcualis longirostris (de Blainville, 1818), ?Aulostomoides tyleri Blot, 1980, Monte Bolca, Verona, Italy.

**Extant**

**Intervening:** RUP, UMI.

**Order** DACTYLOPTERIFORMES Regan, 1914


**First and Last:** Pterygocephalus paradoxus Agassiz, 1839, Monte Bolca, Verona, Italy. This fish may be related to dactylopterids (Blot, 1984b).

**F.** DACTYLOPTERIDAE Gill, 1885 (= Cephalacanthidae Lacepede, 1802) T. (PRB)–Rec. Mar.

**First:** Prevoltans faedensis Gayet and Barbin, 1985, PRB, River Faedo, northern Italy.

**Extant**

**Intervening:** PLI.

**Order** SCORPAENIFORMES Garman, 1899

**Suborder** SCORPAENOIDEI Garman, 1899

**SCORPAENOIDEI** incertae sedis O T. (YPR) Mar.

**First:** O ‘Scorpaenoides prominens’ (Stinton, 1978), London Clay Formation, southern England, UK.
F. SCORPAENIDAE Risso, 1826

First: O 'Scorpaenidarum' acutus (Frost, 1934), London Clay Formation, southern England, UK. No scorpaenid skeletons are reported earlier than MMI, apart from an isolated LUT opercular from the Subathu Formation, Jammu and Kashmir, referred to Scorpaena by Khare (1976).

Intervening: O BRT—PLE.

First: Eosynanceja brabantica Casier, 1966, Argile des Flandres, Quenast, Brabant, Belgium; known only by a premaxilla, a quadrate, and a few vertebrae. No other fossils recorded. Extant

F. CARACANTHIDAE* Gill, 1889, APLOACTINIDAE Regan, 1913, PATAECIDAE Gill, 1872, CONGIPODIDAE Gill, 1889 Extant Mar.

First: Lepidotrigla' cadenati Steurbaut, 1984, Couches de Cauneille (PRB), Cauneille, Chalosse, France; 'Triglidarum' cor (Koken, 1888), Jacksonian, Jackson, Mississippi, USA. Earliest skeletal remains RUP. Extant Intervening: RUP—PLE.

Suborder PLATYCEPHALOIDEI Greenwood et al., 1966
F. PLATYCEPHALIDAE Bleeker, 1859
First: Platyccephalus janeti (Priem, 1911), Argile de Gan, Gan, Pyrénées-Atlantiques, France. Extant

Intervening: O LUT—MMI.

F. HOPLICHTHYIDAE* Gill, 1889

Intervening: O BRT, MMI, PLI.

Suborder ANOPLOPOMATOIDEI Nelson, 1984
F. ANOPLOPOMATIDAE Gill, 1863 Extant Mar.

Suborder HEXAGRAMMOIDEI Greenwood et al., 1966
F. HEXAGRAMMIDAE Gill, 1889
First: Achrestogrammus achrestus (Jordan and Gilbert, 1919), Monterey Formation, Lompoc, California, USA. Placed in this family with a query by David (1946). Extant

Intervening: O PLE.

F. ZANIOLEPIDIDAE* Jordan, 1923
First: Zaniolepis latipinnis Girard, 1857, Palos Verdes Sand, Playa del Rey, Los Angeles, California, USA.

Suborder COTTOIDEI Bleeker, 1859
F. NORMANICHTHYIDAE* Clark, 1937 Extant Mar.

F. COTTIDAE Bonaparte, 1832 (including Icelidae Jordan, 1923) T. (?LUT/RUP)—Rec. Mar./FW
First: ?Eocottus veronensis (Volta, 1796), Monte Bolca, Verona, Italy. This form is conventionally placed in the Cottidae (e.g. Woodward, 1901; Blot, 1980), but needs revision. Regan (1913) thought that it was a goby, and J. R. Norman (MS) placed it in the Electrotridae, where it was placed in the first edition of this compilation (Patterson, 1967). If Eocottus is not a cidd, the first record is Cottus cervicornis Storms, 1894, Argile de Boom, etc. (RUP), Belgium. Extant


Intervening: O RUP, UMI, PLI.

F. CYCLOPTERIDAE Bonaparte, 1832
First: Liparis minusculus Nolf, 1977, Argile de Boom, Kruikebeke, Belgium. Extant

Intervening: O PLE.


Order PERCIFORMES Bleeker, 1859
PERCIFORMES incertae sedis
O K. (CON) Mar.

Suborder PERCOIDEI Bleeker, 1859
The percoids include the major remaining problems in teleost systematics. Johnson (1984) reviewed the Recent percoids from a phylogenetic viewpoint, and estimated that there are 80 families (26 of them monotypic) and 12 incertae sedis genera. Johnson’s arrangement is followed here, listing the incertae sedis genera as if they were families, adjacent to the families in which they are conventionally placed.

PERCOIDEI incertae sedis
O K (CMP), S T (DAN)
First: Perciformorum transitus (Sieber and Weinfurter, 1967), Tiefe Gosau, Ennstaler Alpen, Austria (CON); 'Perciformorum' cepoloides Nolf and Dockery, 1990, Tupelo Tongue of Coffee Sand Formation, Lee County, Mississippi, USA (CMP).
County, Mississippi, USA; S. Proserranus lundensis (Davis, 1890), Danian, Limhamn, southern Sweden; Eoserranus hislopi Woodward, 1890), Danian, Limhamn, southern Sweden; Eoserranus hislopi Woodward, 1890, Lameta Formation (? DAN), Dongargaon, Madhya Pradesh, India. On Platacodon (K (MMA)) see below under Sciaenidae.

F. CENTROPOMIDAE Poey, 1868
T. (YPR)–Rec. Mar./FW

Intervening: PRB, CHT—PLI.

F. PERCICHTHYIDAE Jordan and Eigenmann, 1890
(sensu Johnson, 1984, including GADOPSIDAE
Günther, 1862, Maccullochellidae
McCulloch, 1929, Macquaridiidae Munro, 1961, Pectorinidae Jordan, 1923, Plectroplitidae Munro, 1961) T. (THA)–Rec. FW
First: P. lonquimayensis Chang and Arratia, 1978, P. sandovali Arratia, 1982, Lonquimay Mountains, Chile; Properca angusta (Agassiz, 1834), Menat, Puy-de-Dome, France.

Intervening: YPR—PLI.

F. MORONIDAE Fowler, 1907
First: O Morone eschmeyeri Nolf and Lapierre, 1979, Calcaire Grossier, Paris Basin, France; S Palaeoperca proxima Micklich, 1985, Messel Formation (LUT), Darmstadt, Germany, described as a percichthyid, was referred to Moronidae by Gaudant (1988); otherwise Morone vogdtii (Bogatshov, 1942), LMI, Taman, former USSR.

Intervening: PRB, LMI—PLI.

Genus Hapalogenys Richardson, 1844, Hemilutjanus Bleeker, 1876, Howella Ogilby, 1899 Extant Mar.

Genus Lateolabrax Bleeker, 1857
7T. (AQ)–Rec. FW
First: ?Avitolabrax denticulatus Takai, 1942, Siramizu Formation, Joban Coalfield, Hukusima, Japan, said to be ‘ancestral’ to Lateolabrax.

Extant

Genus Polyprion Oken, 1817 Extant Mar.

Genus Siniperca Gill, 1862 T. (MMI)–Rec. FW

Extant

Intervening: PLI.

Genus Stereolepis Ayres, 1859 Extant Mar.

F. ACROPOMATIDAE Gill, 1891
First: O Acropoma antiqua Schwarzhans, 1985, Dartmoor Formation, Mt. Gambier, South Australia; S A. lepidotus (Agassiz, 1833), LUT, Monte Bolca, Verona, Italy.

Extant

Intervening: O YPR—PLE.

F. AMBASSIDAE Boulenger, 1904 (= Chandidae)
O T. (DAN/THA)–Rec. Mar./FW

Extant

Intervening: YPR—MMI.

F. SERRANIDAE Swainson, 1839 (including GRAMMISTIDAE Gill, 1892,
Pseudogrammatidae Greenwood et al., 1966)
T. (THA)–Rec. Mar./FW
First: O Tretoperca vestita Svitchevskaya, 1986, Cherkassy, Ukraine, former USSR; O 'Serranidarum' serranoides (Stinton, 1965), Woolwich and Reading Formation, SE England, UK.

Extant

Intervening: YPR—MMI.


F. OSTRACOBERYCIDAE* Fowler, 1934
First: O Ostracoberyx pattersoni Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France.

Extant


F. CENTROGENYSIDAE* Weber and de Beaufort, 1931 Extant Mar.

F. DINOPECIDAE Heemstra and Hecht, 1986 Extant Mar.

Genus Symphysanodon Bleeker, 1878 Extant Mar.

F. PSEUDOCHROMIDAE Müller and Troeschel, 1849 (including Anisochromidae Smith, 1954,
Congrogadidae Gill, 1861, Pseudoplesiopidae Bleeker, 1875

Extant


F. PLESIOPIDAE Günther, 1861 (including ACANTHOCLINIDAE Günther, 1861)
Extant Mar.

F. BANJOSIDAE* Jordan, 1923 Extant Mar.

F. ELASSOMIDAE* Jordan and Gilbert, 1882 Extant FW

F. CENTRARCHIDAE Bleeker, 1859
T. (Eoc.)–Rec. FW
First: Undescribed centrarchids, NW Montana, USA (Cavender, 1986).

Extant

Intervening: RUP, LMI—PLE.

F. PERCIDAE Cuvier, 1817
O T. (RUP)–Rec. FW
First: O Perca hassiaca Weiler, 1961, Melanienton, Hesse, Germany; S not recorded before UMI.

Extant

Intervening: O LMI; S PLI, PLE.

F. PRIACANTHIDAE Gill, 1872
de Gan, Gan, Pyrénées-Atlantiques, France; S Pristigeryn substratiuss (de Blainville, 1818), Monte Bolca, Verona, Italy (LUT).

**Intervening:** LUT, RUP–UMI.

**F. APOGONIDAE** Jordan and Gilbert, 1882

- **O K. (CON)–Rec. Mar.**
- **First:** O 'Apogonidarium' weinbergeri Sieber and Weinfurter, 1967, Tiefe Gosau, Ennstaler Alpen, Austria (CON); Apogonidae (Nolf and Dockery, 1990), Tupelo Tongue of Coffee Sand Formation, Lee County, Mississippi, USA (CMP); S Apogon spinosus Agassiz, 1836, Monte Bolca, Verona, Italy (LUT).

**Intervening:** O MAA–PLI.

**F. EPIGONIDAE** Fraser, 1972

- **O T. (YPR)–Rec. Mar.**

**Intervening:** O LMI, UMI, PLI.

**F. DINOLESTIDAE** Whitley, 1948

- **Extant** Mar.
- **F. SILLAGINIDAE** Richardson, 1846

- **O T. (LUT)–Rec. Mar.**
- **First:** O Sillago sp. Schwarzhans, 1980, Bartonian, Waihao River, Canterbury, New Zealand (two eroded juvenile specimens); the next records are RUP, Sillago hassouvis (Koken, 1891), Meeressande, Waldbockelheim, Mainz County, Germany, and S. lamberti (Priem, 1906), Sables d’Ormoy, Ormoy, Paris Basin, France.

**Intervening:** O LMI, MMI, PLI.

**F. MALACANTHIDAE** Günther, 1861 (including Branchiostegidae Jordan, 1923)

- **O T. (RUP)–Rec. Mar.**
- **First:** O 'Malacanthidarum' cadenati Steurbaut, 1984, Sables d’Yrieu, St-Martin-de-Seignanx, Landes, France. These otoliths were originally described as 'aff. Lepidotrigla'; according to D. Nolf (pers. comm.) a number of other O records of supposed triglids are malacanthids. S Mio. (m), Lopholatilus sp., Calvert Formation, Maryland and Virginia, USA.

**Intervening:** O CHT–MMI, S MMI, MES.

**F. LACTARIIDAE** Jordan, 1923

- **O T. (YPR)–Rec. Mar.**
- **First:** O Lactarius sp. Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France.

**Intervening:** O LUT, CHT–LMI.

**F. MENIDAE** Gill, 1885

- **T. (DAN)–Rec. Mar.**
- **First:** Mene phosphaticus Astre, 1927, Montian, Tunis.

**Intervening:** THA–RUP.

**F. LEIOGNATHIDAE** Jordan, 1923

- **O T. (LUT)–Rec. Mar.**

**Intervening:** O RUP–CHT.

**F. BRAMIDAE** Lowe, 1836

- **T. (?YPR/PLI)–Rec. Mar.**
- **First:** Bramoides brieni Casier, 1966 and Goniochrion arambourgi Casier, 1966, London Clay Formation, SE England, UK, were both assigned to Bramidae by Casier, but the attribution is not well supported. Brama sp. Sorbini, 1988, PLI, Marecchia River, NE Italy, is the only other record of the family.

**Extant**

**F. CARISTIIDAE** Gill and Smith, 1905 (including Exelliidae Blot, 1969, = Semiophoridae Jordan, 1923)

- **T. (THA)–Rec. Mar.**
- **First:** Exelia sp., Fur Formation (Mo Clay), NW Denmark (Bonde, 1987). Blot (1969) placed his Exelliidae closest to Caristiidae.

**Extant**

**F. YPR, LUT, UMI.**

**F. EMMELICHTHYIDAE** Jordan and Evermann, 1898

- **O T. (LUT)–Rec. Mar.**
- **First:** O Emmelichthys sp. Nolf and Lapierre, 1977, Sables du Bois-Gouet, Loire-Atlantique, France.

**Extant**

**F. LUTJANIDAE** Gill, 1884

- **O T. (LUT)–Rec. Mar.**
- **First:** O Apsilus latus Stinton, 1980, Selsey Formation, southern England, UK; S Hyposcelus atlanticus Swift and Ellwood, 1972, Crystal River Formation (PRB), Jackson County, Florida, USA.

**Intervening:** RUP.

**F. CAESIONIDAE** Klunzinger, 1870

- **O T. (LUT)–Rec. Mar.**
- **First:** O 'Caesio' boudoti (Priem, 1906), Calcaire Grossier, Paris Basin, France.

**Extant**

**F. PARASCORPIDIDAE** Smith, 1949

- **Extant** Mar.
- **Genus Caesioscorpis** Whitley, 1945

- **Extant** Mar.

**F. LOBOTIDAE** Gill, 1883

- **Extant** Mar.

**Genus Datiroides** Bleeker, 1853

- **Extant** FW/Mar.

**F. GERREIDAE** Bleeker, 1853

- **T. (YPR)–Rec. Mar./FW**

**First:** O Gerres latidens Stinton, 1980, Wittering Formation, southern England, UK; 'Gerreidarum' aquitanicus Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France.

**Extant**

**O LUT, PRB.**

**F. HAEMULIDAE** Richardson, 1848

(= Pomadasyidae Regan, 1913)

- **O T. (THA)–Rec. Mar./FW**

**First:** O Isacia remensis (Leriche, 1908), Sables de Chalons-sur-Vesle, Marne, France; Oldhaven Formation, SE England, UK; 'Pomadasyidarum' gullentopsi Nolf, 1978, Landen Formation, Wansin, Belgium; S Pomadasyi furcatas (Agassiz, 1839), Monte Bolca, Verona, Italy (LUT).

**Extant**

**O YPR–PLE.**

**F. SPARIDAIDAE** Bonaparte, 1832

- **T. (?THA/YPR)–Rec. Mar.**

**First:** O Inermiidae Jordan, 1923

- **Extant** Mar.

Intervening: YPR-PLE.


First: O Centracanthus cahuzaci Nolf, 1988, Argile de Gan, Gan, Pyrénées-Atlantiques, France. Extant

Intervening: O LUT, LMI–MMI.

F. LETHRINIDAE Regan, 1913 Extant Mar.

F. NEMIPTERIDAE Regan, 1913 (including Pentapodidae Smith, 1941) Extant Mar.

F. SCIAENIDAE Cuvier, 1829 T. (?LUT/CHT)–Rec. Mar./FW Extant

First: O ‘Sciaenidarum’ claybornensis Koken, 1888, Claiborne, Mississippi, USA. Sciaenids are otherwise unknown before the CHT: S Larimus ignotus (Smirnov, 1936), Maikop, Caucasus, former USSR; O ‘Sciaenidarum’ eperrectus Koken, 1888, Vicksburg, Newton, Mississippi, USA; Platacodon nanus Marsh, 1889, Lance Formation (MAA), Wyoming, USA, contains isolated pharyngeals (not dentaries: see Wilson et al., 1988) referred to Sciaenidae by Estes (1964), but compared with Cichlidae by Cavender (1986). According to M. V. H. Wilson (pers. comm.), they are not sciaenid, may not be acanthomorph, and could be ostariophysan. Extant

Intervening: CHT–PLE.


First: Undescribed mullid (Blot, 1980), Monte Bolca, Verona, Italy. Extant

Intervening: LMI–PLI.

F. MONODACTYLIDAE* Jordan, 1923 T. (LUT)–Rec. Mar./FW Extant

First: Pasaichthys pleuronectiformis Blot, 1969, Psettopsis
Animals: Vertebrates

subarcuatus (de Blainville, 1818), Monte Bolca, Verona, Italy.

F. GLAUCOSOMATIDAE* Jordan, 1923


F. PEMPHERIDIDAE Gill, 1862

First: O Pempheris sp. Nolf, 1988, Saint-Estephe Formation, Blaye, Gironde, France. Extant

F. GLAUCOSOMATIDAE* Jordan, 1923


F. PEMPHERIDIDAE Gill, 1862

First: O Pempheris sp. Nolf, 1988, Saint-Estephe Formation, Blaye, Gironde, France. Extant

F. GLAUCOSOMATIDAE* Jordan, 1923


F. PEMPHERIDIDAE Gill, 1862

First: O Pempheris sp. Nolf, 1988, Saint-Estephe Formation, Blaye, Gironde, France. Extant

F. GLAUCOSOMATIDAE* Jordan, 1923


F. PEMPHERIDIDAE Gill, 1862

First: O Pempheris sp. Nolf, 1988, Saint-Estephe Formation, Blaye, Gironde, France. Extant

F. GLAUCOSOMATIDAE* Jordan, 1923

F. CICHLIDAE Gill, 1872  

Intervening: LMI–PLI.

F. EMBIOTOCIDAE Günther, 1862  
First: Eriquius plectrodes Jordan, 1924, Monterey Formation, Lompoc, California, USA. Extant

Intervening: PLI–PLE.

F. POMACENTRIDAE Girard, 1858  
First: Izuus nakamurai Tokunaga and Saito, 1938, Yugasima Group, Izu, Japan. This fish was compared by Tokunaga and Saito with Recent pomacentrids and with Odonteus Agassiz, from Monte Bolca, Verona, Italy (LUT), and conventionally assigned to Pomacentridae. Blot (1980), who had begun revising Odonteus, repeated Arambourg's (1927) comment that the genus has nothing to do with Pomacentridae. The only other fossil pomacentrid is MES, Chromis savornini Arambourg, 1927, Raz-el-Ain, Oran, Algeria. Extant

Intervening: PRB–RUP, MMI–PLE.

Suborder ZOARCOIDEI Garman, 1899
F. BATHYMASTERIDAE Jordan, 1885  
Extant Mar.

F. ZOARCIDAE Cuvier, 1829  
First: O Lycodopsis pacifica (Collett, 1879), unspecified PLI, California, USA. Extant

Intervening: O PLE.

F. STICHAEDIIDAE Gill, 1872  

F. CRYPTACANTHODIDAE Gill, 1861  
First: O Lyconectes aleutensis Gilbert, 1895, unspecified PLI, California, USA. Extant

Intervening: O PLE.

F. PHOLIDIDAE Gill, 1893  
First: Anarchidas lopus L. 1758, Coralline Crag, Suffolk, England, UK. Extant

Intervening: O PLE.

F. PERCOPHIDAE Adams, 1854  
First: O Pseudoscopelus grossheimi (Danil'chenko, 1960), lower Khadum, Caucasus, former USSR. Extant

Intervening: O PRB–LMI, PLI.

F. TRICHONOTIDAE Regan, 1913  
First: Pseudoscopelus grossheimi (Danil'chenko, 1960), lower Khadum, Caucasus, former USSR. Extant

Intervening: O PLE.
Animals: Vertebrates

F. CHAMPSODONTIDAE* Jordan, 1923
Extant Mar.

F. LEPTOSCIPOIDAE Gill, 1872
Intervening: O LMI--UMI.

F. AMMODYTIDAE Bonaparte, 1832
Intervening: PRB--MMI, PLI.

F. TRACHINIDAE* Risso, 1826
Intervening: LUT--PLI.

F. URANOSCIPOIDAE Bleeker, 1859
Intervening: O MMI, PLI.

Suborder BLENNIOIDEI Bleeker, 1859


F. TRIPTERYGIIDAE Hubbs, 1952
First: Tripterygion pronasus Arambourg, 1927, Oran, Algeria.

F. DACTYLOSCOPIDAE Gill, 1872 Extant Mar.
F. LABRISOMIDAE Hubbs, 1952
First: Labrisomus pronuchipinnis Arambourg, 1927, Oran, Algeria.

First: Undescribed otolith, Hispaniola (Nolf, 1985).

F. CHAENOPSIDAE Gill, 1856 Extant Mar.
F. BLENNIIDAE Rafinesque, 1810
Intervening: PRB--RUP, UMI, PLE.

Suborder ICOSTEOIDEI Berg, 1937

F. ICOSTEIDAE* Jordan and Gilbert, 1882
Extant Mar.

Suborder CALLIONYMOIDEI Berg, 1937
F. CALLIONYMIDAE Bonaparte, 1832
T. (YPR)--Rec. Mar./FW
First: Callionymus eocaenus Casier, 1946, Sables de Forest, Forest-lez-Bruxelles, Belgium (isolated preoperculars); otoliths of Callionymus in Calcaire Grossier (LUT), Paris Basin, France.
Intervening: LUT, RUP, UMI.

F. DRACONETTIDAE Jordan and Fowler, 1903
Extant Mar.

Suborder GOBIESOCOIDEI Berg, 1896
F. GOBIESOCIDAE Bleeker, 1859
Suborder GOBIIDAE Bleeker, 1859 (including ALABETIDAE Gill, 1906)

Suborder GOBIOIDEI Jordan and Evermann, 1896
GOBIOIDEI incertae sedis (F. PIRSKENIIDAE Obrhelova, 1961) T. (CHT/LMI) Mar./FW
First and Last: Pirskenius diatomaceus Obrhelova, 1961, diatomite, Hrazeny, northern Bohemia, Czechoslovakia.

F. RHYACICHTHYIDAE* Jordan, 1923 Extant FW
F. ELEOTRIDAE Gill, 1861 O T. (RUP)--Rec. Mar./FW
Intervening: O LMI.

F. GOBIIDAE Bonaparte, 1832
T. (?LUT/PRB)--Rec. Mar./FW
First: 'Gobius' microcephalus Agassiz, 1839, Monte Bolca, Verona, Italy, doubtfully a gobiid or even a gobioid. One gobiid otolith is reported by Nolf and Bajpai (in press) from the Harudi Formation (LUT), Katchchh, India, and two gobiid otoliths from the Naggulan Formation (BRT), Java. The first reliably identified skeletal gobiids are PRB: Pomatoschistus (?) cf. bleicheri (Sauvage, 1883), Fishbourne Member of Headon Hill Formation, Isle of Wight, England, UK (Gaudant and Quayle, 1988); also PRB is O 'Gobidiarum' sp. Steurbaut, 1984, Sables d'Yrieu, Landes, France.
Intervening: RUP--PLE.

F. XENISTHMIDAE Miller, 1973 Extant Mar.
F. SCHINDLERIIDAE* Gilty, 1934 (Johnson and Brothers, 1990) Extant Mar.
F. GOBIOIIDAE Jordan, 1923 Extant Mar./FW
F. TRYPARCHENIDAE Günther, 1861
Extant Mar./FW
F. KRAEMERIIDAE Whitley, 1935 Extant Mar./FW
F. MICRODESMIDAE Regan, 1912 Extant Mar.
Suborder KURTOIDEI Regan, 1909
F. KURTIDAE* Bleeker, 1859 Extant FW/Mar.
**Suborder** ACANTHURIDAE Berg, 1937
*(sensu lato, Tyler et al., 1989)*

F. DREPANIDAE* Kaup, 1860  Extant  Mar.
F. CHAETODONTIDAE Bonaparte, 1832
First:  Pygaeus Agassiz, 1838 (about six nominal species), Malacopygaeus Leriche, 1906 (one species) and Parapygaeus Fellegrin, 1907 (one species), all from Monte Bolca, Verona, Italy, are conventionally assigned to Chaetodontidae, but all are in need of revision. *Chaetodon penniger* Bogatschov, 1964, RUP, Moroskin, Transcaucasia, former USSR, is otherwise the first chaetodontid.  Extant
Intervening: RUP-PLI.

First:  Archaephippus asper (Volta, 1796), Eoplatax papilio (Volta, 1796), Monte Bolca, Verona, Italy.  Extant
Intervening: ?RUP, PLI.

First:  Scatophagus frontalis Agassiz, 1835, Monte Bolca, Verona, Italy.  Extant
Intervening: RUP.

**Suborder** ACANTHUROIDEI s.s. (Tyler et al., 1989)

ACANTHUROIDEI incertae sedis (F. Kushlukiidae Danil’chenko, 1968)  T. (YPR) (see Fig. 36.6)
First and Last:  Kushlukia permira Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR; *Kushlukia* may also occur in the YPR Fuller’s Earth, Barmer, SW Rajasthan, India (J. C. Tyler, pers. comm.).  Extant
First:  Siganopygaeus rarus Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR  Extant
Intervening: LUT, RUP.

First:  Siganopygaeus ingens Casier, 1966, Danatinsk Formation, Kopetdag, Turkmenia, former USSR  Extant
Intervening: LUT, RUP.

First:  Proluvarus necopinatus Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR; *Beerichthys imperialis* Casier, 1966, London Clay Formation, SE England, UK. *Eoluvarus bondei* Sahni and Choudhary, 1977, YPR, Barmer, SW Rajasthan, India, was accepted as a luvarid by Tyler et al. (1989), but Tyler (pers. comm.), after examining the type material and confirmed that it is unrelated to *Luvarus*.  Extant
First:  Eoluvarus bondei Casier, 1966, London Clay Formation, southern England, UK; Ieper Formation, Belgium; Phosphates, Morocco (isolated teeth).  Extant
Intervening: LUT–PLE.

First:  Eutrichiurides orpiensis (Leriche, 1906), Montian

First:  Eight genera (Blot and Tyler, 1991), Monte Bolca, Verona, Italy, and one unnamed acronurus-like specimen (Bannikov and Tyler, 1992), Dabakham Formation, Tbilisi, Georgia, former USSR.  Extant
Intervening: Eoc. (u), RUP, MMI; these records are of *Caprovesposus*, long thought to be a zeiform, which Bannikov and Tyler (1992) show to be acronurus-stage larvae of acanthurids.

**Suborder** SCOMBROIDEI Bleeker, 1859 s.l.  (Johnson, 1986)

First:  Palimphyes palaeocenicus Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR.  Extant
Last:  Three genera (David, 1943), Modelo and Monterey Formations, southern California, USA.  Extant
Intervening: LUT/BRT, RUP–LMI.  Extant
Comment: This nominal family, discussed by David (1943: ‘nearly related to the Gempylidae’) and Danil’chenko (1960: ‘intermediate between Scombrids and Gempylidae’), seems to lack most of the characters of Scombroidae s.s. and of Gempylidae listed by Johnson (1986). There is no indication that it is monophyletic.

First:  Scombrops sp. Nolf, 1888, Argile de Gan, Gan, Pyrénées-Atlantiques, France.  Extant


F. POMATOMIDAE* Gill, 1865

First:  Palimphyes palaeocenicus Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR  Extant
Last:  Three genera (David, 1943), Modelo and Monterey Formations, southern California, USA.  Extant
Intervening: LUT/BRT, RUP–LMI.  Extant
Comment: This nominal family, discussed by David (1943: ‘nearly related to the Gempylidae’) and Danil’chenko (1960: ‘intermediate between Scombrids and Gempylidae’), seems to lack most of the characters of Scombroidae s.s. and of Gempylidae listed by Johnson (1986). There is no indication that it is monophyletic.

First:  Pseudoseriola spp., London Clay Formation, southern England, UK; Ieper Formation, Belgium; Phosphates, Morocco (isolated teeth).  Extant
Intervening: LUT–PLE.
Phosphates, Morocco; *E. africanus* Darrevelle and Casier, 1949, Landana, Cabinda, Angola (isolated teeth). **Extant**

**Intervening:** THA–PLI.

F. **SCOMBRIDAE** Rafinesque, 1815 (including Istiophoridae Lütken, 1875, Xiphiidae Swainson, 1839, Xiphiorhynchidae Regan, 1909)

T. (DAN)–Rec. Mar. (Bannikov, 1985a)

**Tribe** GASTEROCHEMATININI Gill, 1892

**Extant** Mar.

**Tribe** SCOMBRINI Rafinesque, 1815


**First:** *Scombroserda turkmenica* Danil’chenko, 1968, Danatinsk Formation, Kopetdag, Turkmenia, former USSR; *S. decipiens* (Casier, 1966), London Clay Formation, SE England, UK.

**Intervening:** LUT–PLI.

**Tribe** GRAMMATORCYNNINI* Johnson, 1986


**First:** Grammatorcynus scomberoides Arambourg, 1967, Elam, Luristan, Iran. **Extant**

**Intervening:** MMI.


**First:** *Serdha palaeocaena* (Leriche, 1909), Landana, Cabinda, Angola (isolated teeth); earliest complete fish is YPR, *Palaeothunnus parvidentatus* Danil’chenko, 1968, Danatinsk
Formation, Kopetdag, Turkmenia, former USSR. 

**Intervening:** YPR–PLF.

**Tribe** SCOMBEROMORINI* Starks, 1910 


**Intervening:** THA–UMI.

**Tribe** ACANTHOCYBILINI* Starks, 1910 

**First:** *Hemirhabdorhynchus depressus* Casier, 1946, *H. ypresiensis* Casier, 1946, Sables de Forest, Forest-Iez-Bruxelles, Belgium; *Aglyptorhynchus* spp., London Clay Formation, SE England, UK; and Sables de Forest, Belgium. 

**Intervening:** LUT–PLI.

**Tribe** XIPHIINI* Swainson, 1839 

**First:** *Xiphias rupeliensis* Leriche, 1909, Argile de Boom, Belgium, and Bohlener Schichten, Leipzig, Germany. 

**Intervening:** MMI–PLI.

**Suborder** STROMATEOIDEI Regan, 1929 s.l. (Johnson and Fritzsche, 1989) 

**F. ARRIPIDAE* Regan, 1913** Extant Mar. 

**First:** Undescribed fishes, questionably referred to the suborder (Bonde, 1987), Fur Formation (Mo Clay), NW Denmark.

**F. AMARSPORTIDAE* Haedrich, 1969** Extant Mar. 


**First:** *Osphronemus goramy* Lacepede, 1802, Padang, Indonesia. 

**Intervening:** PLI.


**First:** *Tetragonurus* sp. Sorbini, 1988, Marrechia River, NW Italy.

**Intervening:** RUP, LMI.

**Suborder** ANABANTOIDEI Regan, 1909 

**F. ANABANTIDAE Richardson, 1836** Extant FW 

**F. BELONTIIDAE Liem, 1963** (= Polycanthidae Gill, 1893) Extant FW 

**Comment:** Hora (1939) assigned a scale from Interappean beds (?DAN), Deothan, Madhya Pradesh, India, to the extant *Macropodus*, but I doubt the determination. Nair (1945) and Khare (1976) also assigned isolated Tertiary scales from India to *Macropodus*.

**F. HELOSTOMATIDAE* Gill, 1872** Extant FW 

**F. OSPHRONEMIDAE* Bleeker, 1859** T. (?Eoc.)–Rec. FW 

**First:** *Osphronemus goramy* Lacépède, 1802, Padang,
Sumatra. The Eocene age of the fish shales at Padang is still dubious. Extant

**Suborder** LUCIOCEPHALOIDEI Berg, 1937
F. LUCIOCEPHALIDAE* Bleeker, 1859 Extant FW

**Suborder** OPHICEPHALOIDEI Bleeker, 1859 (= Channiformes Greenwood et al., 1966)
F. CHANNIDAE* Berg, 1940 (= Ophicephalidae Bonaparte, 1831) T. (YPR)–Rec. FW
Intervening: SLUT, MMI–PLE, 0 PRB, LM!.

Jebel Tourah, Egypt. Extant
First: S Luciocephalus* Bleeker, 1859 Extant FW Formation, Chorlakki, Kohat, Pakistan. Extant
First: S LUCIOCEPHALIDAE* Bleeker, 1859 Extant FW
Intervening: SLUT, MMI–PLE, 0 PRB, LM!.
Jebel Tourah, Egypt. Extant
First: S Luciocephalus* Bleeker, 1859 Extant FW Formation, Chorlakki, Kohat, Pakistan. Extant
First: S Luciocephalus* Bleeker, 1859 Extant FW
Intervening: 0 PRB–PL!.

Gan, Pyrenees-Atlantiques, France; S LUT d’Yrieu, Landes, France; S UMI, Algeria and California, USA. Extant
Intervening: 0 PRB–PL!.

First: P. sp. NoIf and Steurbaut, 1990, leper Formation, Belgium; First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
Intervening: 0 PRB–PL!.

Monte Bolca, Verona, Italy; First: F. AMPHISTIIDAE Boulienger, 1902 T. (LUT) Mar., southern England, UK and Argile de Gan, Gan, Pyrenees-Atlantiques, France. Extant
Intervening: 0 PRB–PL!.

First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
Intervening: 0 PRB–PL!.

First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
Intervening: 0 PRB–PL!.

First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
Intervening: 0 PRB–PL!.

First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
First: P. sp. NoIf, 1988, Kuldana Formation, Chorlakki, Kohat, Pakistan. Extant
Intervening: 0 PRB–PL!.
**Last:** *Eotrigonodon* spp., LUT, Belgium, France, Egypt.  
**Intervening:** DAN–YPR.  
**Comment:** Eotrigonodontids, although conventionally treated as tetraodontiforms, are probably not teleosts but pycnodonts, a group whose stratigraphical range includes that of eotrigonodontids.

**Suborder TRIACANTHOIDEI** Winterbottom, 1974  
**F. TRIACANTHODIDAE** Gill, 1862  
*T. (RUP)–Rec. Mar.*  
**First:** *Cryptobalistes brevis* (Rath), Glarus, Switzerland. Tyler (1980) places *Cryptobalistes* in the succeeding family, and it includes four monotypic LUT genera from Monte Bolca, Verona, Italy, in this one.  
**Extant**  

**F. TRIACANTHIDAE** Bleeker, 1859  
*T. (LUT)–Rec. Mar.*  
**First:** *Proacanthonodes ombonii* (de Zigno, 1884), Monte Bolca, Verona, Italy.  
**Intervening:** RUP, Mio.  

**Suborder TETRAODONTOIDEI** Berg, 1937  
**Infra-order BALISTIDEO Berg, 1937**  
**BALISTIDEO incertae sedis** T. (YPR)  
**First and Last:** *Eospinus danilshenki* Tyler and Bannikov, 1992, Danatinsk Formation, Kopetdag, Turkmenia, former USSR.  
**Extant**  

**F. SPINACANTHIDAE** Tyler, 1968  
*T. (LUT)–Mar.*  
**First and Last:** *Spinacanthus cuneiformis* (de Blainville, 1818) and *Protobalistum imperiale* (Massalongo, 1857), Monte Bolca, Verona, Italy.  

**Superfamily BALISTOIDEO Rafinesque, 1810**  
**F. BALISTIDAE** Rafinesque, 1810  
*T. (RUP)–Rec. Mar.*  
**First:** *Balistomorphus ovalis* (Agassiz, 1842), *B. spinosus* (Agassiz, 1842), *B. orbiculatus* (Heer, 1865), Glarus, Switzerland; *Oligobalistes robustus* Danil'chenko, 1960, Khadum Horizon, Maikop Series, Caucasus, former USSR.  
**Extant**  

**F. MONACANTHIDAE** Nardo, 1844  
**First:** *O Amanses sulcifer* Stinton, 1966, London Clay Formation, southern England, UK; *Alutera* sp. Sorbini, 1988, Marecchia River, NE Italy.  
**Intervening:** PLI.  

**Superfamily OSTRACIOIDEA** Rafinesque, 1810  
**OSTRACIOIDEA incertae sedis** T. (THA)–Mar.  
**First:** ‘*Ostracion*’ *meretrix* Daimeries, 1891, Aqua Formation, Virginia, USA (dermal plates), also in Woolwich and Reading Formation, SE England, UK. *Ostracion* is reported by Gayet et al. (1984) from the ?DAN, Intertrappean beds, Gitti Khadan, Madhya Pradesh, India, and from K. (MAA), In Beceten, Niger, but both records require confirmation.  

**F. ARACANIDAE** Hollard, 1860  
*T. (LUT)–Rec. Mar.*  
**First:** *Proaracana dubia* (de Blainville, 1818), Monte Bolca, Verona, Italy.  
**Intervening:** CHT.  

**F. OSTRACIIDAE** Rafinesque, 1810  
*T. (LUT)–Rec. Mar.*  
**First:** *Eolactoria sorbinii* Tyler, 1975, Monte Bolca, Verona, Italy.  
**Extant**  

**T. (YPR)–Rec. Mar.*  
**First and Last:** *Eoslactus bloti* Tyler, 1975 and *Zignoichthys oblongus* (Zigno, 1874), Monte Bolca, Verona, Italy.  

**Superfamily TRIODONTOIDEA** Bleeker, 1865  
**F. TRIODONTIDAE** Bleeker, 1859  
*T. (YPR)–Rec. Mar.*  
**First:** *Triodon antiquus* Leriche, 1905, Ieper Formation, Belgium, and London Clay Formation, southern England, UK. Tyler (1980) pointed out that the isolated jaws on which this species is based could be equally well from primitive diodontids as from *Triodon*, but a recently collected London Clay skull indicates that the fish is a *Triodon*.  
**Extant**  

**Intervening:** LUT–BRT.  

**Superfamily TETRAODONTOIDEA** Bonaparte, 1832  
**F. TETRAODONTIDAE** Bonaparte, 1832  
*T. (LUT)–Rec. Mar.*  
**First:** *Eotetraodon pygmaeus* (de Zigno, 1887), Monte Bolca, Verona, Italy.  
**Extant**  
**Intervening:** MMI–PLI.  

**F. DIODONTIDAE** Bibron, 1855  
**(including Eodiodontidae Tavani, 1955)**  
*T. (YPR)–Rec. Mar.*  
**First:** *Diodon* sp. Kumar and Loyal, 1987, lower Subathu Formation, Solan, Himachal Pradesh, India; *Kyrtogymnodon* sp. Weems and Horman, 1983, lower Nanjemoy Formation, Popes Creek, Maryland, USA (both records isolated tooth plates, not surely diodontid). The first intact skeletons are LUT, *Prodiodon erinaceus* (Agassiz, 1844), *P. tenuispinus* (Agassiz, 1833), Monte Bolca, Verona, Italy.  
**Extant**  
**Intervening:** LUT–PLI.  

**Superfamily MOLOIDEA** Ranzani, 1837  
**F. MOLIDAE** Ranzani, 1837  
*T. (LUT/PRB)–Rec. Mar.*  
**First:** *Eoranzania* Tyler and Bannikov (in press), isolated jaws from the Kumskii Formation, Pshekha River, northern Caucasus, former USSR.  
**Extant**  
**Intervening:** ?CHT (Woodward, 1901, p. 576), LAN–PLI.  

**REFERENCES**


Blot, J. and Tyler, J. C. (1991) New genera and species of fossil surgeon fishes and their relatives (Acanthuroidei, Teleostei) from the Eocene of Monte Bolca, Italy, with application of the Blot formula to both Recent and fossil forms. Studi e Ricerche sui giacimenti Terziari di Bolca, 6, 13–92.


Animals: Vertebrates


OSTEICHTHYES: SARCOPTERYGII

H.-P. Schultze

Actinopterygians and sarcopterygians are the two divisions of the osteichthyans. The sarcopterygians are a monophyletic taxon that include piscine representatives (Dipnoiformes, Onychodonta, Actinistia and Rhipidistia) and Tetrapoda (Schultze, 1987). The Tetrapoda, together with the Panderichthyida and the Osteolepidida, form the Choanata, a subdivision of the infraclass Rhipidistia. This classification reflects the position of the Tetrapoda and their closest relatives in a phylogenetic system. Of course, herpetologists, ornithologists and mammalogists ascribe to their respective groups a higher taxonomic rank than the phylogenetic position of these groups would require. Thus, it is customary to retain the divisions found in the traditional Linnean classification. However, I prefer not to elevate the rank of the piscine sarcopterygians based on their early branching points (Hennig, 1966). The piscine sarcopterygians form a relatively small group compared to the tetrapods.

In this chapter, only the piscine sarcopterygians are considered. The sequence of higher taxa (infraclass and order) follows Schultze (1987) with a sequential change in the position of Onychodonta and Actinistia. The Dipnoi are united with their sister group Diabolepidida nov. order in the infraclass Dipnoiformes. The Dipnoiformes do not include Youngolepis as proposed by Cloutier (1993). Youngolepis is the sister taxon to Powichthys within the Youngolepiformes. Within the Dipnoi, the families listed are monophyletic according to Marshall's 1987 strict consensus tree (his fig. 5); some families contain only one genus (Conchopomatidae, Uronemidae). Suborders of Dipnoi as proposed by Vorobyeva and Obruchev (1964) are all paraphyletic except for the Ceratodontoidae.

At present, an acceptable division of the Actinistia into families and orders is not available. Cladistic analyses (Forey, 1981, 1984, 1988; Cloutier, 1991a,b) give a sequence of genera without grouping into higher categories. Here I base the assignment of genera on Cloutier's analysis, so that the 49 nominal genera are divided into closely related groups. The families Miguashaiidae nov., Diploceridae, Hadronectoridae, Whiteidae nov., Mawsoniidae nov. and Latimeriidae are monophyletic. The other three families, Rhabdodermatidae, Laugiiidae and Coelacanthidae, are paraphyletic, each including a section of sequentially arranged genera on the cladogram of Cloutier (1991a). Contrary to common usage, the family Laugiiidae is not restricted to Laugia; here it also includes Rhabdoderma madagascariensis, Synaptotylus, Coccoderma and Coelacanthus granulatus. Above family level, there are no monophyletic units except for the suborder Latimerioidae; all other orders are paraphyletic with respect to their descendants.

The infraclass Rhipidistia comprises five orders and the tetrapods, and of the five orders three contain only one family. Representatives of the Youngolepiformes, Holoptychiida and Rhizodontida possess two external nasal openings, in contrast to Osteolepidida and Panderichthyida with one external and one internal opening, a true choana. Therefore, only the last two orders, together with the Tetrapoda, can be classified as Choanata. The division of Osteolepidida into families follows Worobjewa (1975) with the exception of two families raised to the rank of order (Rhizodontida and Panderichthyida) and for Lampropolepididae, a family based on one species of one genus. The family Canowindridae has recently been placed within the Osteolepidida (Young et al., 1992).

Acknowledgements – The author is indebted to R. Cloutier for review and criticism of this MS.

**Class** SARCOPTERYGII Romer, 1955

**Infraclass** DIPNOIFORMES Cloutier, 1993 (see Fig. 37.1)

**Order** DIABOLEPIDIDAE nov.

**F. DIABOLEPIDIDAE fam. nov.**  D. (LOK)  Mar.

**First and Last:**  *Diabolepis speratus* (Chang and Yu, 1984), Xitun Member, Cuifengshan Formation, Yunnan, China (Chang and Yu, 1984).

**Order DIPNOI Müller, 1844**

The dipnoans can be traced back to the Gedinnian, based on unpublished records from southern China.


**Suborder DIPTEROIDEI** Vorobyeva and Obruchev, 1964

**F. DIPTERIDAE** Owen, 1846  D. (PRA–FAM) Mar./?FW

*First:* *Dipterus* sp., Water Canyon Formation, Idaho, USA (Denison, 1968).

*Last:* *Dipnorhynchus suessmilchi* (Etheridge, 1906), Warroo Limestone, Taemas region, New South Wales, Australia (Thomson and Campbell, 1971).

**Suborder DIPTEROIDEI** Vorobyeva and Obruchev, 1964

**F. DIPTERIDAE** Owen, 1846  D. (PRA–FAM) Mar./?FW

*First:* *Dipterus* sp., Water Canyon Formation, Idaho, USA (Denison, 1968).

*Last:* *Conchodus jerofejevi* Pander, 1858, Zagare Formation, Estonia, former USSR (Blieck *et al*., 1988).

**Intervening:** EIF–FRS.

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Fig. 37.1

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658  Animals: Vertebrates
Fig. 37.1

F. PHANEROPLEURIDAE Huxley, 1861
D. (FRS, FAM) FW/Mar.

First: *Scaumenacia curta* (Whiteaves, 1881), Escuminac Formation, Quebec, Canada (Orvig, 1957).

F. RHYNCHODIPTERIDAE Berg, 1940
D. (FRS, FAM) FW/ Mar.

First: *Fleurantia denticulata* Graham-Smith and Westoll, 1937, Escuminac Formation, Quebec, Canada (Orvig, 1957).

F. CONCHOPOMATIDAE Berg, 1940
C. (MOS)—P. (SAK) FW/ Mar.


Last: *Conchopoma gadiforme* Kner, 1868, Lebach Group, Lower Rotliegend, Palatinate, Germany (Heidtke, 1986).

Suborder CTENODONTOIDEI Vorobyeva and Obruchev, 1964

F. URONEMIDAE Traquair, 1890
C. (VIS, BSH) FW/ Mar.

First: *Ganopristodus lobatus* (Agassiz, 1844), Burdiehouse Limestone, Midlothian, Scotland, UK (Henrichsen, 1972).
Last: *Ganopristodus splendens* Traquair, 1881, Burghlee Ironstone, Namurian E1, Midlothian, Scotland, UK (Henrichsen, 1972).

Intervening: SPK.

F. CTENODONTIDAE Woodward, 1891
C. (TOU—MOS) FW

Animals: Vertebrates

Last: Ctenodus murchisoni Ward, 1890, Phalen Coal, Sydney coalfield, Nova Scotia, Canada (Baird, 1978).

**Intervening:** VIS–BSH.

F. SAGENODONTIDAE Romer, 1966
D. (FAM)–P. (ART) FW/Mar.

**First:** Proceratodus wagneri (Newberry, 1889), Cleveland Shale, Cleveland, Ohio, USA (Romer and Smith, 1934).

Last: Sagenodus periprion (Cope, 1878), Vale Formation, Hennessey Group, Oklahoma, USA (Simpson, 1979).


F. Gnathorhizidae Miles, 1977
C. (MOS)–Tr. (OLK) FW/Mar.

**First:** Palaeophichthys parulus Eastman, 1908, Francis Creek Shales, Carbondale Formation, Illinois, USA (Eastman, 1908).


**Intervening:** KAS–ART, TAT, IND.

**Suborder** Ceratodontidae Vorobyeva and Obruchev, 1964

F. CERATODONTIDAE Gill, 1872
Tr. (DIE)–T. (LUT) FW/Mar.

**First:** Paraceratodus germani Lehman et al., 1959, Middle Sakamena Group, Madagascar (Schaeffer and Mangus, 1976).


**Intervening:** ANS–RHT, J.(l), CLV, TTH, NEO–CEN, CON, CMP, MAA, Pal.

F. NEOCERATODONTIDAE Miles, 1977
Tr. (SCY)–Rec. FW/Mar.

**First:** Epiceratodus sp., Lower Triassic, Orenburg Region (southern Urals), (Vorobyeva and Obruchev, 1964).

**Intervening:** ALB, Mio., PLE.

F. LEPIDOSIRENIDAE Bonaparte, 1841
K. (CMP)–Rec. FW.

**First:** Protopterus ? regulatus Schaal, 1984, Mut Formation, Campan, Egypt (Schaal, 1984).

**Extant**

**Intervening:** MAA–PLE.

**Infraclass** ONYCHODONTIDA Andrews, 1973

F. ONYCHODONTIDAE Woodward, 1891
D. (EMS)–(FAM) Mar.

**First:** Struniiiform crossopterygian, gen. et sp. indet. Spirifer yassensis Limestone, New South Wales, Australia (Örvig, 1969). Earlier records refer probably to acanthodian teeth.

Last: Onychodus dellei Gross, 1942, Ketleri Beds, Latvia (Bliek et al., 1988). Later records from the Carboniferous (C(u)): Huene, 1943: lower Westphalian, Silesia; or Schultz, 1973: Desmoinesian (MOS), North America) may be teeth of rhizodonts (Strepsodus).

**Intervening:** EIF–FRS.

**Infraclass** ACTINISTIA Cope, 1871

**Suborder** DIPLOCERCIDOIDEI Berg, 1937


**First and Last:** Miguashaia bureau Schultze, 1973, Escuminac Formation, Quebec, Canada (Schultze, 1973).

F. DIPLOCERCIDAE Stensiö, 1922

**First:** Diplocercides heiligenstockiensis (Jessen, 1966), Oberer Plattenkalk (early FR), Germany (Jessen, 1966).


**Suborder** HADRONECTOROIDEI Lund and Lund, 1984

F. HADRONECTOROIDIDAE Lund and Lund, 1984

**First:** Euporosteus eifelianus Jaekel, 1927, Crinoidenmergel, Germany (Gross, 1950).


**Intervening:** FAM.

F. Rhabdodermatididae Berg, 1958
C. (VIS–MOS?GZE) Mar./FW

**First:** Coelacanthopsis curta Traquair, 1901, and Rhabdoderma aridrossense Moy-Thomas, 1937, Calciferous Sandstone Series, Scotland, UK (Henrichsen, 1972).

Last: Rhabdoderma elegans (Newberry, 1856), Allegheny Group, Ohio, USA (Hook and Baird, 1986). May extend into GZE, if Coelacanthidae gen. et sp. indet. (Zidek, 1975) from the Wild Cow Formation, New Mexico, USA, and Coelacanthidae indet. (Schultze and Chorn, 1989) from the Bern Limestone Formation, Wabaunsee Group, Kansas, USA, belong to the family.

**Intervening:** SPK.

**Suborder** COELACANTHOIDEI Berg, 1937


**First:** Synaptotylus newelli (Hibbard, 1933), Stanton Limestone, Lansing Group, Kansas, USA (Echols, 1963).

Last: Coccoderma sueticum Quenstedt, 1858, Lithographic Limestone, Bavaria, Germany (Reis, 1888).

**Intervening:** IND: GRI, DIE, KIM.

F. WhiteIIDAE fam. nov. Tr. (DIE) Mar.

**First and Last:** Whiteia woodwardi Moy-Thomas, 1935, Middle Sakamena Group, Madagascar (Schaeffer and Mangus, 1976).

F. COELACANTHIDAE Agassiz, 1843

**First:** Coelacanthus granulatus Agassiz, 1839, Kupferschiefer, Germany and England, UK (Schauberg, 1978).

Last: Heptanema willemoesi (Vetter, 1881), Lithographic Limestone, Bavaria, Germany (Reis, 1888).

**Intervening:** KAZ, TAT, OLK, ANS, LAD, ?CRN, RHT.

**Suborder** LATIMERIOIDEI subord. nov.

F. MAWSONIIDAE fam. nov. Tr. (LAD)–K. (CEN) FW/Mar.

**First:** Alcoveria brevis Beltan, 1972, Upper Muschelkalk, Spain (Beltan, 1972).

**Intervening:** RHT, HET, OXF–ALB.

F. **LATIMERIDAE** Berg, 1940


**Extant**

**Intervening:** SIN, TTH, CEN, TUR, CMP.

*Infraclass* RHIPIDISTIA Cope, 1889

**Order** YOUNGOLEPIFORMES Gardiner, 1984

F. **YOUNGOLEPIDIDAE** Gardiner, 1984

First and Last: *Youngolepis praecursor* Zhang and Yu, 1981, Xitun Member of Cuifengshan Series, Yunnan, China (Chang, 1982); and *Powichthys thorsteinssoni* Jessen, 1975, Drake Bay Formation, Prince of Wales, Canadian Arctic (Jessen, 1980).

**Order** HOLOPTYCHIIA Andrews, 1967

F. **POROLEPIDIDAE** Berg, 1940
D. (PRA–GIV) Mar./?FW


Last: *Porolepis posnaniensis* (Kade, 1858), Aruküla Beds, Estonia, former USSR (Blieck et al., 1988).

**Intervening:** EMS, ElF.

F. **HOLOPHTHYIIDAE** Owen, 1860
D. (EIF–C) (TOU) FW/Mar.

First: *Glyptolepis leptocephalus* Agassiz, 1844, Tynet Burn Fish Beds, Morayshire, Scotland, UK (Westoll, 1951).


**Intervening:** GIV, FRS.

**Order** RHIZODONTIDA Andrews and Westoll, 1970

F. **RHIZODONTIDAE** Traquair, 1881
D. (?)FRS–C. (BSH) Mar./FW


Cloutier, R. (1991b) Interrelationships of Palaeozoic actinistians:
Osteichthyes: Sarcopterygii


Vorobyeva, E. I. and Obrucheva, Y. D. (1977) [Rhizodont crossopterygian fish (fam. Rhizodontidae) from middle Paleozoic deposits of the Asiatic part of the USSR], in Ocherki po Filogenii i Sistematike Iskopayemykh Ryb i Beschezylastnykh (ed. V. V. Menner), Izdeltelstvo Nauka, Moscow, pp. 89–97.


The term ‘Amphibia’ is generally used for all tetrapods between the fish grade and the amniote clade of vertebrate organization. In this review I have divided these forms into four groups:

1. the Stem Tetrapoda, comprising the forms believed to be branches off the common stem of all living tetrapods;
2. the Aistopoda, a group of early tetrapods, the relationships of which are enigmatic;
3. the Amphibia sensu stricto, comprising the living Lissamphibia and a series of stem groups referred to as Stem Amphibia;
4. the Stem Amniota.

This follows the general pattern put forward by Smithson (1985b) and Panchen and Smithson (1988), but differs in that those authors did not recognize any groups as stem tetrapods whereas I have placed two genera and four families in this category.

**STRATIGRAPHICAL NOTES**

There does not seem to be a precise correlation of the Moscow Basin late Carboniferous ages used by Harland et al. (1982) with the Westphalian/Stephanian stages widely used for western Europe. The following approximate correlations are used for the Moscow Basin ages which are asterisked (*) throughout the text.

| NOG* | Stephanian C |
| KLA* | upper Stephanian B |
| DOR* | middle Stephanian B |
| CHV* | lower Stephanian B |
| KRE* | Stephanian A |
| MYA* | middle/upper Westphalian D |
| POD* | upper Westphalian C/lowestmost Westphalian D |
| KSK* | uppermost Westphalian B/lowest Westphalian C |
| VRK* | lower/middle Westphalian B |
| MEL* | upper Westphalian A |
| CHE* | lower Westphalian A |

The stratigraphical terminology for the formations within the lower Texas Red Bed sequence follows that of Hentz (1989) and Hook (1989). Stratigraphical correlation of the European Lower Permian with the Pre-Ural standard is currently in a state of flux. In this work, most of the Autunian/lowest Rotliegendes is equated with the Asselian, while the uppermost lowest Rotliegendes is treated as indeterminate Asselian/Sakmarian. The Tambach and Wadern Schichten are treated as indeterminate Sakmarian/Artinskian.

**STEM TETRAPODA**

**STEM TETRAPODA incertae sedis**

D. (FRS/FAM) FW? (Fig. 38.1)

**First and Last:** *Metaxygnathus denticulus* Campbell and Bell, 1977, Cloghnian Shale, Forbes, New South Wales, Australia (Campbell and Bell, 1977).

**Comment:** This specimen is a mandible which has not been placed in a family but is diagnostically tetrapod (Clack, 1988), and therefore merits inclusion as probably the earliest recorded tetrapod fragment.

**F. ICHTHYOSTEGIDAE** Säve-Söderbergh, 1932

D. (FAM) FW

**First:** Ichthyostega spp., Aina Dal Formation, East Greenland.

**Last:** Ichthyostega stensioi Säve-Söderbergh, 1932 and Ichthyostegopsis wimani Säve-Söderbergh, 1932, Britta Dal Formation, East Greenland (Clack, 1988).

**F. ACANTHOSTEGIDAE** Jarvik, 1952

D. (FAM) FW

**First:** Acanthostega gunnari Jarvik, 1952, undescribed referred material from Aina Dal Formation, East Greenland (J. A. Clack, pers. comm.).

**Last:** Acanthostega gunnari Jarvik, 1952, Britta Dal Formation, East Greenland (Clack, 1988).

**F. UNNAMED** D. (FAM) FW/Terr.

**First and Last:** Tulerpeton curtum Lebedev, 1984, Suvorov, Tula Province, former USSR (Lebedev, 1984).

**Comments:** This specimen has not yet formed the basis of
a separate family but is clearly distinct from all other early tetrapods, and will ultimately merit a new family.

**F. CRASSIGYRINIDAE** Watson, 1929  
(C. BRI—PND) FW

**First:** *Crassigyrinus scoticus* (Lydekker, 1890), Lower Limestone Group, Gilmerton, Scotland, UK.  
**Last:** *Crassigyrinus scoticus* (Lydekker, 1890), referred material from Limestone Coal Group, Cowdenbeath, Fife, Scotland, UK (Panchen, 1985).

**F. BAPHETIDAE** Cope, 1875 (= LOXOMMATIDAE  
Lydekker, 1889)  
(C. BRI—MYA*) FW

**First:** *Loxomma allmanni* Huxley, 1862, Lower Limestone Group, Gilmerton, Scotland, UK.  
**Last:** *Baphetes bohemicus* (Fritsch, 1885), Gaskohle, Kladno Formation, Nýřany, Czechoslovakia. (Beaumont, 1977).  
**Intervening:** PND, CHE*, VRK*—KSK*.

**TETRAPODA INcertae Sedis**  
Order AISTOPODA Miall, 1875

The most recent general review of the aistopods is that of Baird, 1964.

**F. LETHISCIDAE** Wellstead, 1982  
(C. HLK) Terr./FW

**First and Last:** *Lethiscus stocki* Wellstead, 1982, Wardie Shales, lower Oil Shale Group, Wardie, Edinburgh, Scotland, UK.
F. OPHIDERPETONTIDAE Schwarz, 1908
C. (BRI–KLA*) Terr./FW
First: Unnamed material, East Kirkton Limestone, Bathgate, Scotland, UK (A. C. Milner, pers. comm.).
Last: Ophiderpeton vicinum Fritsch, 1880, Kounov Series, Slaný Formation, Kounov, Czechoslovakia.

F. PHLEGETHONTIDAE Cope, 1875
C. (MEL*)–P. (ART) Terr.
First: Phlegethontia phanerapha Thayer, 1985, Black Prince Limestone, Swisselm Mountains, Arizona, USA.
Last: Sillerpeton permianum Lund, 1978, upper Garber Formation, Fort Sill Fissures, Oklahoma, USA.
Intervening: POD*–MYA*.
Comments: A slightly older possible phlegethontiid is ‘Dolichosoma’ emersoni Thayer, 1886, Jarrow Coal, Kilkenny, Republic of Ireland (= CHE*). This material is very poorly preserved and though often reported as a phlegethontiid, might equally be a juvenile ophiderpetontid (K. Bossy, cited by Lund, 1978, p. 54).

AMPHIBIA
The term ‘Amphibia’ is here taken to include the clade Lissamphibia and all those extinct amphibian groups which are more closely related to the lissamphibians than to the amniotes.

‘STEM AMPHIBIA’

Order NECTRIDEA Miall, 1875
The major source for data on nectrideans is A. C. Milner (1980).

F. DIPOLOCAULIDAE Cope, 1881
C. (CHE*)–P. (UFI) FW
First: Keraterpeton galvani Wright and Huxley, 1866, Jarrow Coal, Kilkenny, Republic of Ireland.
Last: Diplocaulus parvus Olson, 1972, Chickasha Formation, Blaine County, Oklahoma, USA.

F. SCINCOSAURIDAE Jaekel, 1909
C. (MYA*)–P. (ASS) Terr.
First: Scincosaurid specimen mentioned by A. C. Milner (1980), Allegheny Group, Linton, Ohio, USA.
Last: Sauravus cambrayi Thevenin, 1910, Les Télots, Autun, France.
Intervening: CHV/KLA*.

F. UROCORDYLIDAE Lydekker, 1889
C. (CHE*)–P. (ART) FW
First: Urocordylus wandesfordii and Lepterpeton dobbsi Wright and Huxley, 1866, Jarrow Coal, Kilkenny, Republic of Ireland.
Last: Crossotels annulatus Case, 1902, Wellington Formation, Orlando, Oklahoma, USA.
Intervening: MEL*–MYA*, CHV/KLA*, SAK.

Order COLOSTEIDAE Tatarinov, 1964 sensu Hook, 1983
The most recent general source for data on the colosteoids is Hook (1983).

F. COLOSTEIDAE Cope, 1875
C. (ASB–MYA*) FW
First: Pholidogaster pisciformis Huxley, 1862 (referred specimen originally described as Otocratia modesta Watson, 1929; see Panchen, 1975), upper Oil Shale Group, Burdhouse, Scotland, UK.
Last: Colosteus scutellatus (Newberry) Cope, 1871, Allegheny Group, Linton, Ohio, USA.
Intervening: BRI–PND, CHE*.

F. ACHERONTISCIDAE Carroll, 1969
C. (?PND) FW
First: Palaeomolgophis scoticus Brough and Brough, 1967, Pumpherton Oil Shale, Broxburn, Scotland, UK.
Last: Adelogyrinus sp., Shale above South Parrot Coal Seam, Niddrie, Edinburgh, Scotland, UK (Smithson, 1985a).
Intervening: None.

Order MICROSAURIA Dawson, 1863
The most recent review of the microsaurs is that of Carroll and Gaskill (1978).

Suborder MICROBRACHOMORPHA Carroll and Gaskill, 1978

MICROBRACHOMORPHA incertae sedis
C. (ALP/KIN) FW
First: Microbrachis pelikani Fritsch, 1883, Gaskohle, Kladno Formation, Nýřany, Czechoslovakia.
Last: Paramicrobrachis fritschi Kuhn, 1959, Lauterecken-Oderheim Formation, Glan Group, Lebach, Saarpfalz region, Germany.
Intervening: None.
Comments: A specimen from the Jarrow Coal, Kilkenny, Republic of Ireland (= CHE*) described as ?microbrachid by Carroll and Gaskill (1978) is a poorly preserved member of the Cucynitidae.

F. HYLOPLESIONTIDAE Carroll and Gaskill, 1978
C. (MYA*) Terr./FW
First: Hyloplegia longicostatum Fritsch, 1876, Gasköhle, Kladno Formation (= upper MYA*), Nýřany, Czechoslovakia.
Last: Hyloplegia longicostatum Fritsch, 1876, Platekohlke (= uppermost MYA*), Třemošná, Czechoslovakia.

F. BRACHYSTELECHIDAE Carroll and Gaskill, 1978
P. (ASS/SAK–?ART) Terr.
First: Batropetes fritschi (Geinitz and Deichmuller),

**Last:** *Quasicaecilia texana* Carroll, 1990, ?Arroyo Formation, ?Baylor County, Texas, USA (locality data uncertain).

**F. ODONTERPETONTIDAE** Carroll and Gaskill, 1978

_C.(MYA*)_ FW

**First and Last:** *Odonterpeton triangulare*, Moodie, 1909, Allegheny Group, Linton, Ohio, USA.

**Suborder** TUDITANOMORPHA Carroll and Gaskill, 1978

_C.(VRK*-KLA*)_ Terr.

**First:** *Asaphestera intermedia* (Dawson, 1894), Joggins Formation, Joggins, Nova Scotia.

**Last:** *Boii crassidens* (Fritsch, 1876), Kounov Series, Slany Formation, Kounov, Czechoslovakia.

**Intervening:** MYA*.

**F. HAPSIDOPAREIONTIDAE** Daly, 1973

_P.(ART)_ Terr.

**First:** *Hapsidopareion lepton* Daly, 1973, Hennessy Formation, South Grandfield, Oklahoma, USA.

**Last:** *Llistrofus pricei* Carroll and Gaskill, 1978, upper Garber Formation, Fort Sill Fissures, Oklahoma, USA.

**Comments:** Following Schultze and Foreman (1981), *Ricnodon* is not included in the Hapsidopareiontidae but is considered to be indeterminate.

**F. PANTYLIDAE** Case, 1911

_C./P. (NOG*/ASS)-P. (ART) Terr._

**First:** *Stegotretus agyrus* Berman et al., 1988, Cutler Formation, New Mexico, USA.

**Last:** *Pantylus cordatus* Olson, 1939, Arroyo Formation, Brushy Creek, Texas, USA.

**Intervening:** SAK.

**F. GYMNARTHIDAE** Case, 1910

_C.(MEL*)-P. (ART)_ Terr.

**First:** *Elfridia bulbidens* Thayer, 1985, Black Prince Lime­stone, Swisshelm Mountains, Arizona, USA.

**Last:** *Euryodus primus* Olson, 1939, Arroyo Formation, Brushy Creek, Texas, USA.

**Intervening:** VRK*, MYA*, KLA*, SAK.

**F. OSTEODOLPIDAE** Romer, 1945

_P.(ASS) FW/Terr._

**First and Last:** *Ostodolepis brevispinatus* Williston, 1913 and *Peladosotis elongatum* Carroll and Gaskill, 1978, Arroyo Formation, Coffee Creek, Texas, USA.

**F. TRIHECATONTIDAE** Vaughn, 1972

_C.(KRE/CHV*)_ Terr.

**First and Last:** *Trihecaton howardinus* Vaughn, 1972, Sangre de Cristo Formation, Colorado, USA.

**F. HYRHCHONKIDAE** Zanon, 1988

_P.(ART)_ Terr.

**First and Last:** *Rhynchonkos stovalli* (Olson, 1970), Hennessy Formation, South Grandfield, Oklahoma, USA.

**Order** LYSOROPHIA Romer, 1930

The most recent review of the lysorophians is that of Wellstead (1991).

**F. COCYTINIDAE** Cope, 1875 (= LYSOROPHIDAE Williston, 1908); _C.(CHE*)-P. (ART/KUN) FW._

**First:** Indeterminate cocytinid (Wellstead, 1991), Jarrow Coal, Kilkenny, Republic of Ireland.

**Last:** *Brachydectes elongatus* Wellstead, 1991, referred material (as *Lysorophus cf. L. tricarinatus* Cope), Chocha Formation, Texas, USA (Olson, 1956).

**Intervening:** KSK*, MYA*, KRE/CHV*, ASS–ART.

**Grade** TEMNOSPONDYLi Zittel, 1888 (P.)

There is no comprehensive work on temnospondyls subsequent to that of Romer (1947), and much of the following data is compiled by the author from primary sources, and is a summary of the families used in the *Temnospondyli* volume of the *Handbuch der Palaeoherpetologie* (Milner, in prep.). Four useful reviews summarizing earlier literature are Cosgriff (1984: Lower Triassic assemblages), Kalandadze et al. (1968: Russian Permo-Triassic temnospondyls), Milner (1987: Westphalian assemblages) and Werneburg (1989: Lower Permian of Europe).

**STEM TEMNOSPONDYLs**

**F. CAERORHACHIDAE** Carroll, 1988

_C.(?PND) Terr._

**First and Last:** *Caerorhachis bairdi* Holmes and Carroll, 1977, Limestone Coal Group, Loanhead, Scotland, UK (locality and horizon uncertain).

**F. DENDRERPETONTIDAE** Fritsch, 1889

_C.(BRI–VRK*)_ Terr.

**First:** Unnamed material, East Kirkton Limestone, Bathgate, Scotland, UK (Milner et al., 1986).

**Last:** *Dendrerpeton acadianum* Owen, 1853, Joggins Formation, Joggins, Nova Scotia, Canada.

**Intervening:** CHE*.

**F. EDOPIDAE** Romer, 1945

_P.(ASS) FW/Terr._

**First:** *Edops craigi* Romer, 1936, Markley Formation, Texas, USA.

**Last:** *Edops craigi* Romer, 1936, Archer City Formation, Texas, USA.

**F. COCHLEOSAURIDAE** Broili, 1923

_C.(VRK*-C./P. NOG*/SAK) FW_.

**First:** Unnamed vomers from Joggins Formation, Joggins, Nova Scotia, Canada (Carroll, 1967, fig. 7 A, as *Dendrerpeton*).

**Last:** *Chenoprosopus milleri* Mehl, 1913, Cutler Formation, Arroyo de Agua, New Mexico, USA.

**Intervening:** MYA*.

**THE TRIMERORHACHOID–BRACHYOPOID GROUP**

**F. COCHRLEOSAURIDAE** Broili, 1923

_C.(VRK*-C./.P. NOG*/SAK) FW_.

**First:** Unnamed vomers from Joggins Formation, Joggins, Nova Scotia, Canada (Carroll, 1967, fig. 7 A, as *Dendrerpeton*).

**Last:** *Chenoprosopus milleri* Mehl, 1913, Cutler Formation, Arroyo de Agua, New Mexico, USA.
**First:** Dawsonerpeton polydens (Fritsch, 1879), Kounov Series, Slany Formation, Kounov, Czechoslovakia, is probably a trimerorhachid as suggested by Romer (1945) and is currently being restudied by Dr. M. Maňourová (Prague). The first certain trimerorhachid is: Lafonius lehmani Berman, 1973, Wild Cow Formation (= NOG*), Manzanita Mountains, New Mexico, USA.

**Last:** Trimerorhachis rogersi Olson, 1955, Choza Formation, Foard County, Texas, USA.

**Intervening:** NOG*

**F. DVINOSAURIDAE** Watson, 1919  
P. (TAT) FW

**First and Last:** All dvinosaurs are from the Zone IV (= TAT) of the former USSR (Shishkin, in Kalandadzie et al., 1968). They are as follows: Dvinosaurus primus Amalitsky, 1921, Kotlas, Arkhangel Province; Dvinosaurus egregius Shishkin, 1968, Vyazniki, Vladimir Province; and Dvinosaurus puriensis Shishkin, 1968, Purla, Gorkiy Province.

**Intervening:** NOG*-SAK.

**F. EUGRINIDAE** Watson, 1940  
C. (MEL*) FW

**First and Last:** Eugyrinus wildi (Woodward, 1891), Lower Coal Measures, Trawden, Lancashire, England, UK.

**F. SAURERPETONTIDAE** Chase, 1965  
C. (FOD*)–P. (ART) FW

**First:** Saurerpeton obtusum (Cope, 1868), referred specimen from Carbondale Formation, Mazon Creek, Illinois, USA (Milner, 1982).

**Last:** Isodectes megalops Cope, 1869, referred specimen (Acheloma casei of Broili, 1913) from Arroyo Formation, Coffee Creek, Texas (Baird, in Welles and Estes, 1969).

**Intervening:** MYA*.

**F. TUPILAKOSAURIDAE** Kuhn, 1960  
Tr. (DIE) ?Mar.

**First and Last:** Tupilakosaurus heilmani Nielsen, 1954, Wordy Creek Formation, Kap Stosch, East Greenland, and Tupilakosaurus wutlensis Shishkin, 1961, Veltuga Series, Spasskoye, Veltuga Basin, former USSR.

**F. BRACHYPOIDAE** Lydekker, 1885  
P. (KAZ-TAT)–J. (CLV) FW

**First:** Bothriceps major Woodward, 1909, Lithghow Coal Measures, Airly, New South Wales, Australia.

**Last:** Ferganobatrachus riabinini Nessov, 1990, Baldansbay Formation, Tashkumyr, Kirgizistan, former USSR.

**Intervening:** GRI–ANS, NOR, BAI/HTH.

**Comments:** Nessov (1990) described Ferganobatrachus as a 'capitosaurid' but the holotype clavicle appears to be brachyopid. Shishkin (1991) has described a brachyopid, Gobiops desertus, from the Upper Jurassic (stage uncertain) of Shara-Teg, Mongolia.

**STEM STEREOSPONDYLS**

**F. ACTINODONTIDAE** Lydekker, 1885  
P. (ASS–UFI) FW (see Fig. 38.2)

**First:** Sclerocephalus bavaricus (Branca, 1886), Altenglan Formation, Kusel Group, Ohmbach, Saarpfalz region, Germany.

**Last:** Syndiodosuchus tetricus Konzhukova, 1956, Inta Formation, Komi, former USSR.

**Intervening:** SAK.

**F. INTASUCHIDAE** Konzhukova, 1953  
P. (ASS/SAK–UFI) FW

**First:** Cheliderpeton vranyi Fritsch, 1877, Broumov Formation, Olšávětín, Czechoslovakia.

**Last:** Intasuchus silvicola Konzhukova, 1956, Inta Formation, Komi, former USSR.

**Intervening:** None.

**F. ARCHEGOSAURIDAE** Lydekker, 1885  
P. (ASS/SAK–TAT) FW

**First:** Archegosaurus decheni Goldfuss, 1847, Lauterecken-Odernheim Formation, Glan Group, Lebach, Saarpfalz region, Germany.

**Last:** Platyposaurus vjuschkovi Gubin, 1989, lower Tatarian, Malaya Kinel' River, Orenburg Region, former USSR; and Platyposaurus sp. (as Platyops sp.) Barberena and Daemon (1974), Rio do Rasto Formation, Para State, Brazil.

**Intervening:** KAZ.

**CROWN-GROUP STEREOSPONDYLS**

**F. RHINESUCHIDAE** Watson, 1919  
P. (KAZ–KAZ/TAT) FW

**First:** Rhinesuchus whatisi Broom, 1908, Tapinocephalus Zone, Cape Province, South Africa.

**Last:** Rhinesuchus africanus (Lydekker, 1890), R. capensis Haughton, 1925, R. bromianus Huene, 1931 and R. rubidgei Broom, 1948, all Cistecephalus Zone, Cape Province, South Africa.

**F. URANOCENTRODONIDAE** Romer, 1947  
P. (TAT)–Tr. (GRI) FW

**First:** Laccocephalus insperatus Watson, 1919 and Lacco­saurus watsoni Haughton, 1925, Daptocephalus Zone, South Africa.

**Last:** Uranocentrodon senekalensis (van Hoepen, 1911), Lystrosaurus Zone, Orange Free State, South Africa.

**F. SCLEROTHORACIDAE** Romer, 1947  
Tr. (SPA) Terr.

**First and Last:** Sclerotherax hypselonotus Huene, 1932, middle Bunter, Queck, Oberhessen, Germany.

**F. WETLUGASAURIDAE** Säve-Söderbergh, 1935  
Tr. (DIE–SPA) FW

**First:** Wetlagasaurus greenlandicus Säve-Söderbergh, 1935, Wordy Creek Formation, Kap Stosch, East Greenland.

**Last:** Wetlagasaurus kizilajensis Ochev, 1966, Zone VI, Andreyevka, Orenburg Province, former USSR.

**Intervening:** None.

**Comments:** Most species of Wetlagasaurus occur in the Veltuga Series of the former USSR which is variously correlated with the Dienerian and the Spathian (Cosgriff, 1984, p. 38). The species quoted above are those of least equivocal stratigraphical position.

**F. CAPITOSAURIDAE** Watson, 1919  
Tr. (GRI/DIE–NOR) FW

**First:** Parotosuchus rewanensis Warren, 1980, P. gunganj Warren, 1980, and P. aliciae Warren and Hutchinson, 1988b, Arcadia Formation, Queensland, Australia (= GRI/DIE); and Parotosuchus madagascariensis (Lehman, 1961),...
Sakamena Formation, Madagascar (= DIE) (Warren and Hutchinson, 1988a).

Last: *Cyclotosaurus carinidens* (Jaekel, 1914) (including *Hercynosaurus carinidens* Jaekel, 1914, *Hemprichisaurus keuperianus* Kuhn, 1939 and *Cyclotosaurus hemprichi* Kuhn, 1942), Knollenmergel, Halberstadt, Germany. This is the latest certain capitosaurid material.  

**Intervening:** SMI–CRN.
Comments: Nessov (1988) reported capitosaurid? material from the Jurassic (CLV) of former Soviet Central Asia, and later described it as *Ferganobatrachus riabinini* (Nessov, 1990). The material is certainly temnospondyl but is not critically diagnostic. The type clavicle appears to belong to a brachyopid.

**F. BENTHOSUCHIDAE** Efremov, 1940  
Tr. (DIE–SPA) FW

**First:** All species of *Benthosuchus* derive from Vetluga Series horizons in the European part of the former USSR. They include: *B. sushkini* (Efremov, 1937), Sharzhenga River, Vologda Province; *B. bashkiricus* Ochev, 1967, Muraptalovo, Bashkirian, former USSR; *B. korobkovi* Ivakhnenko, 1972, Tikhvinskoye, Yaroslavl Province; *B. uralenis* (Ochev, 1966), Blumental Site, Orenburg Province.

**Last:** *Benthosphenus lozovskii* Shishkin, 1979, Zone VI?, Russkiy Island near Vladivostock, former USSR.

**Intervening:** None.

**Comment:** As used here, the family Benthosuchidae (restricted to *Benthosuchus* and *Benthosphenus*) is probably paraphyletic with respect to the Heylerosauridae, Mastodontosauridae, Thoosuchidae, Trematosauridae, Latiscopidae and Metoposauridae.

**F. HEYLEROSAURIDAE** Shishkin, 1980  
Tr. (SMI–SPA/ANS) FW

**First:** *Odenwaldia heidelbergensis* Morales and Kamphausen, 1984, upper Konglomerat Horizon, Middle Buntsandstein, near Heidelberg, Germany.

**Last:** *Eocyclotosaurus woschmidti* Ortlam, 1970, Lower Rot, upper Buntsandstein, Rötfelden, Schwarzwald, Germany.

**Comment:** As used here, the Heylerosauridae is probably paraphyletic with respect to the Heylerosauridae. This family was revised, as the Heylerosaurinae, by Kamphausen (1989).

**F. MASTODONSauridae** Lydekker, 1885  
Tr. (SPA/ANS–CRN) FW

**First:** *Mastodonsaurus cappelensis* Wepfer, 1923, upper Buntsandstein, Kappel, Baden-Württemberg, Germany.

**Last:** *Mastodonsaurus keuperinus* Fraas, 1889, Schilfsandstein, Stuttgart, Germany.

**Intervening:** LAD.

**F. THOOSUCHIDAE** Getmanov, 1982  
Tr. (DIE/SPA) FW

**First and Last:** All thoosuchids derive from the Zone V horizons of European part of the former USSR. They include: *Thoosuchus jakovlevi* (Riabinin, 1926), Vetluga Series, Yaroslavl Province and *Trematotegmen otchewi* Getmanov, 1982, Kyzyl-Say Formation, Orenburg Province.

**Comments:** As used here, the Thoosuchidae is probably paraphyletic with respect to the Trematosauridae. The same stratigraphical ambiguities apply here as for the Wettugasauridae (q.v.).

**F. TREMATOSAURIDAE** Watson, 1919  
Tr. (GRI–CRN) Mar./FW

**First:** *Gonioglyptus longirostris* Huxley, 1865, *Glyptognathus fragilis* Lydekker, 1882, and *Panchetosaurus panchetensis* Tripathi, 1969, are all fragments of long-snouted trematosaurid from the Panchet Formation, Bengal, India (Cosgriff, 1984).

**Last:** *Hyperokynodon keuperinus* Pleninger, 1852, Schilfsandstein, Heilbronn, Baden-Württemberg, Germany (Hellrung, 1987).

**Intervening:** DIE–SPA.

**F. LATISCOPIDAE** Wilson, 1948  
Tr. (CRN–NOR) FW

**First:** *Almasaurus habbazi* Dutuit, 1972, t.5 Beds, Argana Formation, Alma, Morocco.

**Last:** *Latisaurus disjunctus* Wilson, 1948, upper Dockum Group, Texas, USA.

**F. METOPOSAURIDAE** Watson, 1919  
Tr. (LAD–NOR) FW

**First:** *Trigonosternum latum* Schmidt, 1931, Lettenkeuper, Kolleda, Germany. This taxon is a *nomen vanum*, but is nevertheless a metoposaurid. Also from the Lettenkeuper is an undescribed skull from Eschenau, Baden-Württemberg, Germany (Moraes, 1988).

**Last:** *Metoposaurus stuttgartensis* Fraas, 1913, Lehrbergstufe, Stuttgart-Sonnenberg, Germany.

**Intervening:** CRN.

**Comments:** Murry (1987) suggested that metoposaurid material from the Redonda Formation, Apache Canyon, New Mexico, USA, was post-Carnian and might prove to be Hettangian. Hunt and Lucas (1990) have argued that this site is late Triassic (Norian) in age.

**F. LYDEKKERINIDAE** Watson, 1919  
Tr. (GRI–SMI) FW

**First:** *Lydekkerina huxleyi* (Lydekker, 1889), and *Limnoiketes paludinatans* Parrington, 1948, both *Lystrosaurus* Zone, Orange Free State, South Africa.

**Last:** *Chomatobatrachus halei* Cosgriff, 1974, Knocklofty Formation, Tasmania, Australia.

**Intervening:** DIE.

**Comments:** As used here and elsewhere, the Lydekkerinidae (comprising Lydekkerina, Limnoiketes, Luzocephalus and Chromatobatrachus) is probably paraphyletic with respect to the Rhytidosteidae.

**F. RHYTIDOSTEIDAE** Huene, 1920  
Tr. (GRI–SPA) FW/Mar./Terr.

**First:** *Pneumatostega potamica* Cosgriff and Zawiskie, 1979, *Lystrosaurus* Zone, Cape Province, South Africa; and *Indobrachyops panchetensis* Huene and Sahni, 1958, Panchet Formation, Bengal, India.

**Last:** *Laidleria gracilis* Kitching, 1957, *Cynognathus* Zone, Cape Province, South Africa.

**Intervening:** DIE–SMI.

**F. CHIGUTISaurIDAE** Rusconi, 1951  
Tr. (GRI–DIE)–K. (BER/ALB) FW

**First:** *Keratobrachyops australis* Warren, 1981, Arcadia Formation, Queensland, Australia.

**Last:** Unnamed material, Strzelecki Formation, Victoria, Australia (Jupp and Warren, 1986).

**Intervening:** CRN, NOR, PLB/TOA.

**THE ERYOPID–DISSOROPHOID GROUP**
F. ZATRACHYDIDAE Cope, 1882  
P. (ASS—ART) FW  
First: *Acanthostomatops vorax* (Credner, 1883), Niederhäslich-Schweinsdorf Beds, Niederhäslich, Germany.  
Last: *Zatracys* sp., Arroyo Formation, Coffee Creek, Texas, USA (Murry and Johnson, 1987).  
Intervening: SAK.  
Comments: Most North American zatrachydids are either former USSR or of uncertain stratigraphical position. The late record is one of relatively secure stratigraphical position.  
F. ERYOPIDAE Cope, 1882  
C. (KRE/NOG*)—P. (UFI) FW/Terr.  
First: *Eryops avinoffi* (Romer, 1952), Conemaugh Group, Pennsylvania, USA.  
Last: *Clamorosaurus nocturnus* Gubin, 1983, Sheshminsky Horizon, and *C. borealis* Gubin, 1983, Inta Formation, Komi, former USSR.  
Intervening: ASS—ART.  
First: *Clamorosaurus nocturnus* Gubin, 1983, Sheshminsky Horizon, and *C. borealis* Gubin, 1983, Inta Formation, Komi, former USSR.  
Intervening: ASS—ART.  
F. PARIJOXYIDAE Moustafa, 1955  
P. (SAK—ART) Terr.  
First: *Parioxyx bolii* Carroll, 1964, Archer City Formation, Archer City Bone bed, Texas, USA.  
Last: *Parioxyx ferriculosis* Cope, 1878, Petrolia Formation, Texas, USA.  
Intervening: None.  
F. PELTOBATRACHIDAE Kuhn, 1960  
P. (KAZ/TAT) Terr.  
First and Last: *Peltobatrachus pustulatus* Panchen, 1959, Kawinga Formation, Ruhuhu Valley, Tanzania.  
F. PLAGIOSAURIDAE Jaekel, 1914  
Tr. (GRI/DIE—RHT) FW  
First: *Plagiobatrachus australis* Warren, 1985, Arcadia Formation, Queensland, Australia.  
Intervening: SPA—NOR.  
F. TREMATOPIDAE Williston, 1910  
C. (DOR*)—P. (ART) Terr.  
First: *Actiobates peabodyi* Eaton, 1973, Stanton Formation, Garnett, Kansas, USA (Berman et al., 1987a).  
Last: *Acheloma cumminsi* Cope, 1882, Arroyo Formation, Coffee Creek, Texas, USA.  
Intervening: NOG*—SAK.  
F. DISSOROPHIDAE Boulenger, 1902  
C. (MYA*)—P. (KAZ) Terr.  
First: *Stegops newberryi* (Cope, 1875), Allegheny Group, Linton, Ohio, USA (Hook and Baird, 1986). Although widely cited as an early zatrachydid, undescribed material shows this to be an armoured dissorophid (R. Hook, pers. comm.). The earliest dissorophid described as such is: *Astreptorhachis ohiensis* Vaughn, 1971, Conemaugh Group (= KRE/NOG*), Wayne Township, Ohio, USA.  
Last: *Kamacops acrivalis* Gubin, 1980, Belebej Formation, Perm and Orenburg Provinces, former USSR.  
Intervening: KRE/NOG*—UFI.  
F. MICROPHOLIDAE Watson, 1919  
Tr. (GRI) Terr./FW  
F. MICROMELERPETONTIDAE Boy, 1972  
C. (MYA*)—P. (SAK/ART) FW  
First: *Limnogninus elegans* (Fritsch, 1881), Gaskohle, Kladno Formation, Nýřany, Czechoslovakia.  
Last: *Eimerosaurus ('Tersomius') graumanni* (Boy, 1980), lower Wadern Beds, Nahe Group, Nahe Group, Germany.  
Intervening: KLA/NOG*—SAK.  
F. BRANCHIOSAURIDAE Fritsch, 1883  
C. (MYA*)—P. (SAK/ART) FW  
First: *Branchiosaurus salamandroides* Fritsch, 1876, Gaskohle, Kladno Formation, Nýřany, Czechoslovakia.  
Last: *Melanerpeton* sp. (as *Branchiosaurus* sp.), Prosečné Formation, Horní Kalná, Czechoslovakia (Maňourová 1981).  
Intervening: KLA*—SAK.  
F. AMPHIBAMIDAE Moodie, 1910  
C. (POD*)—P. (ART) Terr./FW  
First: *Amphibamus grandiceps* Cope, 1865, Carbondale Formation, Mazon Creek, Illinois, USA.  
Last: *Delerpeton annectens* Bolt, 1969, Upper Garber Formation, Fort Sill fissures, Oklahoma, USA.  
Intervening: MYA*—ASS—SAK.  
Crown division LISSAMPHIBIA Haeckel, 1866  
The most recent major summary of data on lissamphibians is that of Duellman and Trueb (1986) and the recent families used in the following section are those used in that work. The higher-group taxonomy and the indeterminate position of the Albanerpetontidae follows Milner (1988).  
**Superorder** GYMNOPHIONA Rafinesque, 1814  
**GYMNOPHIONA incertae sedis** J. (SIN)  
First: Undescribed material, family undesigned, Kayenta Formation, Arizona, USA (Jenkins and Walsh, 1990).  
Comments: The earliest described specimen is an unnamed vertebra, indeterminate at family level, unnamed formation (=MAA), Triupampa, Bolivia (Rage, 1986).  
F. RHINOTREMATICHAUSSBAUM, 1977  
**Extant** Terr.  
F. ICHTHYOPHIDAE Taylor, 1968 **Extant** Terr.  
F. URAEOTYPHLIDAE Nussbaum, 1979  
**Extant** Terr.  
F. SCOLECOMORPHIDAE Taylor, 1969  
**Extant** Terr.  
F. CAECILIIDAE Gray, 1825  
T. (THA)—Rec. Terr.  
Extant Intervening: None.  
F. TYPHLONEGCTIDAECope, 1875  
**Extant** Terr.  
Superorder BATRACHIA Bronniant, 1799
**Order SALIENTIA Laurenti, 1768**

There is no recent review of all fossil frogs. The latest major source of data on Mesozoic and some Cenozoic fossil frogs is Estes and Reig (1973).

**F. TRIADOBATRACHIDAE Kuhn, 1962**

Tr. (DIE) FW.

**First and Last:** *Triadobatrachus massinoti* (Piveteau, 1936), marine shales, Betsieka, Madagascar (Rage and Roček, 1989).

**Crown order ANURA Rafinesque, 1815**

F. ANURA incertae sedis J. (HET/TOA)

**First:** *Vieraella herbstii* Reig, 1961, Roca Blanca Formation, Santa Cruz Province, Argentina.

**Comment:** This is the earliest fossil with the suite of anuran skeletal characters, and merits inclusion for this reason even though it is not placed in a family. Estes and Reig (1973) placed it in the Leiopelmatidae (under the synonym Ascaphidae) and most subsequent authors have followed them. However, that position was entirely based on primitive characters and *Vieraella* could equally be a 'stem frog' with no immediate relationship to any living family. For this reason it is left as Anura incertae sedis.

**Suborder DISCOGLOSSOIDEI Sokol, 1977**

F. LEIOPELMATIDAE Mivart, 1869

J. (ITH)-Rec. FW

**First:** *Notobatrachus degiustoi* Reig, 1955, La Matilde Formation, Santa Cruz Province, Argentina. Extant

**Intervening:** None.

F. DISCOGLOSSIDAE Guenther, 1859

J. (BTH)-Rec. FW

**First:** *Eodiscoglossus oxoniensis* Evans et al., 1990, Forest Marble Formation, Kirtlington, Oxfordshire, England, UK. Extant

**Intervening:** TTH, BER/VAL, BRM/APT, MAA-DAN, PRB-RUP, AQ/T-SRV, ZAN-PLE.

**Suborder RANOIDEI Sokol, 1977**

**Superfamily PIPOIDEA Fitzinger, 1843**

F. PIPIDAE Gray, 1825

K. (HAU?)–Rec. FW

**First:** *Shomronella jordanica* Estes et al., 1978, Tayasir Formation, Shomron, Israel. Extant

**Intervening:** BRM, SAN/CMP, THA, RUP, BUR/LAN.

F. RHINOPHRYNIDAE Guenther, 1859

T. (THA)–Rec. Terr.

**First:** *Eorhinophrynus* sp., Fort Union Formation, Princeton Quarry, Wyoming, USA (Estes, 1975). Extant

**Intervening:** LUT, RUP, PLE.

F. RHINODERMATIDAE Bonaparte, 1850

**Extant**

F. PSEUDIDAE Fitzinger, 1843

Extant FW

F. HYLIDAE Gray, 1825

T. (THA)–Rec. Terr./FW

**First:** *Bufonidae* sp. Undescribed material from the Itaborai Fissures, Rio de Janeiro Province, Brazil (Estes and Reig, 1973). Extant

**Intervening:** AQ/T–TOR, ZAN–PLE.

F. BRACHYCEPHALIDAE Guenther, 1859

**Extant**

F. RHINODERMATIDAE Bonaparte, 1850

**Extant**

F. PSEUDIDAE Fitzinger, 1843

**Extant** FW/Terr.

F. HYLIDAE Gray, 1825

T. (THA)–Rec. Terr./FW
### Key for both diagrams.

1. Pelobatidae  
   ANTHRACOSAURIA
2. Pelodytidae  
   22. Eoherpetontidae
3. Myobatrachidae  
   23. Gephyrostegidae
4. Leptodactylidae  
   24. Proterogyrinidae
5. Bufonidae  
   25. Anthracosauridae
6. Hylidae  
   26. Eogyrinidae
7. Ranidae  
   27. Archeriidae
8. Rhachophoridae  
   28. Chroniosuchidae
9. Microhylidae  
   SEYMOURIA-
   CAUDATA
10. Caudata Incertae sedis  
   29. Seymouriidae
11. Karauridae  
   30. Discosaurusidae
12. Sirenidae  
   URODELA
13. Cryptobranchidae  
   31. Leptorhynchoidea-
   MORPHA
14. Proteidae  
   32. Enosuchidae
15. Batrachosaurusidae  
   33. Nycterothelyridae
16. Scapherpetontidae  
   34. Tokosaurusidae
17. Amphiumidae  
   35. Lanthanosuchidae
18. Plethodontidae  
   36. Limnoscelidae
19. Ambystomatidae  
   37. Solenodonsauridae
20. Salamandridae  
   38. Tseajaiidae
21. Albanerpetontidae  
   39. Diadectidae

### Fig. 38.3

First: Undescribed material from the Itaborai Fissures, Rio de Janeiro Province, Brazil (Estes and Reig, 1973). **Extant**

Intervening: RUP, AQT, ZAN, PLE.

F. CENTROLENIDAE Taylor, 1951 **Extant** Terr.

F. DENDROBATIDAE Cope, 1865 **Extant** Terr.

**Superfamily** RANOIDEA Fitzinger, 1826

F. RANIDAE Gray, 1825 T. (PRB)–Rec. FW/Terr.

First: Unnamed ranid material from Rohiac-equivalent horizon, Grisolles, France (Rage, 1984). **Extant**

Intervening: RUP, AQT–BUR/LAN, ZAN–PLE.

F. HYPEROLIIDAE Laurent, 1943 **Extant** Terr.

F. RHACHOPHORIDAE Hoffman, 1932 Q. (PLE)–Rec. Terr.


**Superfamily** MICROHYLOIDEA Duellman, 1975


First: *Gastrophryne* cf. *G. carolinensis*, Thomas Farm deposits, Gilchrist County, Florida, USA (Holman, 1965). **Extant**

Intervening: PLE

**Order** CAUDATA Oppel, 1811

The most recent major review of fossil caudates is Estes (1981). Later work by Nessov is summarized in Nessov (1988).
Fig. 38.3

F. CAUDATA incertae sedis J. (BTH) FW
First: Marmorerpeton kermacki and M. freemani Evans et al., 1988, Forest Marble Formation, Kirtlington, Oxfordshire, England, UK.

F. KARAURIDAE Ivakhnenko, 1978 J. (BTH–KIM) FW?
First: Kokartus honorarius Nessov, 1988, black and red shales, Kizylsu River, Kirghizia, former USSR.
Last: Karaurus sharovi Ivakhnenko, 1978, Karabastau Formation, Kazakhstan, former USSR.
Intervening: None.

Crown order URODELA Latreille, 1825

F. SIRENIDAE Gray, 1825 K. (CMP)-Rec. FW
Extant
Intervening: MAA–THA, LUT, AQT–LAN, MES/ZAN, PLE.
Comment: The ‘sirenid’ material reported from the Liassic Kota Formation of India (Yadagiri, 1986) is not diagnostically urodelan.

F. HYNOBIIDAE Cope, 1859 Extant FW

F. CRYPTOBRANCHIDAE Fitzinger, 1826 T. (THA)–Rec. FW
Extant
Intervening: YPR, PRI–CHT, BUR–PLE.

F. PROTEIDAE Gray, 1825 T. (THA)–Rec. FW
First: Necturus krausei Naylor, 1978, upper Ravenscrag Formation, Saskatchewan, Canada.
Extant
Intervening: LAN/SRV, PIA–PLE.

F. BATRACHOSAUROIDIDAE Auffenberg, 1958 J. (TTH)–T. (ZAN) FW
First: Unnamed material from the Freshwater Member, Purbeck Limestone Formation, Langton Matravers, Dorset, England, UK (Ensom et al., 1991).
Last: Peratosauroides problematica Naylor, 1981, ‘San Pablo’ Formation, California, USA.
Intervening: CON, CMP–LUT, AQT–LAN.
Comment: The earliest fully described batrachosauroidid is Mynbulakia surgayi Nessov, 1981, Middle Taikarshin Beds (= CON), Dzharakhuduk, former USSR.

F. DICAMPTODONTIDAE Tihen, 1958 Extant FW
Ambystomichnus montanensis (Gilmore, 1928) from the Palaeocene of Montana is frequently cited as a dicamptodont footprint trail, but I have excluded it as not susceptible to further phylogenetic investigation. Estes (1981) has included a series of four fossil genera in the Dicamptodontidae, namely Bargmannia Herre, 1955, Chrysotriton Estes, 1955, Geyeriella Herre, 1950 and Woltersdorfiella Herre, 1950. All of them have a vertebral structure similar to that of Dicamptodon, but this is a gradistic resemblance and not a cladistic one.

F. SCAPERPETONTIDAE Auffenberg and Goin, 1959 Extant FW
Extant
Intervening: YPR, PRI–CHT, BUR–PLE.

F. AMPHIUMIDAE Gray, 1825 K. (MAA)–Rec. FW
F. PROTEROGYRINIDAE Romer, 1970
C. (BRI–PND) FW
First: Proterogyrinus scheeli Romer, 1970, Bluefield Formation, Greer, West Virginia, USA.

F. ANTHRACOSAURIDAE Cope, 1875
C. (MEL*–KS*) Terr.
Last: Anthracosaurus russeli Huxley, 1863, referred material from Low Main Seam, upper Modiolaris Zone, Newsham, Northumberland, England, UK.

Intervening: VRK*

F. EOGYRINIDAE Watson, 1929
C. (CHE*)–P. (UFI) FW
First: Pholiderpeton scutigerum Huxley, 1869, Black Coal Bed, Tofthaw, Yorkshire, England, UK.
Last: Aversor dmitrievi Guibin, 1985, Sheshma Horizon, Komi, former USSR.

Intervening: MEL*–KSK*, MYA*, CHVIDOR*, ASS.

Comment: Several earlier poor embolomere specimens have been attributed to the Eogyrinidae but none is diagnosis eogyrinid. The earliest of these is ‘Pholiderpeton bretonense’ Romer, 1958, Point Edward Formation, Nova Scotia, Canada.

F. ARCHERIIDAE Kuhn, 1965
C. (MYA*)–P. (ART) FW
First: Undescribed archeridi, Linton, Ohio, USA (reported but not described by Hook and Baird, 1986: p. 183).
Last: Archeria cassinensis (Cope, 1884), referred material from middle Garber Formation, Cotton County, Oklahoma, USA (Holmes, 1989).

Intervening: ASS–SAK.

F. CHRONIOSUCHIDAE Viushkov, 1957
P. (TAT) FW/Terr.
First and Last: All known chroniosuchids are from upper TAT horizons in the former USSR. The genera and species are: Chroniosuchus mirabilis Viushkov, 1957, Gorkiy and Orenburg Provinces; C. paradoxus Viushkov, 1957, Pronkino, Orenburg Province; C. licharevi (Riabinin, 1962), Sokolki, Arkhangel Province, and Chroniosaurus dongusensis Tverdokhlebova, 1972, Donguz River, Orenburg Province.

Order SEYMOURIAMORPHA Watson, 1917
Information on Russian material is mainly derived from Ivakhnenko, 1987.

Suborder SEYMOURIIDA Tatarinov, 1971
F. SEYMOURIIIDAE Williston, 1911
P. (ASS–TAT) Terr./FW
First: Seymouria sanjuanensis Vaughn, 1966, referred material from Cutler Formation, New Mexico, USA, equivalent to Archer City Formation of Texas (Berman et al., 1987b).
Last: A wide range of seymouriids sensu Ivakhnenko (1987) (i.e. including the kotlassiids) occur in formations of
Zone IV Permian (= TAT) in pre-Ural former USSR. These include: Kotlassia prima Amalitsky, 1921, Arkhangelsk Province; and Karpinskiosaurus secundus (Amalitsky) Sushkin, 1925, Arkhangelsk Province.

**Intervening:** SAK–KAZ.

**F. DISCOSAURISCIDAE** Romer, 1947

C. /P. (???)–P. (KAZ/TAT) FW

**First:** Utegenia schipinari Kuznetsov and Ivakhnenko, 1981, Alma-Ata, Kazakhstan, former USSR, may be late Carboniferous or early Permian in age.

**Last:** Discosauriscus netschaevi (Riabinin, 1911), Orenburg Province, former USSR.

**Intervening:** ASS/SAK–ART.

**Comment:** Many discosaurusids derive from basins in Central Asia which are poorly correlated with those of Europe.

**Suborder** LEPTOROPHIDA Ivakhnenko, 1987

**F. LEPTOROPHIDAE** Ivakhnenko, 1987

P. (KAZ–TAT) FW/Terr?

**First:** Leptoropa talonophora (Tchudinov, 1955), Shikovo-Cherki, Kirov Province, former USSR.

**Last:** Raphanodon ultimus (Tchudinov and Viushkov, 1956), Pronkino, Orenburg Province; and R. tverdokhlebovae Ivakhnenko, 1987, Donguz VI, Orenburg Province, former USSR.

**F. ENOSUCHIDAE** Konzhukova, 1955

P. (TAT) FW

**First and Last:** Enosuchus breviceps Konzhukova, 1955, Isheevko, Tatarian, former USSR.

**Order** NYCTEROLETEROMORPHA Ivakhnenko, 1987

Information on this order is mainly derived from Ivakhnenko (1987).

**Suborder** NYCTEROLETERIDERA Tatarinov, 1972

**F. NYCTEROLETERIDAE** Romer, 1956

P. (KAZ–TAT) Terr.

**First:** Nycteroleter bashkircus Efremov, 1940, Belebey, Bashkirian, former USSR; and N. kassini Tchudinov, 1955, Shikhovo-Cherki, Kirov Province, former USSR.

**Last:** Nycteroleter ineptus Efremov, 1938 and Macroleter poecicus Tverdokhlebova and Ivakhnenko, 1984, both from Mezen River Basin, Arkhangelsk Province, former USSR.

**F. TSEAJAIDAE** Vaughn, 1964

P. (KRE/CHV*) FW

**First and Last:** Tseajaia campi Vaughn, 1964, Organ Rock Shale, Utah, USA.

**F. DIADECTIDAE** Cope, 1880

C. (KRE/CHV*)–P. (ART) Terr.

**First and Last:** Solenodonaurus janensis Broili, 1924, Gaskohle, Klado Formation, Nýřany, Czechoslovakia.

**F. TSEAJAIDAE** Vaughn, 1964

P. (ART) Terr.

**First and Last:** Tseajaia campi Vaughn, 1964, Organ Rock Shale, Utah, USA.

**F. DIADECTIDAE** Cope, 1880

C. (MYA*) Terr.

**First and Last:** Solenodonaurus janensis Broili, 1924, Gaskohle, Klado Formation, Nýřany, Czechoslovakia.

**F. TSEAJAIDAE** Vaughn, 1964

P. (ART) Terr.

**First and Last:** Tseajaia campi Vaughn, 1964, Organ Rock Shale, Utah, USA.

**F. DIADECTIDAE** Cope, 1880

C. (KRE/CHV*)–P. (ART) Terr.

**First and Last:** Desmatodon hollandi Case, 1908, Conemaugh Group, Pennsylvania, USA; and Desmatodon hesperis Vaughn, 1969, Sangre de Cristo Formation, Colorado, USA.

**Last:** Diadectes sp. Vale Formation, Taylor County, Texas (Olson and Mead, 1982).

**Intervening:** ASS–SAK.

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REPTILIA
M. J. Benton

The stratigraphical assignments of many of the terrestrial deposits containing fossil reptiles were difficult because of doubtful correlations with the marine standard stages summarized in Harland et al. (1982, 1990). This is particularly true for the Carboniferous and Lower Permian. Assignments of the Carboniferous units are based on Carroll (1984) and Milner (1987), and the Lower Permian formations of the south-western United States were dated according to summary tables in Olson and Vaughn (1970), Hentz (1989) and Hook (1989). The stage-level ages of many terrestrial Mesozoic formations were obtained from Weishampel's (1990) compilation on dinosaurian localities, and many Cainozoic ages were based on Savage and Russell's (1983) compilation of mammalian faunas. Note that the Guimarota locality in Portugal is accepted as Oxfordian in age on the basis of several lines of evidence, rather than the oft-quoted Kimmeridgian (see Evans, 1989), although the question is not settled.

Faunal zones in South Africa have been revised recently. The scheme used here (Rubidge, 1992) is:

- **Eodicynodon-Tapinocaninus Assemblage Zone** (= lower part of the *Tapinocephalus* Zone, and lower portion of the Dinocephalian Assemblage Zone of Keyser and Smith (1979)).
- **Tapinocephalus-Brady­saurus Assemblage Zone** (= middle part of the *Tapinocephalus* Zone, and upper portion of the Dinocephalian Assemblage Zone of Keyser and Smith (1979)).
- **Pristerognathus-Dictodon Assemblage Zone** (= 'upper' *Tapinocephalus* Zone).
- **Tropidostoma-Endothiodon Assemblage Zone** (= *Endothiodon* Zone, or *Tropidostoma micro trema* Assemblage Zone of Keyser and Smith (1979)).
- **Aulacephalodon-Cistecephalus Assemblage Zone** (= *Cistecephalus* Zone, or Aulacephalodon baini Assemblage Zone of Keyser and Smith (1979)).
- **Dicynodon-Theriognathus Assemblage Zone** (= *Daptocephalus* Zone, or *Dicynodon lacerticeps* Assemblage Zone of Keyser and Smith (1979)).
- **Lystrosaurus-Procolophon Assemblage Zone** (= *Lystrosaurus* Zone).
- **Cynognathus-Diademodon Assemblage Zone** (= *Cynognathus* Zone, or Kannemeyeria Assemblage Zone of Keyser and Smith (1979)).

Paraphyletic taxa are indicated by (p).

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**Series AMNIOTA**

**AMNIOTA incertae sedis**

F. **UNNAMED** C. (VIS) Terr. (see Fig. 39.1)

**First and Last:** *Westlothiana lizziae* Smithson and Rolfe, 1991, East Kirkton Limestone, Brigan­tian, West Lothian, Scotland, UK.

**Comment:** This specimen is said to be the oldest reptile, but the preliminary description (Smithson, 1989) did not indicate a familial assignment.

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**F. BOLOSaurIDAE Cope, 1878**

P. (ART-KAZ) Terr.

**First:** *Bolosaurus striatus* Cope, 1878, lower Wichita Beds, Texas, USA.


**F. ACLEISTORHINIDAE Daly, 1969**

P. (ART) Terr.
First and Last: Acleistorhinus pteroticus Daly, 1969, Garber Formation, Oklahoma, USA.


First and Last: Eunotosaurus africanus Seeley, 1892, Abrahamskraal Formation, Tapinocephalus-Bradysaurus Assemblage Zone, Beaufort West, Karoo Basin, South Africa.

Class REPTILIA Laurenti, 1768 (p)

Subclass ANAPSIDA Williston, 1917

The Procolophonidae have been proposed (Reisz and Laurin, 1991) as the closest known sister group of the Testudines. The Nyctiphruretidae are generally reckoned to be close relatives of the Procolophonidae, so they are placed here. The Captorhinidae were earlier (Gaffney and McKenna, 1979) proposed as turtle relatives, but Reisz and Laurin (1991) regard them as more distant than the procolophonids.

General information on the stratigraphical distribution of early anapsids was obtained from Kuhn (1969) and Anderson and Cruickshank (1978). The Mesosauridae, Milleretidae, Procolophonidae and Pareiasauridae were tentatively included in a new clade ‘Parareptilia’ by Gauthier et al. (1988). However, the Procolophonidae have been removed to the Anapsida, as a close sister group of the Testudines (Reisz and Laurin, 1991), and the Pareiasauridae and others may follow suit (P. S. Spencer, pers. comm., 1993).


First and Last: Mesosaurus tenuidens Gervais, 1865, White Band, Ecca Group, South Africa, White Band equivalent, south-western Africa, and Irati Formation, Passa Dois Group, Paraná Basin, Brazil.

### Reptilia

#### Key for both diagrams

1. Westlothiana  
2. Bolosauridae  
3. Cleistostoma  
4. Eunotosauridae  
5. Mesosaurus  
6. Milleretidae  
7. Pareiasauridae  
8. Captorhinidae  
9. Nyctiphruretidae  
10. Procolophonidae  
11. Proganochelyidae  
12. Pareiasauridae  
13. Dermochelyidae  
14. Pelomedusidae  
15. Chelidae  
16. Kayentachelyidae  
17. Pterosternidae  
18. Baenidae  
19. Plesiochelyidae  
20. Meiolaniidae  
21. Sinemyidae  
22. Chelydridae  
23. Toxochelyidae  
24. Unnamed  
25. Cheloniidae  
26. Osteopygidae  
27. Desmatochelyidae  
28. Protostegidae  
29. Dermochelyidae  
30. Trionychidae  
31. Carettochelyidae  
32. Nanhsiungchelyidae  
33. Adocidae  
34. Dermatemydidae  
35. Kinosternidae  
36. Emydidae  
37. "Bataguridae"  
38. Testudinidae  
39. Protorothyrididae  
40. "Bataguridae"  
41. Drepanosauridae  
42. Mesenosauridae  
43. Mesenosauridae  
44. Mesenosauridae  
45. Weigeltisauridae  
46. Claudiosauridae  
47. Chelidae  
48. Galesphryidae  
49. Apisaurus  
50. Paliguaniidae  
51. Monjurosuchidae  
52. Nanchangosauridae

#### Fig. 39.1

**First:** Broomia perplexa Watson, 1914, Tapinocephalus–Bradysaurus Assemblage Zone, Karoo Basin, South Africa.

**Last:** Millerretta rubidgei Broom, 1938, and three or four other possible species, Aulacephalodon–Cistecephalus Assemblage Zone, Karoo Basin, South Africa.

**F. PAREIASAURIDAE** Cope, 1896  
**P. (UFI–TAT)** Terr.

**First:** ?Rhiphaeosaurus tricuspidens Efremov, 1940, Leptorophanojilovi Chudinov, 1955 and Parabraodysaurus udmurticus Efremov, 1954, all from Zone II, Bashkir Republic and Kirov Province, former USSR.

**Last:** Pareiasaurus serridens Owen, 1876, Dichydron–Theriochelys Assemblage Zone of the Karoo Basin, South Africa, and several other species from that formation, and equivalents, in the former USSR, China and Scotland, UK.

**Intervening:** KAZ.

**F. CAPTORHINIDAE** Case, 1911  
**P. (SAK–TAT)** Terr.

**First:** Romeria primus Clark and Carroll, 1973, Moran Formation, Wichita Group, Archer County, Texas, USA (Clark and Carroll, 1973).

**Last:** Moradasaurus grandis Ricolès and Taquet, 1982, Moradi Formation, Niger, and Protocaptorhinus sp., Middle Madumabisa Mudstones, Middle Zambezi Basin, Zimbabwe (Gaffney and McKenna, 1979).

**Intervening:** ART–KAZ.

**F. NYCTIPHURETIDAE** Efremov, 1938  
**P. (UFI–KAZ)** Terr.

**First:** Nyctiphruretus acudens Efremov, 1938, Zone III, Mesen district, former USSR.

**Last:** Barasaurus besairiei Piveteau, 1955, ?Upper Permian, Madagascar.

**Comment:** It has been assumed that nyctiphruretids and procolophonids are related, but the material is poorly known. Nyctiphruretus may be related to procolophonids, but Barasaurus shows no clear affinities (P. S. Spencer, pers. comm., 1992).

**F. PROCOLOPHONIDAE** Cope, 1889  
**P. (KAZ)–Tr. (NOR)** Terr.

**First:** Owenetta rubidgei Broom, 1939, Aulacephalodon–Cistecephalus Assemblage Zone, South Africa.

**Last:** Hypsognathus fenneri Gilmore, 1928, upper Passaic Formation, New Jersey and Pennsylvania, USA.

**Intervening:** ANS–CRN.

**Comment:** Sphodrosaurus pennsylvanicus Colbert, 1960, also upper Passaic Formation, New Jersey and Pennsylvania, USA, seems to be a diapsid, while the RHT or latest NOR ‘procolophonoid’ described by Cuny (1991) from the St Nicolas de Port locality in France is incorrectly identified (P. S. Spencer, pers. comm., 1992).

**Order** TESTUDINES Batsch, 1788

The classification of turtles used here is based on that of Gaffney and Meylan (1988), and information on stratigraphical distributions comes from Młynarski (1976), de Broin (1988) and Gaffney (1990). Authors of familial names are based on those authors, with corrections from Bour and Dubois (1984).
Animals: Vertebrates

F. PROGANOCHELYIDAE Baur, 1888

Tr. (NOR)–J. (HET) Terr./FW

First: *Proganochelys quenstedtii* Baur, 1887, Mittlere and Obere Stubensandstein, Baden-Württemberg and Halberstadt, Germany.

Last: Unnamed proganochelyid, upper Elliot Formation (Red Beds), Orange Free State, South Africa (Gaffney, 1986).

Comment: The age of *P. ruchae* is assumed to be equivalent to the German formations, but that is not certain.

Suborder PLEURODIRA Cope, 1868

F. PROTEROCHERSIDAE Nopcsa, 1928

Tr. (NOR) Terr./FW

First and Last: *Proterochersis robusta* E. Fraas, 1913, Untere Stubensandstein, Baden-Württemberg, Germany.

F. PLATYCHELYIDAE Bram, 1965

J. (OXF–TTH) FWfferr.


Last: *Platychelys oberndorferi* A. Wagner, 1853, Solothurn, Switzerland.

Intervening: KIM.

F. PELOMEDUSIDAE Cope, 1868

K. (APT)–Rec. FW/Mar.

First: *Araripemys barretoi* Price, 1975, Santana Formation, Brazil. Extant


Comment: Following Gaffney and Meylan (1988), the podocnemines and bothremydines are included here in the Pelomedusidae. Other authors, however, maintain the Podocnemidae Baur, 1888 (ALB–Rec) and Bothremyidae Baur, 1891 (ALB–YPR) as separate families (Antunes and de Broin, 1988; de Broin, 1988).

F. CHELIDAE Lindholm, 1929 (Gray, 1825)

T. (Eoc.)–Rec. FW

First: Unnamed form, Eocene, Tasmania, Australia (Gaffney, 1992). Extant


Comment: The oldest records of chelids given by de Broin (1988) are based on indeterminate material of uncertain age. The next oldest chelids noted by de Broin (1988, p. 136) are several species from the Campanian (Upper Cretaceous) and Palaeocene of Chubut Province, Argentina, but Gaffney (pers. comm.) regards these as pelomedusids. De Broin (1988, p. 138) also notes the chelid *Hydromedusa* sp. Wagler 1830, from the Upper Eocene of Chubut Province, Argentina. Gaffney (1975, 1990) indicates that the oldest chelid is Eocene.

Suborder CRYPTODIRA Gaffney et al., 1987

Infra-order SELMACRYPTODIRAE Gaffney et al., 1987

Superfamily PLEUROSTEROIDEA Romer, 1956

F. PLEUROSTERNIDAE Cope, 1868

J. (KIM/TTH)–T. (DAN) Mar./FW

First: *Glytops plicatulus* (Cope, 1877), Morrison Formation, Colorado, USA (Gaffney, 1979).

Last: *Compsemys victa* Leidy, 1859, Torrejonian, San Juan Basin, New Mexico, USA (Hutchison, 1987).

Intervening: BER, MAA.

Superfamily BAENOIDEA Williams, 1950

F. BAENIDAE Cope, 1882

K. (ALB)–T. (BRT) FW

First: *Trinitichelys hiatti* Gaffney, 1972, Trinity Sand, Trinity Group, Montague County, Texas, USA.

Last: *Chisternon undatum* (Leidy, 1871) and *Baena arenosa* Leidy, 1870, both with types from the Bridger Formation of Wyoming and Utah, but latest records from the Uinta Formation of Utah, USA (Gaffney, 1972).

Intervening: CMP–LUT.

Infra-order STEM POLYCRYPTODIRAE

F. PLEISOCHELYIDAE Rütimeyer, 1873


First: *Plesiochelys etalloni* (Pictet and Humbert, 1857), Kimmeridgian, Solothurn, and other localities, Switzerland (Gaffney, 1975).


F. MEIOLANIIDAE Lydekker, 1887

K. (MAA?)–Q. (PLE) Terr.


Last: *Meiolania platyceps* Owen, 1881, *M. mackayi* Anderson, 1925, and *M. oweni* Woodward, 1888, Pleistocene of Lord Howe Island, Walpole Island (New Caledonia), and Queensland and New South Wales, Australia, respectively (Gaffney, 1981).

Intervening: YPR?, MAA (?) (Chikhvadze, 1988).

Infra-order POLYCRYPTODIRAE

F. SINEMYIDAE Wiman, 1930

J. (KIM–TTH)–Rec. FW

First: *Sinemys lens* Wiman, 1930, Upper Jurassic, China.

Last: *Protochelydra zangerli* Erickson, 1973, Tongue River Formation, Billings County, North Dakota, USA (Erickson, 1973).

Intervening: TTH, APT, ALB, CMP, MAA (?) (Chkhivadze, 1988).

Superfamily CHELYDROIDEA Gaffney and Meylan, 1988

F. CHELYDRAEIDAE Gray, 1831

K. (TUR)–Rec. FW

First: *Sinemyidae* Wiman, 1930, Upper Jurassic, China.

Last: *Protochelydra zangerli* Erickson, 1973, Tongue River Formation, Billings County, North Dakota, USA (Erickson, 1973).

Intervening: TTH, APT, ALB, CMP, MAA (?) (Chkhivadze, 1988).

Suborder CRYPTODIRA Cope, 1868

Infra-order STEM SELMACRYPTODIRAE

F. KAYENTACHELYIDAE Gaffney et al., 1987

J. (SIN/PLB) Terr./FW

First and Last: *Kayentachelys aprix* Gaffney et al., 1987, Kayenta Formation, Coconino County, Arizona, USA (Gaffney et al., 1987).
Superfamily CHELONIOIDEA Baur, 1889

First and Last: Toxochelys latiremis Cope, 1873, Niobrara Formation, Kansas, USA.

First and Last: Ctenochelys tenuitesta Zangerl, 1953 and C. acris Zangerl, 1953, Selma Formation, Alabama, USA.

First: Dollochelys ('Toxochelys') atlantica (Zangerl, 1953), Hornerstown Formation, Gloucester County, New Jersey, USA. Extant
Intervening: DAN-PLE.

First: Osteopygis emarginatus Cope, 1868, Hornerstown Formation, Gloucester County, New Jersey, USA.
Last: Erquelinnesia gosseleti (00110, 1886), Erquelinnes Sands, Upper Landenian and Sparnacian, Belgium.
Intervening: ?DAN.

First: Notochelone costata (Owen, 1882), Toolebuc Formation, Flinders River, Queensland, Australia (Gaffney, 1981).
Last: Desmatochelys lowi Williston, 1898, Benton Group, Nebraska and South Dakota, USA (Zangerl and Sloan, 1960).
Intervening: CMP.

First: Protostega eaglefordensis Zangerl, 1953, Eagle Ford Shale, McLennan County, Texas, USA (Zangerl, 1953).
Intervening: SAN, CMP.

F. DERMATEMYDIDAE Gray, 1870 T. (YPR)–Rec. Terr./FW
First: Baptemys tricarinata Hay, 1908, Wind River Formation, Wasatchian, Wyoming, USA (Hutchison, 1980).
Extant
Intervening: LUT, BRT, LMI.

F. KINOSTERNIDAE Gray, 1869 T. (YPR)–Rec. Terr./FW
Intervening: PLI, PLE.
Comments: Earlier records of supposed MAA kinosternids are given by Hutchison and Archibald (1986).

Superfamily TESTUDINOIDEA Baur, 1893

F. EMYDIDAE Gray, 1825 T. (YPR)–Rec. Terr./FW
First: Chrysemys bicarinata (Bell, 1849) and C. testudiniformis (Owen, 1844), London Clay, Kent, England, UK. Extant
Intervening: LUT–PLE.
Comment: Hutchison (pers. comm., 1991) notes that these European forms could be batagurids, and that all Eocene records of Chrysemys are in question.

F. BATAGURIDAE' Gray, 1869 T. (YPR)–Rec. Terr./FW
First: Echmatemys testudinea (Cope, 1872), Wasatch Formation, Wyoming, USA. Extant
Intervening: LUT–PLE.

First: Hadrianus majusculus Hay, 1904, Willwood and Wasatch Formations, Wasatchian, Wyoming, USA. Extant
Intervening: LUT–PLE.

**STEM DIAPSIDA**

**F. PROTOROTHYRIDIDAE** Price, 1937
C. (VRK)–P. (ART) Terr.

First: *Hylonomus lyelli* Dawson, 1860, Cumberland Group, Joggins, Nova Scotia, Canada.

Last: Unnamed protorothyridid, Arroyo Formation, Clear Fork Group, Fort Sill, Oklahoma, USA (Reisz, 1980).

Intervening: POD, MYA, ASS.

**Subclass** DIAPSIDA Osborn, 1903

The classification of early diapsids is based on Benton (1985), Evans (1988) and Laurin (1991). Stratigraphical ranges are taken from papers cited by those authors, as well as Kuhn (1969) and Anderson and Cruickshank (1978), as well as more recent references cited.

**DIAPSIDA incertae sedis**

**F. ENDENNASAURIDAE** Carron, 1987
Tr. (NOR) Terr.

First and Last: *Endennasaurus acutirostris* Renesto, 1984, Calcare di Zorzino, Bergamo, Italy (Renesto, 1984).

**F. DREPANOSAURIDAE** Carron, 1987
Tr. (NOR) Terr.

First and Last: *Drepanosaurus unguicaudatus* Pinna, 1980, Calcare di Zorzino, Bergamo, Italy (Pinna, 1980).

**Order** ARAEOSCELIDIA Williston, 1913

**F. ARAEOSCELIDIDAE** Williston, 1910
P. (ASS–ART) Terr.

First: *Zarcasaurus tanyderus* Brinkman et al., 1984, Cutler Formation, Rio Arriba County, New Mexico, USA (Brinkman et al., 1984).

Last: *Araeoscelis gracilis* Williston, 1910, Arroyo Formation, Baylor County, Texas, USA.

**F. PETROLACOSAURIDAE** Peabody, 1952
C. (KAS) Terr.

First and Last: *Petrolacosaurus kansensis* Lane, 1945, Stanton Formation, Lansing Group, Garnett, Kansas, USA.

**STEM-GROUP NEODIAPSIDA**

**F. MESENOSAURIDAE** Romer, 1956
P. (KAZ) Terr.

First and Last: *Mesenosaurus romeri* Efremov, 1940, Zone II, Mezen' River, Archangel Province, former USSR.

**F. WEIGELTISAUROIDAE** Romer, 1933
P. (UFI)–Tr. (SCY) Terr.

First: *Weigeltisaurus jaekeli* (Weigelt, 1930), Kupferschiefer, Hesse, Germany; Marl Slate, Durham, England, UK.


Intervening: KAZ.

First and Last: *Claudiosaurus germani* Carroll, 1981, upper part of the Lower Sakamena Formation, Leoposa, Madagascar.

**F. HELEOSAURIDAE** Haughton, 1924
P. (TAT) Terr.

First and Last: *Heleosaurus scholtzi* Broom, 1907, *Aulacephalodon–Cistecephalus* Assemblage Zone, Victoria West, Karoo Basin, South Africa.

**F. GALESPHYRIDAE** Currie, 1981
P. (TAT) Terr.

First and Last: *Galesphyrus capensis* Broom, 1914, *Aulacephalodon–Cistecephalus* Assemblage Zone, Cape Province, South Africa.

**F. UNNAMED** P. (ASS) Terr.


**Infraclass** NEODIAPSIDA Benton, 1985
NEODIAPSIDA incertae sedis

**F. PALIGUANIDAE** Broom, 1926
Tr. (SCY) Terr.

First and Last: *Paliguana whitei* Broom, 1903, ?*Lystrosaurus–Procolophon* Assemblage Zone, Tarkastad, Karoo Basin, South Africa.

**F. MONJUROSUCHIDAE** Endo, 1940
J. (u) Terr.

First and Last: *Monjurosuchus splendens* Endo, 1940, Chiufotang Formation, Lingyung Basin, Manchuria, China.

**F. NANCHANGOSAURIDAE** Wang, 1959
Tr. (ANS) Mar.

First and Last: *Nanchangosaurus suni* Wang, 1959 and *Hupehsuchus nanchangensis* Young and Dong, 1972, Jialingjiang Formation and Daye Limestone, Hubei Province, China (Carroll and Dong, 1991).

**Division** YOUNGINIFORMES Romer, 1933

**F. UNNAMED** P. (TAT) Terr. (see Fig. 39.2)


**F. YOUNGINIDAE** Broom, 1914
P. (TAT) Terr.

First and Last: *Youngina capensis* Broom, 1914, *Dicynodon–Theriognathus* Assemblage Zone, New Bethesda, Karoo Basin, South Africa.

**F. TANGASAURIDAE** Camp, 1945
P. (TAT)–Tr. (SCY) FW


Order ICHTHYOSAURIA de Blainville, 1835

Ichthyosaur classification and stratigraphical distributions are taken from Mazin (1982, 1988) and Massare and Callaway (1990), but there has been no recent comprehensive phylogenetic analysis of the group, and the families are rather fluid in composition. Massare and Callaway (1990) argue that the ichthyosaurs are closely related to the younginiforms.

F. UNNAMED Tr. (SCY) Mar.
**First and Last:** *Grippa longirostris* Wiman, 1928, Sticky Keep Formation (Spithian), Svalbard, Spitsbergen.

**F. OMPHALOSAURIDAE** Merriam, 1906

*Tr. (SCY–ANS)* Mar.

**First:** *Omphalosaurus nettariahynchus* Mazin and Bucher, 1987, Prida Formation (Spithian), Humboldt Range, Nevada, USA.

**Last:** *Omphalosaurus neovadanus* Merriam, 1906, Prida Formation, West Humboldt Range, Nevada, USA.

**F. MIXOSAURIDAE** Baur, 1887

*Tr. (SCY–LAD)* Mar.

**First:** *Mixosaurus* cf. *M. nordenskioeldii* (Hulke, 1873), Sulphur Mountain Formation, Wapiti Lake, British Columbia, Canada.

**Last:** *Mixosaurus* nordenskioeldii (Hulke, 1873), Tschermakfjellet Formation, Svalbard, Spitsbergen; *Mixosaurus* sp., upper Muschelkalk, Bavaria and Baden-Württemberg, Germany.

**Intervening:** ANS.

**F. UNNAMED** Tr. (SCY) Mar.

**First and Last:** *Utaltasaurus hataii* Shikama, Kamei and Murata, 1978, Osaka Formation, northern Honshu, Japan.

**F. UNNAMED** Tr. (SCY) Mar.

**First and Last:** *Svalbardosaurus crassidens* Mazin, 1981, Sticky Keep Formation, Svalbard, Spitsbergen.

**F. SHASTASAURIDAE** Merriam, 1902

*Tr. (SCY–NOR)* Mar.

**First:** *Cymbospondylus* sp., Thaynes Formation, Idaho, USA (Massare and Callaway, 1992).

**Last:** *Shastasaurus* cf. *S. osmonti* Merriam, 1902, Martin Bridge Formation, Wallowa Mountains, Oregon, USA.

**Intervening:** ANS–CRN.

**Comment:** Mazin (1988, p. 54) notes possible RHT shastasaurids from the Germanic Basin.

**F. SHONISAURIDAE** Camp, 1980

*Tr. (CRN–NOR/RHT)* Mar.

**First:** *Shonisaurus popularis* Camp, 1976, *S. mulleri* Camp, 1976, and *S. silberlingi* Camp, 1976, Luning Formation, Nye County, Nevada, USA.

**Last:** *Shonisaurus* sp., Kossen Formation, Switzerland.

**F. ICHTHYOSAURIDAE** Bonaparte, 1841

*J. (HET–TTH)* Mar.

**First:** *Ichthyosaurus communis* Conybeare, 1821, Lower Lias (Psiloceras planorbis Zone), Somerset, England, UK.

**Last:** *?Ophthalmosaurus* sp., Purbeck Beds, Dorset, England, UK.

**Intervening:** SIN.

**Comment:** McGowan (1978) notes a humerus of *Ichthyosaurus* sp. from the Lower Cretaceous of North-west Territories, Canada, but its exact age is uncertain.

**F. STENOPTERYGIIDAE** Kuhn, 1934

*J. (TOA)* Mar.

**First:** *Stenopterygius quadriscissus* (Quenstedt, 1858), and six other species, Posidonionschiefer (Dactylioceras tenuicostatum and Harpoceras falciferum Zones), Baden-Württemberg, Germany.

**Last:** *Stenopterygius acutirostris* (Owen, 1840), Alum Shales Formation (Hildoceras bifrons Zone), Yorkshire, England, UK.

**F. LEPTOPTERYGIIDAE** Kuhn, 1934

*Tr. (RHT)–K. (CEN)* Mar.

**First:** *Leptopterygius teniarostris* Conybeare, 1822, Kössen Formation, Switzerland (McGowan, 1989).

**Last:** *??Platypterygius* sp., lower SAN, Western Australia (Wade, 1990). If these are derived from older rocks, then *Platypterygius americanus* (Nace, 1939), Mowry Shales, Wyoming, USA, *P. kipjianoffi* (Romer, 1968), Sewerish Sandstone, former USSR, and *P. campydolon* (Carter, 1846), upper Greensand and Lower Chalk, Cambridgeshire and Kent, England, UK (all CEN), are the youngest.

**Intervening:** HET, SIN, BTH, CLV, KIM, TTH, HAU–CEN.

**Comment:** Supposedly later ichthyosaurs, one from the New Egypt Formation of New Jersey, USA (late MAA in age), and one from the Bearpaw Shale of Saskatchewan, Canada (late CMP), turn out to be isolated bones of plesiosaurs (Baird, 1984). Ventura (1984) notes a Miocene ichthyosaur from Malta, but is doubtful of its true provenance!

**Division** LEPIDOSAUROMORPHA Benton, 1983

**F. UNNAMED** Tr. (SCY) Terr.

**First and Last:** *Palaeoqama vielhaueri* Broom, 1926, *?Lystrosaurus–Procolophon Assemblage Zone*, Mount Frere district, Karoo Basin, South Africa.

**STEM-GROUP** LEPIDOSAURIA

**?F. SAUROSTERNIDAE** Haughton, 1924

*P. (TAT)* Terr.

**First and Last:** *Saurosternon bainii* Huxley, 1868, *Cistecephalus or Dicyonodon–Therioognathus Assemblage Zone*, Sneeuwberg, Karoo Basin, South Africa.

**F. KUEHNEOSAURIDAE** Romer, 1966

*Tr. (CRN–RHT)* Terr.

**First:** *Icarosaurus sieferi* Colbert, 1966, Lockatong Formation (upper Carnian), North Bergen, New Jersey, USA; and *?Kuehneosaurus jaw fragments*, Petrified Forest Member (uppermost Carnian), Chinle Formation, St Johns, Arizona, USA (Murry, 1987).

**Last:** *Kuehneosaurus latus* Robinson, 1962, Pant-y-yfynnon Quarry, Glamorgan, Wales (Crush, 1983).

**Comment:** Pant-y-yfynnon Quarry is dated as RHT. The type material of *K. latus* comes from Emborough Quarry, Somerset, England, UK, whose age is probably NOR, but this is not certain. Later supposed kuehneosaurs, or close relatives, such as *Cteniogenys antiquus* Gilmore, 1928 from the Upper Jurassic and *Litakis gilmorei* Estes, 1964 from the Upper Cretaceous (Estes, 1983) are very doubtful. *Cteniogenys* has been reclassified as a choristodere (Evans, 1989).

**Superorder** LEPIDOSAURIA Haeckel, 1866

* (Duméril and Bibron, 1839)

**Order** SPHENODONTIA Williston, 1925

**F. SPHENODONTIDAE** Cope, 1870

*Tr. (CRN)–Rec. Terr. (p)*

**First:** *sphenodontian cf. Planocephalosaurus*, Turkey
Branch Formation, ?lower CRN, Virginia, USA (Sues and Olsen, 1990); *Brachyrhinodon taylori* Huene, 1912, Lossiemouth Sandstone Formation, ?Upper CRN, Elgin, Scotland, UK.

**Extant**

**Intervening:** NOR, KIM, TTH, APT.

**Comment:** *Brachyrhinodon* is probably the oldest confirmed sphenodontid. Other upper CRN examples have been reported from Arizona, New Mexico and Texas (Murry, 1986, 1987). Other Upper Triassic taxa from England, Germany, Zimbabwe, and the USA (Fraser and Benton, 1989) are probably NOR in age. Older supposed sphenodontids, such as *Palacrodon* from the Lower Triassic of South Africa, and *Anisosodontosaurus* from the Middle Triassic of Arizona, may be procolophonids (Murry, 1987; Evans, 1988). *Elachistosuchus* is an archosauromorph (Evans, 1988). The family Sphenodontidae, as presented here, is paraphyletic because of the exclusion of the Pleurosauridae. *Sapheosaurus* is included here within the Sphenodontidae (Evans, 1988; Fraser and Benton, 1989) and is not given in a separate family. In addition, *Gephyrosaurus briensis* Evans, 1980, from a fissure fill, Glamorgan, South Wales, UK (HET/SIN), is included within Sphenodontidae, and is not regarded as the representative of a separate family (Fraser and Benton, 1989).

**Order** SQUAMATA Oppel, 1811

Cladistic analyses of squamates (Evans, 1984; Estes et al., 1988; Rieppe1, 1988) show that the snakes (Serpentes) are a monophyletic group nested among the squamates. Hence the lizards (Sauria) form a paraphyletic group, which is retained here. The location of Serpentes among the ‘lizard’ groups is uncertain. The classification and stratigraphical distribution of families of Squamata are based on Estes (1983), Estes et al. (1988), and Rage (1984).

**Suborder** SAURIA McCartney, 1802 (p)

**Infra-order** IGUANIA Cuvier, 1817 (Cope, 1864)

F. IGUANIDAE Gray, 1827 K. (MAA)—Rec. Terr.

**First:** *Pristiguama brasiliensis* Estes and Price, 1973, Baurú Formation, Minas Gerais, Brazil. 

**Extant**

**Intervening:** THA—HOL.


**First:** *Mimoseaurus crassus* Gilmore, 1943, Djadokhta Formation, Mongolia. 

**Extant**

**Intervening:** THA—PRB, UMI—HOL.

F. EUPOSAURIDAE Camp, 1923 J. (KIM) Terr.

**First and Last:** *Euposaurus thiolierei* Lortet, 1892, *E. cirinensis* Lortet, 1892, and *E. lorteti* Hofstetter, 1964, all from Calcaire lithographique, Cerin (Ain), France.


**First and Last:** *Arretosaurus ornatus* Gilmore, 1943, Ulan Gochu Formation, Shara Murun, Mongolia.


**First:** *Anquingosaurus brevicephalus* Hou, 1976, Wang-Hu-Dun Series, Qian-Shan District, Anhui, China. 

**Extant**

**Intervening:** LMI—UMI, PLE, HOL.

**Infra-order** SCLEROGLOSSA Estes, de Queiroz and Gauthier, 1988

**SCLEROGLOSSA incertae sedis**

Included here are the Dibamidae, Amphisbaenia and Serpentes (listing follows all the ‘lizard’ groups), according to Estes et al. (1988).

F. DIBAMIDAE Bouleneger, 1884 **Extant** Terr.

**Parvorder** AMPHISBAENIA Gray, 1844


**First and Last:** *Oligodontosaurus wyomingensis* Gilmore, 1942, Fort Union Formation, Park County, Wyoming, and *Oligodontosaurus* sp., Tongue River Formation, Carter County, Montana and Bison Basin deposits, Fremont County, Wyoming, USA. 

**Comment:** Possible amphibiaenians have been reported from the Upper Cretaceous (?MAA) of Spain (Astibia et al., 1990).


**First:** *Omoiophlops edwardsi* (de Rochebrune, 1884), Phosphorites de Quercy, France. 

**Extant**

**Intervening:** LMI, UMI.


**First:** *Plesiureina tsentasi* Sullivan, 1985, upper part of Nacimiento Formation (Torrejonian), Torreon Wash, New Mexico, USA (Sullivan, 1985). 

**Extant**

**Intervening:** THA—LUT, RUP—UMI, PLE.


**First:** *Hyporhina tertia* Berman, 1972, White River Formation, Fremont County, Wyoming, USA. 

**Last:** *Hyporhina antiqua* Baur, 1893, White River Formation, Washington County, South Dakota, USA.

F. BIPEDIDAE Taylor, 1951 **Extant** Terr.

F. TROGONOPHIDAE Gray, 1865 **Extant** Terr.

**Parvorder** GEKKOTA Cuvier, 1817

F. ARDEOSAURIDAE Camp, 1923 J. (THH) Terr.

**First and Last:** *Ardeosaurus brevipes* Meyer, 1855, *A. digitalellus* Grier, 1914, and *Eichstaettosaurus Schroederi* Broili, 1938, Solnhofener Schichten, Eichstätt, Germany.
Comment: Estes (1983) includes Yabeinosaurus tenuis Endo and Shikama, 1942, Tsaozushan Formation, Manchuria, and Y. youngi Hoffstetter, 1964, Ketzuting, Liaoning, China, in this family. These occurrences are dated merely as ‘Upper Jurassic’, so may extend the range of the family.

First and Last: Bavarisaurus macrodactylus Wagner, 1852 and Palaeolacerta bavarica Cocude-Michel, 1961, Solnhofener Schichten, Bavaria, Germany.

Extant Intervening: MAA, THA, YPR, PRB, RUP, LMI–HOL.

F. PYGOPodidae Gray, 1845 Extant Terr.
Parvorder SCINCOMORPHA Camp, 1923
First: Becklesius hoffstetteri (Seiffert, 1973), Saurillodon proraformis (Seiffert, 1973), and S. henkeli (Seiffert, 1973), Guimarota Lignite Mine, Leiria, Portugal.
Intervening: KIM.

First: Palaeoxantusia fera Hecht, 1956, Tongue River Formation, Carbon County, Wyoming, USA. Extant Intervening: LUT–RUP, UMI, PLE, HOL.
Comment: Exostinus lancensis Gilmore, 1928, Lance Formation, Natrona County, Wyoming and Judith River Formation, Chouteau County, Montana, and ‘cf. Gerrhonotus’, Fruitland Formation, San Juan County, New Mexico, USA.
Extant Intervening: MAA–HOL.

First: Odaxosaurus piger Gilmore, 1928, Mesaverde Formation, Natrona County, Wyoming and Judith River Formation, Chouteau County, Montana, and ‘cf. Gerrhonotus’, Fruitland Formation, San Juan County, New Mexico, USA.
Extant Intervening: DAN–YPR, CHT.

F. NECROSAURIDAE Hoffstetter, 1967 J. (OX–TTH) Terr. (see Fig. 39.3)

Last: Necrosaurus eucarinatus (Kuhn, 1940), ‘Middle’ Oligocene, Europe (Augé, 1986).
Intervening: MAA–RUP.

First: Paraderma bogerti Estes, 1964, Lance Formation, Niobrara County, Wyoming, USA.
Extant Intervening: THA, PRB–LMI, HOL.
**Reptilia**

| QU | HOL | PLE | 16 |
|    | PLI | UMI | 20 |
|    | MMI | LMI | 25 |
|    | CHT | RUP | 23 |
|    | PRB | BRT | 24 |
|    | LUT | YPR | 23 |
|    | THA | DAN | 22 |
|    | MAA | 2  |    |
|    | CMP | 3  |    |
|    | SAN | 1  |    |
|    | CON | 4  |    |
|    | TUR | 1  |    |
|    | ALB | 6  |    |
|    | APT | 7  |    |
|    | BRM | 12 |    |
|    | HAU |    |    |
|    | VLG |    |    |
|    | BER |    |    |
|    | TTH |    |    |
|    | KIM | 5  |    |
|    | OXF | 1  |    |
|    | CLV | 1  |    |
|    | BTH | 1  |    |
|    | BAJ | 1  |    |
|    | AAL | 1  |    |
|    | TOA | 1  |    |
|    | TOA | 1  |    |
|    | TIT | 1  |    |
|    | SIN | 1  |    |
|    | PLB | 1  |    |
|    | HET | 1  |    |

1. Dorsetisauridae
2. Necrosauridae
3. Helodermatidae
4. Varanidae
5. Aigialosauridae
6. Dolichosauridae
7. Mosasauridae
8. Paravaranidae
9. Baniauidae
10. Typhlopidae
11. Lapparantophiidae
12. Simoliophiidae
13. Aniliidae
14. Dinilysidae
15. Boidae
16. Bolyeridae
17. Tropidophiidae
18. Madstoidae
19. Palaeophiidae
20. Acrochordidae
21. Nesperophiidae
22. Anomolophiidae
23. Russellophiiidae
24. Colubridae
25. Elapidae

**Fig. 39.3**

**F. VARANIDAE Gray, 1827** K. (SAN/CMP)–Rec. Terr. (includes LANTHANOTIDAE Steindachner, 1978)

**First:** *Telmasaurus grangeri* Gilmore, 1943, Djadokhta Formation, ?upper SAN and/or ?lower CMP, Bayn Dzak, Gobi Desert, Mongolia (Borsuk-Bialynicka, 1984). **Extant Intervening:** CMP–HOL.


**First:** *Proaigialosaurus huenei* Kuhn, 1958, Solnhofener Schichten, Eichstätt, Bavaria, Germany. **Last:** *Aigialosaurus dalmaticus* Kramberger, 1892, *Opetiosaurus bucchi* Kornhuber, 1901, and *Carsosaurus marchesseti* Kornhuber, 1893, Fischschiefer, Lesina and Comeno, Dalmatia, former Yugoslavia (Russell, 1967). **Intervening:** CEN. **Comment:** *Proaigialosaurus* is based on limited material, and it is not clear whether it is an aigialosaurid or not (Carroll and Debraga, 1992). *Carsosaurus* lacks a skull, and is also of uncertain familial assignment (Carroll and Debraga, 1992).


**First:** *Dolichosaurus longicollis* Owen, 1850, Lower Chalk, Kent and Sussex, England, UK (Russell, 1967); *Coniasaurus crassidens* Owen, 1850, Lower Chalk, Sussex, England and Eagle Ford Group, Texas, USA (Bell et al., 1982). **Last:** *Acteosaurus tommasini* Meyer, 1866, *Pontosaurus lesinensis* Kornhuber, 1873, and *Eidolosaurus nopcsa* Meyer, 1923, Fischschiefer, Lesina and Comeno, Dalmatia, former Yugoslavia (CEN–TUR; Russell, 1967). **Intervening:** CEN.


**First:** Mosasaur jaws, Middle Chalk, Cuxton, Kent (Russell, 1967); undescribed specimens, Eagle Ford Formation (CEN/TUR), Texas, USA.
Animals: Vertebrates

**Vertebrates**

Last: *Mosasaurus hoffmanni* Mantell, 1829, Maastricht Calcarenite, upper Gulpen Formation, Maastricht, The Netherlands; *Leidodon sectorius* Cope, 1871, Tuffeau of Maastricht, Maastricht Formation, Maastricht, The Netherlands; *Carinodens fraasi* (Dollo, 1913) and *Plioplatecarpus marshi* Dollo, 1882, both Craie Grossierea Silex Gris, Maastricht Formation, Limburg, The Netherlands; *Goronyosaurus nigeriensis* (Swinton, 1930) and *Mosasaurus sp.*, Dukamaje Formation, Sokoto, NW Nigeria and Niger (T. Lingham-Soliar, pers. comm., 1992); *Mosasaurus dekayi* Bronn, 1838, *M. maximus* Cope, 1869, *Liodon sectorius* Cope, 1871, and *Plioplatecarpus depressus* (Cope, 1869), all 'Navesink Formation and younger Cretaceous' (Russell, 1967), New Jersey, USA; *Prognathodon rapax* (Hay, 1902) and *Halisaurus platyspondylus* Marsh, 1869, New Egypt Formation, New Jersey, USA; all upper MAA (Russell, 1967).

Intervening: TUR-CMP.

**SAURIA incertae sedis**

F. **PARAVARANIDAE** Borsuk-Bialynicka, 1984


F. **BAINGUIDAE** Borsuk-Bialynicka, 1984


**Suborder** **SERPENTES** Linnaeus, 1758

The classification, and distributions, are taken from Rage (1984), unless otherwise stated.

**Suborder** **SCOLECOPHIDIA** Duméril and Bibron, 1844

F. **TYPOLOPIIDAE** Gray, 1825

First: Scolophidia indet., Lower Eocene, Dormaal, Belgium. Extant

Intervening: PRB, MMI, HOL.

**Suborder** **ALETHINOPHIDIA** Hoffstetter, 1955

**Superfamily** **SIMOLIOPHEOIDEA** Nopcsa, 1925

F. **LAPPARANTOPHIIDAE** Hoffstetter, 1968


F. **SIMOLIOPHIDAE** Nopcsa, 1925

First and Last: *Simoliophis rochebrunei* Sauvage, 1880, CEN, south-western France, Portugal; *Simoliophis sp.*, CEN, Egypt.

**Superfamily** **ANILIIOIDEA** Fitzinger, 1826

F. **ANILIIDAE** Fitzinger, 1826

First: *Coniophis cosgriffinii* Armstrong-Ziegler, 1978, Fruitland Formation, New Mexico, USA. Extant

Intervening: MAA, LUT, PRB, MMI, PLI.

F. **UROPELTIDAE** Müller, 1832 Extant Terr.

**Superfamily** **BOOIDEA** Hoffstetter, 1955


Comment: The Rio Colorado Formation has been dated as tentatively CON by Bonaparte (1991).

F. **XENOPELTIDAE** Bonaparte, 1845 Extant Terr.


First: Indeterminate boid, Hell Creek Formation, Montana, USA, and from equivalent deposits in Portugal and India (J.-C. Rage, pers. comm., 1991). Extant

Intervening: DAN-PLE.

F. **BOLYERIIDAE** Hoffstetter, 1946 Q. (HOL)-Rec. Terr.

First: Subfossil *Casarea*, Mauritius. Extant

F. **TROPIDOPHIIDAE** Cope, 1894 T. (THA?)-Rec. Terr.

First: 'Tropidophiid', Palaeocene, South America. Extant

Intervening: YPR.


Intervening: CMP, YPR, PRB.

F. **PALAEOPHIIDAE** Lydekker, 1888 K. (MAA)-T. (PRB) FW

First: *Palaeophis sp.*, MAA, Morocco. Last: *Pterosphenus schucherti* Lucas, 1889, Jackson Formation, Alabama, USA; *P. schweinfurthi* (Andrews, 1901), Qasr el Sagha Formation, Fayum Basin, Egypt; and *P. sheppardi* Hoffstetter, 1958, Seca Formation, Ancon, Ecuador.

Intervening: DAN-BRT.

**Superfamily** **ACROCHORDOIDEA** Bonaparte, 1838

F. **ACROCHORDIDAE** Bonaparte, 1838 T. (MMI)-Rec. FW/Mar.

First: *Acrochordus dehmi* Hoffstetter, 1964, Chinji Formation, Siwalik Group, Chhoinja, Pakistan. Extant


First: *Nigerophis mirus* Rage, 1975, Palaeocene, Kreeb de Sessao, Niger.

Superfamily COLUBROIDEA Fitzinger, 1826
F. ANOMALOPHIIDAE Oppel, 1811 T. (YPR) FW
First and Last: Anomalophis bolcensis (Massalongo, 1859), Monte Bolca, Veneto, Italy.

F. RUSSELLOPHIIDAE Rage, 1978 T. (YPR–PRB) FW
First: Russelophilis sp., Lower Eocene, Dormaal, Belgium.
Last: Russellophiiid indet, Phosphorites de Quercy, France.

First: Coluber cadurci Rage, 1974 and Natrix mlynskii Rage, 1988, Phosphorites de Quercy, upper Suevian, Lot, France.
Extant: CHT–PLE.

F. ELAPIDAE Boie, 1827 T. (LMI)–Rec. Terr. (see Fig. 39.4)
First: Viperid, Agenian, France. Extant
Intervening: MMI, UMI–PLE.

Division ARCHOSAUROMORPHA Huene, 1946
Order CHORISTODERIA Cope, 1876
Relationships of the group, and division into families, are based on the cladogram of Evans (1990).

F. PACHYSTROPHIEIDAE Kuhn, 1961 Tr. (RHT) FW/Mar.

F. UNNAMED J. (BTH–KIM) FW
Last: Cteniogenys antiquus Gilmore, 1928, Morrison Formation, Wyoming, USA.
Intervening: OXF.

Comments: The familial assignment of these early choristoderes has not been confirmed, and relationships to the pachystropheids and to later champsosaurs are unclear at present. Earlier choristoderes, perhaps belonging to this group have been noted from the Kayenta Formation (SIN/PLB: J. Clark, pers. comm., 1991).

F. CHAMPSOSAURIDAE Cope, 1876 (1884?) K. (APT/ALB)–T. (RUP) FW
First: Tchoria namsarai Efimov, 1985, Lower Cretaceous, Khamaril-Khural, Mongolia.
Intervening: CMP–YPR.

F. SIMOEDOSAURIDAE Lemoine, 1884 K. (ALB/CEN)–T. (YPR?) FW
Last: Simoedosaurus sp., Clarkforkian, Park County, Wyoming, USA (Uppermost Palaeocene or Lowermost Eocene).
Intervening: CMP–THA.

Order RHYNCHOSAURIA Osborn, 1903
F. RHYNCHOSAURIDAE Huxley, 1887 (Cope, 1870) Tr. (SCY–CRN) Terr.
First: Hoxesia browni Broom, 1905 and Mesosuchus browni Watson, 1912, Cynognathus–Diademodon Assemblage Zone, Karoo Basin, South Africa.
Intervening: ANS, LAD.
Comment: Carroll (1976) suggested that Noteosuchus colletti (Watson, 1912) from the Lystrosaurus–Procolophon Assemblage Zone of South Africa was the oldest rhynchosaur, but it lacks diagnostic characters of the group (Benton, 1985). Other upper Carnian rhynchosaurids are known, but these are dated as ‘early’ late Carnian by Hunt and Lucas (1991b), while the ‘Lasts’ listed above are given as ‘late’ late Carnian.

Order THALATTOSAURIA Merriam, 1904
F. ASKEPTOSAURIDAE Kuhn, 1952 Tr. (ANS/LAD) Mar.
First: Askeptosaurus italicus Nopcsa, 1925, Grenzbilumenzone, Monte San Giorgio, Kt. Tessin, Switzerland.
Last: Thalattosaurus indet., Pardonet Formation, British Columbia, Canada (Storrs, 1991b).

F. THALATTOSAURIDAE Merriam, 1904 Tr. (CRN–NOR) Mar.
First: Thalattosaurus alexandrae Merriam, 1904, and Nectosaurus balii Merriam, 1905, Hosselkus Limestone, California, USA.
Last: Thalattosaurus indet., Pardonet Formation, British Columbia, Canada (Storrs, 1991b).

First and Last: Clarazia schinzi Peyer, 1936, and Heschelheria ruebeli Peyer, 1936, Grenzbilumenzone, Monte San Giorgio, Kt. Tessin, Switzerland.

F. TRILOPHOSAURIDAE Gregory, 1945 Tr. (CRN–RHT) Terr.
First: Trilophosaurus buettneri Case, 1928, lower Dockum Group, Crosby County, Texas, USA.
Last: Tricuspisaurus thomasi Robinson, 1957, Upper Triassic (NOR/RHT), Ruthin Quarry fissure, Glamorgan, Wales, UK (Fraser, 1986).
Intervening: NOR.
Fig. 39.4

Comment: Earlier supposed trilophosaurids, such as Doniceps, Anisodontosaurus, and Gomphiosaurus, as well as Toxolophosaurus from the Lower Cretaceous, are probably not trilophosaurids (Murry, 1987). It is unclear whether Tricuspisaurus and Variodens, both from the English-Welsh fissures, are trilophosaurids or not.

First and Last: Megalancosaurus preonensis Calzavara et al., 1980, Dolomia di Forni, Udine, Italy.

Order PROLA Ceriformes Camp, 1945

Animals: Vertebrates
**Reptilia**

F. PROTOROSAURIDAE Baur, 1889 (Cope, 1871)  
P. (KAZ) Terr.  
**First and Last:** Protosaurus speneri Meyer, 1832, Kupferschierfer, Thuringia, Germany.

**F. PROLACERTIDAE** Parrington, 1935  
Tr. (SCY–CRN) Terr.  
**First:** Prolacerta broomi Parrington, 1935, Lystrosaurus–Procolophon Assemblage Zone, Karoo Basin, South Africa, and Fremouw Formation, Antarctica.  
**Last:** Malerisaurus robinsonae Chatterjee, 1980, Maleri Formation, Andhra Pradesh, India; and M. langstoni Chatterjee, 1986, Tecovas Member, lower Dockum Group, Howard County, Texas, USA.  
**Intervening:** ANS, LAD.

**F. TANYSPTHEIDAE** Romer, 1945 (Gervais, 1859)  
Tr. (ANS–NOR) Terr./Mar.  
**First:** 'Tanystropheus' conspicus Huene, 1931, Obere Buntsandstein, southern Germany.  
**Last:** Tanystropheus fossai Wild, 1980, Argillite di Riva di Solto, Val Brembana, Italy.  
**Intervening:** LAD, CRN.

**Subdivision** ARCHOSAURIA Cope, 1869  
The classification of basal archosaurs ('thecodontians') is based on Benton and Clark (1988), Sereno and Arcucci (1990), and stratigraphical distributions are taken from Charig (1976), and more recent references noted.

**F. PROTEROSUCHIDAE** Huene, 1908  
P. (TAT)–Tr. (ANS) Terr./FW  
**First:** Archosaurus rossicus Tatarinov, 1960, Zone IV, Vladimir region, former USSR.  
**Last:** Chasmatosaurus ultimus Young, 1964, Er-Ma-Ying Series, SE Shansi Province, China.  
**Intervening:** SCY.

**F. ERYTHROSUCHIDAE** Watson, 1917  
Tr. (SCY–LAD) Terr.  
**First:** Fugusuchus heijapensis Cheng, 1980, He Shang-gou Formation, Fuku County, Shanxi Province, North China, and Garjainia prima Ochev, 1958, Yarenskian Horizon, upper part of Stage V, Orenburg region, southern Ural, former USSR, both mid to late Scythian in age.  
**Last:** Cayosuchus huenei Reig, 1961, Cacheuta Formation, Mendoza Province, Argentina.  
**Intervening:** ANS.

**F. CTENOSAURISCIDAE** Kuhn, 1964  
Tr. (SCY–ANS/LAD) Terr.  
**First:** Ctenosaurus koeneni (Huene, 1902), Mittlere Buntsandstein, Göttingen, Germany.  
**Last:** Lotosaurus adentus Zhang, 1975, Batung Formation, Hunan, China.  
**Comment:** These two taxa of (?) archosaurs share long dorsal neural spines, but their systematic position is uncertain. It is not clear whether they are related to each other or not.

**F. EUPARKERIIDAE** Huene, 1920  
Tr. (SCY–ANS) Terr.  
**First:** Euaparkeria capensis Broom, 1913, Cynognathus–Diademodon Assemblage Zone, Karoo Basin, South Africa.  
**Last:** Halazaisuchus giąonensis Wu, 1982, Lower Er-Ma-Ying Formation, Shansi Province, China; Turfanosuchus dabanesiens Young, 1973, Er-Ma-Ying equivalent, Sinkiang, China; and T. shagediens Wu, 1982, Lower Er-Ma-Ying Formation, Inner Mongolia, China.  
**Comment:** Turfanosuchus may be a pseudosuchian (J. M. Parrish, pers. comm., 1991).

**F. PROTEROCHAMPSIDAE** Sill, 1967  
Tr. (LAD–CRN) Terr./FW  
**First:** 'Rutiodon sp.', Pekin Formation, middle CRN, North Carolina, USA (Olsen et al., 1989).  
**Last:** Rutiodon sp., Rhät, Switzerland, North Germany; 'phytosaurs', upper Passaic Formation, New Jersey, Upper New Haven Arkose, Connecticut, USA.  
**Intervening:** NOR.  
**Comment:** Apparently older phytosaurs, Mesorhinusuchus fracsi (Jaekel, 1910) from the Mittlere Buntsandstein (SCY) of Bernburg, Germany, and others from the Muschelkalk of Germany (ANS–LAD) are all doubtful records (Westphal, 1976). There are numerous upper CRN phytosaurs, Paleorhinus bransoni Williston, 1904, Popo Agie Formation, Fremont County, Wyoming, USA, and other species of Paleorhinus from Arizona and Texas, USA, Morocco, Germany, Austria and India (Hunt and Lucas, 1991a).

**F. PHYTOSAURIDAE** Lydekker, 1888  
Tr. (CRN–RHT) FW/Terr.  
**First:** 'Ruitiodon sp.', Pekin Formation, middle CRN, North Carolina, USA (Olsen et al., 1989).  
**Last:** Rutiodon sp., Rhät, Switzerland, North Germany; 'phytosaurs', upper Passaic Formation, New Jersey, Upper New Haven Arkose, Connecticut, USA.  
**Intervening:** NOR.  
**Comment:** There are numerous late CRN stagonolepidids, Stagonolepis robertsoni Tatarinov, 1960 and Proterochampsia barrionuevoi Reig, 1959, Ichigualasto Formation, San Juan Province, Argentina.

**Infradivision** CRUROTARSID Sereno and Arcucci, 1990

**F. PHYTOSAURIDA Lydekker, 1887**  
Tr. (CRN–RHT) Terr.  
**First:** cf. *Pytoptheron*, Pekin Formation, middle CRN, Chatham County, North Carolina, USA (Olsen et al., 1989); Longosuchus meadei (Sawin, 1947), lower Dockum Group, Howard County, Texas; Salitral Member, Chinle Formation, Rio Arriba County, New Mexico, USA (Hunt and Lucas, 1990).  
**Last:** Neoaetosauroides engaeus Bonaparte, 1969, upper Los Colorados Formation, La Rioja, Argentina; aetosaur elements, Penarth Group ('Rhaetian'), SW England (Fraser, 1988).  
**Intervening:** NOR.  
**Comment:** There are numerous late CRN stagonolepidids, Stagonolepis robertsoni Agassiz, 1844, Losiemouth Sandstone Formation, Morayshire, Scotland, UK; Aetosauroides scagliai Casamiquela, 1960 and Argentiniosuchus bonapartei Casamiquela, 1960, Ichigualasto Formation, San Juan, Argentina; Desmatosuchus haplocerus (Cope, 1892), lower units of the Chinle Formation and Dockum Group, New Mexico and Texas, USA; unnamed aetosaur, Wolfville Formation, Nova Scotia, Canada.

**F. RAUISUCHIDAE** Huene, 1942  
Tr. (ANS–RHT) Terr.
First: Wangisuchus tzycki Young, 1964 and Fenhosuchus cristatus Young, 1964, Er-Ma-Ying Series, Shansi, China; Vjushkovisoravisus berdjanensis Ochev, 1982, Donguz Series, Orenburg region, former USSR; Stagonosuchus major (Haughton, 1932) and 'Mandasuchus', upper bone bed of the Manda Formation, Ruhuhu region, Tanzania; 'rauisuchid', Yarrapalli Formation, India.


Intervening: LAD–NOR.

Comment: Some of the early 'rauisuchids' are of uncertain affinities, particularly Fenhosuchus, Vjushkovisoravisus, and Wangisuchus (Bonaparte, 1984; Benton, 1986). Parrish (pers. comm., 1991) regards this family as non-monophyletic.

F. POPOSAURIDAE Nopcsa, 1928
Tr. (ANS–NOR) Terr.


Last: Poposaurus, upper Redonda Formation, ?late NOR, New Mexico, USA.

Intervening: LAD, CRN.

Comment: If the 'last' record is not confirmed, there are several lower and middle NOR poposaurids, Teratosaurus suevicus Meyer, 1861, Mittlere Stubensandstein, Baden-Württemberg, Germany; Postosuchus kirkpatricki Chatterjee, 1985, upper Dockum Group, Texas, USA.

F. ORNITHOSUCHIDAE Huene, 1908
Tr. (CRN–RHT) Terr.


Last: Riojasuchus tenueiceps Bonaparte, 1969, upper Los Colorados Formation, La Rioja, Argentina.

Intervening: None.

Superorder CROCODYLOMORPHA Walker, 1968

The classification of crocodilomorphs is based on Clark, in Benton and Clark (1988), and stratigraphical distributions are taken from Steel (1973), Buffetaut (1982) and references cited below.

F. SALTOPOSAURIDAE Crush, 1984
Tr. (NOR–RHT) Terr.

First: Saltoposaurus connectens Huene, 1921, Mittlere Stubensandstein, Württemberg, Germany.

Last: Terrestrisuchus gracilis Crush, 1984, Ruthin Quarry, Glamorgan, Wales, UK.

F. SPHENOSUCHIDAE Huene, 1922
Tr. (CRN–J. (SIN/PLB)) Terr. (p)

First: Hesperosuchus agilis Colbert, 1952, lower Chinle Group, Cameron, Arizona, USA.

Last: Kayentasuchus sp., Kayenta Formation, Arizona, USA (Clark, 1993).

Intervening: RHT, HET.

Comment: Hallopus victor (Marsh, 1877) is a crocodilomorph which may belong to this clade (Clark, in Benton and Clark, 1988). It is probably from the lower Ralston Creek Formation (CLV) of Fremont County, Colorado, USA (Norell and Storrs, 1989).

Order CROCODYLIA Gmelin, 1788

F. PROTOSUCHIDAE Brown, 1934
Tr. (RHT–J. (PLB/TOA)) Terr.

First: Hemiprotosuchus leali Bonaparte, 1969, upper Los Colorados Formation, La Rioja, Argentina.

Last: Unnamed form, Kayenta Formation (SIN/PLB), Arizona, USA (Clark, in Benton and Clark, 1988), or Stegmosuchus longipes Lull, 1953, upper Portland Group (PLB/TOA), Connecticut, USA.

Intervening: HET, SIN.

Comment: The range of Protosuchidae could be much greater if one includes Dupolax arecales Fraas, 1867, Schilfsandstein, Germany (CRN), as Walker (1961) suggests, and Edentosuchus tienshanensis Young, 1973, Wuerho, China (VLG/ALB), as Clark (in Benton and Clark, 1988) suggests.


First and Last: Orthusosuchus stormbergi Nash, 1968, upper Elliot Formation, Lesotho, South Africa.

Suborder MESOEUCROCODYLIA Whetstone and Whybrow, 1983

Infra-order THALATTOSUCHIA Fraas, 1901

F. TELEOSAURIDAE Geoffroy, 1831

First: Stereosaurus bollensis (Jaeger, 1828), S. brevior Blake, 1876, and S. gracilirostris Westphal, 1961, Whitby Mudstone Formation, Yorkshire, England, UK; Posidonienschiefer, Baden-Württemberg, Germany.

Last: 'Teleosaurid', Valanginian, Bouches-du-Rhône, France.

Intervening: AAL–TTH.

Comment: Huene and Mauherge (1954) reported teleosaurid vertebrae from the Lotharingian (HET/SIN) of Lorraine, France.

F. METRIORHYNCHIDAE Fitzinger, 1843
J. (BTH)–K. (HAU) Mar./FW

First: Teleidosaurus calvadosi (J. A. Eudes-Deslongchamps, 1866), T. gaudryi Collot, 1905, and T. bhamonicus (Mercier, 1933), Bathonian, Normandy and Burgundy, France.

Last: Dakosaurus maximus (Plieninger, 1846), Hauterivian, Provence, France.

Intervening: CLV–TTH.

?F. CROCODILEIMIDAE Buffetaut, 1979
J. (KIM) Mar.

First and Last: Crocodileimus robustus Jourdan, 1871, Calcaires lithographiques, Cerin, Ain, France.

Infra-order METAMESOSUCHIA Clark, in Benton and Clark, 1988


Reptilia


**F. BAURUSUCHIDAE** Price, 1945

K. (CON–MAA) Terr.

First: **Cynodontosuchus rothi** Woodward, 1896, Río Colorado Formation, Neuquén, Argentina.

Last: **Baurusuchus pachecoi** Price, 1945, BaurU Formation, São Paolo, Brazil.

**F. LIBYCOSUCHIDAE** Stromer, 1914

K. (BRM-CEN) Terr.

First: 'Libycosuchid', BRM, Niger.

Last: **Libycosuchus brevirostris** Stromer, 1914, Cenomanian, Baharija, Egypt.

Intervening: ALB.

**F. SEBECIDAE** Simpson, 1937

T. (THA-PLI) Terr.

First: **Sebecus** sp., Upper Palaeocene, Itaborai, Brazil.

Last: cf. **Sebecus**, Pliocene, Australia.

Intervening: YPR, PRB-CHT, MM!

**F. PEIROSAURIDAE** Gasparini, 1982

K. (?CON-MAA) Terr.


Last: **Peirosaurus tormini** Price, 1955, BaurU Formation, State of Minais Gerais, Brazil.

Parvorder **NEOSUCHIA** Clark, in Benton and Clark, 1988

**F. ATOPOSAURIDAE** Gervais, 1871

K. (KIM)-K. (APT) Terr./FW

First: **Alligatorium meyeri** Gervais, 1871, Calcaire lithographique, Cerin, Ain, France.

Last: Atoposaurid, BRM/APT, Spain.

Intervening: TTH, BRM.

Comment: The atoposaurids are essentially an Upper Jurassic group, but extend into the Lower Cretaceous if Theriosuchus is included in the family (Buffetaut, 1982; Clark, in Benton and Clark, 1988).

**F. DYROSAURIDAE** de Stefano, 1903

K. (MAA)–T. (PRB) FW/Mar.

First: **Sokotosuchus iamaisoni** Halstead, 1975, Dukumaje Formation, Sokoto, Nigeria; **Hyposaurus roggersii** Owen, 1849, Hornerstown Formation, New Jersey, USA; H. derbianus Cope, 1886, MAA, Pernambuco Province, Brazil.

Last: 'Dyrosaurid', Upper Eocene, Burma.

Intervening: DAN-BRT.

Comment: An older possible dyrosaurid is reported from the CEN of Nazaré, Portugal (Buffetaut, 1982).

F. **TREMATOCHAMPSIDAE** Buffetaut, 1974

K. (HAU)–T. (LUT) FW/Terr.

First: **Amargosuchus minor** Chiappe, 1988, La Amarga Formation, Neuquén Province, Argentina (Chiappe, 1988).

Last: **Bergisuchus dietrichbergi** Kuhn, 1968, Messel lignite, Hesse, Germany (Buffetaut, 1988).

Intervening: ?CON, CMP, MAA, YPR, BRT.

F. **HSISOSUCHIDAE** Young and Chow, 1953

J. (KIM)–K. (CMP) Terr.

First: **Hsisosuchus chungkingensis** Young and Chow, 1953, Upper Jurassic, Szechwan, China.

Last: ?**Doratodon archariensis** (Bunzel, 1871), Gosau Formation, Austria.

Intervening: None.

**F. GONIOPHOLIDIDAE** Cope, 1875

K. (CEN) FW


Last: 'Goniopholis' kirtlandicus' Wiman, 1931, MAA, New Mexico, USA.

Intervening: KIM–ALB.

**F. PARALLIGATORIDAE** Konjukova, 1954

K. (CEN/TUR–CMP/MAA) FW

First: **Shamosuchus major** Efimov, 1981, S. ulgicus Efimov (Efimov, 1981), Bayshirenskaya Svita, Mongolia (Efimov, 1981).

Last: **Shamosuchus ancestralis** (Konjukova, 1954), Nemegt Formation, Omnogov, Mongolia.

Intervening: SAN.

**F. BERNISSARTIIDAE** Dollo, 1883

K. (OXF)–K. (BRM) Terr/FW

First: **Bernissartia** sp., Guimarota, Leiria, Portugal.

Last: **Bernissartia** sp., Wealden, Isle of Wight, England, UK.

Intervening: VLG, HAU.

F. **BRILLANCEAUSUCHIDAE** Michard et al., 1990

K. (BRM) Terr/FW

First and Last: **Brillanceausuchus babouriensis** Michard et al., 1990, from the Lower Cretaceous of Babouri-Figuil Basin, north Cameroon (Michard et al., 1990).

Suborder **EUSUCHIA** Huxley, 1875

**F. HYLAEOCHAMPSIDAE** Andrews, 1913

K. (BRM) Terr/FW

First and Last: **Hylaeochampsa vectiana** Owen, 1874, Wealden, Isle of Wight, England, UK.

**F. STOMATOSUCHIDAE** Stromer, 1925

K. (CEN) FW

First and Last: **Stomatosuchus inermis** Stromer, 1925, ?**Aegyptosuchus peyeri** Stromer, 1933, Baharija Formation, Marsa Matruh, Egypt.

**F. GAVIALIDAE** Cuvier, 1807

T. (PRB)–Rec.

First: **Eogavialis africanus** (Andrews, 1905), Upper Eocene,
Fayum, Egypt.

**Intervening**: LUT–HOL.

F. **THORACOSAURIDAE** Cope, 1871
K. (CEN/TUR)–T. (THA) FW

**First**: *Thoracosaurus cherifiensis* Lavocat, 1955, southern Morocco.

**Last**: *Thoracosaurus macrorhynchus* (Blainville, 1839–1864), Bourgogne, Marne, France.

**Intervening**: CMP–DAN.

**Comment**: *T. cherifiensis* may be a pholidosaurid (E. Buffetaut, pers. comm., 1991), in which case the oldest *Thoracosaurus* species are MAA in age (Hornerstown Formation, New Jersey; Ripley Formation, Mississippi, USA).

F. **DOLICHOCHAMPSIDAE** Gasparini and Buffetaut, 1980
K. (MAA) FW

**First and Last**: *Dolichochampsa minima* Gasparini and Buffetaut, 1980, Yacoraite Formation, Salta Province, Argentina and El Molino Formation, southern Bolivia (Buffetaut, 1987).

F. **UNNAMED** T. (YPR–PLE) FW

**First**:

*?Eosuchus lerichei* Ostrom, 1901, Ypresian, Jeumont, northern France.

**Last**:

Unnamed form, Quaternary?, Murua Island, Solomon Sea (Molnar, 1982).

**Intervening**: LUT, LMI, UMI, PLI.

F. **CROCODYLIDAE** Cuvier, 1807
K. (TUR/SAN)–Ree. FWfTerr.

**First**:

*?Tadzhikosuchus macrodentis* Efimov, 1982, Yalovachskaya Formation, Tadzhikistan (Efimov, 1982).

**Extant**

**Intervening**: CMP–HOL.

F. **PRISTICHAMPSIDAE** Kuhn, 1968

**First**:

*Planocrania datangensis* Li, 1976, Nonshan Formation, Guangdong, China; *P. hengdongensis* Li, 1984, Palaeocene (?) red beds, Hunan, China; *Wanosuchus atresus* Zhang, 1981, Palaeocene (?), Anhui, China.

**Last**:


**Intervening**: YPR–BRT, PLI.

F. **ALLIGATORIDAE** Gray, 1844 (Cuvier, 1807)
K. (CMP)–Rec. FW/Terr.

**First**:

*Albertochampsa langstoni* Erickson, 1972, Judith River Formation, Alberta, Canada; *Bottosaurus pernugasus* Cope, 1874, Belly River Formation, Alberta, Canada.

**Extant**

**Intervening**: YPR–BRT, PLI.

F. **NETTOSUCHIDAE** Langston, 1965
T. (UMI–PLI) FW

**First**:

*Mourasuchus atopus* (Langston, 1965), Honda Beds, La Venta, Huila, Colombia.

**Last**:

*Mourasuchus amazonensis* Price, 1964, Acre State, Brazil.

**Infradivision**: ORNITHODIRA Gauthier, 1986

F. **LAGOSUCHIDAE** Arcucci, 1987
Tr. (LAD) Terr.


F. **PODOPTERYGIDAE** Sharov, 1971
Tr. (CRN/NOR) Terr.

**First and Last**: *Sharovipteryx mirabilis* (Sharov, 1971), Madygenskaya Svia, Fergana, Kirgizia, former USSR.

F. **UNNAMED** Tr. (CRN/NOR) Terr.

**First and Last**: *Longisquama insignis* Sharov, 1970, Madygenskaya Svia, Fergana, Kirgizia, former USSR (Haubold and Buffetaut, 1987).

F. **SCLEROMOCHLIDAE** Huene, 1914
Tr. (CRN) Terr.

**First and Last**: *Scleromochlus taylori* Woodward, 1907, Lossiemouth Sandstone Formation, Morayshire, Scotland, UK.

**Order**: PTerosauria Owen, 1840 (Kaup, 1834) (see Fig. 39.5)

The classification of pterosaurs is based on Wellnhofer (1978, 1991), Howse (1986), Bennett (1989), and Unwin (1991), with distribution data from Wellnhofer (1978, 1991), and other references noted.

**Suborder**: RHAMPHORHYNCHOIDEA

Plieninger, 1901 (p)

F. **UNNAMED** Tr. (NOR) Terr.

**First and Last**: *Preondactylus buffarini* Wild, 1983, lower middle part of the 'Dolomia Principale', Udine Province, Italy (Wild, 1983).

F. **DIMORPHODONTIDAE** Seeley, 1870
Tr. (NOR)–J. (SIN) Terr.


**Last**: *Dimorphodon macronyx* (Buckland, 1829), upper Blue Lias, Dorset, England, UK.

**Intervening**: None.

F. **EUDIMORPHODONTIDAE** Wellnhofer, 1978
Tr. (NOR)–J. (OXF) Terr.

**First and Last**: *Eudimorphodon ranzii* Zambelli, 1973, upper half of the Calcare di Zorzino, Bergamo, Italy.

F. **ANUROGNATHIDAE** Kuhn, 1937
J. (TTH) Terr.

**First and Last**: *Anurognathus ammoni* Döderlein, 1923, Solnhofener Schichten, Bavaria, Germany; and *Batrachognathus volans* Riabinin, 1948, Upper Jurassic, Karatau Mountains, Michałówka, Kazakhstan, former USSR.

F. **UNNAMED** J. (OXF–TTH) Terr.

**First**: *Nesodactylus hesperius* Colbert, 1969, OXF, Province Pinar del Rio, west Cuba.

**Last**: *Comodus anostri* Galton, 1981, upper part of Morrison Formation, Wyoming, USA.

**Intervening**: KIM?

F. **RHAMPHORHYNCHOIDEA** Seeley, 1870
J. (TOA–TTH) Terr.
**Suborder** PTERODACTYLOIDEA Plieninger, 1901

**Superfamily** DSUNGARIPTEROIDEA Young, 1964

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**First:** *Parapsicephalus purdoni* (Newton, 1888), upper Lias, Yorkshire, England, UK; *Dorygnathus banthensis* (Theodori, 1930), upper Lias, Germany.


**Intervening:** BTH–KIM.

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**Suborder** PTERODACTYLOIDEA Plieninger, 1901

**Superfamily** DSUNGARIPTEROIDEA Young, 1964

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**First:** *Dermodactylus montanus* (Marsh, 1878), Morrison Formation, Wyoming, USA.

**Last:** *Araripedactylus dehmi* Wellnhofer, 1977, Santana Formation, Estado do Ceará, Brazil.

**Intervening:** None.

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**F. UNNAMED** J. (KIM/TTH)–K. (APT) Terr.

**First:** *Dermodactylus montanus* (Marsh, 1878), Morrison Formation, Wyoming, USA.

**Last:** *Araripedactylus dehmi* Wellnhofer, 1977, Santana Formation, Estado do Ceará, Brazil.

**Intervening:** None.

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**F. GERMANODACTYLIDAE** Young, 1964 J. (KIM–TTH) Terr.

**First:** *Germanodactylus* sp., Kimmeridge Clay, Dorset, England, UK (Unwin, 1987).

**Last:** *Germanodactylus cristatus* (Wiman, 1925), Solnhofener Schichten, Bavaria; *G. rhamphastinus* (Wagner, 1851), Mönchsheimer Schichten, Bavaria, Germany.
F. DSUNGARIPTERIDAE Young, 1964
J. (KIM)–K. (APT/ALB) Terr.
First: ?Dsungaripterus brancai (Reck, 1931), Tendaguru Beds, Tendaguru, Tanzania (Calton, 1980).
Last: Dsungaripterus weii Young, 1964 and Noripterus complicidens Young, 1973, Tugulu Group, Junggar Basin, Xinjiang, China; ‘dsungaripterid’, Qingshan Formation, Shandong, China.
Intervening: BER–HAU.
Comment: Dsungaripterus brancai is not noted as a dsungaripterid by Bennett (1989), so that the oldest certain member of the family is Dsungaripterus parvus Bakhurina, 1982, from the Tsagantsabskaya Svita, Khovd, Mongolia (VLG).

Superfamily UNNAMED
F. PTERODACTYLIDAE Bonaparte, 1838 (p)
J. (OXF–TTH) Terr.
First: Pterodactylus sp. (teeth), Guimarota lignite mine, Leiria, Portugal.
Last: Pterodactylus antiquus (Soemerring, 1812), P. kochi (Wagner, 1837), P. micronyx Meyer, 1856, P. elegans Wagner, 1861, and P. longicollum Meyer, 1854, Solnhofener Schichten, Bavaria, Germany.

F. GALLODACTYLIDAE Fabre, 1974
J. (KIM–TTH) Terr.
First and Last: Gallodactylus suevicus (Quenstedt, 1855), Solnhofener Schichten, Bavaria and G. canjuersensis Fabre, 1974, ‘Portlandien’, Var, France.

F. CTENOCHASMATIDAE Nopcsa, 1928
J. (KIM)–K. (APT) Terr.
Last: Ceaeactadactylus atrox Leonardi and Borgomanero, 1985, Santana Formation, Estado do Ceará, Brazil.
Comment: Aidachar paludalis Nesson, 1981, Taykarshinskaya Member (TUR/SAN), Uzbekistan, former USSR, turns out to be based on the remains of a teleost fish (P. Wellnhofer, pers. comm., 1991). Ceaeactadactylus is included here according to Unwin’s (1991) cladistic analysis, although Wellnhofer (1991) places it in a separate family.
Intervening: None.

F. PTERODAUSTRIDAE Bonaparte, 1971
K. (I.) Terr.

Last: Lonchodectes compressirostris (Owen, 1851), Middle Chalk, Kent, England, UK.
Intervening: ALB, CEN.
Comment: This family is based on Unwin’s (1991) work.

F. AZHDARCHIDAE Nessov, 1984
J. (TTH)–K. (MAA) Terr.
First: Doratorhynchus validus Seeley, 1875, Purbeck, Dorset, England, UK.
Last: Quetzalcoatlus northropi Lawson, 1975, Tornillo Group, Brewster County, Texas, USA; Quetzalcoatlus sp., Lance Formation, Wyoming, USA; MAA, New Jersey, USA; Arambourgiana philadelphica (Arambourg, 1959), Maastrichtian, Amman, Jordan (Nesson, 1984; Bennett, 1989).
Intervening: ALB–CON, CMP.

Superfamily ORNITHOCHEIROIDEA Seeley, 1891
F. NYCTOSAURIDAE Williston, 1903
K. (SAN–MAA) Terr.
First: Nyctosaurs gracilis Marsh, 1876, Smoky Hill Chalk Member, upper Niobrara Formation, western Kansas, USA.
Last: Nyctosaurus lamegoi (Price, 1953), Gramame Formation, Paraíba, Brazil.
Intervening: None.

F. ORNITHODESМИDАЕ Hooley, 1913
K. (BRM) Terr.
First and Last: Ornithodesmus latidens Seeley, 1901, Wealden, Isle of Wight, England, UK.
Comment: O. cliniculus (Hooley, 1913), also from the Wealden of the Isle of Wight, is based on a dinosaur sacrum (A. R. Milner, in prep.).

F. ORNITHOCHEIRIDAE Seeley, 1870
K. (VLG–CEN) Terr.
First: Coloborhynchus clavirostris (Owen, 1874), Hastings Sand, Sussex, England, UK.
Last: Anhanguera cuvieri (Bowerbank, 1851), Lower Chalk, Kent, England, UK.
Intervening: APT, ALB.
Comment: This family is based on Unwin’s (1991) analysis, and includes the Anhangueridae Campos and Kellner, 1985.

F. TAPEJARIDAE Kellner, 1990

F. PTERANODONTIDAE Marsh, 1876
Last: Pteranodon longiceps Marsh, 1876 and P. sternbergi Hawksen, 1966, Smoky Hill Chalk Member, upper Niobrara Formation and Pierre Shale, Kansas, South Dakota, and Wyoming, USA.
Intervening: CEN–SAN.
Comment: The Pteranodontidae, according to Bennett (1989) should be expanded to include pterosaurs assigned by Wellnhofer (1978, 1991), and others, to the families Criorhynchidae, Ornithocheiridae and Ornithodesmidae. However, the ornithodesmids and ornithocheirids are retained as separate families here, according to Unwin’s (1991) work. Species of Pteranodon other than those named are regarded as synonyms or nomina dubia by C. Bennett (pers. comm., 1991).
Superorder DINOSAURIA Owen, 1842 (P)
The classification of dinosaurs, and stratigraphical distributions of families are taken from Weishampel et al. (1990).

Order SAURISCHIA Seeley, 1877

Suborder THEROPODA Marsh, 1881

F. HERRERASAURIDAE Benedetto, 1973


Infra-order CERATOSAURIA Gauthier, 1986

F. PODOKESURIDAE Huene, 1914

First: Coelophysis bauri (Cope, 1889), lower part of Petrified Forest Member, Chinle Formation, Arizona, USA.

Last: Syntarsus kayentakatae Rowe, 1989, Kayenta Formation, Willow Springs, Arizona, USA.

Intervening: PLB.

Comment: The famous Coelophysis quarry at Ghost Ranch, New Mexico, USA, is in the upper part of the Petrified Forest Member, dated lower NOR.

F. CERATOSAURIDAE Marsh, 1884 (P)

J. (SIN–KIM/TTH) Terr.


Last: Ceratosaurus nasicornis Marsh, 1884, Morrison Formation, Canyon City, Colorado, USA.

Intervening: PLB.

F. VELOCISAURIDAE Bonaparte, 1991

K. (CON) Terr.


Infra-order CARNOSAURIA Huene, 1920

F. ALLOSAURIDAE Marsh, 1879

J. (CLV)–K. (ALB) Terr.

First: Piatnitzkysaurus floresi Bonaparte, 1979, Cañadon Asfalto Formation, Chubut, Argentina.

Last: Chilantaisaurus marotuensis Gilmore, 1924, unnamed unit, Nei Mongol Zizhqu, China.

Intervening: OXF–HAU, APT

F. TYRANNOSAURIDAE Osborn, 1905

K. (?CEN–MAA) Terr.

First: Alectrosaurus olsenii Gilmore, 1933, Iren Dabasu Formation, Nei Mongol Zizhqu, China.

Last: Tyrannosaurus rex Osborn, 1905, Hell Creek Formation, Montana, and numerous other upper Maastrichtian formations in the mid-west of Canada and USA.

Intervening: CMP.

F. MEGALOSAURIDAE Huxley, 1869

Tr. (RHT)–K. (VLG/ALB) Terr.

First: Megalosaurus cambrensis (Newton, 1899), Rhaetic, Glamorgan, Wales, UK.

Last: Kelmayisaurus petriolicus Dong, 1973, Lianmugin Formation, Xinjiang Uygyur Zizhqu, China.

Intervening: AAL–BTH, OXF.

Comment: The famous Coelophysis quarry at Ghost Ranch, New Mexico, USA, is in the upper part of the Petrified Forest Member, dated lower NOR.

Infra-order ORNITHOMIMOSAURIA Barsbold, 1976

F. HARPYMIMIDAE Barsbold and Pede, 1984

K. (APT/ALB) Terr.

First and Last: Harpyimus okladnikovi Barsbold and Perle, 1984, Shinekhudukskaya Svita, Dundgov, Mongolia.

F. GARUDIMIMIDAE Barsbold, 1981

K. (CEN/TUR) Terr.

First and Last: Garudimus brevipes Barsbold, 1981, Baynshirenkskaya Svita, Omnogov, Mongolia.

F. ORNITHOMIMIDAE Marsh, 1890

K. (?CEN–MAA) Terr.

First: Archaeornithomimus asiaticus (Gilmore, 1933), Iren Dabasu Formation, Nei Mongol Zizhqu, China.

Last: Ornithomimus velox Marsh, 1890, Denver Formation, Colorado; Kaiparowits Formation, Utah, USA.

Intervening: CMP.

Comment: An older ‘ornithomimid’ has been reported from the Sebayashi Formation (BRM/APT) of Japan (Manabe and Hasegawa, 1991), but its exact affinities are unclear.

STEM-GROUP MANIRAPTORANS

?F. ALVAREZOSAURIDAE Bonaparte, 1991

K. (CON) Terr.

First and Last: Alvarezerosaurus calvii Bonaparte, 1991, Bajo de la Carpa Member, Río Colorado Formation, Neuquén Province, Argentina (Bonaparte, 1991).

F. ELMISAURIDAE Osmólska, 1981

K. (CMP–MAA) Terr.

First: Elmisaurus ischigualastensis (Manabe and Hasegawa, 1991), but its exact affinities are unclear.

Comment: The family Megalosauridae is not accepted by Molnar et al. (1990), although they suggest that Megalosaurus, Magnasaurus, and Kelmayisaurus may be related. There is little evidence that M. cambrensis is a true megalosaur. If not, the earliest records of Megalosaurus are AAL and BAJ.

F. UNNAMED J. (CLV–KIM/TTH) Terr.


Last: Torvosaurus tanneri Galton and Jensen, 1979, Morrison Formation, Colorado, USA.

Intervening: None.

Comment: This family is hinted at by Molnar et al. (1990, p. 209), in suggesting a phyletic link between Eustreptospondylus, Torvosaurus, and Yangchuanosaurus.
**Animals: Vertebrates**

**F. DEINOCHEIRIDAE** Osmólska and Roniewicz, 1970
K. (CMP/MAA) Terr.

**First and Last:** Deinocheirus mirificus Osmólska and Roniewicz, 1970, Nemegt Formation, Omnogov, Mongolia.

**F. NOASAURIDAE** Bonaparte and Powell, 1980
K. (CMP/MAA) Terr.

**First and Last:** Noasaurus leali Bonaparte and Powell, 1980, Lecho Formation, El Brete, Salta, Argentina.

**F. THERIZINOSAURIDAE** Maleev, 1954
K. (CMP/MAA) Terr.

**First and Last:** Therizinosaurus cheloniformis Maleev, 1954, Nemegt Formation, Omnogov, and White Beds of Khermeen Tsav, Bayankhongor, Mongolia.

**Suborder** SAUROPODOMORPHA Huene, 1932

**Infra-order** PROSAUROPODA Huene, 1920 (p)

**F. THECODONTOSAURIDAE** Huene, 1908
Tr. (CRN-RHT) Terr.

**First:** Azendhosaurus laaroussi Dutuit, 1972, Argana Formation, Marrakech, Morocco.

**Last:** Thecodontosaurus antiquus Riley and Stutchbury, 1836, Magnesian Conglomerate, Avon, England, UK; fissure fillings, Glamorgan, Wales, UK.

**Intervening:** NOR.

**F. ANCHISAURIDAE** Marsh, 1885
J. (PLBITOA) Terr.

**First and Last:** Anchisaurus polyzelus (Hitchcock, 1865), Upper Portland Formation, Connecticut and Massachusetts, USA.

**F. MASSOSPONDYLIDAE** Huene, 1914
J. (HET-SIN/PLB) Terr.

**First:** Massospondylus carinatus Owen, 1854, upper Elliot Formation, South Africa; Forest Sandstone, Zimbabwe; upper Elliot Formation, Lesotho.

**Last:** Massospondylus sp., Kayenta Formation, Arizona, USA.

**F. YUNNANOSAURIDAE** Young, 1942
J. (HET/SIN) Terr.

**First and Last:** Yunnanosaurus huangi Young, 1942, upper and lower Lufeng Series, Yunnan, China.

**F. PLATEOSAURIDAE** Marsh, 1895
Tr. (NOR)-J. (PLBITOA) Terr.

**First:** Sellosaurus gracilis Huene, 1907–1908, Untere Stubensandstein, Baden-Württemberg, Germany.

**Last:** Ammosaurus major (Marsh, 1891), upper Portland Formation, Connecticut; Navajo Sandstone, Arizona, USA.

**Intervening:** RHT.

**F. MELANOROSAURIDAE** Huene, 1929
Tr. (NOR–HET/SIN) Terr.

**First:** Euskelosaurus browni Huxley, 1866, lower Elliot Formation and Bushveld Sandstone, South Africa; lower Elliot Formation, Lesotho; Mpandien Formation, Zimbabwe; Melanorosaurus radix Haughton, 1924, lower Elliot Formation, South Africa.
Infra-order SAUROPODA Marsh, 1878

F. VULCANODONTIDAE Cooper, 1984 (p?)
J. (HET—TOA) Terr.

Intervening: BTH, CLV.


Infra-order SAUROPODA Marsh, 1878

F. CETIOSAURIDAE Lydekker, 1888 (p)
J. (BAJ—KIM/TTTH) Terr.

Last: Hoplocanthosaurus priscus (Hatcher, 1903) and H. delfsi McIntosh and Williams, 1988, Morrison Formation, Colorado and Wyoming, USA.

Intervening: BTH, CLV.

F. BRACHIOSAURIDAE Riggs, 1904
J. (?AAI/BTH)—K. (ALB) Terr.

Last: Brachiosaurus nougaredi Lapparent, 1960, 'Continental Intercalaire', Wargla, Algeria; Chubutisaurus insignis Lapparent, 1960, 'Con­
modified

Intervening: BTH, CLV, KIM, TTH, ALB, SAN.

Comment: If the Northamptonshire brachiosaurid is not confirmed, definite BTH examples include: Bothriopсидylus robustus Owen, 1875, Forest Marble, Wiltshire, England, UK; B. madagascariensis Lydekker, 1895 and Lapparentosaurus madagascariensis Bonaparte, 1979, Isalo Formation, Majunga, Madagascar.

F. CAMARASAURIDAE Cope, 1877
J. (OXF)—K. (CMP/MAA)Terr.

First: Tienshanosaurus chitalensis Young, 1937, Shishigou Formation, Xinjiang, China.
Last: Opisthothecauda starzynskii Borisuk-Bialynicka, 1977, Nemegt Formation, Omnogov, Mongolia.

Intervening: KIM, TTH, HAU—BRM.

F. DIPLODOCIDAE Marsh, 1884
J. (BAJ)—K. (CMP/MAA) Terr.

First: Cetiosaurus longus (Owen, 1842), Inferior Oolite, West Yorkshire, England, UK.

Intervening: BTH, CLV, KIM, TTH, ALB, SAN.

F. TITANOSAURIDAE Lydekker, 1885
J. (KIM)—K. (MAA) Terr. (Fig. 39.6)

First: Tornieria robusta (Fraas, 1908), upper Tendaguru Beds, Mtwara, Tanzania.
Last: Alamosaurus sanjuanensis Gilmore, 1922, Javelina Formation, upper MAA, Texas, USA; Magyarosaurus dacus (Nopcsa, 1915), M. transylvanicus Huene, 1932, and M. hungaricus Huene, 1932, Sinpetru Beds, upper MAA, Hunedoara, Romania.

Intervening: VAL—BRM, ALB, TUR—CMP.

Comment: Titanosaurs are known from numerous CMP/MAA formations in Asia, South America, North America and Europe, but most are not dated as late MAA.

SAURISCHIA incertae sedis

F. SEGNOUSAURIDAE Perle, 1979
K. (CEN/TUR—CMP) Terr.

Last: Nanxunhosaurot brevispinus Dong, 1979, Nanxiong Formation, Guandong, China.

Intervening: SAN, CMP.

Order ORNITHISCHIA Seeley, 1887

F. PISANOSAURIDAE Casamiquela, 1967
Tr. (CRN) Terr.

First and Last: Pisanosaurus merti Casamiquela, 1967, Ichigualasto Formation, La Rioja Province, Argentina.

F. FABROSAURIDAE Galton, 1972
J. (HET/SIN) Terr.

First and Last: Lesothosaurus diagnosticus Galton, 1978, Upper Elliot Formation, Mafeting District, Lesotho.

Comment: Other supposed fabrosaurids such as Technosaurus and Reuellosaurus (CRN), Scelidosaurus (HET), Fabrosaurus, Tava­saurus, and Fulenia (HET/SIN), Xiaosaurus (BTH), Alcodon and Trumacrodon (OXF), Nanosaurus (KIM), and Echinodon (BER) are not regarded as fabrosaurids, but merely Ornithischia incertae sedis, or thyreophorans (e.g. Scelidosaurus), or prosauropods (e.g. Fulenia, Tava­saurus, Technosaurus) (Weishampel and Witmer, 1990; Sereno, 1991a).

Suborder THYREOPHORA Nopcsa, 1915

F. SCELIDOSAURIDAE Huxley, 1869 (?p)
J. (SIN—TTH?) Terr.

First: Scelidosaurus harrisoni Owen, 1861, lower Lias, Dorset, England, UK.
Last: Echinodon becklesi Owen, 1861, middle Purbeck Beds, Dorset, England, UK.

Intervening: ?PLB.

Comment: The family Scelidosauridae is equated here with the 'basal Thyreophora' of Coombs et al. (1990). If Echinodon is not a 'basal thyreophoran', the family range becomes SIN—PLB?, with Scelidosaurus lawleri Colbert, 1981, as the youngest member.

Infra-order STEGOSAURIA Marsh, 1877

F. HUAYANGOSAURIDAE Dong et al., 1982
J. (HET/PLB—BTH/CLV) Terr.

First: Tatisaurus oehleri Simmons, 1965, Dark Red Beds of the Lower Lufeng Group, Yunnan, China (Dong, 1990).
Last: Huayangosaurus taihuii Dong et al., 1982, Xiashaximiao Formation, Szechuan, China.
Fig. 39.6

### F. STEGOSAURIDAE Marsh, 1880

J. (BTH)--K. (CON)  Terr.

**First:** Unnamed stegosaur, Chipping Norton Formation, lower BTH, Gloucestershire, England, UK (Metcalf et al., 1993); and from other BTH localities in Gloucestershire and Oxfordshire, England, UK (Evans and Milner, 1991).

**Last:** Dravidosaurus blanfordi Yadagiri and Ayyasami, 1979, Trichinopoly Group, Tamil Nadu, India.

**Intervening:** CLV--ALB.

**Infra-order** ANKYLOSAURIA Osborn, 1923

F. NODOSAURIDAE Marsh, 1890

J. (CLV)--K. (MAA)  Terr.
Reptilia

F. ANKYLOSAURIDAE Brown, 1908
K. (APT/ALB-MAA) Terr.

F. HETERODONTOSAURIDAE Romer, 1966
J. (HET/SIN-SIN) Terr.


F. CAMPTOSAURIDAE Marsh, 1885
J. (KIM)-K. (BRM) Terr.


F. BACTRANOPODA Sereno, 1986

Infra-order ORNITHOPODA Marsh, 1881

F. HADROSAURIDAE Cope, 1869
K. (?CEN-MAA) Terr.

F. CAMPTOSAURIA Brown, 1908
K. (APT/ALB-MAA) Terr.


Last: ‘Struthiosaurus translabilicus’ Nopcsa, 1915, Sinepetau Beds, Hunedoara, Romania; Gosau Formation, Niederösterreich, Austria; Denvirosaurs schlesiani Bakker, 1988, Lance Formation, South Dakota, USA.

Intervening: KIM, VLG-CEN, CMP.


CI: 1923 K. (BRM-ALB) Terr.

First: Iguanodon hoffi Owen, 1874, upper Purbeck Beds, Dorset, England, UK.


Intervening: VLG-APT.

First: Lydekker, 1893, Xiashaximiao Formation, Nei Mongol Zizhiqu, China. The Iren Dabasu Formation is dated variously as CEN or MAA. If the latter, the oldest hadrosaurid is Araiosaurus tubiferus Rozhdestvensky, 1968, Beleutinskaya Svita, Kazakhstan, former USSR (?TUR/SAN).

First: Edmontosaurus regalis Lambe, 1917, E. annectens (Marsh, 1892), E. saskatchewanensis (Sternberg, 1926), and ‘Anatosaurus’ copei Lull and Wright, 1942, Scollard Formation, Alberta, Canada; Frenchman Formation, Saskatchewan, Canada; Hell Creek Formation, Montana, North Dakota, South Dakota, USA; Lance Formation, South Dakota, Wyoming, USA; Laramie Formation, Colorado, USA.

Intervening: TUR-CMP.

First: Goyocephale latimori Perle et al., 1982, unnamed unit, Ovorkhangai, Mongolia.


First: Psittacosaurus guoyangensis Brown and Schlaikjer, 1943, Lance Formation, Wyoming, USA; Hells Creek Formation, South Dakota, Montana, USA; Stegoceras edmontonense (Brown and Schlaikjer, 1943), Hell Creek Formation, Montana, USA; Stygimoloch spinifer Galton and Sues, 1983, Hell Creek Formation, Montana, USA; Lance Formation, Wyoming, USA.

Intervening: CMP.

First: Psittacosaurus mongoliensis Osborn, 1923, Shestakovskaya Svita, Gorno-Altayskaya Autonomous Region, former USSR, and several formations in Mongolia and China.

First: Psittacosaurus guiyangensis Cheng, 1983, and P. osborni Young, 1931, Lisangou Formation, Nei Mongol Zizhiqu, China; and possibly other species of Psittacosaurus from China (Sereno, 1990, p. 589) in rocks dated as APT-ALB.

Intervening: APT.

Comment: An older ‘psittacosaurid’ has been reported from the Kitadani Formation (BRM) of Japan (Manabe and Hasegawa, 1991).


First: Protoceratops andrewsi Granger and Gregory, 1923, Beds of Toogregg and Beds of Alag Teg, Omnogov, Mongolia.
**Last:** *Leptoceratops gracilis* Brown, 1914, Scollard Formation, Alberta, Canada; Lance Formation, Wyoming, USA.

**F. CERATOPSIDAE** Marsh, 1890
K. (CMP–MAA) Terr.

**First:** *Chasmosaurus mariscalis*ensis Lehman, 1989, Aguja Formation, Texas, USA; *Torosaurus latus* Marsh, 1891 and *Triceratops horridus* Marsh, 1889, Lance Formation, Wyoming, USA; Evanston Formation, Wyoming, USA; Hell Creek Formation, Montana, South Dakota, USA; Laramie Formation, Colorado, USA; Javelina Formation, Texas, USA; Scollard Formation, Alberta, Canada; Frenchman Formation, Saskatchewan, Canada.

**ARCHOSAUROMORPHA incertae sedis**


**First and Last:** *Helveticosaurus zollingeri* Peyer, 1943, Grenzbitumen Horizon, Monte San Giorgio, Kanton Tessin, Switzerland.

**NEODIAPSIDA incertae sedis**

**Superorder** SAUROPTERYGIA Owen, 1860


**Order** PACHYPLEUROSAURIA Sanz, 1980

**F. PACHYPLEUROSAURIDAE** Nopcsa, 1928
Tr. (ANS–LAD) Mar.

**First:** *Dactylosaurus gracilis* Gürich, 1884, lower Muschelkalk, Silesia, Poland; *Anatosaurus multidentatus* Huene, 1958, base of the Muschelkalk, Lechtaler Alpen, Germany; *Keichousaurus yuansensis* Young, 1965, basal Ansian, Kweichow, China.

**Last:** *Neusticosaurus pusillus* (Fraas, 1881), terminal Muschelkalk, Baden-Württemberg, Germany; *Psilotrachelosaurus toepfisch*i Nopcsa, 1928, upper Muschelkalk, Töplitz, Germany.

**Order** NOTHOSAURIFORMES Storrs, 1991

**Suborder** PLACODONTIA Zittel, 1887–1890 (Owen, 1859)

**F. PLACODONTIDAE** Meyer, 1863
Tr. (SCY–LAD) Mar.

**First:** *?Placodus impressus* Agassiz, 1839, upper Buntsandstein, Pfalz, Germany. A reputed upper SCY record from Makhtech Ramon, Israel is not a placodontian, but is rather a temnospondyl (Zanon, 1991).

**Last:** *Placodus gigas* Agassiz, 1833, Tonplatten, upper Muschelkalk, Bayreuth, Germany.

**Intervening:** ANS.

**F. CYAMODONTIDAE** Nopcsa, 1923
Tr. (ANS–LAD) Mar.

**First:** *Cyamodus tarnowitzensis* Gürich, 1884, lower Muschelkalk, Silesia, Poland.

**Last:** *Cyamodus rostratus* (Münster, 1830), upper Muschelkalk, Bayreuth, Germany.

**F. PLACOCHELYIDAE** Jaekel, 1907
Tr. (ANS–RHT) Mar.

**First:** *Saurophargis volzi* Frech, 1903, Wellenkalk, lower Muschelkalk, Silesia, Poland.

**Last:** *Psephoderma alpinum* Meyer, 1858 and *P. raeticum* (Schubert-Klempnauer, 1975), Rät, Bavaria, Germany; *P. anglicum* Meyer, 1867, Rhaetic, Avon, England, UK.

**Intervening:** LAD, CRN, ?NOR.

**F. HENODONTIDAE** Huene, 1936
Tr. (CRN) Mar./FW

**First and Last:** *Henodus chelyops* Huene, 1936, Gipskeuper, Baden-Württemberg, Germany.

**Suborder** EUSAUROPTERYGIA Tschanz, 1989

**Infra-order** NOTHOSAURIA Seeley, 1882 (p)

**F. COROSAURIDAE** Kuhn, 1964 Tr. (SCY) Mar.

**First and Last:** *Corosaurus alcovenensis* Case, 1936, Alcova Limestone, Chugwater Group, Natrona County, Wyoming, USA (Storrs, 1991a).

**F. SIMOSAURIDAE** Gervais, 1859
Tr. (LAD–CRN) Mar.

**First:** *Simosaurus gaillardi*ti Meyer, 1842, upper Muschelkalk, France, Germany.

**Last:** *Simosaurus guilelmi* Meyer, 1855, Lettenkohle, Hoheneck, Germany.

**F. NOTHOSAURIDAE** Baur, 1889
Tr. (SCY–CRN) Mar.

**First:** *?Nothosaurus mirabilis* Münster, 1834, Obere Buntsandstein, Germany; *?Kuangsisaurus orientalis* Young, 1959, Lower Triassic, Kwangsi, China.

**Last:** *Nothosaurus edingerae* Schultze, 1970, Gipskeuper, Bayreuth, Germany.

**Intervening:** ANS, LAD.

**Infra-order** PLESIOSAURIA Blainville, 1835


**F. PISTOSAURIDAE** Baur, 1887 Tr. (ANS) Mar.

**First and Last:** *Pistosaurus longaevus* Meyer, 1847–1855, upper Muschelkalk, Bayreuth, Bavaria, Germany.

**F. PLESIOSAURIDAE** Gray, 1825
Tr. (LAD??/RHT)–J. (TOA) Mar.

**First:** *Plesiosaurus priscus* Huene, 1902, Lettenkohle of Bibersfeld, Germany, is based on plesiosaur-like vertebrae (Mazin, 1988, p. 119). Other plesiosaurian vertebrae are known from the Middle Triassic German Muschelkalk and the Ladinian of the former USSR (Storrs, 1991a, p. 81). If these are not plesiosaurid, then the oldest remains are *Plesiosaurus costatus* Owen, 1840, and other species, from the Rhaetic of Avon, Leicestershire, and Nottinghamshire, England, UK; Morayshire, Scotland, UK; Autun, France; and Baden-Württemberg, Germany.

**Last:** *Plesiosaurus brachypterygius* Huene, 1923 and *P. guileiimperatoris* Dames, 1895, Lia–č, Posidonien-chiefer, Baden-Württemberg, Germany.

**Intervening:** HET–PLB.
F. CRYPTOCLEIDIDAE Williston, 1925  
Last: Aristonectes parvidens Cabrera, 1941, Cañadon del Loro, Chubut, Argentina; Turneria seymourensis Chatterjee and Small, 1989, Lopez de Bertodano Formation, Seymour Island, Antarctica (Chatterjee and Small, 1989).  
Intervening: KIM.  

F. ELASMOSAURIDAE Cope, 1869  
First: Microcleidus macropterus (Seeley, 1865) and M. homalospodylous (Owen, 1840), Alum Shale Member, Yorkshire, England, UK.  
Last: Mausaurus haasti Hector, 1874, Haumurian, South Island, New Zealand (Welles and Gregg, 1971); elasmosaurid vertebrae, Nacatoch Formation, Texas, USA (Storrs and Langston, 1993); elasmosaurid vertebrae and tooth, Fox Hills Formation, New Mexico, USA.  
Intervening: OXF–TTH, ALB–CMP.  

F. PLIOSAURIDAE Seeley, 1874  
First: ?Eurycleidus arcuatus (Owen, 1840), and others, lower Lias, Zone of Psiloceras planorbis, Dorset, England, UK.  
Intervening: SIN–TOA, BTH–TTH, APT–CEN.  
Comment: If Eurycleidus arcuatus and relatives are not pliosaurs, then the oldest confirmed examples are CLV and OXF from Europe.  

F. POLYCOTYLIDAE Williston, 1908  
First: Trinacomerum sp., Kiamichi Formation, Denton County, Texas, USA (Storrs and Langston, 1993).  
Last: Polycotylus sp., Haumurian, South Island, New Zealand (Welles and Gregg, 1971), Fox Hills Formation, New Mexico, USA.  

Subclass SYNAPSIDA Osborn, 1903(p)  
Order PELYCOSAURIA Cope, 1878(p)  
All pelycosaur records were obtained from Reisz (1986), unless otherwise stated. The ages of the terrestrial Lower Permian tetrapod-bearing formations of the United States are hard to correlate with the type Russian marine sections, so there is some uncertainty over the dating of many pelycosaur records (Olson and Vaughn, 1970).  

F. EOTHYRIDIDAE Romer and Price, 1940  
P. (SAK–? ART) Terr.  
First: Oedaleops campi Langston, 1965, Abo/Cutler Formation, Cutler Group, Rio Arriba County, New Mexico, USA.  
Last: Eothyris parkeyi Romer, 1937, Belle Plains Formation, Wichita Group, Archer County, Texas, USA.  

F. CASEIDAE Williston, 1912  
P. (ART–KAZ) Terr.  
First: Casea broilii Williston, 1910, uppermost Arroyo Formation or lowermost Vale Formation, Clear Fork Group, Baylor County, Texas, USA.  
Last: Ennatosaurus lector Efremov, 1956, Zone II, Kazanian, Pinega River, former USSR.  
Intervening: KUN.  

F. VARANOPSISIDAE Romer and Price, 1940  
First: Aerosaurus greenleeorum Romer, 1937, Abo/Cutler Formation, Cutler Group, Rio Arriba County, New Mexico, USA.  
Last: Varanodon agilis Olson, 1965, Chickasha Formation, equivalent of the middle Flowerpot Formation, Blaine County, Oklahoma, USA.  
Intervening: SAK, ART.  

F. OPHIACODONTIDAE Nopcsa, 1923  
First: Archaeothyris florensis Reisz, 1972, Morien Group, Newfoundland, Nova Scotia, Canada.  
Last: Ophiacodon major Romer and Price, 1940, Clyde Formation, Clear Fork Group, Baylor County, Texas, USA.  
Intervening: KRE/CHV, KLA–SAK.  
Comment: A possible ophiacodontid, Varanossaurus acutoirostris Broili, 1904, from the Arroyo Formation, Clear Fork Group of Texas, would be the youngest representative of that family (ART) if correctly determined. However, Reisz (1986, p. 85) regards it as 'Pelycosauria incertae sedis'.  

F. EDAPHOSAURIDAE Case, 1907  
First: Edaphosaurus ? raymoudi (Case, 1908), Round Knob Formation, Conemaugh Group, Pennsylvania, USA.  
Last: Edaphosaurus pogonias Cope, 1882, Arroyo Formation, Clear Fork Group, Baylor County, Texas, USA.  
Intervening: KLA/NOG–SAK.  

F. SPHENACODONTIDAE Williston, 1912  
C. (KRE–P. (UFI) Terr. (Fig. 39.7)  
First: Haptodus garnettensis Currie, 1977, Santon Formation, Lansing Group, Garnett, Kansas, USA.  
Last: Dimetrodon angelensis Olson, 1962, upper San Angelo Formation, Pease River Group, Knox County, Texas, USA.  
Intervening: ASS–KUN.  

Order THERAPSIDA Broom, 1905  
### Figure 39.7

**Suborder PHTHINOSUCHIA** Romer, 1961

F. PHTHINOSUCHIDAE Efremov, 1954

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<th>Suborder</th>
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<tr>
<td>PHTHINOSUCHIA</td>
<td>PHTHINOSUCHIDAE</td>
<td>Phthinosaurus borissiaki Efremov, 1940</td>
<td>Phthinosaurus discors Efremov, 1954</td>
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**Suborder BIARMOSUCHIA** Hopson and Barghusen, 1986

F. BIARMOSUCHIDAE Olson, 1962

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<td>BIARMOSUCHIA</td>
<td>BIARMOSUCHIDAE</td>
<td>Biarmosuchus tener Tchudinov, 1960</td>
<td>Biarmosuchus tener Tchudinov, 1960</td>
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**Suborder EOTITANOSUCHIA** Boonstra, 1963

F. EOTITANOSUCHIDAE Tchudinov, 1960

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<tr>
<td>EOTITANOSUCHIA</td>
<td>EOTITANOSUCHIDAE</td>
<td>Eotitanosuchus olsoni Tchudinov, 1960</td>
<td>Eotitanosuchus olsoni Tchudinov, 1960</td>
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**Suborder GORGONOPSIA** Seeley, 1895

F. WATONGIIDAE Sigogneau-Russell, 1989

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<tr>
<td>GORGONOPSIA</td>
<td>WATONGIIDAE</td>
<td>?Watongia meieri Olson, 1974</td>
<td>?Watongia meieri Olson, 1974</td>
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**First and Last:** *Tetraceratops insignis* Matthew, 1908, basal Clear Fork Group, Baylor County, Texas, USA (Laurin and Reisz, 1990).

**Suborder PHTHINOSUCHIA** Romer, 1961

F. PHTHINOSUCHIDAE Efremov, 1954

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**Suborder BIARMOSUCHIA** Hopson and Barghusen, 1986

F. BIARMOSUCHIDAE Olson, 1962

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**Suborder EOTITANOSUCHIA** Boonstra, 1963

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**Suborder GORGONOPSIA** Seeley, 1895

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<td>?Watongia meieri Olson, 1974</td>
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</table>
F. GORGONOPSIDAE Lydekker, 1890  
P. (TAT) Terr.  
First: Broomisaurus planiceps (Broom, 1913), *Eoarctops* vanderbyli Haughton, 1929, *Galesuchus gracilis* Haughton, 1925, and *Scylacognathus parvus* Broom, 1913, *Eodicynodon-Tapinocephalus* Assemblage Zone, South Africa.  

Infra-order DINOCEPHALIA Seeley, 1894  
F. ESTEMMENOSUCHIDAE Tchudinov, 1960  
P. (KAZ-TAT) Terr.  
Last: *Molybdopagus arcanus* Tchudinov, 1964, lower TAT, Kirov, former USSR.  

F. ANTEOSAURIDAE Boonstra, 1954  
P. (IFI-TAT) Terr. (= Brithopidae)  
First: *Eosodon hudsonii* Olson, 1962, San Angelo Formation, Knox County, Texas, USA.  
Intervening: KAZ.  

F. TITANOSUCHIDAE Boonstra, 1972  
P. (KAZ) Terr.  

F. TAPINOCEPHALIDAE Lydekker, 1890  
P. (KAZ) Terr.  
Last: *Struthiocephalus whatsi* Haughton, 1915, and 17 other species, *Tapinocephalus-Bradysaurus* Assemblage Zone, South Africa.  

Infra-order ANOMODONTIA (DICYNODONTIA) Owen, 1859  
F. DROMASAURIDAE Abel, 1919  
P. (KAZ) Terr.  

F. OTSHERIIDAE Tchudinov, 1960  
P. (KAZ) Terr.  
First and Last: *Otsheria netsvetaei* Tchudinov, 1960, Zone II, KAZ, Ezhovo, Ural region, former USSR.  

F. GALEOPIIDAE Broom, 1912  
P. (KAZ) Terr.  
First and Last: *Galeops whatsi* Broom, 1912, *Tapinocephalus-Bradysaurus* Assemblage Zone, South Africa.  

F. VENJUKOVIDAE Efremov, 1940  
P. (KAZ) Terr.  
First: *Venjukovia prima* Amalitsky, 1922, Copper Sandstones, Zone II, KAZ, Ural region, former USSR.  
Last: *Venjukovia invisa* Efremov, 1938, Copper Sandstones, Zone II, KAZ, Ural region, former USSR.  

F. EODICYNODONTIDAE Cluver and King, 1983  
P. (IFI/KAZ) Terr.  
First and Last: *Eodicynodon oosthuizeni* Barry, 1974, *Eodicynodon-Tapinocephalus* Assemblage Zone, Cape Province, South Africa.  

F. ENDOTHIODONTIDAE Owen, 1876  
P. (KAZ-TAT) Terr.  
First: *Chelydontops altidentalis* Cluver, 1975, *Tapinocephalus-Bradysaurus* Assemblage Zone, Cape Province, South Africa.  
Last: *Endothiodon sp., Aulacephalodon-Cistecephalus* Assemblage Zone, South Africa. Equivalents in Brazil, India and Zambia.  

F. CRYPTODONTIDAE Owen, 1859  
P. (KAZ-TAT) Terr.  
First: *Tropidostoma microtremus* (Seeley, 1889), *Cleniosaurus platycetes* Broom, 1935, *Rhachiocephalus magnus* (Owen, 1876), *Oudenodon bainii* Owen, 1860, and other species of these genera, *Tropidostoma-Endothiodon* Assemblage Zone, Beaufort West, South Africa.  
Last: *Oudenodon bainii* (Owen, 1860), *Dicynodon-Therio­gnathus* Assemblage Zone, South Africa. Equivalents from Zambia.  

F. AULACEPHALODONTIDAE Cluver and King, 1983  
P. (KAZ-TAT) Terr.  
First: *Aulacephalodon baini* (Owen, 1845) and *Pelanomodon rubigedi* Broom, 1938, *Aulacephalodon-Cistecephalus* Assemblage Zone, South Africa, and equivalents in Zambia and Tanzania respectively.  
Last: *Gekia elginensis* Newton, 1893, Cutties Hillock Sandstone Formation, Morayshire, Scotland, UK.  

F. DICYNODONTIDAE Owen, 1859  
P. (KAZ-TAT) Terr.  
First: *Dicynodon acutirostris* Broom, 1935, and other species of this genus, *Tropidostoma-Endothiodon* Assemblage Zone, South Africa.
Last: *Dicynodon traquairi* (Newton, 1893), Cuttles Hilllock Sandstone, Morayshire, Scotland, UK.

Comment: Supposedly older species of *Dicynodon*, from the *Pristerognathus–Dictodon* Assemblage Zone of South Africa, are hard to substantiate (King, 1988).

**F. LYSTROSARUIDAE** Broom, 1903

Tr. (SCY) Terr.

**First and Last:** *Lystrosaurus murrayi* (Huxley, 1859), *Lystrosaurus–Procolophon* Assemblage Zone, Cape Province, South Africa; and 12 other species from this zone, and supposedly equivalent zones in Antarctica, the former USSR, China, India and Laos.

**F. KANNEMEYERIIDAE** Huene, 1948

Tr. (SCY–CRN) Terr.


**Last:** *Jachaleria colorata* Bonaparte, 1971, boundary between Ischigualasto Formation and lower Los Colorados Formation, La Rioja Province, Argentina.

Intervening: ANS, LAD.

**F. PRISTERODONTIDAE** King, 1988

P. (KAZ–TAT) Terr.

**First:** *Pristerodon merwevillensis* (Brolly and Schroeder, 1935), *Tapinocephalus–Bradysaurus* Assemblage Zone, South Africa.

**Last:** *Pristerodon mackayi* Huxley, 1868, and 13 other species of that genus, *Aulacephalodon–Cistecephalus* Assemblage Zone, South Africa.

**F. EMYDOPIDAE** Cluver and King, 1983

P. (KAZ)–Tr. (SCY) Terr.

**First:** *Emydops sp.*, *Tapinocephalus–Bradysaurus* Assemblage Zone, South Africa.

**Last:** *Myosaurus gracilis* Haughton, 1917, *Lystrosaurus–Procolophon* Assemblage Zone, South Africa.

Intervening: TAT.

**F. ROBERTIIDAE** Cluver and King, 1983

P. (KAZ–TAT) Terr.

**First:** *Robertia broomiana* Boonstra, 1948, *Dictodon jouberti* (Broom, 1905), and four other species of the latter genus, *Tapinocephalus–Bradysaurus* Assemblage Zone, South Africa.

**Last:** *Dictodon nanus* (Broom, 1936), *Dicynodon–Theriognathus* Assemblage Zone, South Africa.

**F. KINGORIIIDAE** King, 1988

P. (TAT)–Tr. (SCY) Terr.

**First:** *Kingoria nowacki* (Huene, 1942), Kawinga Formation, Kongori, Tanzania; *K. recurvidens* (Owen, 1876), and four other species of that genus, and *Dicynodontoides parringtoni* Broom, 1940, *Aulacephalodon–Cistecephalus* Assemblage Zone, South Africa.

**Last:** *Kombuisia freensis* Hotton, 1974, *Cynognathus–Diademodon* Assemblage Zone, Cape Province, South Africa.

**Suborder THEROCEPHALIA** Broom, 1903

**F. PRISTEROGNATHIDAE** Broom, 1906

P. (KAZ) Terr.

**First:** *Porosteognathus eoremovii* Vjuskov, 1952, Zone I, Urals region, former USSR; *pristerognathid*, upper Ecca Group, Cape Province, South Africa (Rubidge et al., 1983).

**Last:** *Pristerognathus polyodon* Seeley, 1895, and other species, upper *Pristerognathus–Dictodon* Assemblage Zone, South Africa.

**F. HOFMEYERIIDAE** Hopson and Barghusen, 1986

P. (TAT) Terr.

**First and Last:** *Hofmeyria atavus* Broom, 1935 and *Ictidos­toma hemburyi* (Broom, 1912), *Aulacephalodon–Cistecephalus* Assemblage Zone, South Africa (Brink, 1960).

**F. EUCHAMBERSIIDAE** Boonstra, 1934

P. (TAT)–Tr. (SCY) Terr. (= Moschorhinidae; Annatherapsidae; Akidnognathidae)

**First:** *Euchambertia mirabilis* Broom, 1931, *Aulacephalodon–Cistecephalus* Assemblage Zone; *Annatherapsidus petri* (Amalitzky, 1922), Zone IV, Urals region, former USSR.

**Last:** *Moschorinus kitchingi* Broom, 1920, *Lystrosaurus–Procolophon* Assemblage Zone, South Africa.

**F. WHAITSIIDAE** Haughton, 1918

P. (TAT) Terr.

**First:** *Whaitsia sp.*, *Aulacephalodon–Cistecephalus* Assemblage Zone, Graaf-Reinet, South Africa.

**Last:** *Whaitsia platyceps* Haughton, 1918, *Dicynodon–Theriognathus* Assemblage Zone, South Africa and equivalent, Ruhuhu Valley, Tanzania; *Moschorhaisia vjuskovi* Tatarinov, 1963, Zone IV, TAT, Urals region, former USSR.

**F. ICTIDOSUCHIDAE** Broom, 1903

P. (KAZ)–Tr. (SCY) Terr.

**First:** *Icticepsuchus polycynodon* Broom, 1915, *Tapinocephalus–Bradysaurus* Assemblage Zone, South Africa.


**F. SCALOPOSAURIDAE** Broom, 1914

P. (TAT)–Tr. (SCY) Terr.

**First:** *Scalopsaurus constictus* Owen, 1876 and *Nanicto­cephalus richardi* Broom, 1940, *Aulacephalodon–Cistecephalus* Assemblage Zone, South Africa (Mendrez-Carroll, 1979).

**Last:** *Pediaesaurus parus* Colbert and Kitching, 1981, Fremouw Formation, Antarctica.

Comment: Mendrez-Carroll (1979) and Hopson and Barghusen (1986) noted that the *Lystrosaurus–Procolophon* Assemblage Zone examples of scaloposaurids belong to other taxa, but Colbert and Kitching (1981) described *Pediaesaurus* as a scaloposaurid.

**F. REGISAUROIDAE** Hopson and Barghusen, 1986

Tr. (SCY) Terr.

**First and Last:** *Regisaurus jacobi* Mendrez, 1972, *Lystro­saurus–Procolophon* Assemblage Zone, Cape Province, South Africa.

**F. LYCIDEOPSIDAE** Broom, 1931

P. (TAT) Terr.

**First and Last:** *Lycideops longiceps* Broom, 1931,
Aulacephalodon–Cistecephalus Assemblage Zone, South Africa.

F. ERICIOLACERTIDAE Watson and Romer, 1956
Tr. (SCY) Terr.

First and Last: Ericiolacerta parva Watson, 1931, Lystrosaurus–Procolophon Assemblage Zone, Orange Free State, South Africa; Fremouw Formation, Antarctica (Colbert and Kitching, 1981).

F. BAURIIDAE Broom, 1911 Tr. (SCY–ANS) Terr.
First: Bauria cynops Broom, 1909, Sesamodon browni Broom, 1932, Cynognathus–Diademodon Assemblage Zone, South Africa.

Last: Dongusaurus schepeletovi Vjuschkov, 1964 and Noto gomphodon damilovi Tatarinov, 1974, Donguz Series, Urals region, former USSR; Herpetogale marsupialis Keyser and Brink, 1979, Omingonde Formation, Etjo Mountain, southwestern Africa (Keyser and Brink, 1979).

Suborder CYNODONTIA Owen, 1860


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1–80.
Tschanz, K. (1989) Lariosaurus buzzii n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland), with comments on the classification of nothosaurs. Palaeontographica, Abteilung A, 208, 153–79.
Avian palaeontology has experienced a tremendous growth in popularity during the last two decades, as clearly shown by a simple index based on rate of publication (Unwin, 1988), which demonstrates that activity is now at an all-time high. It is also reflected in the data presented here; the temporal ranges of fewer than 70 of the 200 or so families listed by Fisher in 1967 remain unchanged, and during the intervening period, some 33 new families, four new orders and a new subclass have been proposed.

Archaeopteryx remains the earliest bird and, with the recent discovery of a sixth specimen (Wellnhofer, 1988), one of the best-known forms from the Mesozoic. Molnar’s recent review (1985) of contenders for the title of earliest-known bird, mostly represented by very fragmentary remains, concluded that none could definitely be assigned to Aves. Two putative Jurassic avians, Laopteryx Marsh, 1881 and Palaeopteryx Jensen, 1981, have recently been reidentified as pterosaurian (Jensen, 1981; Ostrom, 1986; Jensen and Padian, 1989). Praeornis sharovi (Rutnian, 1978) is almost certainly not a plant frond as has been suggested (Bock, 1986; Nessov, 1992), but its true identity (feather, prefeather, scale or perhaps none of these) remains unclear, as does the identity of the animal upon which it was borne.

The systematic layout of this section largely follows traditional lines, and only where a clear consensus of opinion seems to have emerged, have taxa been relocated. Practically all references prior to 1985 can be found in Brodkorb’s Catalogue of Fossil Birds (1963, 1964, 1967, 1971, 1978) or Olson’s recent review of the avian fossil record (1985). Only references not included in these works are given. Please note the additional abbreviation: Lit. = littoral.

Avian systematics continues to be riven by disputes, particularly with respect to the composition and phylogenetic arrangement of families. This stems, in part, from the variety of systematic methods employed by avian palaeontologists (Cracraft, 1988), and while some approaches may yield more durable results than others, none can fairly claim to have a monopoly on objectivity, or, for that matter, ‘the truth’. In fact, the imposition of a single system may have a stultifying rather than invigorating effect on avian systematics. The interminable taxonomic wrangles have led to a continual shuffling of taxa between families. The data presented here represent the latest state of play, but many changes in composition of families and their temporal range are to be expected.

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Class AVES

Order ARCHAEOPTERYGYIFORMES Fürbringer, 1888

F. ARCHAEOPTERYGYIDAE Huxley, 1872

J. (ITH)–K. (BER?) Terr. (see Fig. 40.1)

First: Archaeopteryx lithographica Meyer, 1861, Solnhofener Schichten, Altmüh-Alb, Bavaria, Germany.

Last: Archaeopteryx sp., Cornet, Padurea Cralui Mountains, Bihor, Romania (Kessler, 1984)? Until this identification is confirmed, A. lithographica remains the only certain record for this family.
**Order** IBEROMESORNITHIFORMES Sanz and Bonaparte, 1992

**F. IBEROMESORNITHIDAE** Sanz and Bonaparte, 1992  
K. (HAU/BRM)  
Terr.

**First and Last:** *Iberomesornis romerali* Sanz and Bonaparte (1992), La Huergina Formation, Las Hoyas, La Cierva Township, Cuenca Province, Spain.

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![Table and Diagram](image-url)
Bajan-Khongor aimak, currently referred to as ‘Holobotia ponomarenskoi’ and thought to be pterosaur (Kurochkin, 1991), probably belong in the Ambiortidae, and possibly to Ambiortus.

**Order** HESPERORNITHIFORMES Fürbringer, 1888

**F. ENALIORNITHIDAE** Fürbringer, 1888

**K. (ALB–CEN)** Mar.

**First:** Enaliornis barreti Seeley, 1864 and E. sedgwickii Seeley, 1864, Cambridge Greensand, Cambridge, England, UK.

**Last:** ‘Enaliornis like’ tarso-metatarsus, Greenhorn Formation, Kansas, USA (Martin, 1983).

F. BAPTORNITHIDAE American Ornithologists’ Union, 1910

**K. (SAN–CMP) Mar.**

**First:** Baptornis advenus Marsh, 1877, Smoky Hill Chalk, Niobrara Formation, Kansas, USA.

**Last:** Baptornis sp., Judith River Formation, Saskatchewan Landing, Saskatchewan, Canada (Tokaryk and Harington, in press).

**Comment:** Neogaeornis, earlier thought to be a baptornithid, has recently been transferred to the Gaviidae (Olson, 1992).

**F. HESPERORNITHIDAE** Marsh, 1872

**K. (SAN–MAA?) Mar.**

**First:** Hesperornis regalis Marsh, 1872, H. crassipes Marsh, 1876, H. gracilis Marsh, 1876 and Parahesperornis alexi Martin, 1983, Smoky Hill Chalk, Niobrara Formation, Kansas, USA. Note, the three species of *Hesperornis* are probably conspecific (Martin, 1980).

**Last:** Hesperornithid remains have been recovered from the Kanguk Formation (MAA), of Bylot Island, north-west of Baffin Island, North-west Territories, Canada (Currie, pers. comm., 1989), but until this is confirmed, the youngest reliable record is *Hesperornis* cf. *H. regalis*, from the Foremost Formation (middle CMP), South Saskatchewan River, Alberta, Canada (Fox, 1974).

**Order** ICHTHYORNITHIFORMES Marsh, 1873

**F. ICHTHYORNITHIDAE** Marsh, 1873

**K. (TUR–CMP)** Lit./Mar.

**First:** Ichthyornis sp., Vimen Member, Kaskapau Formation, Watino, Alberta, Canada (Fox, 1984). Note, teeth with some similarity to those of *Ichthyornis* have been recovered from upper Lower Cretaceous (APT/ALB) sediments of Hoboor, Central Mongolia (Kurochkin, 1988).

**Last:** Ichthyornis, Pembina Formation, Pierre Shale, Manitoba, Canada (Martin and Stewart, 1982) and the Mooreville Chalk, of Alabama and Mississippi, USA (Nicholls and Russell, 1990).

**Intervening:** CON, SAN.

**F. APATORNITHIDAE** Fürbringer, 1888

**K. (CON–MAA?)** Lit./Mar.

**First:** Apatornis celer (Marsh, 1873), Smoky Hill Chalk, Niobrara Formation, Kansas, USA.

**Last:** Palintropus retusus (Marsh, 1892), Lance Formation, Lance Creek, Niobrara County, Wyoming, USA. Studies currently in progress suggest that this form is indeed an apatornithid (C. Coy, pers. comm., 1990; Tyrrell Museum of Palaeontology, 1988). Otherwise, the earliest reliable record consists of undescribed remains from the Judith River Formation (CMP), Dinosaur Provincial Park, Alberta, Canada (C. Coy, pers. comm., 1990). Note, there may be some grounds for supposing the Apatornithidae to belong within the Charadriiformes (Olson, 1985).

F. ZHYRAORNITHIDAE Nessov, 1984

**K. (TUR/CON) Lit.**

**First and Last:** Zhyraornis kashkarovi Nessov, 1984, Bissekty Formation, Dzhyrakhuduk water well, Bukhara region, central Kyzylkum desert, Uzbekistan, former USSR.

**Comment:** There is some doubt as to the relationship of this family with ichthyornithiformes (Nessov, 1992).

**Order** ENANTIORNITHIFORMES Walker, 1981

**F. ENANTIORNITHIDAE** Nessov and Borkin, 1983

**K. (MAA) Terr.**

**First and Last:** Enantiornis leali Walker, 1981, Lecho Formation, El Brete, Salta Province, Argentina. *Sazavis prisa* Nessov, 1989, based on very fragmentary remains from the Taykarshin Beds (TUR/CON) of Dzhyrakhuduk, Bukhara region, Uzbekistan, former USSR, might possibly represent an earlier record for this family (Nessov, 1984; Nessov and Yarkov, 1989).

**F. ALEXORNITHIDAE** Brodkorb, 1976

**K. (CMP) Terr.**

**First and Last:** Alexornis antecedens Brodkorb, 1976, Bocana Roja Formation, Baja California del Norte, Mexico.

**F. AVISAURIDAE** Brett-Surman and Paul, 1985

**K. (MAA?)** Terr.

**First and Last:** Avisaurus archibaldi Brett-Surman and Paul, 1985, Hell Creek Formation, Garfield County, Montana, USA. Described as a new family of theropods, recent authors (e.g. Cracraft, 1986; Chiappe and Calvo, 1989a) regard the Avisauridae as probably avian.

**F. UNNAMED** Chiappe and Calvo, 1989a

**K. (CON) Terr.**

**First and Last:** Undescribed remains from the Rio Colorado Formation, Neuquén, Neuquén Province, Argentina (Chiappe and Calvo, 1989a). These remains may be shown eventually to belong within the Enantiornithidae (Chiappe, 1991).

**F. UNNAMED** Molnar, 1986

**K. (ALB) Terr.**

**First and Last:** Nanantis eos Molnar, 1986, Toolebuc Formation, Warra Station, Queensland, Australia.

**Order** GOBIPTERYGIFORMES Elzanowski, 1974

**F. GOBIPTERYGIDAE** Elzanowski, 1974

**K. (CMP) Terr.**

**First and Last:** Gobipteryx minuta Elzanowski, 1974, Barun Goyot Formation, Khulsan, Nemegt Basin, Mongolia.

**Order** PATAGOPTERYGIFORMES Alvarenga and Bonaparte, 1992

**F. PATAGOPTERYGIDAE** Alvarenga and Bonaparte, 1992

**K. (CON) Terr.**

**First and Last:** Patagopteryx deferrarii Alvarenga and Bonaparte, 1992, Rio Colorado Formation, Neuquén,
Neuquén Province, Patagonia, Argentina (see Chiappe and Calvo, 1989b; Bonaparte, 1991).

**Order** LITHORNITHIFORMES Houde, 1988

F. LITHORNITHIDAE Houde, 1988

T. (THA—LUT) Terr.

**First:** Lithornis celetius Houde, 1988, Fort Union Formation, Bangtail Quarry, Park County, Montana, USA.

**Last:** Lithornithidae genus indet., Bridgerian sediments, Henry’s Fork, Bridger Basin, Wyoming, USA (Houde, 1988).

**Intervening:** YPR.

**Order** STRUTHIONIFORMES Latham, 1790

F. ELEUTHERORNITHIDAE Wetmore, 1951

T. (LUT—RUP?) Terr.

**First:** Eleutherornis helveticus Schaub, 1940, Egerkingen gamma, Bohnerz, Switzerland. Fischer (1987) has reidentified Sauornis matthesi Fischer, 1967 from Neumark West, Saxony, Germany, as a perissodactyl.

**Last:** Proceriavis martini Harrison and Walker, 1979a, Hampstead Beds, Yarmouth, Isle of Wight, England, UK. Proceriavis is only tentatively included within the Eleutherornithidae (Harrison and Walker, 1979a), thus Eleutherornis may represent the sole occurrence of this family.

F. STRUTHIONIDAe Vigors, 1825

T. (UMI)—Rec. Terr.

**First:** A pedal phalanx and egg-shell fragments (!) tentatively ascribed to Struthio brachydactylus Burchak-Abramovich, 1939, lower to middle Upper Miocene, Anatolia, Turkey (Sauer, 1979). The earliest reliable record is Struthio orlovi Kurochkin and Lungu, 1970, from the Upper Miocene (MES), Varnitsa, Bendersky Region, Moldavia, former USSR.

**Intervening:** ZAN—HOL.

F. PALAEOTIDIDAE Houde and Haubold, 1987

T. (LUT) Terr.

**First:** Palaeotis weigelti Lambrecht, 1928, lowermost LUT, Messel Oil Shale, Messel Quarry, Hessen, Germany (Houde and Haubold, 1987; Peters, 1988).

**Last:** Palaeotis weigelti Lambrecht, 1928, Braunkohle des Geiseltasles, Saxony, Germany (Houde, 1986).

**Order** REMIORNITHIFORMES Martin, 1992

F. REMIORNITHIDAE Martin, 1992

T. (THA) Terr.

**First and Last:** Remiornis heberti Lemoine, 1881. Cernay les Reims, Dept. Haut-Rhin and Mont du Berru, France.

**Order** AEPYORNITHIFORMES Newton, 1884

F. AEPYORNITHIDAE Bonaparte, 1853

Q. (PLE/HOL) Terr.


**Order** CASUARIIFORMES Sclater, 1880

F. CASUARIIDAE Kaup, 1847

T. (PI)—Rec. Terr.

**First:** Casuarius sp., Awe fauna, Bulolo, south-east New Guinea (Plane, 1967).

**Intervening:** PLE.

**Order** DINORNITHIFORMES Gadow, 1893

F. DINORNITHIDAE Bonaparte, 1853

Q. (PLE/HOL) Terr.

**First and Last:** Dinornis novaezelandiae Owen, 1843, D. ingens Owen, 1844, D. giganteus Owen, 1844, D. gazella Oliver, 1849, and D. hercules Oliver, 1849 from North Island, New Zealand and D. torosus Hutton, 1891, D. robustus Owen, 1846 and D. maximus Owen, 1867, South Island, New Zealand.

**Order** ANOMALOPTERYGIDAE Oliver, 1930


**First:** Anomalopteryx antiquus Hutton, 1892, Timaru, South Island, New Zealand.

**Last:** Megalapteryx didius Owen, 1883, Takahe Valley, South Island, New Zealand; the last remaining anomalopterygid became extinct about 200 years ago (Scarlett, 1974).

**Intervening:** PLE, HOL.

**Order** APTERYGIFORMES Haeckel, 1866

F. APTERYGIDAE Gray, 1840

Q. (PLE?)—Rec. Terr.

**First:** Pseudapteryx gracilis Lydekker, 1891, possibly Upper Pleistocene but probably Holocene, New Zealand. Extant

**Intervening:** HOL.

**Order** RHEIFORMES Forbes, 1884

F. OPISTHODACTYLDae Ameghino, 1895

T. (THA—AQT) Terr.

**First:** Diogenornis fragilis Alvarenga, 1983, Basal Lime­stone of Itaborai, Cabuçu district, Rio de Janeiro State, Brazil.

**Last:** Opisthodactylus patagonicus Ameghino, 1891, Santa Cruz Formation, Santa Cruz Province, Argentina. This genus may represent both the first and last occurrence of this family, as Alvarenga (1983) only tentatively assigns Diogenornis to the Opisthodactylidae.

**F. RHEIDAE Bonaparte, 1853**

T. (PIA)—Rec. Terr.

**First:** Heterorhea dabbenei Rovereto, 1914, Monte Hermoso Formation, Buenos Aires Province, Argentina. Extant

**Intervening:** PLE, HOL.
Order TINAMIFORMES Huxley, 1872
First: Eudromia sp. indet. Epecuen Formation, Salinas Grandes de Hidalgo, La Pampa Province, Argentina (Tambussi, 1987). Remains of a tinamou from the Santacrucian Beds (LMI) of Patagonia have recently been identified by R. Chandler, but remain unpublished (L. Chiappe, pers. comm., 1989).
Intervening: ZAN–HOL.

Order SPHENISCIFORMES Sharpe, 1891
F. SPHENISCIDAE Bonaparte, 1831
First: Pachydyptes simpsoni Jenkins, 1974, Blanche Point Marls (lower PRB), Blanche Point, South Australia.
Extant
Intervening: RUP–HOL.

Order GAVIIIFORMES Wetmore and Miller, 1926
F. GAVIIDAE Allen, 1897
K. (u.?)-Rec. FW/Lit.
First: Neogaeornis wetzeli Lambrecht, 1929, Quirquina Formation, San Vincente bay, Concepti6n Province, Chile. Originally placed within the Baptornithidae, Olson (1992) has reidentified this bird as a diver. In addition, the partial skeleton of another diver has recently been recovered from the Lopez de Bartodano Formation, Seymour Island, Antarctica (Chatterjee, 1989).
Extant
Intervening: PRB, AQT–HOL.

Order PODICIPEDIFORMES (Fürbringer, 1888)
F. PODICIPEDIDAE Bonaparte, 1831
T. (BUR)–Rec. FW/Lit.
Extant
Intervening: TOR–HOL.

Order PROCCELLARIIFORMES Fürbringer, 1888
F. DIOMEDEIDAE Gray, 1840
First: Diomedeaedae gen. et sp. indet., La Meseta Formation, Seymour Island, Antarctica (Tambussi and Tonni, 1988).
Extant
Intervening: CHT–HOL.
F. DIOMEDEIDIDAE Fischer, 1985
First and Last: Diomeedoides minimus Fischer, 1985, phosphorite nodule horizons, Braunkohlentagebau, Espenhain, south of Leipzig, Germany.
Extant
Intervening: AQT–HOL.
F. PLOTOPTERIDAE Howard, 1969
First: Phocavis maritimus Goedert, 1988, Keasey Formation, Vernonia, Washington County, Oregon, USA.
Last: Unnamed form, Central Japan (Hasegawa et al., 1977; Olson, 1985).
Extant
Intervening: RUP, CHT?, LMI.

Order PELECANIFORMES Sharpe, 1891
Extant
Intervening: HOL.

F. PELECANOIDIDAE Gray, 1871
T. (RUP?)–Rec. FW/Mar.
First: Miopelecanus gracilis (Milne-Edwards, 1863), Labeur, Commune de Vaumas, Allier, France, Recent stratigraphical studies suggest that the beds which yielded Miopelecanus may only be early Miocene (AQT) in age (Cheneval, 1984).
Extant
Intervening: AQT–HOL.
F. ELOPTERYGIDAE Lambrecht, 1933
K. (MAA?)–T. (MEO?) Mar./FW
First: Elopteryx nanopoi Andrews, 1913, Transylvanian freshwater limestone, Hatszeg, Romania. Considerable doubt has been expressed about the nature of remains ascribed to Elopteryx, including suggestions that they are non-avian (Olson, 1985); an avian skull has now apparently been discovered (Kessler, 1987), although whether it can be legitimately assigned to Elopteryx remains to be demonstrated. According to Milikovsky (1987) the holotype mandible is avian, but possibly belongs within the Sulidae.
Last: Eostega lebedinsky Lambrecht, 1929, ‘coarse chalk’, near Cluj–Napoca (formerly Kolozsvár), Romania. While Eostega may be pelecaniform, there is some doubt as to whether it belongs here (Olson, 1985). The only remaining fragmentary paired frontal (!), can be established, the oldest reliable record is Puffinus raemdonckii (Van Beneden, 1871), Rupelian Sand (RUP), Edeghem, Antwerp, Belgium (Brodkorb, 1962).

**F. SULIDAE** Reichenbach, 1849  
T. (RUP?)-Rec.  
**First**: *Sula ronzoni* Milne-Edwards, 1867, calcareous marl of Ronzon, Auvergne, France. This material is difficult to interpret and cannot definitely be assigned to the Sulidae ( Olson, 1985); it may even belong in the Phalacrocoracidae ( Harrison, 1976). The earliest reliable record is *Empherasula avenersis* (Milne-Edwards, 1867–1871), Calcaire de Gannat (CHT), Allier, France (Cheneval, 1984), but see also comments on *Elopteryx* above.  
**Extant**  
**Intervening**: AQT-HOL.

**F. PHALACROCORACIDAE** Bonaparte, 1854  
T. (PRB/RUP)-Rec.  
**Extant**  
**Intervening**: RUP–HOL.

**F. ANHINGIDAE** Ridgway, 1887  
T. (LMI)-Rec.  
**First**: *Anhinga subvolans* (Brodkorb, 1956), Thomas Farm, Gilchrist County, Florida, USA (Becker, 1986).  
**Extant**  
**Intervening**: LLA-HOL.

**F. UNNAMED** Rich et al., 1986  
T. (Eoc./Mio.).  
**First and Last**: *Protoplotos beauforti* Lambrecht, 1930, freshwater fish beds, whose age may be anywhere between Eocene and Miocene (Rich et al., 1986), Sipang, Sumatra.

**F. FREGATIDAE** Garrod, 1874  
T. (YPR)-Rec.  
**First**: *Limnofregata azygosternon* Olson, 1977, Green River Formation, Wyoming, USA.  
**Extant**  
**Intervening**: PLE-HOL.

**F. PELAGORNITIDAE** Fürbringer, 1888  
T. (THA-PIA?)-Mar.  
**First**: *Pseudodontornis tenuirostris* Harrison, 1985, Oldhavens Beds, Herne Bay, Kent, England, UK.  
**Last**: *Pseudodontornis stirtoni* Howard and Warter, 1969, Greta Silstone, Motunae Beach, South Island, New Zealand. As *P. stirtoni* is of uncertain age, pelagornithid material from the Middle Pliocene of Waihi Beach, Hawera, North Island, New Zealand, may represent the youngest record for this family (McKee, 1985).

**Intervening**: YPR-ZAN.  
**Comment**: Following Olson (1985), I assume here that Pelagornithidae = Odontopterygidae, Cyphornithidae, Pseudodontornithidae and possibly Dasornithidae (see also Goedert, 1989).  
**Order** ARDEIFORMES Wagler, 1830  
**F. ARDEIDAE** Vigors, 1825  
T. (BRT/CHT)-Rec.  
**First**: *Proardea amissa* (Milne-Edwards, 1892), Phosphorites du Quercy, France.  
**Extant**  
**Intervening**: RUP–HOL.

**F. XENERODIOPIDAE** Rasmussen, Olson and Simons, 1987  
T. (RUP)-FW/Terr.  
**First and Last**: *Xenerodipteryx mcyter* Rasmussen et al., 1987, upper sequence of the Jebel Qatrani Formation, Quarry M, Fayum Province, Egypt.

**Order** CICONIIFORMES Bonaparte, 1854  
**F. SCOPIDAE** Bonaparte, 1853  
T. (ZAN)-Rec.  
**First**: *Scopus xenopus* Olson, 1984, Varswater Formation, eastern Quarry, Langebaanweg, Cape Province, South Africa.  
**Extant**  
**F. CICONIIIDAE** (Gray, 1840)  
T. (MEO?)-Rec.  
**First**: *Eociconia sangequensis* Hou, 1989, Xi-Xi-Bai-La Formation, Sangequan, Xinjiang, China. While this is probably the oldest known stork, until confirmed, *Palaeo­phyrnchus dietrichi* Lambrecht, 1930, from the Jebel Qatrani Formation (RUP), north of Qasr Quarun and possibly also from Quarry M in the upper sequence of the Jebel Qatrani Formation, Fayum Province, Egypt, are the earliest reliable records for this family (Rasmussen et al., 1987).  
**Extant**  
**Intervening**: AQT-HOL.

**F. BALAENICIPITIDAE** Bonaparte, 1853  
T. (RUP)-Rec.  
**First**: *Goliathia andrewsi* Lambrecht, 1930, lower sequence of Jebel Qatrani Formation, Fayum Province, Egypt.  
**Extant**  
**Intervening**: UMI.

**F. PLATALEIDAE** Bonaparte, 1838  
T. (LUT)-Rec.  
**First**: *Rhynchaeites messeleensis* Wittich, 1899, Messel Oil Shales, Messel Quarry, Hesse­n, Germany (Peters, 1983).  
**Extant**  
**Intervening**: PRB, AQT-ZAN, PIA, PLE-HOL.  
**Order** CATHARTIFORMES Coues, 1884  
**F. VULTURIDAE** Illiger, 1811  
T. (BRT)-Rec.  
**First**: *Diatropornis elliottii* (Milne-Edwards, 1892), Le Breton, Phosphorites du Quercy, France (Mourer-Chauvire, 1988a).  
**Extant**  
**Intervening**: RUP, BUR, MMI, TOR, ZAN-HOL.

**F. TERATORNITHIDAE** Miller, 1909  
T. (MES)-Q. (PLE)-Terr.  
**First**: *Argentavis magnificens* Campbell and Tonni, 1980, Epecuén Formation, Salinas Grandes de Hidalgo, La Pampa, Buenos Aires Province, Argentina.  
**Last**: *Teratornis merriami* Miller, 1909, and *Cathartornis gracilis* Miller, 1910, Rancho La Brea, Los Angeles County, California and *Teratornis incredibilis* Howard, 1952, Smith Creek Cave, White Pine County, Nevada, USA.  
**Extant**  
**Intervening**: ZAN.
### Fig. 40.2

**Order ACCIPITRIFORMES** Vieillot, 1816

- **F. SAGITTARIIDAE** Finsch and Hartlaub, 1870
  - **First**: *Pelagopappus schlosseri* (Gaillard, 1908), Phosphorites du Quercy, France (Mourer-Chauvire and Cheneval, 1983).
  - **Intervening**: CHT, AQT.

**F. ACCIPITRIDAE** (Vieilliot, 1816)
  - **First**: *Miltopterus kempi* Harrison and Walker, 1979b, upper Bracklesham Beds (probably LUT), Lee on Solent, Hampshire, England, UK. A small raptor belonging to the Accipitridae has recently been identified in the Messel Oil Shale (LUT) Messel Quarry, Hessen, Germany (Peters, 1991).
  - **Extant**: RUP—HOL.
  - **Intervening**: LUT, PRB/RUP, LMI, MMI, ZAN—HOL.

**F. PANDIONIDAE** Sclater and Salvin, 1873
- T. (RUP)—Rec. FW/Terr.
  - **First**: Genus and species indet., aff. *Pandion*, upper sequence of the Jebel Qatrani Formation, Quarry M, Fayum Province, Egypt (Rasmussen et al., 1987).
  - **Extant**: MMI, TOR, ZAN—HOL.

**F. FALCONIDAE** Vigors, 1824
  - **First**: *Stintonornis mitchelli* Harrison, 1984a, London Clay, Isle of Sheppey, Kent, England, UK. *Paravultur watteli* Harrison, 1982, also from the London Clay, is slightly older, but is only provisionally assigned to the Falconidae (Harrison, 1982).
  - **Extant**: LUT, PRB/RUP, LMI, MMI, ZAN—HOL.

**F. HORUSORNITHIDAE** Mourer-Chauvire, 1991
  - **First**: *Horusornis vianeyliaudae* Mourer-Chauvire, 1991, La Bouffie, Phosphorites du Quercy, France.
  - **Last**: Unnamed species, Lower Oligocene, USA (Mourer-Chauvire, 1991).

**Order ANSERIFORMES** Wagler, 1831
F. ANHIMIDAE Stejneger, 1885
T. (YPR) - Rec. FW
First: Remains of an anhimid have recently been recovered from the Lower Eocene (Tyberg, pers. comm., 1992).

Intervening: RUP, HOL.
F. ANATIDAE Vigors, 1825 T. (EOC) - Rec. Mar./FW
First: Undetermined remains from Burgin Xian, Xinjiang and Erenhot, Inner Mongolia, China (Rich et al., 1986), and possibly Palaeopapua eous from the Lower Headon Beds (PRB) of Hordle, Hampshire, England, UK (Harrison and Walker, 1976).

Intervening: RUP - HOL.
F. PRESBYORNITHIDAE Wetmore, 1926
K. (CMP?) - T. (RUP?) FW/Lit.
First: Presbyornithidae gen. et sp. indet. from the Barun-Goyot Formation, Udan-Sair, Southern Mongolia (Kurochkin, 1988). Based on a single, fragmentary, tarso-metatarsus this record is difficult to confirm. The oldest certain record is Presbyornis sp., Palaeocene (THA) of Utah, USA (Olson, 1985).

Last: Headonornis hantoniensis (Lydekker, 1891) Hamstead Beds, Hamstead, and Bembridge Marls, Burnt Wood, Isle of Wight, England, UK (Harrison and Walker, 1979a). These might represent the youngest records for this family, but until confirmed, the youngest certain records are Presbyornis peretus Wetmore, 1926, and Presbyornis antiquus (Howard, 1955), Green River Formation (YPR), Uintah County, Utah, USA, and Casamayor Formation (YPR), Cañadón Vacas, Chubut Province, Argentina (Tonni and Tambussi, 1986).

Order GALLIFORMES Temminck, 1820
F. CRACIDAE Vigors, 1825 T. (AQT) - Rec. Terr.
First: Boreorhala laevis Brodkorb, 1954, Thomas Farm Beds, Thomas Farm, Gilchrist County, Florida, USA.

Intervening: MMI, UMI, ZAN, PLE, HOL.
F. GALLINULOIDIDAE Lucas, 1900 T. (YPR-AQT) Terr.
First: Gallinuloides wyomingensis Eastman, 1900, Green River Shales, Lincoln County, and Bridger Formation, Uinta County, Wyoming, USA.

Last: Taoperdix gallica (Milne-Edwards, 1869), T. brevipes (Milne-Edwards, 1869) and T. phasianoides (Milne-Edwards, 1869), Langy and St Gérard-le-Puy, Dept. Allier, France.

Intervening: PRB, RUP.
First: Paraortyx lorteti Gaillard, 1908, La Bouffie, Phosphorites du Quercy, France.

Last: Pirortyx major (Gaillard, 1938), Pech du Fraysse, Phosphorites du Quercy, France.

Intervening: RUP.
First: Quercymegapodius brodkorbi Mourer-Chauviré (1992), Lavergne, France.


Intervening: PRB.
Comment: Crowe and Short (1992) would place both this family and the Paraortygidae within the Gallinuloididae.

F. MEGAPODIIDAE Swainson, 1837 T. (YPR) - Rec. Terr.

Intervening: HOL.
F. PHASIANIDAE Vigors, 1825 T. (PRB/RUP) - Rec. Terr.
First: Nanortyx inexpectatus Weigel, 1963, Irdin Manha Formation, Shara Murun Region, Suiyuan Province, Inner Mongolia, China. This is only tentatively assigned to the Numididae (Olson, 1974; Mourer-Chauviré, 1992), thus the oldest certain guinea-fowl is Numida meleagris (Linnaeus, 1758), from six, putative, Upper Pleistocene sites in Hungary, Czechoslovakia and Germany (Brodkorb, 1964).

Intervening: AQT-HOL.
First: Undescribed remains from the Miocene of Virginia, USA (Olson, 1989).

Intervening: ZAN, PLE, HOL.
Order GRUIFORMES Bonaparte, 1854
First: Undescribed remains from the Miocene, USA (Olson, 1989).

Intervening: ZAN, PLE, HOL.
Comment: Recent authors (Mourer-Chauviré, 1981; Olson and Steadman, 1981; Olson, 1985; Hesse, 1988b) would exclude the button quails from the Gruiformes.

F. GERANOIDIDAE Wetmore, 1933 T. (YPR-LUT?) Terr.

Last: Geranodornis aenigma Cracraft, 1969, Uinta County, Wyoming, USA. Olson (1985) expresses considerable doubt over the identity of this form, thus the Geranoididae may be confined to the Ypresian.

**Last:** Amphilaelurus dzabghanensis Kurochkin, 1985, Hirgis Nur Suite (Upper Middle Pliocene), Dzagso Hirhan, western part of People’s Republic of Mongolia.

**Intervening:** LMI, UMI, ZAN.

**Comments:** Some authors (e.g. Mikhailovský, 1985) consider the Ergolanthiidae and Eogruidae to be a single family.

F. EOGURUIDAE Wetmore, 1934

First: Eogrurus turanicus (Bendukidze, 1971), Obayla Formation, Kalmakpai River, eastern Kazakhstan, former USSR, Iridin Manha, Shara Murun region, Suiyan Province, Inner Mongolia, China, and similar remains from Upper Eocene beds near Iren Dabasu, Inner Mongolia, China (Kurochkin, 1981).

Last: Eogrus wetmorei Brodkorb, 1967, Tung Gur Formation, Iren Dabasu, Inner Mongolia, China. Until the identity of this form is confirmed, the youngest record for this family is Somogrus gregalis Kurochkin, 1981, Lower Oligocene (RUP), Khoer Dzan, People’s Republic of Mongolia.

**Comment:** The Geranoididae, Ergolanthiidae and Eogruidae quite possibly belong in the Struthioniformes (e.g. Olson, 1985).

F. GRUIDAE Vigors, 1925


Intervening: CHT, AQT, TOR–HOL.

F. ARAMIDAE Bonaparte, 1849

First: Badistornis aramus Wetmore, 1940, Brule Formation, Washington County, South Dakota, USA. Extant

Intervening: ZAN, PLE, HOL.

F. PSOPHIIDAE Bonaparte, 1831

First: Anisolornis excavatus Ameghino, 1891, Santa Cruz Formation, Southern Patagonia, Argentina. Anisolornis is only very tentatively identified as a trumpeter (Olson, 1985), otherwise they have no fossil record. Extant

F. SONGZIDAE Hou, 1990

First and Last: Sosisia heidangkouensis Hou, 1990, Yangxi Formation, Heidangkou, Songzi County, Hubei Province, China.


Intervening: LUT/BRT?–TOR, ZAN–HOL.

F. HELIORNITHIDAE Gray, 1849 Extant Terr.

F. MESITORNITHIDAE Wetmore, 1960 Extant Terr.

F. MESSELORNITHIDAE Wetmore, 1960 ExtantTerr.

First: Remains from Mont Berru, France (Mourer-Chauviré, 1992b).

Last: Undescribed species from the BRT–CHT of France and North America (Hesse, 1988a).

Intervening: LUT.

F. EURYPYGIDAE Bonaparte, 1849

First: Remains from the Lower Eocene of Wyoming, USA, are tentatively ascribed to this family (Olson, 1989). Otherwise, sun bitterns have no fossil record. Extant

F. RHYNOCHECIDAE Newton, 1868

First: Rhynchos azalis Baloutet and Olson, 1989, Holocene deposits, Pindai Cave, Nepou Peninsula, New Caledonia. Extant

F. APTORNITHIDAE Olson, 1985

First: Apterornis otidiformis (Owen, 1848), meneencine beds at Te Rangatapu, Waingongoro and Wainganui, North Island, New Zealand.

Last: Apterornis otidiformis (Owen, 1848), Pyramid Valley Swamp and fourteen other sites (Brodkorb, 1964), South Island, New Zealand.

F. CARIAMIDAE Bonaparte, 1853

First: Riacama caliginea Ameghino, 1899, Deseado Formation, Santa Cruz Province, Argentina. As Riacama may not be a cariamid (Mourer-Chauviré, 1981), the oldest certain record is Chunga incerta from the lower Middle Pliocene (PIA), Monte Hermoso Formation, Buenos Aires Province, Argentina (Toni, 1974).

Intervening: PLE, HOL.

F. BATHORNITIDAE Wetmore, 1927

First: ‘Neocathartes grallatore‘ (Wetmore, 1944), Washakie Formation, Sweetwater County, Wyoming, USA (Olson, 1985).

Last: Bathornis fricki Cracraft, 1968, Willow Creek, Converse County, Wyoming, USA.

Intervening: PRB, RUP, CHT.

Comment: Both this family and the Idiornithidae probably belong within the Cariamidae (Mourer-Chauviré, 1981; Hesse, 1988b).

F. IDIORNITIDAE Brodkorb, 1965

First: Remains from the Messel Oil Shale, Messel, Germany (Peters, 1988) possibly represent the earliest idiornithids. Until confirmed, the oldest are Elaphrocnemus alfiidae (Shufeldt, 1915), Washakie Formation (BAR), Sweetwater County, Wyoming, USA and Idiornis gailardi (Cracraft, 1973) Le Bretou (BAR), Phosphorites du Quercy, France (Mourer-Chauviré, 1988a).


Intervening: PRB, RUP.

F. PHORORHACIDAE Brodkorb, 1963

First: Paleopsilopterus bitaeniensis Alvarenga, 1985, Basal Limestone of the Povoado de San José, Cabaçu District, Itaborai, Brazil.

Last: Titanis walleri Brodkorb, 1963, Santa Fé River,
boundaries of Gilchrist and Columbia Counties, Florida, USA, recently redated from Pleistocene to late Pliocene (Olson, 1985).

**Intervening:** YPR, LUT, PRB–ZAN.


**First and Last:** *Cunampaia simplex* Rusconi, 1946, Divisadero Largo Formation, Las Heras, Mendoza Province, Argentina.

**F. OTIDIDAE** (Gray, 1840) T. (BRT/CHT)–Rec. Terr.

**First:** Undetermined remains, Phosphorites du Quercy, France (Mourer-Chauviré, 1982).

**Extant**

**Comment:** There are some grounds for believing that the bustards belong within the Charadriiformes, near to the Glaucolithicidae (see Olson, 1985).


**First and Last:** *Gryzaja odesana* Zubareva, 1939, Koltovina, southern Ukraine and Etulya, Vulkanskey District, Moldavia, former USSR (Bochenski and Kurochkin, 1987).

**Comment:** This family probably belongs within the Otidae (see Olson, 1985, p. 180).

**Order** GASTORNITHIFORMES Stejneger, 1885


**First:** *Gastornis parisiensis* Hébert, 1885, Conglomerate de Meudon, Seine-et-Oise; and Sables de Réilly and Conglomerate de Cernay, Marne, France; a fissure fill, Walbeck, Haldensleben County, Magdeburg District, Saxony, Germany; Upper Palaeocene beds of Meusin near Mons, Hainault, Belgium; and Bottom Bed, lower Woolwich Beds, Hendon, London, England, UK, and *G. russelli* Martin, 1992, Berru in Reims, France.

**Last:** *Zhongyuaurus xichuanensis* Hou, 1980, Yu-Huang-Ding Series, Xichuan district, Hunan Province, China.

**F. DIATRYMIDAE** Shufeldt, 1913 T. (YPR–LUT) Terr.

**First:** *Diatryma gigantea* Cope, 1876, Wasatchian of Park County, and Graybull Member, Willwood Formation, South Elk Greek, Big Horn County, Wyoming, USA.

**Last:** *Diatryma geiselensis* Fischer, 1978, Braunkohle des Geiseltales, Neumark West, Saxony, Germany, and Messel Oil Shale, Messel Quarry, Hessen, Germany (Fischer, 1978).

**Comment:** There is a growing consensus (e.g. Olson, 1985; Andors, 1992; Martin, 1992) for combining Gastornithidae with Diatrymidae.

**Order** PHOENICOPTERIFORMES Fürbringer, 1888

**F. PHOENICOPTERIDAE** Bonaparte, 1831 T. (LUT)–Rec. FW/Terr.

**First:** *Junctarius merkeli* Peters, 1887, Messel Oil Shales, Messel Quarry, Hessen, Germany. **Extant**

**Intervening:** PRB?, RUP, AQT, MMI–ZAN, PIA, PLE, HOL.

**F. PALAEOLODIDAE** (Stejneger, 1885) T. (RUP–ZAN) FW/Terr.

**First:** Genus indet. aff. *Palaebodus* species 1 and 2, upper sequence of Jebel Quatrani Formation, Quarry M, Fayum Province, Egypt (Rasmussen et al., 1987).

**Last:** *Megalopeleolodus opsigonus* Brodkorb, 1961, Juntura Formation, Malheur County, Oregon, USA (Brodkorb, 1961). This family might range into the Pleistocene (Baird and Rich, quoted in Cheneval and Escuillé, 1992).

**Intervening:** AQT, MMI, UMI.

**Order** CHARADRIIFORMES Huxley, 1867

**F. JACANIDAE** Stejneger, 1885 T. (RUP)–Rec. FW/Terr.

**First:** *Nupharanassa sulataria* Rasmussen et al., 1987, lower sequence of the Jebel Qatrani Formation, Quarry E, Fayum Province, Egypt.

**Extant**

**Intervening:** TOR, PIA, PLE, HOL.

**F. ROSTRATULIDAE** Ridgway, 1919 T. (ZAN)–Rec. FW/Terr.

**First:** *New species of painted snipe*, Langebaanweg, south-western Cape Province, South Africa ( Olson and Eller, 1989).

**Extant**

**F. HAEMATOPODIDAE** (Gray, 1840) T. (ZAN)–Rec. Lit./Terr.

**First:** *Haematopus* sp., Lee Creek, North Carolina, USA ( Olson 1985) and *Haematopus sulatus* (Brodkorb, 1955), Bone Valley Mining District, Polk County, Florida, USA.

**Extant**

**Intervening:** PIA–HOL.

**F. CHARADRIIDAE** Vigors, 1825 T. (BUR?)–Rec. Lit./Terr.

**First:** Very fragmentary charadriid remains have been described from a siderolithic fissure fill, Vieux-Collonges, Dept. Rhône, France (Ballmann, 1972), but until they can be verified the earliest certain record is *Charadrius* sp., Ribielse Kröleswiek I, southern Poland (Jánossy, 1974), now dated as late Pliocene (PIA) following recent stratigraphical revision (Z. Bochenski, pers. comm., 1989; J. Milkovský, pers. comm., 1990).

**Extant**

**Intervening:** PLE, HOL.

**F. SCOLOPACIDAE** Vigors, 1825 T. (BRT/CHT)–Rec. Lit./Terr.

**First:** *Totanus edwardsi* Gaillard, 1908, Phosphorites du Quercy, France.

**Extant**

**Intervening:** RUP, AQT, MMI–HOL.

**F. RECURVIROSTRIDAE** Bonaparte, 1854 T. (YPR)–Rec. Lit./Terr.

**First:** *Fluviatilavis antunesi* Harrison, 1983, Lower Mondego Region, Silveirinha, central Portugal.

**Extant**

**Intervening:** PRB, MMI, PIA, PLE, HOL.

**F. GRACULAVIDAE** Fürbringer, 1888 K. (MAA) Mar./Lit.


**Extant**

**Intervening:** PRB, MMI, PIA, PLE, HOL.

**F. PHALAROPODIDAE** Bonaparte, 1831 T. (PIA)–Rec. Mar./Lit.
First: *Phalaropus eleonorae* Kurochkin, 1985, Chikoskaya Suite, Beregovaya, Buichurski Region, Buryatia, former USSR. **Extant**

Intervening: PLE.

F. DROMADIDAE (Gray, 1840) **Extant** Lit./Terr.

F. BURHINIDAE Matthews, 1913 **Extant**

First: *Burhinus lucorum* Bickart, 1982, Middle Sheep Creek Formation, Thomson Quarry, Sioux City, Nebraska, USA. **Extant**

Intervening: PLI, PLE, HOC

F. GLAREOLIDAE Brehm, 1831 **Terr.**

First: *Paractiornis perpusillus* Wetmore, 1930, Harrison Formation, Sioux County, Nebraska; USA. **Extant**

Intervening: MMI, PLE.

F. THINOCORIDAE Gray, 1845 **Q.** **Extant**

First: *Thinocorus koepckeae* Campbell, 1979 and *T. rumicivorus* Eshscholtz, 1829, Talara, Piura, Peru (Cuello, 1987). **Extant**

F. PEDIONOMIDAE **Extant**

F. CHIONIDIDAE Bonaparte, 1832 **Extant**

First: *Larus desnoyersii* Milne-Edwards, 1863, Saint-Gerand-Ie-Puy, Allier, France. **Probably a skua, but needs to be confirmed (Olson, 1985).** The oldest certain record is *Stercorarius* sp., Calvert Formation (MMI), Maryland, USA (Olson, 1985). **Extant**

Intervening: ZAN, PLE, HOL.

F. RHYNCHOPIDAE Bonaparte, 1832 **Extant**

First: An isolated sternum from the Moler Diatomite, Fur Formation, Limfjorden West, Denmark has been tentatively identified as that of a turaco (Bonde, 1987). The earliest certain record is genus and species indet., aff. *Crinifer*, upper sequence of the Jebel Qatrani Formation (RUP), Quarry M, Fayum Province, Egypt (Rasmussen et al., 1987). **Extant**

Intervening: CHT, BUR, TOR.

Order COLUMBIFORMES Latham; 1790

F. COLUMBIDAE (Illiger, 1811)

First: *Gerandia calcaria* (Milne-Edwards, 1871), Aquitanian beds between St-Gerand-le-Puy and Langy, Allier, France. **Extant**

Intervening: UMI-HOL.

F. RAPHIDAE Wetmore, 1930 **Q.** (PLE/HOL) **Terr.**

First and Last: *Raphus cucullatus* (Linnaeus, 1758), Mauritius, *R. solitaria* (Selys-Lonchamps, 1846), Reunion Island and *Pezophas solitarius* (Gmelin, 1789), Rodriguez.

Order PSITTACIFORMES Wagler, 1830

F. PSITTACIDAE (Illiger, 1811) **Terr.**

First: *Hydrotherikornis oregonus* Miller, 1931, Sunset Bay, Coos County, Oregon, USA? According to R. Chandler (pers. comm., 1989) *Hydrotherikornis* is probably not an auk, thus *Petralca austriaca* (Mlikovsky, 1987), from the Schieferton (part of the Puchkircher Schichtengruppe) (CHT) of Traun near Linz, Austria, is the oldest reliable record. **Extant**

Intervening: MMI, UMI-HOL.

Order MUSOPHAGIFORMES Seebohm, 1890

F. MUSOPHAGIDAE Bonaparte, 1831 **T.** (THA?) **Terr.**

First: An isolated sternum from the Moler Diatomite, Fur Formation, Limfjorden West, Denmark has been tentatively identified as that of a turaco (Bonde, 1987). The earliest certain record is genus and species indet., aff. *Crinifer*, upper sequence of the Jebel Qatrani Formation (RUP), Quarry M, Fayum Province, Egypt (Rasmussen et al., 1987). **Extant**

Intervening: CHT, BUR, TOR.

Order CUCULIFORMES Wagler, 1830

F. CUCULIDAE Vigors, 1825 **T.** (BRT/CHT) **Terr.**

First: *Dynamopterus velox* Milne-Edwards, 1892, Phosphorites du Quercy, France. **Extant**

Intervening: RUP, LMI, ZAN, PLE, HOL.

F. PARVICUCULIDAE Harrison, 1982 **T.** (YPR?) **Terr.**


F. OPISTHOCOMIDAE Gray, 1840 **T.** (MMI) **Terr.**

First: *Hoazinoides magdalenae* Miller, 1953, La Venta Formation, Magdalena Valley, Huila, Colombia. **Extant**

F. FORATIDAE Olson, 1992 **T.** (YPR) **Terr.**


F. OPISTHOCOMIDAE Gray, 1840 **T.** (MMI) **Terr.**

First: *Hoazinoides magdalenae* Miller, 1953, La Venta Formation, Magdalena Valley, Huila, Colombia. **Extant**

F. FORATIDAE Olson, 1992 **T.** (YPR) **Terr.**

First and Last: *Foro panarium* Olson, 1992, Fossil Butte Member of Green River Formation, Thompson Quarry, Kemmerer, Lincoln County, Wyoming, USA.

Order STRIGIFORMES Wagler, 1830
### Animals: Vertebrates

<table>
<thead>
<tr>
<th>Period</th>
<th>Family</th>
<th>Subdivision</th>
<th>Extant</th>
<th>Intervening</th>
</tr>
</thead>
<tbody>
<tr>
<td>CRETACEOUS</td>
<td>CUCULIFORMES</td>
<td>1. Glareolidae</td>
<td>27. Aegialornithidae</td>
<td>LUT/BRT, PRB.</td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>2. Thinocoridae</td>
<td>28. Hemiprocnidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>3. Stercorariidae</td>
<td>29. Trochilidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>4. Laridae</td>
<td>30. Sandcoleidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>5. Alcidae</td>
<td>31. Coliidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>6. Pteroclididae</td>
<td>32. Eurylaimidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>7. Columbidae</td>
<td>33. Fumariidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>8. Raphidiidae</td>
<td>34. Bucerotidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>9. Psittacidae</td>
<td>35. Coraciiformes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>11. Cuculidae</td>
<td>37. Passeriformes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>12. Parvicuculidae</td>
<td>38. Momotidae</td>
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</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>14. Foratidae</td>
<td>40. Coracidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>15. Tytonidae</td>
<td>41. Primobucoconidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>16. Strigidae</td>
<td>42. Atelornithidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>17. Protostrigidae</td>
<td>43. Upupidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>18. Tytonidae</td>
<td>44. Phoeniculidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>19. Caprimulgidae</td>
<td>45. Coliidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>20. Steatomithidae</td>
<td>46. &quot;Primobucco&quot;</td>
<td></td>
</tr>
<tr>
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<td>CUCULIFORMES</td>
<td>21. Aegothelidae</td>
<td>47. Bucconidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>22. Podargidae</td>
<td>48. Capitonidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>23. Caprimulgidae</td>
<td>49. Indicatoridae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>24. Nyctibiidae</td>
<td>50. Ramphastidae</td>
<td></td>
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<tr>
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<td>CUCULIFORMES</td>
<td>25. Opisthocoemidae</td>
<td>51. Picidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>26. Apodidae</td>
<td>52. Eurylaimidae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>CUCULIFORMES</td>
<td>27. Steatornithidae</td>
<td>53. Furnariidae</td>
<td></td>
</tr>
</tbody>
</table>

**Fig. 40.3**

**F. TYTONIDAE** Ridgway, 1914

_T. (LUT?)—Rec. Terr._

First: *Necroyas rossignoni* Milne-Edwards, 1892, Gisement de Perrière and *Nocturnavis incerta* (Milne-Edwards, 1892), Gisement d'Escamps, Phosphorites du Quercy (PRB), France. Extant

Intervening: RUP—AQT, MMI—MES, PIA—HOL.

**F. SOPHIORNITHIDAE** Mourer-Chauvire, 1987

_T. (THA—RUP) Terr._

First: Unnamed genus, Mont Berru, France (Mourer-Chauvire, 1987).

Last: *Sophornis quercynus* Mourer-Chauvire, 1987, Belgaric 1, Phosphorites du Quercy, France.

**F. PROTOSTRIGIDAE** Wetmore, 1933

_T. (YPR—RUP) Terr._


Last: *Oligostrix rupelensis* Fischer, 1983, Middle Oligocene, Weisselsterbecken, near Leipzig, Germany. Extant

Intervening: LUT/BRT, PRB.

**F. OGYGOPTYNGIDAE** Rich and Bohaska, 1981

_T. (THA) Terr._

First and Last: *Ogygoptynx vetmorei* Rich and Bohaska, 1976, San Juan River, south-west Colorado, USA.

**F. STRIGIDAE** Vigors, 1825

_T. (LUT?)—Rec. Terr._


Intervening: AQT—HOL.
Order CAPRIMULGIFORMES Ridgway, 1881
F. STEATORNITHIDAE (Gray, 1846)
T. (YPR)–Rec. Terr.
First: *Prefica nivea* Olson, 1987, Green River Formation, Lincoln City, Wyoming, USA. Extant
Intervening: CHT?
F. AEGOTHELIDAE Bonaparte, 1853
T. (BRT/CHT?)–Rec. Terr.
First: Fragment of a sternum from the Phosphorites du Quercy, France, tentatively assigned to the Aegothelidae by Mourer-Chauvire (1982). The next oldest record is *Quipollornis koniberi* Rich and McEvey, 1977, from a caldera lake deposit (LLA), Warrumbungle Mountains, eastern New South Wales, Australia. Extant
Intervening: PLE, HOL.
F. PODARGIDAE (Gray, 1840)
T. (LUT?)–Rec. Terr.
First: Undescribed remains from the Messel Oil Shale, Messel Quarry, Hessen, Germany (Peters, 1988). The earliest certain record is *Quercypodargus olsoni* Mourer-Chauvire, 1988b, Phosphorites du Quercy (BRT), France. Extant
Intervening: PLE, HOL.
F. CAPRIMULGIDAE Vigors, 1825
T. (LUT?)–Rec. Terr.
First: Undescribed remains from the Messel Oil Shale, Messel Quarry, Hessen, Germany (Peters, 1988). The earliest certain record is *Ventivorus ragei* Mourer-Chauvire, 1988b, Le Bretou, Phosphorites du Quercy (BRT), France. Extant
Intervening: PLE, HOL.
F. NYCTIBIIDAE (Bonaparte, 1853)
First: *Euronyctibius kurochkini* Mourer-Chauvire, 1988b, Phosphorites du Quercy, France. Extant
Intervening: PLE, HOL.
Order APODIFORMES Peters, 1940
F. JUNGORNITHIDAE Karkhu, 1988
Last: *Jungornis tessellatus* Karkhu, 1988, Maykop Formation, Abadzekhskaya Station, Adygey, northern Caucasus, former USSR.
F. APODIDAE Hartert, 1897
T. (LUT/BRT)–Rec. Terr.
First: *Scaniacypsela wardi* Harrison, 1984b, Resnaes Clay, Øst, Jutland, Denmark.
Intervening: LUT.
F. HEMIPROCNIDAE Oberholser, 1906
T. (YPR)–Rec. Terr.
Intervening: BRT.
Comment: Some authors (e.g. Milkovský, 1985) would combine Aegialornithidae with Hemiprocnidae.
Order TROCHILIFORMES Wagler, 1830
F. TROCHILIDAE Vigors, 1825
T. (PLE)–Rec. Terr.
First: Sandcoleus copiosus Houde and Olson, 1992, Sand Coulee Beds, Willwood Formation, Clark’s Ford Basin, Clark Quadrangle, Park County, Wyoming, USA.
Last: *Eobucco brodkorbi* Feduccia and Martin, 1976, 56 km north of Green River, Sweetwater County, Wyoming, USA.
Order COLIIFORMES Murie, 1872
F. COLIIDAE Swainson, 1837
T. (BRT)–Rec. Terr.
First: *Primocolius sigei* Mourer-Chauviré, 1988a, Le Bretou, Phosphorites du Quercy, France. Extant
Intervening: PRB, AQT, MMI–ZAN.
Order TROGONIFORMES American Ornithologists’ Union, 1886
F. ARCHAEOTROGONIDAE Mourer-Chauvire, 1980
First: *Archaeotrogon venustus* Milne-Edwards, 1892, Mouillac, Tarn-et-Garonne, France (Mourer-Chauvire, 1982).
Intervening: RUP.
F. TROGONIDAE Swainson, 1831
T. (RUP)–Rec. Terr.
First: Unnamed specimen originally referred to *Protonis glarniensis* Meyer, 1854, Glarner Fischschiefer, Sernftal, Glarus Canton, Switzerland (Olson, 1976). Extant
Intervening: AQT, PLE.
Order CORACIIFORMES Forbes, 1884
F. HALCYORNITHIDAE Harrison and Walker, 1974
T. (YPR) Terr.
F. HALCYONIDAE Vigors, 1825
T. (BRT/CHT)--Rec. Terr.
First: Undetermined remains, Phosphorites du Quercy, France (Mourer-Chauvire, 1982).
Extant

Intervening: ZAN, PLE, HOL.

F. TODIDAE Vigors, 1825
T. (PRB/RUP)--Rec. Terr.
Extant

F. SYLPHORNITHIDAE Mourer-Chauvire, 1988
T. (LUT-BRT) Terr.
First: Undescribed remains from the Messel Oil Shale, Messel Quarry, Hessen, Germany (Peters, 1991).
Extant

F. MOMOTIDAE (Gray, 1840)
T. (RUP)--Rec. Terr.
First: *Protornis glarniensis* Meyer, 1854, Glarner Fischschiefer, Sernftal, Glarus Canton, Switzerland (Olson, 1976).
Extant

Intervening: UMI, PLE, HOL.

F. MEROPIDAE Vigors, 1825
T. (BRT/CHT)--Rec. Terr.
First: Undetermined remains, Phosphorites du Quercy, France (Mourer-Chauvire, 1982).
Extant

Intervening: PLE, HOL.

F. CORACIIDAE Vigors, 1825
T. (LUT)--Rec. Terr.
First: Undescribed remains from the Messel Oil Shale, Messel Quarry, Hessen, Germany (Peters, 1988).
Extant

Intervening: BRT/CHT, PRB, PLE, HOL.

F. SYLPHORNITHIDAE Mourer-Chauvire, 1988
T. (LUT--BRT) Terr.
First and Last: *Prionornis glarniensis* Meyer, 1854, Glarner Fischschiefer, Sernftal, Glarus Canton, Switzerland (Olson, 1976).
Extant

F. PRIMOBUCCONIDAE Feduccia and Martin, 1976
T. (YPR) Terr.
First and Last: *Primobucco mcgrewi* Brodkorb, 1970, Green River Formation, Fossil, Lincoln County, Wyoming, USA.
Extant

F. ATELORNITHIDAE Bonaparte, 1854
T. (LUT?)--Rec. Terr.
First: Undescribed remains from the Messel Oil Shale, Messel Quarry, Hessen, Germany (Peters, 1988). Otherwise, this family has no fossil record.
Extant

F. LEPTOSOMIDAE Bonaparte, 1831 Extant Terr.
First: *Nystalus chacuru* Vieillot, 1816 and *Malacoptila striata* Spix, 1824 Lapa de Escrivania, Minas Gerais Province, Brazil.
Extant

F. CAPITONIDAE Bonaparte, 1840
T. (BUR)--Rec. Terr.
First: *Capitonides europaeus* Ballmann, 1969, Wintershof West, near Eichstatt, Bavaria, Germany.
Extant

Intervening: SER/TOR, PLE.

F. INDICATORIDAE Swainson, 1837
T. (ZAN)--Rec. Terr.
First: Undescribed remains, Varswater Formation, Langebaanweg, South Africa (Olson, 1985).
Extant

F. RAMPHASTIDAE Vigors, 1825
Q. (PLE)--Rec. Terr.
First: *Ramphastos dicolorus* Linnaeus, 1758, and *R. toco* Müller, 1846, Lapa de Escrivania, Minas Gerais Province, Brazil.
Extant

F. BUCEROTIDAE Vigors, 1825
T. (LUT?)--Rec. Terr.
First: Candidates include *Geiseloceros robustus* Lambrecht, 1935 (LUT), possibly a vulture (Olson, 1985), but almost certainly not a hornbill (Mlíkovský, pers. comm., 1990); *Cryptornis antiquus* Gervais, 1852 (PRB), possibly a coraciid (Harrison, 1979) and *Homoalopus picoideus* Milne-Edwards, 1871 (MMI), which might be a phoeniculid but is almost certainly not a hornbill (Olson, 1985). The oldest reliable record for this family is *Bucorvus brailoni* Brunet, 1971, Middle Miocene of Beni Mellal, north of Atlas Mountains, Morocco (Olson, 1985).
Extant

Order PICIFORMES Meyer and Wolf, 1810

F. GALBULIDAE Bonaparte, 1831 Extant Terr.
F. UNNAMED Houde and Olson, 1989 T. (YPR) Terr.
First and Last: *Primobucco* olsoni (Feduccia and Martin, 1976), Green River Formation, Nugget, Lincoln County, Wyoming (Houde and Olson, 1989).
Extant

Order PASSERIFORMES Linnaeus, 1766

F. EURYLAIMIDAE (Swainson, 1837) Q. (PLE)--Rec. Terr.
First: *Eurylaimid gen. et sp. indet.* Wintershof West, near Eichstatt, Bavaria, Germany.
Extant

F. FURNARIIDAE (Gray, 1840) T. (BUR)--Rec. Terr.
Extant

Intervening: BUR.
F. THAMNOPHILIDAE (Vigors, 1825)  
Q. (PLE)—Rec. Terr. (Fig. 40.4)  
*extant: Chamaeza brevicauda* (Vieillot, 1818), Upper Pleistocene, Lapa da Escrivania, Minas Geraes, Brazil.

F. TYRANNIDAE (Vigors, 1825)  
Q. (PLE)—Rec. Terr.  
*First: Tyrannus tyrannus* (Linnaeus, 1758), Reddick Beds (Middle Pleistocene) Reddick, Florida, USA. Eleven other neospecies are listed from the Pleistocene (Brodkorb, 1978).

F. SCYTALOPIDAE (Müller, 1846)  
Q. (PLE)—Rec. Terr.  
*First: ?Scytalopus sp.,* Upper Pleistocene, Cueva de Los Ñiles, north-east of Camagüey, Camagüey Province, Cuba (Olson and Kurochkin, 1987).

F. PITIIDAE Bonaparte, 1850 *extant* Terr.  
F. PHILEPITIDAE (Sharpe, 1870) *extant* Terr.  
F. OXYRUNCIDAE Ridgway, 1906 *extant* Terr.  
F. PIPRIDAE Vigors, 1825 *extant* Terr.  
F. QUERULIDAE (Swainson, 1837) *extant* Terr.  
F. PHYTOTOMIDAE (Swainson, 1837) *extant* Terr.  

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**ig. 40.4**
F. ALAUDIDAE (Vigors, 1825)
T. (BUR/LAN1)–Rec. Terr.
First: Undetermined genus, siderolithic fissure fill, Vieux­Collonges, Dept. Rhône, France (Ballmann, 1972). Extant
Intervening: ZAN, PLE, HOL.

F. HIRUNDINIDAE Vigors, 1825
T. (PIA)–Rec. Terr.
First: Hirundo aprica Feduccia, 1967, Rexroad Formation, Fox Canyon, Mead County, Kansas, USA. Extant
Intervening: ZAN, PLE, HOL.

F. DICRURIDAE (Vigors, 1825)
Q. (PLE)–Rec. Terr.
First: Dicrurus macrocercus (Vieillot, 1816), localities 1 and 15, Zhoukoudian area, Beijing, China (Rich et al., 1986). Extant

F. MENURIDAE (Gray, 1847)
T. (LMI?)–Rec. Terr.
First: Undescribed remains from Riversleigh, north-west Queensland, Australia, are tentatively assigned to this family (W. Boles, pers. comm., 1989), otherwise lyrebirds have no fossil record. Extant

F. ACANTHISITIIDAE (Sundevall, 1872)
Q. (HOL)–Rec. Terr.
First: Dendroscansor decurvirostris Millener and Worthy, 1991, Upper Quaternary (HOL) of New Zealand. Extant

F. ATRICHORNITHIDAE Stejneger, 1855
Q. (PLE)–Rec. Terr.
First: Undescribed remains from the Pleistocene of Australia (P. Rich, pers. comm., 1989). Extant

F. MOTACILLIDAE Vigors, 1825
T. (ZAN)–Rec. Terr.
First: Anthus seductus Kurochkin, 1985, Lower Pavlodarski Suite, Pavlodar, eastern Kazakhstan, former USSR. Extant

F. CAMPEPHAGIDAE (Vigors, 1825) Extant Terr.
F. PYCNONOTIDAE (Gray, 1840)
Q. (PLE)–Rec. Terr.
First: Pycnonotus barbatus (Desfontaines, 1789), 'Ubeidiya Formation, 'Ubeidiya, SW bank of Sea of Galilee, Israel (Tchernov, 1980). Extant

F. LANIIDAE (Swainson, 1832)
T. (AQT?)–Rec. Terr.
First: Lanius miocaenus Milne-Edwards, 1871, Gargano Peninsula, Italy (Ballmann, 1973). Ballmann only tentatively identified these remains as sylviid; the oldest certain records are Sylvia cf. atricapilla, Pedrera de S'Onix (PIA), Mallorca (Mourer-Chauvire et al., 1977), and Hippolais sp., Csarnota 2 (PIA), Hungary (Jánossy, 1979). Extant

F. BOMBYCILLIDAE (Swainson, 1832)
Q. (PLE)–Rec. Terr.
First: Bombycilla garrulus (Linnaeus, 1758), Upper Middle Pleistocene of Orgnac 3, France (Mourer-Chauvire, 1975). Extant

F. PALAEOSCINIDAE Howard, 1957
T. (MMI/UMI) Terr.
First and last: Palaeoscincus turdirostris Howard, 1957, Monterey Formation, Tepusquet Creek, Santa Barbara County, California, USA. Extant

F. TROGLODYTIDAE (Swainson, 1832)
T. (PIA)–Rec. Terr.
First: Troglodytes troglodytes (Linnaeus, 1758), Pedrera de S'Onix, Mallorca. Extant

F. PRUNELLIDAE Richmond, 1908
T. (PIA)–Rec. Terr.
First: Prunella cf. modularis, Pedrera de S'Onix, Mallorca (Mourer-Chauvire et al., 1977). Extant

F. SYLVIIDAE (Vigors, 1825)
T. (UMI?)–Rec. Terr.
First: Gavialis gangeticus (Wied, 1820), Upper Miocene, Rome, Italy. Extant

F. PARIDAE Boie, 1826
T. (PIA)–Rec. Terr.
First: Aegithalos caudatus, Parus cf. ater and P. cf. major, Pedrera de S'Onix, Mallorca (Mourer-Chauvire et al., 1977). Extant

F. SITIIDAE Bonaparte, 1831
First: undetermined genus, siderolithic fissure fill, Vieux­Collonges, Dept. Rhône, France (Ballmann, 1972). Extant

F. VANGIDAE Shelley, 1896 Extant Terr.
First: Sitta, La-Grive-Saint-Alban, France (Ballmann, 1973; see also Olson, 1985). Extant
Intervening: ZAN–HOL.

F. PARADALOTIDAE Bonaparte, 1850 Extant Terr.
F. NECTARINIIDAE Vigors, 1825 Q. (PLE)–Rec. Terr.
First: Nectarinia osea Oustalet, 1904, Upper Pleistocene, Haynim Cave, Israel (Tchernov, 1979). Extant
F. ZOSTEROPIDAE Bonaparte, 1853 Extant Terr.
F. MELIPHAGIDAE Vigors, 1825 Q. (PLE)–Rec. Terr.
First: Prosthemadera noveseelandiae (Gmelin, 1788), Pyramid Valley Swamp and Martinborough Cave V, South Island, New Zealand. Anthornis melanura (Sparrman), Awakino–Mohoenui area, North Island, New Zealand (Medway, 1971). Extant
Intervening: HOL.

First: Ammodramus hatcheri (Shulelda, 1913), Long Island, Phillips County, Kansas, USA (Steadman, 1982). Extant
Intervening: ZAN–HOL.

F. TANAGRIDAE (Vigors, 1825) Q. (PLE)–Rec. Terr.
First: Pyrrhuloxia cardinalis (Linnaeus, 1758), Arredondo Clay member, Wicomico Formation (Middle Pleistocene), Reddick, Marion County, Florida, USA (Fisher, 1967). Extant
Intervening: HOL.

F. COEREBIIDAE (Gray, 1840) Q. (PLE)–Rec. Terr.
First: Geothlypis trichas (Linnaeus, 1766), Reddick Beds (Middle Pleistocene), Reddick, Marion County, Florida, USA (Brodkorb, 1957). Extant
Intervening: HOL.

F. VIREONIDAE Swainson, 1837 Q. (PLE)–Rec. Terr.
First: Cyclarhis gujanensis (Gmelin, 1789), Lapa da Escrivania (Upper Pleistocene), Lagoa Santa, Minas Gerais Province, Brazil; Virgo calidris (Linnaeus, 1758) and V. nanus (Lawrence, 1875), Cerro de San Francisco, Dominican Republic; V. griseus (Boddart, 1783), Haile, Florida, USA (Brodkorb, 1978). Extant
Intervening: HOL.

First: 'Colinus eatoni' Shufeldt, 1915, ?Ogalla Formation, Fort Wallace, western Kansas (Brodkorb, 1978). There is some doubt as to the age of this material (Brodkorb, 1978) thus the oldest certain records are Pandanaris floridana Brodkorb, 1957, Reddick Beds (middle Upper Pleistocene), Reddick, Marion County and Cremaister tytthus Brodkorb, 1959, Arredondo, Alachua County, Florida. Extant
Intervening: HOL.

F. PASSERIDAE (Illiger, 1811) Q. (PLE)–Rec. Terr.
First: Passer domesticus (Linnaeus, 1758), Grotte L’Escale, France (Mourer-Chauviré, 1975). Extant
Intervening: HOL.

First: Genus indet., Chikoyskaya Suite, Selenginski Aimak, Shamar, northern part of People’s Republic of Mongolia (Kurochkin, 1985).
Intervening: PLE, HOL.

F. ORIOLIDAE (Vigors, 1825) Q. (PLE)–Rec. Terr.
First: Oriolus sp., ‘Ubeidiya Formation, ‘Ubeidiya, SW bank of Sea of Galilee, Israel (Tchernov, 1980). Remains of orioles have been found recently in the Upper Pleistocene (PIA) of Varshets, west Balkan Range, Bulgaria (Boev, 1992).
Intervening: HOL.

F. CALLAEATIDAE (Gray, 1841) Q. (PLE)–Rec. Terr.
First: Callaeas cinerea (Gmelin, 1788) and Creadion carrunculatum (Gmelin, 1789), Pyramid Valley Swamp, South Island, New Zealand (Scarlett, 1955). Extant
Intervening: HOL.

F. ARTAMIDAE Blyth, 1849 Extant Terr.
First: Turnagra capensis (Sparrman, 1787) (neosp.), Awakino-Mohoenui area, North Island, and possibly Pyramid Valley Swamp, South Island, New Zealand (Scarlett, 1955; Medway, 1971). Extant

F. PARADISAEIDAE Vieillot, 1825 Extant Terr.
First: Corvidae gen. et sp. indet., Shanwang Formation, Linqu, Shandong, China (Yeh and Sun, 1989). This record has not yet been confirmed, and Microrus larreti (Milne-Edwards, 1871), from the Upper Miocene of Sansan, Dept. Gers, France, also needs to be checked (Brodkorb, 1978). The earliest certain record is Miocitta galbreathi Brodkorb, 1972 (UMI) Kennesaw local fauna, Pawnee Creek Formation, Logan County, Colorado, USA. Extant
Intervening: PIA–HOL.


First and Last: Cimolopters rara Marsh, 1889, C. minima Brodkorb, 1963 and C. maxima Brodkorb, 1963, Palintonops retusus (Marsh, 1892), (see entry for Apatornithidae) and Ceramornis major Brodkorb, 1963, Lance Formation, Lance Creek, Niobrara County, Wyoming, USA; Cimoloptersp., Frenchman Formation, Frenchman Valley, south of Shaunaon, Saskatchewan, Canada (Tokaryk and James, 1989).

F. CLADORNITHIDAE Ameghino, 1895 T. (RUP) Lit.? Terr.
First and Last: Cladornis pachypus Ameghino, 1895, Deseado Formation, Rio Deseado, Santa Cruz Province, Argentina.
Intervening: MMI, UMI, PLI.

Australia, and Mudgee, New South Wales, Australia (Rich, from this locality (W. Boles, pers, comm., 1989). Creek near Burra; Parroo River and Mount Gambier, South 1979).

Last: Homestead, north-western Queensland, Australia.

First and Last: Pleistocene beds of Lake Callabonna, Normanville; Baldina First: and Last: Xiagou Formation, Yumen, Gansu Province, China.

1984, Cornet, Padurea Crailui Mountains, Bihor, Romania. First and Last: First and Last:

Considerable doubt has been cast on the validity of this taxon (Brodkorb, 1978; Steadman, 1981).

F. 'LIMNORNITHIDAE' Kessler and Jurcsak, 1984

F. PRIMOSCENIDAE Harrison and Walker, 1977

F. LONCHODYTIDAE Brodkorb, 1963

F. MARINAVIDAE Harrison and Walker, 1977

F. ONYCHOPTERYGIDAE Cracraft, 1971

F. PALAEOSPIZIDAE Wetmore, 1925


F. DAKOTORNITHIDAE Erickson, 1975 T. (THA) Terr.

First and Last: Dakotornis cooperi Erickson, 1975, Tongue River Formation, Wannagan Creek, Billings County, North Dakota, USA.


Last: Genyornis newtoni Stirling and Zeitz, 1896, Upper Pleistocene beds of Lake Callabonna, Normanville; Baldina Creek near Burra; Parroo River and Mount Gambier, South Australia, and Mudgee, New South Wales, Australia (Rich, 1979).

Intervening: MMI, UMI, PLI.


F. LONCHODYTIDAE Brodkorb, 1963 and Last: Post, west Texas, USA. The identification of the remains of Protoavis as avian is highly controversial (Beardsley, 1986; Ostrom, 1987) and will only be resolved by further study (Ostrom, 1991).


First and Last: Scaniornis lunadreni Dames, 1890, Saltholm Chalk, Annetorp Quarry, Limhamn, Sweden.


First: Parascaniornis stensioi Lambrecht, 1933, Shell Fragment Limestone, Ivö, Sweden.

Last: Torotix clemensi Brodkorb, 1964, Lance Formation, Lance Creek, Niobrara County, Wyoming, USA.


First: Zygodactylus ignotus Ballmann, 1967, Wintershof West, near Eichstatt, Bavaria, Germany.

Last: Zygodactylus grivensis Ballmann, 1969 and possibly also Z. gaudryi (Depéret, 1887), La-Grive-Saint-Alban, Dept. Isère, France (Brodkorb, 1971).

Intervening: MMI?


First and Last: Asiasis phosphatica Nessov, 1986, uppermost Middle Eocene beds of Tashkura, Central Kizylkum, Uzbekistan, former USSR. Represented by a single incomplete wing bone, this bird supposedly belongs in the Gruiformes.


First and Last: Judinornis nogontzavensis Nessov and Borkin, 1983, Nemegt Formation, Nogon-Tsav, southern Mongolia.


First and Last: Sinornis santensis Sereno and Rao, 1992, lake sediments, Jiufuotang Formation, Chaoyoung County, Liaoning Province, north-east China (Rao and Sereno, 1990). Further remains representing two new genera have been recently recovered from the Jiufuotang Formation, which is now generally accepted to be early Cretaceous in age (Zhou et al., 1992).

REFERENCES


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MAMMALIA

R. K. Stucky and M. C. McKenna*

Since the original publication of the chapter on the Mammalia (Butler et al., 1967), a number of critical references on the phylogenetic relations and stratigraphical distributions of mammals have been published. The classification adopted here is based on McKenna (1975), and a current revision of the classification of mammals now in progress by McKenna et al. (MS). Alternative classifications of families and orders are indicated in the references cited for each group. Recent reviews of the relationships of higher taxa include Novacek (1990), Novacek et al. (1988), and references cited therein. Classification is principally the work of MCM and data on ranges and localities were collated by RKS.

Correlations to stage level often are not possible for many taxa of mammals because of difficulties in direct correlation with standard marine sequences. Exceptions to this include ranges for mammals from the Mesozoic and those from Europe. For the many Cainozoic records, occurrences are recorded according to lower (L), middle (M) and upper (U) epochal units, which, at current levels of mammalian biostratigraphical resolution, are generally equivalent from continent to continent. General correlations follow Savage and Russell (1983), with the following exceptions: South American faunal correlation is based on the work of MacFadden (1990) and Pascual and Jaureguizar (1990), and North American correlations follow works in Woodburne (1987), except that:

1. the Palaeocene-Eocene boundary is here considered to coincide with the Clarkforkian–Wasatchian boundary (Krishen et al., 1987; this boundary may lie within the Wasatchian, Lucas, 1989; Wing, 1984; Rea et al., 1990; Beard and Tabrum, 1991);
2. Chadronian faunas are considered to be late Eocene in age, equivalent in part to the Priabonian (Swisher and Prothero, 1990).

Major references from which first and last occurrences of mammalian families are derived, include the temporal and geographic summaries listed below. Data regarding the lithostratigraphical unit are often lacking for many of the reported taxa. In many cases, either the original locality name is reported or the ‘faunal’ unit from which the taxon occurs is listed. This especially applies to the European and South American record. Mesozoic mammals: Clemens et al. (1979); Lillegraven et al. (1979); Cainozoic mammals: Thenius (1959); de Paula Couto (1979); Savage and Russell (1983); Dawson and Krishtalka (1984); Pleistocene mammals: Kurtén and Anderson (1980); Anderson (1984); Martin and Klein (1984); Africa: Simons (1968); Maglio and Cooke (1978); Antarctica: Marshall et al. (1990); Asia: Li and Ting (1983); Russell and Zhai (1987); Australia: Woodburne et al. (1985); Archer et al. (1989); Marshall et al. (1990); Europe: Hooker and Insole (1980); Russell et al. (1982); Savage and Russell (1983); Remy et al. (1987); Schmidt-Kittler (1987b and references therein); Heissig (1987); North America: Webb (1984); Woodburne (1987 and references therein); Archibald et al. (1987); Lillegraven and McKenna (1986); Stucky (1990, 1992); and South America: Ameghino (1906); Pascual et al. (1966); de Paula Couto (1979); Cifelli (1982); Marshall et al. (1983); Marshall et al. (1990).

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*Order of authorship determined by the flip of a coin.
Class MAMMALIA Linnaeus, 1758
Subclass PROTOHERIA Gill, 1872, new rank, McKenna, this volume
Order TACHYGLOSSA Gill, 1872, new rank, McKenna, this volume
F. TACHYGLOSSIDAE Gill, 1872

First: Zaglossus robusta Dun, 1895, Gulgong, Australia. Extant

Order PLATYPODA Gill, 1872, new rank, McKenna, this volume

F. ORNITHORHYNCHIDAE Burnett, 1830
K. (ALB)–Rec. Terr.

First: Steropodon Archer et al., 1985, Griman Creek Formation, Australia. Extant

Intervening: Mio.

Subclass TRICONODONTA Osborn, 1888, new rank, McKenna, this volume

Order MORGANUCODONTA Kermack et al., 1973, new rank, McKenna, this volume

F. MORGANUCODONTIDAE Kühne, 1958
Tr. (RHT)–J. (BTH) Terr.

Last: *Wareolestes rex* Freeman, 1979, Forest Marble Formation, Oxfordshire, England, UK.

**Order** EUTRICONODONTA Kermack et al., 1973, new rank, McKenna, this volume

**F. SINOCOCONODONTIDAE** Mills, 1971

TR. (RHT)–J. (SIN) Terr.

First and Last: *Sinoconodon* Patterson and Olson, 1961, and *Lufengodon* Yang, 1982, both lower Lufeng Formation, Yunnan, China.

**F. AMPHILESTIDAE** Osborn, 1888

J. (SIN)–K.? (CMP) Terr.

First: *Dinnesotherium* Jenkins et al., 1983, Kayenta Formation, Arizona, USA.


**F. TRICONODONTIDAE** Marsh, 1887

J. (KIM)–K. (CMP) Terr.

First: *Triconodon* Owen, 1859, Lulworth Beds, Dorset, England, UK; *Pricodon* Marsh, 1887, Morrison Formation, Wyoming, USA; *Triarctodon* Simpson, 1928, Lulworth Beds, Dorset, England, UK; Morrison Formation, Wyoming, USA.


**Subclass** ALLOOTHERIA Marsh, 1880

**Infraclass** MULTITUBERCULATA Cope, 1884, new rank, McKenna, this volume

**Order** PLAGIAULACIDA McKenna, 1971, new rank, McKenna, this volume

**F. PLAGIAULACIDAE** Gill, 1872

J. (OXF)–K. (BER/APT/ALB) Terr.


Last: *Paulchoffatia* Kühne, 1961, and *Bolodon* Owen, 1871, both Galve, Spain. A plagiaulacid has been reported from the Trinity Sands, Texas, USA (Clemens et al., 1979).

**Order** CIMOLODONOTA McKenna, 1975, new rank, McKenna, this volume

**F. ARGINBAATARIDAE** Hahn and Hahn, 1983

K. (I) Terr.

First and Last: *Arginbaatar* Trofimov, 1980, Khovboor Beds, Mongolia.

**F. NEOPLAGIAULACIDAE** Ameghino, 1890


First: *Cimexomys* Sloan and Van Valen, 1965, and *Mesodroma* Jepsen, 1940, both Milk River Formation, Alberta, Canada.

Last: *Ectypodus* Matthew and Granger, 1921, White River Formation, Wyoming and Nebraska, USA; *Calf Creek* Saskatchewan, Canada (Krishtalka et al., 1982).

**F. PTILODONTIDAE** Gregory and Simpson, 1926

K. (MAA)–T. (THA) Terr.

First: *Kimbetohia* Simpson, 1936, Kirtland and Fruitland Formations, New Mexico, USA.


**F. CIMOLODONTIDAE** Marsh, 1889


First: *Cimolodon* Marsh, 1889, Milk River Formation, Alberta, Canada.

Last: *Anconodon* Jepsen, 1940, Paskapoo Formation, Alberta, Canada; *Liotomus* Cope, 1884, MP6, Cernay, France (Godinot, 1987).

**F. BOFFIIDAE** Hahn and Hahn, 1983

T. (THA) Terr.


**F. EOBAATARIDAE** Kielan-Jaworowska et al., 1987

K. (VGL–APT/ALB) Terr.


**F. SLOANBAATARIDAE** Kielan-Jaworowska, 1974

K. (CMP) Terr.

First and Last: *Sloanbaatar* Kielan-Jaworowska, 1974, Djadokhta Formation, Mongolia.

**F. CIMOLOMYIDAE** Marsh, 1889


First: *Cimolomys* Marsh, 1889, Oldman Formation, Alberta, Canada; *Meniscoecius* Cope, 1882, Milk River Formation, Alberta, Canada.

Last: *Hainina* Vianey-Liaud, 1979, MP6, Cernay, France.

**F. TAENIOLABIDIDAE** Granger and Simpson, 1929


First: *Kamptobaatar* Kielan-Jaworowska, 1970, and *Catopsalis* Cope, 1882, both Djadokhta Formation, Mongolia.

Last: *Prienessus* Matthew and Granger, 1925, Bayan Ulan Formation, Inner Mongolia; *Lambdopsalis* Chow and Qi, 1978, and *Sphenopsalis* Matthew et al., 1928, both Nomogen Formation, Inner Mongolia.

**F. EUUCOSMODONTIDAE** Jepsen, 1940


Last: *Neoliotomus ultimus* Jepsen, 1930, Willwood Formation, Wyoming, USA.
Animals: Vertebrates

F. SUDAMERICIDAE Scillato-Yane and Pascual, 1984
Last: Sudamericia Scillato-Yane and Pascual, 1984, Banco Negro, Argentina.

F. FERUGLIOTHERIIDAE Bonaparte, 1986
K. (CMP) Terr.

Infraclass HARAMYOIDEA Hahn, 1973, new rank, McKenna, this volume

F. HARAMIYIDAE Simpson, 1947
Tr. (NOR) – J. (BTH) Terr.

ALLOTHERIA incertae sedis

F. THEROTEINIDAE Sigogneau-Russell et al., 1986
Tr. (RHT) Terr.
First and Last: Theroteinus Sigogneau-Russell et al., 1986, Saint-Nicolas-de-Port, France.

Subclass TRECHNOTHERIA McKenna, 1975, new rank, McKenna, this volume

Infraclass SYMMETRODONTA Simpson, 1925, new rank, McKenna, this volume

Order AMPHIDONTOIDEA Prothero, 1981, new rank, McKenna, this volume

F. AMPHIDONTIDAE Simpson, 1925
First: Amphidon Simpson, 1925, Morrison Formation, Wyoming, USA.

Order SPALACOTHERIOIDEA Prothero, 1981, new rank, McKenna, this volume

F. SPALACOTHERIIDAE Marsh, 1887
First: Spalacotherium Owen, 1854, Lulworth Beds, England, UK.

F. BARBERENIIDAE Bonaparte, 1990
K. (CMP) Terr.
First and Last: Barberenia Bonaparte, 1990, and Quirogatherium Bonaparte, 1990, both Los Alamitos Formation, Argentina.

SYMMETRODONTA incertae sedis

F. SHUOTHERIIDAE Chow and Rich, 1982
J. (u.) Terr.

Infraclass CLADOTHERIA McKenna, 1975, new rank, McKenna, this volume

Legion DRYOLESTOIDEA Butler, 1939, new rank, McKenna, this volume

Order AMPHITHERIIDAE Prothero, 1981, new rank, McKenna, this volume

F. AMPHITHERIIDAE Owen, 1846 J. (BTH) Terr.
First and Last: Amphitherium De Blainville, 1838, Stonesfield Slate, Oxfordshire, England, UK.

Order DRYOLESTIDA Prothero, 1981, new rank, McKenna, this volume

F. PAURODONTIDAEMarsh, 1887 J. (KIM) Terr.

F. MESUNGULATIDAE Bonaparte, 1986
K. (CMP) Terr.
First and Last: Mesungulatum Bonaparte and Soria, 1985, Los Alamitos Formation, Argentina.

F. REIGITHERIIDAE Bonaparte, 1990
K. (CMP) Terr.
First and Last: Reigitherium Bonaparte, 1990, Los Alamitos Formation, Argentina.

Legion THERIA Parker and Haswell, 1897, new rank, McKenna, this volume

Supercohort MARSUPIALIA Illiger, 1811, new rank, McKenna, this volume

An alternative classification of the Marsupialia is that of Marshall et al. (1990). The earliest known marsupials may be from the Straight Cliffs Formation, Utah, of Turonian age (Cifelli, 1990). The ages of marsupials from the Etadunna Formation and Carl Creek Limestone are currently not precisely known (compare Woodburne et al., 1985; Archer et al., 1989). According to Woodburne (pers. comm. to RKS, 1991), marsupials from the Etadunna Formation are probably early Miocene in age, and those from the Carl Creek Limestone are probably middle Miocene.

Cohort AUSTRALIDELPHIA Szalay, 1982

Magnorder MICROBIOTHERIA Ameghino, 1889, new rank, McKenna, this volume

F. MICROBIOTHERIIDAE Ameghino, 1887

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| F. DASYURIDAE | Goldfuss, 1820 | | | Extant |
| First | Tedford et al. (1975) | report a dasyurid from the Geilston Travertine, Tasmania. | | Extant |

| F. THYLACINIDAE | Bonaparte, 1838 | | | Extant |
| (UMI) | Tedford and Woodburne, 1987 | | | Extant |

| F. THYLACINIDAE | Temminck, 1827 | | | Extant |
| First | Thylacinus | | | Extant |
| Last | Koobor | | | Extant |

| Order DIPROTODONTIA | Owen, 1866 | | | Extant |
| F. ILARIIDAE | Tedford and Woodburne, 1877 | | | Extant |
| (MMI-PLI) | Tedford and Woodburne, 1877 | | | Extant |

| F. ILARIIDAE | Tedford and Woodburne, 1877 | | | Extant |
| First | Ilaria | | | Extant |
| Last | Koobor | | | Extant |

| Order DIPROTODONTIDAE | Gill, 1872 | | | Extant |
| F. DIPROTODONTIDAE | Gill, 1872 | | | Extant |
| (MMI) | Tedford and Woodburne, 1877 | | | Extant |

| F. DIPROTODONTIDAE | Gill, 1872 | | | Extant |
| First | Bematherium | | | Extant |
| Last | Zygomatus | | | Extant |

| F. DIPROTODONTIDAE | Gill, 1872 | | | Extant |
| First | Bematherium | | | Extant |
| Last | Zygomatus | | | Extant |

| F. PHALANGERIDAE | Thomas, 1888 | | | Extant |
| First | Rhizoscapheus | | | Extant |
| First | Termorhynchus | | | Extant |

| F. PHALANGERIDAE | Thomas, 1888 | | | Extant |
| First | Rhizoscapheus | | | Extant |
| First | Termorhynchus | | | Extant |

| F. BURRAMYIDAE | Broom, 1898 | | | Extant |
| First | Rhinolophus | | | Extant |
| First | Phalanger | | | Extant |

| F. BURRAMYIDAE | Broom, 1898 | | | Extant |
| First | Rhinolophus | | | Extant |
| First | Phalanger | | | Extant |

| F. MACROPODIDAE | Gray, 1821 | | | Extant |
| First | Acrobates | | | Extant |
| First | Thylacinus | | | Extant |

| F. PHASCOLARCTIDAE | Owen, 1839 | | | Extant |
| First | Phascolarctos | | | Extant |
| First | Thylacinus | | | Extant |

| F. ACROBATIDAE | Aplin and Archer, 1987 | | | Extant |
| First | Acrobates | | | Extant |
| First | Thylacinus | | | Extant |

| F. THYLACOLEONIDAE | Gill, 1872 | | | Extant |
| First | Thylacolea | | | Extant |
| First | Thylacinus | | | Extant |

| F. MIRALINIDAE | Woodburne et al., 1987 | | | Extant |
| First | Perakura | | | Extant |
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| F. MIRALINIDAE | Woodburne et al., 1987 | | | Extant |
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| F. PALORCHESTIDAE | Tate, 1948 | | | Extant |
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| F. PALORCHESTIDAE | Tate, 1948 | | | Extant |
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| F. MACROPODIDAE | Gray, 1821 | | | Extant |
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| F. PHASCOLARCTIDAE | Owen, 1839 | | | Extant |
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| F. ACROBATIDAE | Aplin and Archer, 1987 | | | Extant |
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| F. THYLACOLEONIDAE | Gill, 1872 | | | Extant |
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| F. MIRALINIDAE | Woodburne et al., 1987 | | | Extant |
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| F. MIRALINIDAE | Woodburne et al., 1987 | | | Extant |
| First | Perakura | | | Extant |
| First | Thylacolea | | | Extant |

| F. PALORCHESTIDAE | Tate, 1948 | | | Extant |
| First | Palorchestes | | | Extant |
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| F. PHASCOLARCTIDAE | Owen, 1839 | | | Extant |
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| F. MIRALINIDAE | Woodburne et al., 1987 | | | Extant |
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| F. PALORCHESTIDAE | Tate, 1948 | | | Extant |
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| First | Thylacinus | | | Extant |
Animals: Vertebrates

Last: Palorchestes Owen, 1873, Upper PLE, Tasmania, Australia.

F. TARSIPEDIDAE Gervais and Verreaux, 1842 Q. (PLE)–Rec. Terr.
First: Tarsiipes Gervais and Verreaux, 1842, Australia.

Cohort EOMETATHERIA incertae sedis
Order NOTORYCTEMORPHIA Kirsch, 1977
F. NOTORYCTIDAE Ogilby, 1892 Extant Terr.
First: Yalkaparidon Archer et al., 1988, Carl Creek Limestone, Queensland, Australia.

Cohort AMERIDELPHIA Szalay, 1982
Order Didelphiphormes Szalay, 1982
F. Sparassocynidae Reig, 1958 T. (UMI–PLI) Terr. (Fig. 41.2)
First and Last: Sparassocynus Mercerat, 1898, Huayquerian, UMI–Upper PLI, Argentina.

Order PAUCITUBERCULATA Ameghino, 1894
F. Caenolestidae Trouessart, 1898 T. (CHT/LMI)–Rec. Terr.
First: Pseudhalmarhiphus Ameghino, 1903, Deseadan, Argentina. Acdestis 1887, all Extant
First and Last: Bonapartherium Pascual, 1980, Casa–mayoran, Argentina.
**Supercohort** PLACENTALIA Owen, 1837  
**Cohort** EDENTATA Cuvier, 1798  
**Order** CINGULATA Illiger, 1811  
F. DASYPODIDAE Gray, 1921  
T. (THA)—Rec. Terr.  
**First:** Prostegotherium Ameghino, 1902, Itaboraí, Brazil (Marshall et al., 1983).  
**Extant**  
F. PELTEPHILIDAE Ameghino, 1894  
T. (YPR—MMI) Terr.  
**First:** Marshall et al. (1983) report Peltephilinae indet. from the Lower Eocene Casamayoran, Argentina.  
**Last:** Epipeltephilus Ameghino, 1904, Chasicoan, Argentina (Pascual et al., 1966).  

**Fig. 41.2**

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Last: *Pediomys* Marsh, 1889, Kirtland and Fruitland Formations, New Mexico, USA; Scollard Formation, Alberta, Canada; Frenchman Formation, Saskatchewan, Canada; Hell Creek Formation, Montana, Lance Creek Formation, Wyoming, and North Horn Formation, Utah, USA.

**F. STAGODONTIDAE** Marsh, 1889  
K. (??TUR/CEN—MAA) Terr.

**First:** *Paridens* Cifelli and Eaton, 1987, Dakota Formation, Utah, USA. Cifelli (1990) questionably refers a premolar to the stagodontids from the Straight Cliffs Formation, Utah, USA, of Turonian age.

Last: *Didelphodon* Marsh, 1889, Lance Creek Formation, Wyoming and Hell Creek Formation, Montana, USA; Scollard Member, Alberta, Canada.

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F. GLYPTODONTIDAE Burmeister, 1879
T. (CHT/TLMI)—Q. (PLE) Terr.

Last: Hoplophorus Lund, 1838, Minas Geraes, Brazil; Buenos Aires, Argentina; Lomaphorus Ameghino, 1889, Buenos Aires, Argentina; Brazil; Plazhaplous Ameghino, 1884, El Paso de la Virgen, Argentina; Bothrops Ameghino, 1889, Buenos Aires, Argentina; Brazil; Plazhaplous Ameghino, 1884, El Paso de la Virgen, Argentina; Doedicurus Burmeister, 1874, Brazil; Buenos Aires, Argentina; Texas; Oklahoma; Kansas, Touro Passo, Brazil. Lower PLE:

First: Ameghino, 1895, both Deseadan, Argentina.

F. SCILLATO-YANIDAE Scillato-Yane, 1977, both Deseadan, Argentina. First: Ameghino, 1891, Santa Isabel, Argentina; Buenos Aires, Argentina; Brazil; Buenos Aires, Argentina; Venezuela; Uruguay; Heterothydon Roselli, 1976, Uruguay; Glyptotherium Osborn, 1903, Texas, USA and Mexico; Sclerocaluptus Ameghino, 1891, Santa Isabel, Argentina; Neothoracophorus Ameghino, 1889, Buenos Aires, Argentina, all Upper PLE (Pascual et al., 1966; Kuntén and Anderson, 1980).


First: Glaptates Ameghino, 1897, Mustersan, Argentina. Last: Glaptates Ameghino, 1897, and Clypeotherium Scillato-Yane, 1977, both Deseadan, Argentina.


First: Machlydotherium Ameghino, 1902, Casamayoran, Argentina. Last: Upper PLE: Pampatherium Ameghino, 1875, Buenos Aires, Argentina; Toca de Esperanca, Bahia, and Arao Touro Passo, Brazil. Lower PLE: Holmesina Simpson, 1930, Uruguay; Coleman 2A, Florida; Texas; Oklahoma; Kansas, USA (Kuntén and Anderson, 1980).


First and Last: Palaeopeltis Ameghino, 1895, Mustersan and Deseadan, Argentina.

Order PILOSA Flower, 1883


First: Eurorhamnus Storch, 1981, MP11, Messel, Germany. Extant


First: Palaeomyrmidon Rovereto, 1914, Tunuyan Formation, Lower PLI, Argentina.

F. OROPHODONTIDAE Ameghino, 1895 T. (CHT/LMI—UMI) Terr.

First: Orophodon Ameghino, 1895, and Octodontotherium Ameghino, 1895, both Deseadan, Argentina. Last: Octomydodon Ameghino, 1904, Chasicoan, Argentina.

F. SCILIDOTHERIIDAE Ameghino, 1899 T. (CHT/LMI)—Q. (PLE) Terr.

First: Chubutherium Cattoi, 1962, Deseadan, Argentina (Marshall et al., 1983). Last: Scilidotherium Owen, 1839, Salado-Indio Rico l.f., Upper PLE, Argentina; Chile; Uruguay; Bolivia; Peru; Brazil.


Last: Glossotherium Owen, 1839 (including Paramylodon Brown, 1903) South and pan-North America (see Anderson, 1984); Leston Gervais, 1865, Buenos Aires, Argentina; Lestodontidion Roselli, 1976, Uruguay, all Upper PLE.

F. BRADYPODIDAE Gray, 1825 Extant Terr.


F. MEGALONYCHIDAE Ameghino, 1889 Extant Terr.

F. ENTELOPSIDAE Ameghino, 1895, Colhuehuapian, Argentina.

First and Last: Entelops Ameghino, 1887, and Delotherium Ameghino, 1889, both Santacrucian, Argentina.

Order PHOLIDOTA Weber, 1904

F. METACHEIROMYIDAE Wortman, 1903 T. (THA—LUT) Terr.

First: Propalaeanodon Rose, 1979, Polecat Bench Formation, Wyoming, USA. Last: Metacheiromys Wortman, 1903, Bridger Formation, Wyoming, USA.


EDENTATA incertae sedis

F. ERNANODONTIDAE Ding, 1979 T. (THA) Terr.

First and Last: Assabradypus Nesov, 1987, Dzhilga, Kazakhstan, former USSR. Ernanodon Ding, 1979, Nung-shan Formation, Kwantung, China.

Cohort EPITHERIA McKenna, 1975

Superorder LEPTICTIDA McKenna, 1975


F. DIDYMOCONIDAE Kretzoi, 1943


Last: Didymoconus Matthew and Granger, 1924, Kansu, China.


First: Prodacodon Matthew, 1929, Tullock Formation, Montana, USA.

Last: Leptictis Leidy, 1868, White River Formation, South Dakota and Colorado, USA.

Superorder PREPTOTHERIA McKenna, 1975, new rank, McKenna

Grandorder ANAGALIDA Szalay and McKenna, 1971

Order MACROSCELIDEA Butler, 1956

F. ANAGALIDAE Simpson, 1931


Last: Anagale Simpson, 1931, Ulun Gochu Formation, Inner Mongolia, China; Anagalopsis Bohlin, 1951, Shih-ehrma-cheng Loc., Gan-su, China.

F. MACROSCELIDIDAE Bonaparte, 1838


Order LAGOMORPHA Brandt, 1855

F. ZALAMBDALESTIDAE Gregory and Simpson, 1926

First and Last: Zalambdalestes Gregory and Simpson, 1926, Djadokhta Formation, Mongolia; Barunlestes Kielan-Jaworowska, 1975, Barun Goyut Formation, Nemegt, Mongolia. See Nesov (1985) for possible Turonian or Coniacian record of Zalambdalestes from Uzbekistan, former USSR.

F. PSEUDICTOPIDAE Sulimski, 1969


Last: Lower Eocene: Pseudictops Matthew et al., 1929, Bayan Ulam Formation, Inner Mongolia, China. Lower Eocene or Upper Palaeocene: Mingotheium Schoch, 1985, Black Mingo Formation, South Carolina, USA.

F. LEPORIDAE Fischer, 1817
T. (LUT/BRT)–Rec. Terr.

First: Lushilagus Li, 1965, Lushih Formation, Honan, China; Procappalagus Gureev, 1960, Swift Current Creek, Saskatchewan, Canada (Storer, 1984); Mytonolagus Burke, 1938, Uinta Formation, Utah; Wagon Bed Formation, Wyoming, USA. Extant

Comments: North American taxa are late Uintan in age.

F. OCOTONIDAE Thomas, 1897
T. (PRB/RUP)–Rec. Terr.

First: Desmatolagus Matthew and Granger, 1923, Ulun Gochu Formation, Hsanda Gol Formation, Inner Mongolia, China. Extant

Order RODENTIA Bowdich, 1821

Papers in Luckett and Hartenberger (1985) provide alternative classifications and additional information on rodents.

Suborder SCIUROMORPHA Brandt, 1855

F. EURYMYLIDAE Matthew et al., 1929


F. ISCHYROMYIDAE Alston, 1876 (including PARAMYIDAE Miller and Gidley, 1918; see Black, 1971)

First: Acritosparamys Korth, 1984, Eagle Coal Mine, Montana; Fort Union Formation, Wyoming, USA (Ivy, 1990); Paramys Leidy, 1871, Togwotee, Wyoming, USA; MP7, Meudon, France (Russell et al., 1988); Microparamys and ‘Pseudoparamys’, both MP7, Meudon, France (Russell et al., 1988).

Last: Paracitellus Dehm, 1950, Europe.

F. CYLINDRODONTIDAE Miller and Gidley, 1918

First: Dawsonomys Gazin, 1961, Wasatch Formation, Wyoming, USA.

Last: Downsimys Flynn et al., 1986, Asia.

F. PROTOPTYCHIDAE Schlosser, 1911
T. (LUT) Terr.

First and Last: Protoptychus Scott, 1895, Washakie Formation, Wyoming; Uinta Formation, Utah, USA.

F. TSAGANOMYIDAE Matthew and Granger, 1923

First and Last: Tsaganomyx Matthew and Granger, 1923, Hsanda Gol, Mongolia; Beatomus Shevyreva, 1972, Ergil Obo, Mongolia; Sepulkomyx Shevyreva, 1972, Takal Gol, Mongolia.

F. APLODONITIDAE Brandt, 1855
T. (LUT/BRT)–Rec. Terr.


F. REITHROPARAMYIDAE Wood, 1962

First and Last: Reithroparamys Matthew, 1920, Western Interior, North America.

F. SCIURIDAE Gray, 1821
T. (PRB–Rec.) Terr.

First: Oligospermophilus Korth, 1987, White River Formation, Nebraska. Earliest European record is Palaeosciurus
### Suborder HYSTRICOMORPHA Brandt, 1855

**F. BATHYERGIDAE Waterhouse, 1841**

- T. (CHT) - Rec. Terr.

### Suborder EUTYPOMYIDAE Miller and Gidley, 1918

- **F. EUTYPOMYIDAE Miller and Gidley, 1918**

  **First:** Mattinyum Korth, 1984, Wind River Formation, Wyoming, USA.
  **Last:** Eutypomys Matthew, 1905, Sharps Formation, South Dakota, USA.

- **F. CASTORIDAE Hemprich, 1820**
  - T. (PRB/RUP) - Rec. FW/Terr.

  **First:** Protadelomys Hartenberger, 1968, MP13, Bouxwiller and Saint Martin, France (Hartenberger, 1990).
  **Last:** Columbomys Thaler, 1962, MP30, level of Coderet, France (Brunet and Vianey-Liaud, 1987).

- **F. RHIZOSPALACIDAE Thaler, 1966**
  - T. (CHT) Terr.

  **First and Last:** Rhizospalax Miller and Gidley, 1919, MP29, Rickenbach, Switzerland; MP30, Coderet, France (Brunet and Vianey-Liaud, 1987).

- **F. MYOXIDAE Gray, 1821**
  - T. (YPR) - Rec. Terr.

  **First:** Eogliravus Hartenberger, 1971, MP13, level of Geiseltal, Germany (Franzen, 1987).
  **Last:** Egliravus Hartenberger, 1971, MP13, level of Geiseltal, Germany (Franzen, 1987). Extant

- **F. SELEVINIIDAE Bashanov and Belosludov, 1939**
  - T. (PLI) - Rec. Terr.

  **First:** Plioselevinia Sulimski, 1962, Poland. Extant

**Suborder HYSTRICOMORPHA Brandt, 1855**

- **F. THERIDOMYIDAE Alston, 1876**
  - T. (LUT–CHT) Terr. (see Fig. 41.3) Extant

  **First:** Theridomyidae, 1876
  **Last:** Theridomyidae, 1876

- **F. JURASSIC**

  - **F. BTH** BTH
    - **CLV** 18. Eocardiidae
      - **36. Armintomyidae**
    - **OXF** 17. Agoutidae
      - **40. Distylomyidae**
    - **KIM** 16. Erethizontidae
      - **52. Coryphodontidae**
    - **TTH** 15. Hystricidae
      - **50. Pantolambodontidae**
    - **HAU** 14. Myoxidae
      - **39. Dipodidae**
    - **VNL** 13. Kenyamyidae
      - **48. Titanoididae**
    - **BRM** 12. Diamantomyidae
      - **47. Pantolambidae**
    - **APT** 11. Myophiomyidae
      - **46. Harpyiodidae**
    - **ALB** 10. Thryonomysidae
      - **45. Pastoralodontidae**
    - **CON** 9. Phoymiidae
      - **44. Bemalambidae**
    - **SAN** 8. Anomaluridae
      - **43. Cimolestidae**
    - **TUR** 7. Pedetidae
      - **39. Dipodidae**
    - **MNI** 6. Bathyergoididae
      - **38. Simiyidae**
    - **LMI** 5. Bathyergidae
      - **37. Geomyidae**
    - **PLI** 4. Seleviniidae
      - **36. Simiyidae**
    - **UMI** 3. Myoxidae
      - **35. Dipodidae**
    - **HOL** 2. Rhizospalacidae
      - **34. Echimyidae**
    - **PLE** 1. Theridomyidae
      - **33. Echimyidae**

**Fig. 41.3**

Vianey-Liaud, 1974, MP21, Mas de Got, Quercy, France. Extant

F. EUTYPOMYIDAE Miller and Gidley, 1918

Mammalia

First: Morosomys Shevyreva, 1972, Middle Oligocene, Ergil Obo, Mongolia. Extant


First and Last: Bathyergoides Stromer, 1926, south-west and east Africa.

F. PEDETIDAE Gray, 1821 T. (AQT)-Rec. Terr. Extant

First: Megapedetes MacInnes, 1957, Negev, Israel. Extant

F. ANOMALURIDAE Gervais, 1849 T. (?YPR/PRB)-Rec. Terr. Extant

First: Nementchamys Jaeger et al., 1985, Nementcha Mountains, Algeria. An indeterminate Lower Eocene anomalurid is recorded from the Kasserine Platform, Tunisia, by Hartenberger et al. (1985).


F. PETROMURIDAE Tullberg, 1899 Q. (PLE)-Rec. Terr. Extant

First: Petromus Smith, 1831, Taung, South Africa.

F. HYSTRICIDAE Fischer de Waldheim, 1817 T. (MMI)-Rec. Terr. Extant

First: Neoprocavia Ameghino, 1889, Barrancos del Parana, Argentina (Ameghino, 1906); Prodolichotis Kraglievich, 1932, Uruguay. Extant

F. EROCHOOERIDAE Gray, 1825 T. (MMI)-Rec. Terr. Extant

First: Procardiatherium Ameghino, 1885, and Cardiatherium Ameghino, 1883, both Chasicoan, Argentina (Bondesio, 1978). Extant

F. NEOEPIBLEMIDAE Kraglievich, 1926 T. (LMI-PLI) Terr. Extant

First: Perimys Ameghino, 1887, Colhuheuapuan, Argentina. Last: Neoepeblema Ameghino, 1889, Parana, Argentina; Phoberomys (= Dabbeina) Kraglievich, 1926, Archipelago de las Antillas, Argentina (Bondesio and Villanueva Bocquentin, 1987).

F. CHINCHILLIDAE Bennett, 1833 T. (MMI)-Rec. Terr. Extant

First: Pliolagostomus Ameghino, 1887, and Prolagostomus Ameghino, 1887, both Santacrucian, Argentina. Extant

F. ABROCOMIDAE Miller and Gidley, 1918 T. (UMI)-Rec. Terr. Extant

First: Protabrocoma Kraglievich, 1927, Huayquerian, Argentina.

F. OCTODONTIDAE Waterhouse, 1839 T. (CHT/LMI)-Rec. Terr. Extant


F. ECHIMYIDAE Gray, 1825 T. (CHT/LMI)-Rec. Terr. Extant

First: Sallamys Hoffstetter and Lavocat, 1970, Salla Beds, Bolivia; Desedamys Wood and Patterson, 1959, and Xylechimys Patterson and Paschau, 1968, both Deseadan, Argentina.
F. HEPTAXODONTIDAE Anthony, 1917

T. (PLI)–Q. (PLE) Terr.

First: Pentastylomys Kraglievich, 1926, and Tetrastylomys Kraglievich, 1926, both Archipelago de las Antillas, Argentina.

Last: Clidomys Anthony, 1920, Jamaica; Amblyrhiza Cope, 1868, Lesser Antilles.

F. CAPROMYIDAE Smith, 1842

T. (MMI)–Rec. Terr.

First: Unnamed capromyids are reported from Santa­


Last: A sciuravid is known from the White River Forma­

 tion of the Douglass area, Wyoming, USA (D. Kron, pers. comm. to RKS).

Suborder MYOMORPHA Brandt, 1855

F. SCIURAVIDAE Miller and Gidley, 1918


First: Knightomys Gazin, 1961, Wasatch and Willwood Formation, Wyoming, USA.

Last: A sciuravid is known from the White River Forma­

 tion of the Douglass area, Wyoming, USA (D. Kron, pers. comm. to RKS).

F. CTENODACTYLIDAE Gervais, 1853

T. (RUP/CHT)–Rec. Terr.


F. COCOMYIDAE De Bruijn et al., 1982


Last: Tsinglingomys Li, 1963, Lushi Formation, Honan, China; Tamquammys Shevyreva, 1971, Zaisan Basin, Kazakhstan, former USSR.

F. DISTYLOMYIDAE Wang, 1988

T. (CHT–MMI) Terr.

First: Prodistylomys Wang and Qi, 1989, Suosuoquan For­

 mation, China.

Last: Distylomys Wang, 1988, Tung Gur, China.

F. YUOMYIDAE Dawson, Li and Qi, 1984

T. (?YPR–RUP) Terr.

First: Advenimus Dawson, 1964, Yu-huang-ding Formation, Sichuan, China; Petrokazlovia Shevyreva, 1972, Mongolia and Kazakhstan, former USSR.

Last: Dianomys Wang, 1984, Caijiachong Formation, Yunan, China.

F. CHAPATTIMYIDAE Hussain et al., 1978


F. EOMYIDAE Winge, 1887

T. (LUT/BRT)–Q. (PLE) Terr.

First: ?Namatomys Black, 1965, Cypress Hills Formation, Saskatchewan, Canada; Ventura County, California, USA; Protadjidaumo Burke, 1934, Cypress Hills Formation, Saskatchewan, Canada; Duchesne River Formation, Utah, USA; Yoderimys Wood, 1955, and Omegodus (= Adjidaumo) Pomer, 1853, both Cypress Hills Formation, Saskatchewan, Canada (Storer, 1987, 1988).


F. ARMINTOMYIDAE Dawson et al., 1990

T. (LUT) Terr.

First and Last: Armintonmys Dawson et al., 1990, Wind River Formation, Wyoming, USA.

F. GEOMYIDAE Bonaparte, 1845

T. (LUT/BRT)–Rec. Terr.

First: Heliscomys Cope, 1873, Wagon Bed Formation, Wyoming, USA (M. R. Dawson, pers. comm. to MCM, 1987); Cypress Hills Formation, Saskatchewan, Canada (Storer, 1988).

Last: F. SIMIMYIDAE Wood, 1980


First: Simimys Wilson, 1935, ?Chambers Formation, Texas; Mission Valley Formation, California, USA.


F. DIPODIDAE Fischer von Waldheim, 1817

T. (LUT/RUP)–Rec. Terr.


Extant F. MURIDAE Illiger, 1811

T. (LUT/BRT)–Rec. Terr.

First: Eumys Leidy, 1856, Cypress Hills Formation, Saskatchewan, Canada (Storer, 1988).

Extant F. FLORENTIAMYIDAE Wood, 1936


First: Ecclesimus Korth, 1989, White River Formation, Cedar Creek Member, Colorado, USA.

Last: Harrymys Munthe, 1988, Split Rock Formation, Wyoming, USA.

F. IVANANTONIIDAE Shevyreva, 1989

T. (YPR) Terr.


Grandorder FERAE Linnaeus, 1758

Order CIMOLESTA McKenna, 1975

Suborder DIDELPHODONTA McKenna, 1975

F. CIMOLESTIDAE Marsh, 1889

First: Otleses Neson, 1985, Uzbekistan, former USSR. Possibly also Deccanoleses Prasad and Sahni, 1988, Andhra Pradesh, India.
Last: Didelphodus Cope, 1882, Swift Current Creek, Saskatchewan, Canada (Storer, 1984).

**Suborder PANTODONTA** Cope, 1873

F. BEMALAMBDIDAE Chow et al., 1973
T. (DAN/THA) Terr.
First: Bemalambda Chow et al., 1973 and Hynpsilolambda Wang, 1975, both Zao-shi Formation, Hunan, China.

F. HARPYODIDAE Wang, 1979
Last: Harpyodus Chiu and Li, 1977, Chi-jiang Formation, Kiangsi, China.

F. PASTORALODONTIDAE Chow and Qi, 1978
Last: Pastoralodon Chow and Qi, 1978, Nomogen, Inner Mongolia, China; Bayan Ulan Formation, Inner Mongolia, China.

F. PANTOLAMBDIDAE Cope, 1883
T. (THA) Terr.
First: Pantolambda Cope, 1882, Nacimiento Formation, New Mexico; Polecant Bench Formation, Wyoming; Lebo and Mervillie formations, Montana, USA.
Last: Caenolambda Gazin, 1956, Polecant Bench Formation, Wyoming, USA; Alberta, Canada.

F. TITANOIDEIDAE Patterson, 1934
T. (THA) Terr.
First and Last: Titanoides Gidley, 1917, Western Interior, North America (Archibald et al., 1987).

F. BARYLAMBDIDAE Patterson, 1937
First: Barylamba Patterson, 1937, Blacks Peak Formation, Texas, USA.
Last: Barylamba Patterson, 1937, Wind River Formation, Wyoming, USA.
Comments: Last record is based on unpublished materials in the collections of Carnegie Museum of Natural History from the Lysite Member, Wind River Formation, Wyoming, USA.

F. PANTOLAMBDOIDONTAIDAE Granger and Gregory, 1934
Last: Pantolambdodon Granger and Gregory, 1934, Irdin Manha Formation, Inner Mongolia, China.

F. CYRIACOTHERIIDAE Rose and Krause, 1982
T. (THA) Terr.
First and Last: Cyriacotherium Rose and Krause, 1982, Paskapoo Formation, Alberta, Canada; Willwood and Polecant Bench Formations, Wyoming; Togwotee, Wyoming, USA.

F. CORYPHODONTIDAE Marsh, 1876
First: Coryphodon Owen, 1845, Wasatch Formation, Colorado, USA; Polecant Bench and Willwood Formations, Wyoming, USA; London Clay, Blackheath and Suffolk Pebble beds, England, UK; Meudon, Argile à Lignites and Argiles Plastiques, France; Vertian and Orp-le-Grand, Belgium; Dabu Formation, Xinjiang, China; Yuli Formation, Shanxi, China; White Beds, Narun-Bulak Beds, Mongolia (Lucas, 1989).
Last: Eudinoceras Osborn, 1924, Shandong, China.

F. WANGLIIDAE Van Valen, 1988
T. (DAN–THA) Terr. (see Fig. 41.4)

**Suborder PANTOLESTA** McKenna, 1975

F. PANTOLESTIDAE Cope, 1884
T. (THA–CHT) Terr.
First: Propalaeosinopa Simpson, 1927, Tongue River Formation, Montana.

F. PAROXYCLAENIDAE Weitzel, 1933
First: Spaniella Crussafont-Pairo and Russell, 1967, Spain; Meralius Russell and Godinot, 1988, MP7, Palette, France (Godinot, 1987).
Last: Paroxylaencaus Teilhard de Chardin, 1922, Quercy, France; Euhookeria Russell and Godinot, 1988, Headon Beds, England, UK.

F. PTOLEMAIIDAE Osborn, 1908
T. (PRB) Terr.
First and Last: Ptolemaia Osborn, 1908, Qaranavan Simons and Gingerich, 1974, and Cleopatrosin Bown and Simons, 1987, all Jebel Qatrani Formation, Egypt.

**Suborder TAEJIDONTA** Cope, 1876

F. STYLINODONTIDAE Marsh, 1875
T. (THA–LUT) Terr.
First: Onychodectes Cope, 1888, Nacimiento Formation, New Mexico; North Horn Formation, Utah; Wortmania Hay, 1899, Nacimiento Formation, New Mexico, USA.
Last: Stylinodon Marsh, 1874, Uinta Formation, Utah, USA.

**Suborder APATOTHERIA** Scott and Jepsen, 1936

F. APATEMYIDAE Matthew, 1909
First: Jepsenidae Simpson, 1940, Fort Union and Polecant Bench Formations, Wyoming; Lebo Formation, Montana, USA.
Last: Sinclairella Jepsen, 1934, White River Formation, South Dakota, USA.

**Suborder TILLODONTIA** Marsh, 1875, new rank, McKenna

F. TILLOHERIDAE Marsh, 1875
Fig. 41.4


Last: *Adapidium* Young, 1937, He-ti Formation, Shansi, China.

**Order CREODONTA** Cope, 1875

F. **OXYAENIDAE** Cope, 1877


First: *Tytthaena* Gingerich, 1980, Jepsen Quarry, Polecat Bench Formation, Wyoming, USA.

Last: *Sarkastodon* Granger, 1938, Irdin Manha Formation, Inner Mongolia, China.

**F. HYAENODONTIDAE** Leidy, 1869


Last: *Pterodon* de Blainville, 1839, Nagri Beds, India.

Comments: A specimen of middle Paleocene age of *Prolimnocyon* has been reported from Swain Quarry, Fort Union Formation, Wyoming, USA (Archibald et al., 1987). According to Ivy (pers. comm. to RKS), these specimens are not from a creodont. Gheerbrant (1987) has reported a proviverrine hyaenodont from the Upper Paleocene of Adrar Mgorn, Morocco.

**Order CARNIVORA** Bowditch, 1821

F. **CANIDAE** Fischer von Waldheim, 1817

T. (PRB–Rec.) Terr.

First: *Hesperocyon* Scott, 1890, White River Formation, Wyoming, USA. Storer (1988) has a queried identifica-
tion of this genus from the Cypress Hills Formation, Saskatchewan, Canada (Duchesnian).

**F. AMPHICYONIDAE** Trouessart, 1885

First: *Daphnoherus* Leidy, 1853, Wagon Bed Formation, Wyoming; Chambers Formation, Texas, USA; *Cynodictis* Bravard and Pomel, 1850, MP18, La Debruge, France.

Last: *Ischyrocyon* Matthew, 1904, Clarendon, Texas, USA; *Agnotherium* Kaup, 1832, Eppelsheim, Germany; *Arctamphicyon* Pilgrim, 1932, Europe; *Pseudarctos* Schlosser, 1899, Tutzing and Hader, Germany.

**F. BRACHYURIDAE** Brachyurus, 1850, MP18, La Debruge, France.

First: *Wyomingia*; Chambers Formation, Texas, USA; *Arctamphicyon* Pilgrim, 1932, Europe; *Pseudarctos* Schlosser, 1899, Tutzing and Hader, Germany.

**F. MUSTELIDAE** Fischer von Waldheim, 1817

First: *Plesioxyx* Schlosser, 1887, Quercy, France; *Cephalogale* Jourdan, 1862, Quercy, France; *Bose Basin, Guanxi, China; ?*Parictis* Scott, 1893 (including *Campylcoydon* Chaffe, 1954), Cypress Hills Formation, Saskatchewan, Canada (Storer, 1987).

Last: *Miocynoidea* Pomel, 1847, all Quercy, France; *Plesiocyon* Daphoenus, 1936, all North America; *Cephalogale* Leidy, 1853, Wagon Bed Formation, Wyoming; *Lebo Formation, Montana, USA.*

**F. URSIDAE** Fischer von Waldheim, 1817

First: *Miocynoidea* Pomel, 1847, all Quercy, France; *Cephalogale* Jourdan, 1862, Quercy, France; *Bose Basin, Guanxi, China; ?*Parictis* Scott, 1893 (including *Campylcoydon* Chaffe, 1954), Cypress Hills Formation, Saskatchewan, Canada (Storer, 1987).

Last: *Miocynoidea* Pomel, 1847, all Quercy, France; *Plesiocyon* Daphoenus, 1936, all North America; *Cephalogale* Leidy, 1853, Wagon Bed Formation, Wyoming; *Lebo Formation, Montana, USA.*

Comments: Family also reported from the Oligocene of Hsanda Gol, Mongolia (Schmidt-Kittler, 1987; Hunt, 1989).

**F. HYAENIDAE** Gray, 1821

First: *Miacis* Cope, 1880, MP22, Quercy, France; *Plesiocyon* Daphoenus, 1936, all North America; *Cephalogale* Leidy, 1853, Wagon Bed Formation, Wyoming; *Lebo Formation, Montana, USA.*

Last: *Miocynoidea* Pomel, 1847, all Quercy, France; *Plesiocyon* Daphoenus, 1936, all North America; *Cephalogale* Leidy, 1853, Wagon Bed Formation, Wyoming; *Lebo Formation, Montana, USA.*

Comments: Family also reported from the Oligocene of Hsanda Gol, Mongolia (Schmidt-Kittler, 1987; Hunt, 1989).

**F. FELIDAE** Fischer von Waldheim, 1817

First: *Proailurus* Barnes, 1979, North America. Extant

First: *Pinnarctidion* Allen, 1880, T. (?CHT/LMI) Rec. Terr./Mar./FW

First: *Miocynoidea* Pomel, 1847, all Quercy, France; *Plesiocyon* Daphoenus, 1936, all North America; *Cephalogale* Leidy, 1853, Wagon Bed Formation, Wyoming; *Lebo Formation, Montana, USA.*

Last: *Miocynoidea* Pomel, 1847, all Quercy, France; *Plesiocyon* Daphoenus, 1936, all North America; *Cephalogale* Leidy, 1853, Wagon Bed Formation, Wyoming; *Lebo Formation, Montana, USA.*

Comments: Family also reported from the Oligocene of Hsanda Gol, Mongolia (Schmidt-Kittler, 1987; Hunt, 1989).

**F. OTARIDAE** Gray, 1821

First: *Pteronarctos* Barnes, 1989, North America. Extant


First: *Proailurus* Barnes, 1979, North America. Extant


First: *Amphictis* Pomel, 1853, *Plesictis* Pomel, 1846, and *Plesiogale* Pomel, 1847, all Quercy, France; *Pseudobassaris* Pohle, 1917, Quercy, France; *North America. Extant


First: * Uintacyon rudis* Matthew, 1915, Willwood Formation, Wyoming, USA.

Last: *Miacis* Cope, 1872, MP17, level of Fons 4, Europe (Legendre, 1987); *Little Egypt and Blue Cliff horizons, Chambers Formation, Texas, USA (Wilson, 1986). Extant


First and Last: *Protictis* Matthew, 1937, Western Interior, North America (Flynn and Galiano, 1982).

F. VIVERRAVIDAE Wortman and Matthew, 1899 T. (THA-PRB) Terr.

First: *Stenonebus* MacIntyre, 1962, Fort Union and Polecat Bench Formations, Wyoming; *Lebo Formation, Montana, USA.*

Last: *Viverravus* Marsh, 1872, Europe; *Tapocyon Stock, 1934, and Plesiomiacis Stock, 1935, both Sespe Formation, California, USA; *Procynoictis Wortman and Matthew, 1899, Quercy, France. Extant


First: *Stenoplopecis* Filhol, 1880, MP22, Villebramar, France; *Stenogale Schlosser, 1887, MP22, Quercy, France; *Palaeeosphonodon* Filhol, 1880, Quercy, France; *Osborne Formation, England, UK; Tatal Gol, Mongolia (Russell and Zhai, 1987). Extant

F. ODOBENIDAE Allen, 1880 T. (?CHT/LMI) Rec. Terr./Mar./FW


First: *Monachopsis* Kretzoi, 1941, Europe; *Monotherium* Van Beneden, 1876, Antwerp Basin, Belgium; *St Marys Formations, Maryland, USA; Properipticyus Ameghino, 1897, Argentina; *Palmidophoca* Ginsburg and Janvier, 1975, Europe; *Praeopusa* Kretzoi, 1941, Crimea, former USSR; *Phocanella* Van Beneden, 1876, Belgium; *Pontophoca* Kretzoi, 1941, Kishenev, former USSR; *Leptophoca* True, 1906, Maryland, USA.

Last: *Nandiniidae* are first reported from the Lower Miocene of Songhor, Kenya (Hunt, 1989). Extant


First: *Nandiniids are first reported from the Lower Miocene of Songhor, Kenya (Hunt, 1989). Extant


First: *Herpestes* Illiger, 1911 (including *Leptoplesictis Forsyth Major, 1903, MN4, France (Hunt, 1989). Extant


First: *Protailurus* Filhol, 1879, MP21, Aubreloing and Somailles, France (Hunt, 1989). Extant


First: *Hoplophonus* Cope, 1874, and *Dinictis* Leidy, 1854, both White River Formation, North America; *?Middle Eocene: cf. Eusmilus* Gervais, 1876, Lushi Formation, Honan, China.

Last: *Barbouroufelis* Schultz et al., 1970, Kimball Formation, Nebraska, USA; Asia; *Sansanosmilus* Kretzoi, 1929, Sansan, France.
Grandorder LIPOTYPHLA Haeckel, 1866, new rank, McKenna

Order ERINACEOMORPHA Gregory, 1910

See Novacek et al. (1985) for an alternative classification of the Erinaceomorpha.

F. ERINACEIDAE Fischer von Waldheim, 1817
T. (THA)—Rec. Terr.
First: Litolestes Jepsen, 1930, Polecat Bench Formation, Wyoming, USA; Tongue River Formation, Montana, USA; Paskapoo Formation, Alberta, Canada. Extant
F. ADAPISORICIDAE Schlosser, 1887
T. (THA—YPR) Terr.
First and Last: Adapisorex Lemoine, 1883, MP6, Cernay, France.
Last: Neomatronella Russell et al., 1975, MP8+9, Mutigny and Avenay, France (Godinot, 1987).
First and Last: Creotarsus Matthew, 1918, Willwood Formation, Wyoming, USA.
F. SESPEDECTIDAE Novacek, 1985
T. (?THA—RUP) Terr.
First: Scenopagus McKenna and Simpson, 1959, Willwood Formation, Wyoming, USA.
Last: Ankylodon Patterson and McGrew, 1937, White River Formation, Wyoming, USA.
F. AMPHILEMURIDAE Heller, 1935
T. (YPR—PRB/RUP) Terr.
First: Macrocranion Weitzel, 1949, Willwood Formation, Wyoming, USA; MP7, Palette, France; Dormaalius Quinet, 1964, MP7, Dormaal, Belgium.
Last: Gesneropithex Hurzeler, 1946, MP18, Gosgen (Solothurn), Switzerland. A ‘dormaliid’ has been reported from the lower Oligocene Caijiachong Formation, China, by Wang (1992).

Order SORICOMORPHA Gregory, 1910
F. TALPIDAE Fischer de Waldheim, 1817
First: Eotalpa Sige et al., 1977, MP17, Headon, England, UK. Extant
F. PROSCALOPIDAE Reed, 1961
T. (PRB—MMI) Terr.
First: Proscalops Matthew, 1901, White River Formation, South Dakota and Nebraska; Renova Formation, Montana, USA; Oligoscalops Reed, 1961, White River Formation, North America.
Last: Mesoscalops Reed, 1960, Deep River Formation, Montana; Split Rock Formation, Wyoming; Batesland and Rosebud Formations, South Dakota and USA, (Barnosky, 1981).
F. DIMYLIDAE Schlosser, 1887
T. (RUP—UMI) Terr.
First: Exoedaenodus Hurzeler, 1944, Quercy, France.
Last: Plesiodimylus Gaillard, 1897, Europe; Cordylyodon von Meyer, 1859, Ulm, Germany.
F. GEOLABIDIDAE McKenna, 1960
K. (MAA)—T. (LMI) Terr.

Grandorder ARCHONTA Gregory, 1910

Order SCANDENTIA Wagner, 1855
First: Batodon Marsh, 1892, Lance Creek Formation, Wyoming, USA.
Last: Centetodon Marsh, 1872, Gering Formation, Nebraska; Monroe Creek Formation, South Dakota, USA (Lillegraven et al., 1982).
F. NYCTITHERIIDAE Simpson, 1928
T. (DAN/THA—RUP) Terr.
First: Leptacodon Matthew and Granger, 1921, Tullock Formation, Montana, USA.
Last: Darbonetus Crochet, 1974, MP23, Itardies, France.
First: Prosarcodon McKenna et al., 1984, Fangou Formation, Shaanxi Province, China.
Last: Micropternodus Matthew, 1903, John Day Formation, Oregon, USA.
F. PALAEORYCTIDAE Winge, 1917
T. (THA—LUT) Terr.
First: Palaeoryctes Matthew, 1913, Nacimiento Formation, New Mexico; Fort Union Formation, Wyoming, USA.
Last: Unnamed taxon, Friars Formation, California, USA (Novacek, 1976).
F. APTERNODONTIDAE Matthew, 1910
T. (YPR—CHT?) Terr.
First: Parapternodus Bown and Schankler, 1982, Willwood Formation, Wyoming, USA.
Last: Apternodus Matthew, 1903, White River Formation, Wyoming, USA.
F. SORICIDAE Fischer von Waldheim, 1817
First: Domnina Cope, 1873, loc. 5, Wagon Bed Formation, Wyoming, USA (Krishtalaka and Setoguchi, 1977). Extant
F. PLESIOSORICIDAE Winge, 1917
T. (YPR/LUT—PLI) Terr.
First: Pakilestes Russell and Gingerich, 1981, Kuldana Formation, Pakistan.
Last: Meterix Hall, 1929, ?Upper PLI, Nevada, USA.
F. CHRYSOCHLORIDAE Gray, 1825
T. (LMI)—Rec. Terr.
First: Prochrysochloris Butler and Hopwood, 1957, Songhor, Kenya.
First: Prochrysochloris Butler and Hopwood, 1957, Songhor, Kenya. Extant
First: Solenodon Brandt, 1833, Cuba; Hispaniola. Extant
F. SOLENODONTIDAE Gill, 1872 Q. (PLE)—Rec. Terr.
First: Solenodon Brandt, 1833, Cuba; Hispaniola. Extant

Order: Vertebrates
F. TUPAIIDAE Gray, 1825
T. (?LUT/BRT/UMI)–Rec. Terr.

Order DERMOPTERA Illiger, 1811
Fossils of dermopterans are unknown from Miocene to Recent.

F. PLAGIOMENIDAE Matthew, 1918
T. (THA–CHT) Terr.
First: Elpidophorus Simpson, 1927, Lebo Formation, Montana, USA.
Last: Mixodectes Cope, 1883, Nacimiento Formation, New Mexico; Fort Union Formation, Wyoming, USA.

F. GALEOPITHECIDAE Gray, 1821 Extant Terr.
F. MICROSYOPIDAE Osborn, 1892
First: Berruvius Russell, 1964, MP6, Berru and Cernay, France; Navajovius Matthew and Granger, 1921, Nacimiento Formation, Colorado; Black Peaks Formation, Texas; Fort Union Formation and Evanston Formations, Wyoming, USA.
Last: Craseops Stock, 1935, Sespe Formation, California, USA.
Comments: See Gunnell (1989) for the most recent re-division of this group.

Order CHIROPTERA Blumenbach, 1779
Despite the occurrence of many bat families during the Eocene, the fossil record of chiropterans is incomplete and discontinuous. Sigé and Legendre (1983) provide a summary of the fossil record of bats in Europe.

F. PTEROPODIDAE Gray, 1821 Extant
First: Archaeopteropus Meschinelli, 1903, Montevialle, Italy.

F. PALAEOCHIROPTERYGIDAE Revilliod, 1917
T. (THA–BRT) Volant
First: Archaeonycteris Revilliod, 1919, MP14, Chamblon and Egerkingen, Switzerland.

F. ICARONYCTERIDAE Jepsen, 1966
T. (THA–LUT–BRT) Volant

F. EMBALLONURIDAE Gervais, 1855
T. (LUT/BRT)–Rec. Volant

F. VESPERTILIONIDAE Gray, 1821 Extant
First: Vespertilious Schlosser, 1887, Ludian, Quercy, France.

F. RHINOPOMATIDAE Bonaparte, 1838 Extant Volant
F. CRASEONYCTERIDAE Hill, 1974 Extant Volant
F. RHINOLOPHIDAE Gray, 1825
T. (LUT)–Rec. Volant
First: Hipposideros Gray, 1821; Rhinolophids are reported from MP16, Robiac, France; Grissolles, France; Chamblon, Switzerland; MP14, Egerkingen, Switzerland; and MP16, Creechbarrow, England, UK.

F. MEGADERMATIDAE Allen, 1864
T. (PRB)–Rec. Volant
First: Necromantis Weithofer, 1887, Quercy, France.

F. NYCTERIDAE Van der Hoeven, 1855
T. (CHT)–Rec. Volant

F. PHYLLOSTOMIDAE Gray, 1825 Extant
First: Notonycteris Savage, 1951, La Venta, Honda Group, Colombia.

F. MORMOOPIDAE de Saussure, 1860 Q. (PLE)–Rec. Volant

F. NOCTILIONIDAE Gray, 1821
Q. (PLE)–Rec. Volant
First: Noctilio Linnaeus, 1766, Upper PLE, West Indies.

F. VESPERTILIONIDAE Gray, 1821 Extant
First: Stehinia Revilliod, 1919, MP14, Chamblon and Egerkingen, Switzerland.

F. MOLOSSIDAE Gervais, 1855 Extant
T. (LUT/BRT)–Rec. Volant
First: Wellia Storer, 1984, Swift Current Creek, Saskatchewan, Canada (Legendre, 1985).

F. PHILISIDAE Sigé, 1985 T. (PRB) Volant
First and Last: Philis Sigé, 1985, Jebel Qatrani Formation, Egypt.

F. NATALIDAE Gray, 1866 Q. (PLE)–Rec. Volant
First: Natalus Gray, 1838, Cuba.

F. MYZOPODIDAE Thomas, 1904 Q. (PLE)–Rec. Volant
First: Myzopoda Milne Edwards and Grandidier, 1878, Lower PLE, Africa.

F. FURIPTERIDAE Gray, 1866 Extant Volant
F. THYROPTERIDAE Miller, 1907 Extant Volant
Animals: Vertebrates

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**Fig. 41.5**

**F. MYSTACINIDAE Dobson, 1875**  
*Extant* Volant

**Order PRIMATES Linnaeus, 1758**

Here only the ‘euprimates’ are considered. As discussed below, a variety of phylogenetic arrangements for Primates have been proposed that have included the paromomyids, plesiadapids, microsyopids and their allies. Paromomyids, plesiadapids, palaechthonids, and picrodontids are included below in Archonta, incertae sedis. At practically all phylogenetic levels, opinions vary as to the included taxa. For different interpretations and reviews of the phylogenetic relationships among Primates, consult Szalay and Delson (1979), Grine et al. (1987), Szalay et al. (1987), Wible and Covert (1987), Simons (1989), Fleagle and Rosenberger (1990), Martin (1990) and Beard et al. (1991).

**F. ADAPIDAE Trouessart, 1879**  

**First:** Donrusselia Szalay, 1976, MP7, Palette, France; Cantius Simons, 1962, MP7, Dormaal, Belgium; Willwood Formation, Wyoming, USA; MP7, Meudon, France (Russell et al., 1988).

**Last:** Sivaladapis Gingerich and Sahni, 1979, and Indraloris Lewis, 1933, both Nagri Beds, India; Sinoadapis Wu and Pan, 1985, Lufeng Formation, Yunnan, China.

**Comments:** Subfossil adapids from Madagascar include species of Varecia Gray, 1863 and Megaladapis Major, 1894. Extant

**F. LEMURIDAE Gray, 1821**  
Q. (HOL)–Rec. Terr.

**Comments:** Subfossil lemurids from Madagascar include species of Varecia Gray, 1863 and Megaladapis Major, 1894. Extant

**F. INDRIIDAE Bumett, 1828**  
Q. (HOL)–Rec. Terr.

**Comments:** Subfossil indriids from Madagascar include species of Mesopropithecus Standing, 1905, Archaeolemur Filhol, 1895, Hadropithecus Lorenz, 1899, Thaumastoilemur Filhol, 1895, and Archaeoindris Standing, 1908. Extant

**F. DAUBENTONIIIDAE Gray, 1863**  
Q. (HOL)–Rec. Terr.

**Comments:** Daubentonia Geoffroy, 1895, subfossil, Madagascar. Extant

**F. LORISIDAE Gray, 1821**  
T. (PRB)–Rec. Terr.

**First:** Lorisidae, gen. indet., Jebel Qatrani Formation, Egypt (Simons et al., 1986). Extant
F. CHEIROGALEIDAE Gray, 1872
Q. (HOL)—Rec. Terr.  
Comments: Szalay and Delson (1979) report subfossil specimens of living taxa from Madagascar. Extant

F. OOMYIIDAE Trouessart, 1879  
T. (DAN/THA—PRB) Terr.  
Last: Macronotarsius Clark, 1941, Renova Formation, Montana, USA; Rooneynia Wilson, 1966, Chambers Formation, Texas, USA.  
Comments: Recent evidence on the basicranial anatomy calls into question the monophyly of the omomyids (sensu Szalay, 1976). Two subfamilies are generally recognized, the Anaptomorphinae Cope, 1883 and the Omomyinae Trouessart, 1879. The former appears to be monophyletic (Bown and Rose, 1987), whereas the latter now appears to be paraphyletic as it has classically been characterized by a number of workers. Shoshonius Granger, 1910 possesses several derived characteristics which suggest that it shares a more recent common ancestry with living Tarsius than other omomyids in which the relevant anatomy is known (Beard et al., 1991; Martin, 1991). If tarsids are the sister group of Anthropoidea, then the earliest anthropoids are earlier than late early Eocene in age (YPR).  

F. MICROCHOERIDAE Lydekker, 1887  
First: Nannopithex Stehlin, 1916, MP13, Bouxwiller, France.  
Last: Microchoerus Wood, 1844, MP19, San Cugat, Spain; MP19, Mormont and Entreroches, Switzerland; Pseudoloris Stehlin, 1916, MP19, San Cugat, Spain (Szalay and Delson, 1979).  

F. TARSIIIDAE Gray, 1825  
T. (1YPR/PRB)—Rec. Terr.  

F. CARPOLESTIDAE Simpson, 1935  
T. (THA) Terr.  
First: Elphidotarsius Gidley, 1923, Polecat Bench Formation, Wyoming; Lebo and Tongue River Formations, Montana, USA.  
Last: Carpoleses Simpson, 1928, Willwood Formation, Wyoming, USA.  

F. CEBIDAE Bonaparte, 1831  
T. (LMI)—Rec. Terr.  
First: Tremacebus Lartet, 1856, numerous localities, principally in East Africa (Szalay and Delson, 1979).  

F. HOMUNCULIDAE Ameghino, 1894  
T. (LMI—MMI) Terr.  
First and Last: Homunculus Ameghino, 1891, Santa Cruz Beds, Santacrucian, Argentina.  

F. CALLITRICHIDAE Gray, 1821  
First: Micodon Setoguchi and Rosenberger, 1985, Mohanamico Luchterhand et al., 1986, both La Venta, Friasian, Columbia. Extant

F. PARAPITHECIDAE Schlosser, 1911  
Last: Oreopithecus Gervais, 1872, numerous localities in Italy, and possibly from the former USSR.  

F. PLOPITHECIDAE Zapfe, 1960  
Last: Pliopithecus Gervais, 1849, Rudibanya, Hungary.  

F. CERCOPITHECIDAE Gray, 1821  
T. (LMJ)—Rec. Terr.  
First: Dryopithecus Lartet, 1856, numerous localities, principally in East Africa (Szalay and Delson, 1979). Extant

ARCHONTA incertae sedis

There is considerable controversy concerning the ordinal affinities of the families included here, many of which have classically been included among the primates. New evidence on the skull and postcranial skeleton of paromomyids and plesiadapids (Szalay and Drawhorn, 1980; Beard, 1990; Kay et al., 1990) suggests that these families are related to galeopithecids rather than primates among living mammals. For this paper, these families are tentatively assigned to the Archonta, incertae sedis. Picrodontids and palaechthonids are included here as well. For varying recent interpretations of the phylogenetic affinities of these taxa see Szalay and Delson (1979), Szalay et al. (1987), MacPhee et al. (1988), Gunnell (1989), Beard (1990), and Kay et al. (1990).  

F. PAROMOMYIDAE Simpson, 1940  
First: ?Cretaceous and/or Lower Palaeocene: Purgatorius Van Valen and Sloan, 1965, Hell Creek Formation, Montana, USA. Palaeocene: Paromomyus Gidley, 1923, North Horn Formation, Utah; Nacimiento Formation, New Mexico, USA.  

F. PALAECHTHONIDAE Szalay, 1969  
T. (THA) Terr.  
First: ?Plesiolestes Jepsen, 1930, North Horn Formation, Utah, USA.
Last: Palaechthon Gidley, 1923, and Palenochtha Simpson, 1935, both Fort Union Formation, Wyoming, USA; Plesiolestes Jepsen, 1930, New Mexico; Utah; Fort Union and Evanston Formations, Wyoming; Montana, USA.

F. PLESIADAPIDAE Trouessart, 1897
First: Pronothodectes Gidley, 1923, Evanston, Fort Union and Polecat Bench Formations, Wyoming; Tongue River and Lebo formations, Montana, Canada; Saunders Creek Formation, Alberta, Canada.

Last: Plesiadapis Gervais, 1887, Willwood Formation, Wyoming, USA; MP7, Meudon, France; Platychoereps Charlesworth, 1854, MP7, Dormaal, Belgium; MP7, Pourcy, France (Szalay and Delson, 1979).

Comments: Kay et al. (1990) suggest that this family is closely allied with Dermoptera.

F. PLESIADAPIDAE Simpson, 1937
T. (THA) Terr.
First: Draconodon Tomida, 1982, North Horn Formation, Utah, USA.
Last: Zanycteris Matthew, 1917, Animas Formation, Colorado, USA; Picroodus Douglass, 1908, Fort Union Formation, Wyoming, USA.

Grandorder UNGULATA Linnaeus, 1766

Miroder EPARCTOCYONA McKenna, 1975

Order ARCTOCYONIDAE Van Valen, 1969
F. ARCTOCYONIDAE Gervais, 1870
K. (MAA)–T. (PRB) Terr.
First: Protungulatum Sloan and Van Valen, 1965, Frenchman Formation, Saskatchewan, Canada.
Last: Lantianius Chow, 1964, Shensi, China.

Order ARTIODACTyla Owen, 1848
F. AGRICHOERIDAE Leidy, 1869
First: Protoxerus Scott and Osborn, 1887, Washakie Formation, Wyoming; Sheep Creek Formation, Nebraska, USA.

F. ANOPLOHERIIDAE Gray, 1821
First: Anoplotherium Pilgrim and Cotter, 1916, Ganda Kas, Pakistan; Siamotherium Suteethorn et al., 1988, Thailand; Probrachyodus Xu and Chiu, 1962, Dongjin Formation, Guanxi, China; Brachyglossus Deperet, 1895, Lumeiyi Formation, Yunnan, China; Bakalovia Nikolov and Heissig, 1985, and Anthracosanx Zdansky, 1930, both Heti Formation, Henan, China; Prominatherium Teller, 1884, former Yugoslavia; Romania; Lulausuwon Hu, 1963, Sharon Murun Formation, Mongolia.

Last: Merycopotamus Falconer and Cautly, 1845, Lower PLI or ?PLE, Sahabi, Libya.

F. ANTILOCAPRIDAE Gray, 1866
T. (LMI)–Rec. Terr.
First and Last: Merycodus Leidy, 1854, Split Rock Formation, Wyoming; Sheep Creek Formation, Nebraska, USA.

Extant

F. BOVIDAE Gray, 1821

Last: Cainotherium Bravard, 1828, Bunol, Spain.

First: Poebrodon kayi Gazin, 1955, Uinta Formation, Utah; Santiago Formation, California, USA (Golz and Lillegraven, 1977).

Extant

F. CEBOCOHERIDAE Lydekker, 1883
First: Cebochoerus Gervais, 1848, MP10, Los Saleros, Spain.
Last: Acotherium Gervais, 1850, MP21, Soumailles, France.

F. CERVIDAE Goldfuss, 1820
T. (CHT/LMI)–Rec. Terr.
First: Lower Oligocene: Cervid, indet. has been reported from Chaganbulage, China (Wang, 1992); Dicrocerus Lartet, 1837, Sansan, France; Tung Gur Formation, China; Actiectus Ginsburg, 1985, Chilleurs-aux-Bois, France; Stephanoceros Colbert, 1936, Europe.

Extant

F. CHOEROPOTAMIDAE Owen, 1845
First: Choeropotamus Cuvier, 1821, Malperie and Quercy, France. Possible early record from MP16, Creechbarrow Limestone, England, UK.

F. CLIMACOCERIDAE Hamilton, 1978
T. (MMI) Terr.
First and Last: Nyanzameryx Thomas, 1984, and Climacoceratidae MacInnes, 1936, both Africa.

F. DACRYTHERIDAE Deperet, 1917
First: Cuisitherium Sudre et al., 1983, MP8, Avenay, France.
Last: Tapirulus Gervais, 1850, MP18, Ranet and Aubrelong, France; Dacyrtherium Filhol, 1876, MP18, level of La Debruge.

F. DIACODEXIEIDAE Gazin, 1955
First: Diacodexis Cope, 1882, Willwood Formation, Wyoming, USA; MP-7, Dormaal, Belgium; MP7, Palette, France; MP7, Silveriniena, Portugal; Kuldana Formation, Pakistan.
Last: Leptochaerus Leidy, 1856, Sharp's Formation, South Dakota, USA.
Comments: Diacodexis is the most primitive artiodactyl and may be paraphyletic as it is currently defined (Sudre et al., 1983; Krishtalka and Stucky, 1985; Stucky and Krishtalka, 1990).

F. DICHOBUNIDAE Turner, 1849
First: Aumelasia Sudre, 1980, and Protodichobune Lemoine, 1879, both from MP10, Grauves and other localities, France.
Last: Metrioatherium Filhol, 1882, MP26, level of Mas de Pauffie, France.
Comments: The dichobunids formerly included taxa here assigned to the Diacodexidae and Homacodontidae (Sudre et al., 1983; Webb and Perrigo, 1984).

F. DROMOMERYCIDAE Frick, 1937
First: Asiagenes Vislobokova, 1983, Mongolia; Barbouro-meryx Frick, 1937, Antelope Creek, Nebraska; Bouroumeryx Frick, 1937, Nebraska, USA; Pediomeryx Stirton, 1936, Coffee Ranch, Texas, USA (Webb, 1983).
Last: Cranioeceras Matthew, 1918, North America.

F. ENTELODONTIDAE Lydekker, 1883
First: Cranioceras Gazin, 1952, Wasatch and Wind River Formations, Wyoming, USA.
Last: Daeodon Cope, 1878, Runningwater Formation, Nebraska, USA.
Comments: An unnamed taxon, formerly referred to Parahyr (see West and Dawson, 1976) from the lower Uinta (Shoshonean) of the Washakie Formation, Colorado, USA, may represent the earliest entelodontid.

F. GELOCIDAE Schlosser, 1886
First: Lophiomeryx Pomel, 1854, Sevkul, Asia; Phaneromeryx Schlosser, 1886, Quercy, France.
Last: Pseudoceras Frick, 1937, Gracias Formation, Honduras; Round Mountain Quarry, New Mexico, USA (Webb and Perrigo, 1984).

F. GIRAFFIDAE Gray, 1821
First: Palaeotragus Gaudry, 1861, Rusinga, Kenya; Gebel Zelten, Libya.

F. HAPLOBUNODONTIDAE Sudre, 1978
First: Rhagatherium Picket and Humbert, 1855, MP10, ?Mas de Gimel, France; MP13, Geiseltal, Germany.
Last: Amphihragatherium Deperet, 1908, MP20, level of Saint Capraise, France (Sudre, 1978; Legendre, 1987).

F. HELOHYIDAE Marsh, 1877
First: Helohyus Marsh, 1872, Bridger and Aycross Formations, Wyoming, USA; Gobiodyus Matthews and Granger, 1925, Lushi Formation, Honan, China.
Last: Gobiodyus Matthew and Granger, 1925, Irdin Manha Formation, Mongolia; Lu-mei-yi Formation, Yunnan and He-ti Formation, Shansi, China.
Comments: Report of a specimen of Helohyus from the Wind River Formation (Stucky, 1984) was in error. The specimen represents a deciduous tooth fragment of the titanotheri Eoitolanops.

F. HIPPOPATAMIDAE Gray, 1821

F. HOMACODONTIDAE Sinclair, 1891
First: Hexacodus Gazin, 1952, Wasatch and Wind River Formations, Wyoming, USA.
Last: Bunocerox Wortman, 1898, Mesomerex Peterson, 1919, Pentacemylus Peterson, 1931, and Mylonomeryx Gazin, 1955, all Uinta Formation, Utah, USA; Tapochoerus McKenna, 1958, Sespe Formation, California, USA.

F. HOPLITOMERYCIDAE Leinders, 1983
First and Last: Hoplitomeryx matthei Leinders, 1983, Gargano, Italy.

F. HYPERTRAGULIDAE Cope, 1879
First: Parvitragulus Emry, 1978, Devil's Graveyard and Capote Mountain Formations, Texas; Vieja Group, Texas; White River Formation, Wyoming, USA; Hypertragulus Cope, 1874, Prietos Formation, Mexico; Devil's Graveyard Formation, Texas, USA (Wilson, 1986); Mioneryx Matthew and Granger, 1925, Sevkul Beds, Asia.

F. LEPTOMERYCIDAE Zittel, 1893
First: Lophiomerex Pomel, 1854, Sevkul, Asia; Phaneromeryx Schlosser, 1886, Quercy, France.
Last: Pseudoceras Frick, 1937, Gracias Formation, Honduras; Round Mountain Quarry, New Mexico, USA (Webb and Perrigo, 1984).

F. MIXOTHERIIDAE Lydekker, 1883
First: Mixotherium Filhol, 1880, Les Badies, Spain; Quercy, France; Creechbarrow Limestone, England, UK.
Animals: Vertebrates

Fig. 41.6

Extant

F. OREODONTIDAE Leidy, 1869  
First: Aclistomycter Wilson, 1971, Devil’s Graveyard Formation, Texas, USA.  
Last: Ustatochoerus Schultz and Falkenbach, 1941, Snake Creek Formation, Nebraska, USA.  

F. OROMERYCIDAE Gazin, 1955  
First: Camelodon arapahovius Granger, 1910, Wagon Bed Formation, Wyoming, USA; Oromeryx Marsh, 1894, Uinta Formation, Utah, USA; Protolepos Wortman, 1888, Uinta Formation, Utah, USA; Mission Valley Formation, California, USA; Merycobunodon Golz, 1976, Friars Formation, California, USA.  
Last: Eotylopus Matthew, 1910, White River Formation, Wyoming, USA; Montanatylopus Prothero, 1986, Renova Formation, Montana; Rubio Peak Formation, New Mexico, USA (Lucas, 1986).

F. PALAEOMERYCIDAE Lydekker, 1883  
First: Palaeomeryx Meyer, 1834, Gebel Zelten, Libya; Artenay, France; Oromeryx Ginsburg, 1985, MN2, Saint-Gerard-le-Puy, France; Propalaeomeryx Lydekker, 1883, Nari Series, Baluchistan.  

F. PROTOCERATIDAE Marsh, 1891  
First: Leptoreodon Wortman, 1898, Uinta Formation, Utah; Friars Formation, California, USA (Golz and Lillegraven, 1977).  
Last: Kyptoceras amatorum Webb, 1981, Bone Valley Formation, Lower PLI, Florida, USA.

F. RAOELLIDAE Sahni et al., 1981  
T. (?YPR–LUT/BRT)  Terr.
**Order CETACEA** Brisson, 1762

**Suborder ARCHAEOCETI** Flower, 1883

**F. PROTOCETIDAE** Stromer, 1908


**First:** Pakicetus Gingerich and Russell, 1981, Gandakasia Deh and Oettingen-Spielberg, 1958, Ichthyolestes Dehm and Oettingen-Spielberg, 1958, all Kuldana Formation, Pakistan. These genera may be Lutetian in age and, as such, first occurrences would also include Indocetis Sahni and Mishra, 1975, Berwali Series, India; Protocetus Fraas, 1904, Mokattum Formation, Egypt; India; Pappocetus Andrews, 1920, Ameki Formation, Nigeria. **Last:** Ecetus Fraas, 1904, Birket-el-Qurum Formation, Egypt.

**F. BASILOSAURIDAE** Cope, 1868


**First:** Prozeuglodon Andrews, 1906, Wadi-Rayan, Egypt; Zygorhiza True, 1908, Creechbarrow Limestone, England, UK; Basilosaurus Harlan, 1834, Europe. **Last:** Basilosaurus Harlan, 1834, Barton Clay, England, UK; Zygorhiza True, 1908, Jackson Formation, Georgia; Harleyville Formation, South Carolina, USA; Barton Clay, England, UK; Dorudon Gibbes, 1845, Kaitaan, New Zealand; Qasr el Sagha, Egypt.

**Suborder ODONTOCETI** Flower, 1867

**F. REMINGTONOCETIDAE** Sahni and Sahni, 1986


**First and Last:** Andreosiphius Sahni and Mishra, 1975, Berwali Series, India (Russell and Zhai, 1987); Remingtonocetus Kumar and Sahni, 1986, India. **Last:** Ziphiiidae Gray, 1850 T. (BUR)–Rec. Mar.

**First:** Squalodelphis Dal Piaz, 1916, Belluno, Italy; Notocetus Moreno, 1892, Chubut, Argentina; Ziphiidae undet. Turkana Grit, Kenya (Barnes and Mitchell, 1978); Medocinia de Muizon, 1958, Girondo, France.

**F. PHYSETERIDAE** Gray, 1821


**First:** Miokogia Pilleri, 1886, and Physeter Linnaeus, 1758, both Europe; Orycterocetus Leidy, 1853, Pontigne and Pont Boutard, France; Diaphorocetus Ameghino, 1894, Chubut, Argentina; Scaldicetus Du Bus, 1867, Belluno, Italy. **Extant**

**F. SQUALODONTIDAE** Brandt, 1873


**First:** Patrioctetus Abel, 1913, Linz, Belgium; Microcetus Kellogg, 1923, Asia; Europe; New Zealand; Metasqualodon Hall, 1911, and Parasqualodon Hall, 1911, both Junjkalian, Australia; Kelloggia Mchedlidze, 1976, Azerbaijan, former USSR; Eosqualodon Rothauser, 1968, Europe; Agriocetus Abel, 1913, Linz, Belgium; Squalodon Grateloup, 1840, Jewett Sand, California, USA; Linz, Belgium; Ashiyu Formation, Japan; Duntronian, New Zealand. **Last:** Squalodon Grateloup, 1840, Europe.

**F. RHABDOSTEIDAE** Gill, 1871


**First:** Macrodelphinus Wilson, 1935, Jewett Sand, California, USA; Phocaenopsis Huxley, 1859, Blue Clay of...
Parimoa, New Zealand; Argyroctes Lydekker, 1894, Jewett Sand, California, USA; Chubut, Argentina.

**Last:** Ziphodelphis Dal Piaz, 1912, Belluno, Italy; Eurhinodelphis Du Bus, 1867, Antwerp, Belgium; Pontigné, France.

**First and Last:** Neophocaena Gervais, 1846 T. (LMI)–Rec. FW/Mar.  
**Extant**

**Last:** Proinia True, 1910, Patagonian, Argentina. Inüid also from Visiano, Italy.

**First:** Propliotes Zhou et al., 1979 T. (MIO)–Rec. FW.

**First:** Microphocaena Gray, 1848, Gironde, France; Schizodelphis Gervais, 1861, Italy; Moghara Formation, Egypt.  
**First:** Delphinodon Lacepede, 1804, Asia.

**Extant**

**First and Last:** Eoplatanista Gray, 1846 T. (UMI)–Rec. Mar.  
**Extant**

**Last:** Allophocaena Wilson, 1935, Pyramid Hill, California, USA.

**First:** Allodelphis Wilson, 1935, Pyramid Hill, California, USA.  
**Extant**

**First and Last:** Brachydelphis de Muizon, 1988, Cerro la Bruja, Peru.  
**Extant**

**First:** Kentriodon Kellogg, 1927, Litholithax Kellogg, 1931, and Delphinodon Leidy, 1869, all Calvert Formation, Maryland, USA; Leptodelphis Kirpichnikov, 1954, and Sarmatodelphis Kirpichnikov, 1954, both Sarmat, Moldavia, former USSR; Microphocaena Kudrin and Tatarinov, 1965, Ternopil, Ukraine, former USSR; Kampholophus Rensberger, 1969, Monterey Formation, California, USA; Atocetus de Muizon, 1988, Pisco Formation, Peru.  
**First:** Kentriodon Kellogg, 1927, Santa Margarita Formation, California, USA.  
**Extant**

**First and Last:** Alodelphis Abel, 1900, Europe; Schizodelphis Gervais, 1861, France.

**First:** Delphinapterus Lacepede, 1804, Asia.  
**Extant**

**First and Last:** Dalpiazinia de Muizon, 1988, Molasses de Bologne, Italy.

**First and Last:** Albireo barnesii, 1984 T. (UMI) Mar.  
**Extant**

**First and Last:** Hemisyntarchelus Brandt, 1873, Lower PLI, Italy.

**Extant**

**First and Last:** Hemisyntarchelus Brandt, 1873, Lower PLI, Italy.

**Comments:** An upper Miocene hemisyntarchelid is reported from California by Savage and Barnes (1972).

**First and Last:** Agorophiiidae Abel, 1913 T. (CHT) Mar.  
**Extant**

**First and Last:** Agorophius Cope, 1895, Ashley Marl, South Carolina, USA.

Suborder MYSTICETI Flower, 1864

**First and Last:** Aetiocetidae Emlong, 1966 T. (CHT) Mar.  
**Extant**

**First and Last:** Aetiocetus Emlong, 1966, North America.  
**Extant**

**First and Last:** Cetotheriidae Brandt, 1872 T. (CHT–PLI) Mar.  
**Extant**

**First:** Cetotheriopsis Brandt, 1871, Linz, Austria.

**Last:** Rhegnopsis Cope, 1896, City Point, Virginia, USA; Cephalotrops Cope, 1896, Yorktown Formation, Maryland, USA, both Upper PLI.

**First and Last:** Balaenopteridae Gray, 1864 T. (LMI)–Rec. Mar.  
**Extant**

**First:** Placodus Van Beneden, 1859, Rio Negro Forma­tion, Argentina; Europe.

**Last:** Balaenidae Gray, 1821 T. (LMI)–Rec. Mar.  
**Extant**

**First:** Morenocetus Cabrera, 1926, Patagonian, Argentina.  
**Extant**

**First and Last:** Eschrichtiidæ Ellerman and Morrison-Scott, 1951 Q. (PLE)–Rec. Mar.  
**Extant**

**First:** Eschrichtius Gray, 1864, Upper PLE, North America.

**Extant**

**First:** Miroorder MERIDIJUNGULATA McKenna, 1975

Order LITOPTERNA Ameghino, 1889

**First and Last:** Proterotheriidae Ameghino, 1887 T. (THA–PLI) Terr.  
**Extant**

**First:** Paraisolambo Cifelli, 1983, and Anisolambo Paula Couto, 1952, both Itaborai, Brazil.

**Last:** Brachytherium Ameghino, 1883, Chapadmalalan, Upper PLI, Argentina; Licþriphium Ameghino, 1887, San Jos£ Formation, Uruguay.

**First:** Macrauchenia Gill, 1864, Upper PLE, North America.

**Extant**

**First:** Macrauchenia Owen, 1838, Buenos Aires, Argentina; Bolivia; Uruguay; Brazil; Windhausenia Kraglievich, 1930, South America (Anderson, 1984); Xenorhineutherium Cartella and Lessa, 1988, Bahia, Brazil, all Upper PLE or Hol.

**First and Last:** Notonychopidae Soria, 1989 T. (THA) Terr.  
**Extant**

**First and Last:** Notonychops Soria, 1989, Rio Loro Formation, Riochican, Tucuman, Argentina.
Mammalia

F. ADIANTHIDAE Ameghino, 1891
T. (YPR–Mio.) Terr.


Last: Adianthus Ameghino, 1891, Santacrucian, Argentina.

F. DIDOLODONTIDAE Scott, 1913


Last: Megadolodus McKenna, 1956, La Venta, Columbia.

Order NOTOUNGULATA Roth, 1903
F. OLDFIELDTHOMASIDAE Simpson, 1945

First: Colbertia de Paula Couto, 1952, and Itaboraitherium Paula Couto, 1970, both from Itaborai, Brazil.

Last: Tsammichoria Simpson, 1936, Mustersan, Argentina.

Comments: Cifelli (1982) indicates that several taxa are known from the Divisadero Largo Formation, Argentina.

F. ISOTEMNIIDAE Ameghino, 1897

First: Isotemnus Ameghino, 1897, Rio Chico, Argentina.

Last: Trimerostephanos Ameghino, 1895, Pleurocoelodon Ameghino, 1895, Trigonolophodon Roth, 1903, and Lophocoeus Ameghino, 1904, all Deseadan, Argentina.

F. ARCHAEOPITHECIDAE Ameghino, 1897
T. (YPR) Terr.

First and Last: Archaeopithecus Ameghino, 1897, and Acrropithecus Ameghino, 1904, both Casamayoran, Argentina. According to Cifelli (1982), these taxa may be Riochican in age as well.

F. NOTOHIPPIDAE Ameghino, 1894

First: Eomorphippus Ameghino, 1901, Mustersan, Argentina.

Last: Notohippus Ameghino, 1891, Santacrucian, Brazil.

F. LEONTINIIDAE Ameghino, 1895
T. (CHT/LMI–MMI) Terr. (see Fig. 41.7)


Last: Huilatherium Villarroel and Guerro Diaz, 1985, La Venta, Columbia.

F. HOMALODOTHERIIIDAE Gregory, 1910

First: Asmodeus Ameghino, 1895, Deseadan, Argentina.

Last: Chasicothierium Cabrera and Kraglievich, 1931, Chasicoan, Argentina.

F. TOXODONTIDAE Gervais, 1847
T. (RUP/LMI)–Q. (PLE) Terr.

First: Proadinotherium Ameghino, 1895, Deseadan, Argentina; Posnanskytherium Lazarte, 1943, Bolivia.

Last: Mixotaxodon van Frank, 1957, Hormiguero, El Salvador; Yeroconte and Orillas del Humuya, Honduras; Toxodon Owen, 1840, Lujan Formation, Argentina; Arroio Touro Passo, Brazil (Pascual et al., 1966; Anderson, 1984), all Upper PLE.

F. INTEROTHERIIIDAE Ameghino, 1887

First: Transpithecus Ameghino, 1901, Rio Chico, Argentina.

Last: Protyotherium Ameghino, 1882, Chasicoan, Argentina.

F. CAMPANORCIDAE Bond et al., 1984
T. (Eoc.) Terr.

First and Last: Campanorca Bond et al., 1984, South America.

F. MESOTHERIIIDAE Alston, 1876

First: Trachytheriinae Ameghino, 1894, Divisadero Largo Formation, Argentina (Simpson et al., 1962). Cifelli (1982) suggests that mesotheriids are present in the Mustersan, Argentina.

Last: Mesotherium Serres, 1867, Deseadan, Argentina; ?Pulchenese (Lower PLE), Argentina (Pascual et al., 1966).

F. ARCHAEOHYRACIDAE Ameghino, 1897
T. (THA–C) Terr.

First: Eohyrax Ameghino, 1901, Rio Chico, Argentina.

Last: Archaeohyrax Ameghino, 1897, Deseadan, Argentina.

F. HEGETOTHERIIDAE Ameghino, 1894
T. (RUP)–Q. (PLE) Terr.

First: Ethegotherium Simpson et al., 1962, Divisadero Largo Formation, Argentina.

Last: Paedotherium Burmeister, 1888, Argentina.

F. HENRICOSBORNIIDAE Ameghino, 1901

First: Othnielmarshia Ameghino, 1901, Itaborai, Brazil.


F. NOTOSTYLOPIDAE Ameghino, 1897

First: Boresistylops Vucetich, 1980, Lumbrera Formation, Argentina; Edwardtrowessartia Ameghino, 1901, Homalostylops Ameghino, 1901, and Notostylops Ameghino, 1897, all Casamayoran, Argentina.

Last: Otronia Roth, 1901, Mustersan, Argentina.

Order ASTRAPOTHERIA Lydekker, 1894
F. TRIGONOSTYLOPIDAE Ameghino, 1901

First: Tetragonostypus de Paula Couto, 1963, Itaborai, Brazil.

Last: Trigonostylops Ameghino, 1897, Mustersan, Argentina (Soria and Bond, 1984).

F. ASTRAPOTHERIIDAE Ameghino, 1887


Last: Astrapotherium Burmeister, 1879, Santacrucian,
Argentina; *Monoeidodon* Roth, 1898, Rio Collon Cura, Argentina.


**First and Last**: *Eoastrapostylops* Soria and Powell, 1981, Rio Loro Formation, Argentina.

**Order** **CONDYLARTHRA** Cope, 1881

**F. PERIPTYCHIDAE** Cope, 1882  K. (MAA)—T. (YPR) Terr.

**First**: *Mimatuta* Van Valen, 1978, Hell Creek Formation, Montana, USA.

**Last**: *Lessnessina* Hooker, 1979, MP8+9, Blackheath Beds, England, UK.

**F. PHENACODONTIDAE** Cope, 1881  T. (THA—LUT/BRT) Terr.

**First**: *Tetaclaenodon* Scott, 1892, Nacimiento Formation, New Mexico; Goler Formation, California, USA.

**Last**: *Phenacodus* Cope, 1873, Wagon Bed and Bridger Formations, Wyoming, USA.

**Comments**: Most recent review by Thewessin (1990).

**F. MIOCLAENIDAE** Osborn and Earle, 1895  T. (DAN—THA) Terr.

**First**: *Bubogonia* Johnson, 1984, Ravenscrag Formation, Saskatchewan, Canada; *Tiznatzinia* Simpson, 1936, North America; *Choeroclaenus* Simpson, 1937, and *Promioclaenus* Trouessart, 1904, both from Nacimiento Formation, New Mexico, USA; *Tiucaleni* de Muizon and Marshall, 1987, and *Molinodus* de Muizon and Marshall, 1987, both El Molino Formation, Bolivia. Also possibly Lower Palaeocene: *Palasiodon* Tong et al., 1976, Shang-hu Formation, Kwantung, China.

**Last**: *Orthaspidotherium* Lemoine, 1885, and *Pleuraspidotherium* Lemoine, 1878, both MP6, Cernay, France; *?Protozene* Matthew, 1897, Blacks Peak Formation, Texas, Togwotee, Wyoming, USA.

**Order** PYOTHERIA Ameghino, 1895

F. PYOTHERIIDAE Ameghino, 1889

First: Proticia Patterson, 1977, north-west Venezuela; Propyrotherium Ameghino, 1901, Mustersan, Argentina.

Last: Pyrotherium Ameghino, 1888, Deseadan, Argentina.

**Order** XENUNGULATA Paula Couto, 1952

F. CARODNIIDAE Paula Couto, 1952
T. (THA) Terr.

First: Carodnia Simpson, 1935, Itaborai, Brazil.  

**Order** DINOCERATA Marsh, 1873

F. UINTATHERIIDAE Flower, 1876
T. (THA–LUT) Terr.

First: Prodinoceras Matthew et al., 1929, Gashato Formation, Mongolia; Polecat Bench Formation, Wyoming, USA.  
Last: Tetheopsis Cope, 1885, Washakie Formation, Wyoming, USA; Uintatherium Leidy, 1872, Uinta Formation, Utah, USA; Ebobsileus Cope, 1872, Washakie Formation, Wyoming and Colorado, USA; Uinta Formation, Utah, USA; Gobiatherium Osborn and Granger, 1932, Irdin Manha Formation, Mongolia.

**Order** MERIDIUNGULATA incertae sedis

F. AMILNEDWARIIDAE Soria, 1984

Last: Acanama Simpson et al., 1962, Divisadero Largo, Argentina.

**Miroder** TETHYHERIA McKenna, 1975

**Order** PROBOSCIDEA Illiger, 1811

Tassy (1990) and Domning et al. (1986) provide information on the relationships among proboscideans. Sirens and desmostylians.

F. PALAEMASTODONTIDAE Andrews, 1906
T. (PRB)–Q. (PLE) Terr.

First: Phiomia Andres and Beadnell, 1902, Jebel Qatari Formation, Egypt; Palaemastodon Andrews, 1901, Dor el Talha, Libya, Qasr el Sagha and Jebel Qatari Formations, Egypt.

Last: Cuvierius Osborn, 1923, Upper PLE, North and Central America; Chile.

F. MAMMUTIDAE Hay, 1922
T. (LMI)–Q. (PLE) Terr.

First: Zygodon Vacek, 1877, Djilancik, Kazakhstan, former USSR; Europe; Mammut Blumenbach, 1799, Lower Miocene, Africa and Europe.

Last: Mammut Blumenbach, 1799, Upper Pleistocene, North America.

F. AMEBELODONTIDAE Barbour, 1927

First: Archaeobelodon Tassy, 1984, Africa and Europe; Platytbelodon Borissiak, 1928, Loperot, Kenya.  

F. STEGODONTIDAE Osborn, 1918
T. (MMI)–Q. (PLE) Terr.

First: Stegolophon Schlesinger, 1917, India.

Last: Stegodon Falconer, 1857, Upper PLE, India; Sulawesi; Timor; Flores (Anderson, 1984).

F. ELEPHANTIDAE Gray, 1821
T. (UMI)–Rec. Terr.

First: Primelephas Maglio, 1970, and Stegotetralodon Petrocchi, 1941, both North and East Africa. Extant

F. ANTHRACOBUNIDAE Wells and Gingerich, 1983

First and Last: Anthracobunia Pilgrim, 1940, Asia; Iathamtherium Sahni and Kumar, 1960, Subath Formation, India; Lammidhania Gingerich, 1977, Kuldana Formation, Pakistan.

Comments: Minchenella Zhang, 1980 from the Upper Paleocene Nonshan Formation, Gungdang, China may be included here (Domning et al., 1986).

F. MOERITHERIIDAE Andrews, 1906
T. (PRB) Terr.

First and Last: Moeritherium Andrews, 1901, Qasr el Sagha, Egypt; Libya; In Tafidet, Gao, Mali; M’Bodione Dadera, Senegal.

F. BARYTHEROIDEA Andrews, 1906
T. (PRB) Terr.

First and Last: Barytherium Andrews, 1901, Qasr el Sagha and Dor el Talha, Egypt.

F. DEINOTHERIIDAE Bonaparte, 1845
T. (BUR)–Q. (PLE) Terr.

First: Prodeinotherium Ehik, 1930, Kuronga Beds, Kenya, Asia, Europe; Deinotherium Kaup, 1835, Asia.


**Order** DESMOSYLIA Reinhart, 1953 (Fig. 41.7)

F. DESMOSYLIDAE Osborn, 1905
T. (CHT–UMI) Terr.

First: Cornwallius Hay, 1923, Sooke Formation, British Columbia, Canada; Behemotops Domning et al., 1986, Japan; Psyht Formation, Washington, USA.

Last: Paleoparadoxia Reinhart, 1959, Santa Margarita Formation, California, USA; Asia.

UNGULATA incertae sedis

F. PERUTHERIIDAE Van Valen, 1978
K. (MAA) Terr.

First and Last: Peruterium Thaler, 1967, Vilquechico, Peru.

**Order** PERISSODACTYLA Owen, 1848

See articles in Prothero and Schoch (1989) for data on Perissodactyla and alternative classifications.

**Mammalia** 765
F. EQUIDAE Gray, 1821
T. (YPR)–Rec. Terr.

First: Hyracotherium Owen, 1840, MP7, Pourcy, France; Willwood Formation, Wyoming, USA; Baja California, Mexico. Extant

F. CHALICOTHERIIDAE Gill, 1872
T. (YPR)–Q. (PLE) Terr.


Last: Nestoritherium Kaup, 1859, Sangiran, Java (Hooijer, 1964); Ancylotherium Gaudry, 1863, Olduvai, Kenya; Makapansgat, South Africa (Anderson, 1984), Lower or ?Middle PLE.

F. BRONTOTHERIIDAE Marsh, 1873
T. (??YPR/LUT)–PRB/RUP) Terr.


Last: Brontotheriidae, indet., White River Formation, Wyoming, USA; Pygmaetitan Miao, 1982, Shinao Formation, China; Embolotherium Osborn, 1929, Houldjinn Formation, Inner Mongolia, China; Titanodectes Granger and Gregory, 1943, Ulun Gochu, Shara Murun, Urtyn Obo, Mongolia.

Comments: The last brontotherium from North America may be either Upper Eocene or Lower Oligocene in age. A skeleton is known from the Brule Member of the White River Formation, a unit that is considered to be early Oligocene in age. A skeleton was found above Ash 5 in the Douglass area, Wyoming, USA, which has a date of 33.7 Ma (Evanoff, 1990).

F. ISECTOLOPHIDAE Peterson, 1919

First: Homogalax Hay, 1899, Wu-tu Formation, Shantung, China; Willwood Formation, Wyoming, USA.

Last: Isectolophus Scott and Osborn, 1887, Uinta Formation, Utah, USA.

F. HELALETIDAE Osborn, 1892

First: Heptodon Cope, 1882, Wu-tu Formation, Shantung, China; Willwood Formation, Wyoming, USA; Wind River Formation, Wyoming; San José Formation, New Mexico, USA; Cymbalophus Hooker, 1984, MP7, Suffolk Pebble Beds, England, UK; MP7, Palette, France; ?Asia (Hooker, 1984).

Last: Colodon Marsh, 1890, Renova Formation, Montana; White River Formation, Wyoming, USA.

F. LOPHIODONTIDAE Gill, 1872

First: Lophiodon Cuvier, 1822, MP7, Epernay, France.

Last: Lophiodon Cuvier, 1822, MP16, Hengistbury, England, UK.

F. TAPIRIDAE Gray, 1825
T. (RUP)–Rec. Terr. (Fig. 41.8)

First: Protapirus Filhol, 1877, Quercy, France; MP21, Mohren, Germany (Heissig, 1987); ?Aral Svita, Kazakhstan, former USSR (Russell and Zhai, 1987).

F. LOPHIALETIDAE Matthew and Granger, 1925

First: Parabreviodon Reshetov, 1975, Mongolia; Kalakotia Ranga Rao, 1972, Kalakot, India; Sabutha, India; Eoletes Biryukov, 1974, Kolpak Svita, Kazakhstan, former USSR (Russell and Zhai, 1987); Breviodon Radinsky, 1965, Mongolia; Schlosseria Matthew and Granger, 1926, Arshanto Formation, Inner Mongolia, China.

Last: Simplaletes Qi, 1980, Bailuyuan, China (Wang, 1992); Breviodon Radinsky, 1965, Mongolia; Schlosseria Matthew and Granger, 1926, Mongolia.

F. DEPERETELLIDAE Radinsky, 1965

First: Pachylophus Tong and Lei, 1984, Hetaoyuan Formation, Henan, China; Teleolophus Matthew and Granger, 1925, Arshanto Formation, Inner Mongolia, China.

Last: Teleolophus Matthew and Granger, 1925, Ergilin Dzo Formation, Mongolia; Chaganbulage, China (Dashzeveg, 1992; Wang, 1992); Haigel Heissig, 1978, MP21, Mohren, Germany.

F. HYRACODONTIDAE Cope, 1879

First: Hyracychus Leidy, 1871, Wind River Formation, Wyoming; Huerfano Formation, Colorado, USA; MP10, Grauves, France; Yimengia Wang, 1988, and Rhodopagus Radinsky, 1965, from Guan-zhuang Formation, Shantung, China; Forstecoperia Wood, 1939, Arshanto Formation, Inner Mongolia, China.

Last: Peracreratherium Forster Cooper, 1911, Agispe-Petrovskoa, former USSR.

F. RHINOCEROTIDAE Gray, 1825
T. (LUT/BRT)–Rec. Terr.

First: Amynodon Marsh, 1877, and Epitriplopus Wood, 1927, both Uinta Formation, Utah, USA; Prohyracodon Koch, 1897, Europe; Euryodon Xu et al., 1979, Da-cang-fang Formation, Honan, China; Lushiamynodon Chow and Xu, 1965, Lushi Formation, Honan, China.

F. PALAEOTHERIIDAE Bonaparte, 1850

First: Propachynolophus Lemoine, 1891, MP10, Grauves, France.

Last: Palaeotherium Cuvier, 1804, MP 21, Soumaine, France; Bembridge Marl, England, UK; Plagiolophus Lemoine, 1891, MP 22, Villebramar, France; Bembridge Marl, England, UK.

Order TUBULIDENTATA Huxley, 1872

F. ORYCTEROPODIDAE Gray, 1821
T. (RUP)–Rec. Terr.

First: Leptomanis Filhol, 1893, Quercy, France (Thewissen, 1985).

Order HYRACOIDEA Huxley, 1869, new rank, McKenna, this volume

Rasmussen (1989) has most recently revised the hyracoids.

F. PLOHYRACIDAE Osborn, 1899
Fig. 41.8

First: ?Lower Eocene: *Titanohyrax* Matsumoto, 1921, Gour Lazib, Algeria.

Last: *Postchizotherium* von Koenigswald, 1932, Lower PLE, Choukoutien, China.

**F. PROCAVIIDAE** Thomas, 1892


First: A procaviid is known from the Upper Miocene of Nakali, Kenya; *Prohyrax* Stromer, 1926, may be a procaviid (Rasmussen, 1989).

**Order** **EMBRITHOPODA** Andrews, 1906


First and Last: *Phenacolophus* Matthew and Granger, 1925, Kashat Svita, Mongolia; *Phenacolophidae, gen. et sp. nov.,* Nung-shan Formation, Kwantung, China.

**EPITHERIA incertae sedis**

**Order** **SIRENIA** Illiger, 1811

F. **DUGONGIDAE** Gray, 1821

T. (LUT/BRT)–Rec. FW

First: *Eotheroides* Palmer, 1899, Mokattam Beds and Qasr el Sagha, Egypt; *Protosiren* Abel, 1904, Mokattam Beds, Egypt; Blaye Limestone, France; Asia (Butler et al., 1967); *Prorastomus* Owen, 1855, Yellow Limestone Group, Jamaica (Butler et al., 1967).

**Extant**
F. TRICHECHIDAE Gray, 1825
T. (LMI)–Rec. FW
Extant

THERIA incertae sedis
F. AEGIALODONTIDAE Kermack et al., 1968
First and Last: Aegialodon Kermack et al., 1965, Cliff End, England, UK; Asia.

F. ENDOTHERHERIAE Slaughter, 1965
K. (ALB) Terr.
First and Last: Endotherium Slaughter, 1964, Fuhshin Coal Field, Liaoning, China.

F. PAPPOTHEREIDAE Slaughter, 1965
K. (ALB) Terr.

F. PICOPSIDAE Fox, 1980
K. (CMP) Terr.
First and Last: Picopsis Fox, 1980, Milk River Formation, Alberta, Canada.

F. DELTATHERIIDAE Gregory and Simpson, 1926
First: Sulistes Nesov, 1985, Uzbekistan, former USSR.
Last: Deltatheridium Gregory and Simpson, 1926, Djadohkha Formation, Mongolia.

F. KERMACKIIDAE Butler, 1978
K. (ALB) Terr.
First and Last: Kermackia Slaughter, 1971, and Trinititherium Butler, 1978, both Trinity Sands, Texas, USA.

F. NECROLESTIDAE Ameghino, 1894
K. (T. M.MI) Terr.
First and Last: Necrolestes Ameghino, 1891, Santacruzan, Argentina.

F. PERAMURIDAE Kretzoi, 1946
Last: Argimus Dashzeveg, 1979, Asia.

F. HOLOCLEMENSIDAE Aplin and Archer, 1987
K. (ALB) Terr.
First and Last: Holocomensia Slaughter, 1968, Paluxy Formation, Texas, USA.

MAMMALIA incertae sedis
F. TINODONTIDAE Marsh, 1887
(including Kuehneotheriidae)
Tr. (NOR)–K. (CMP) Terr.
First: Kuehneotherium Kermack et al., 1968, Bridgend, South Wales, UK.
Last: Mictodon Fox, 1984, Milk River Formation, Alberta, Canada; Bondesius Bonaparte, 1990, El Molino Formation, Argentina.

F. BONDESIIDAE Bonaparte, 1990
K. (CMP) Terr.
First and Last: Bondesius Bonaparte, 1990, Los Alamitos Formation, Argentina.

Order DOCODONTA Kretzoi, 1946
F. DOCODONTIDAE Simpson, 1947
J. (BTH–KIM) Terr.
Last: Haladanodon Kühne and Krusat, 1972, Guimarota, Portugal; Docodon Marsh, 1881, Morrison Formation, Colorado and Wyoming, USA.

REFERENCES


Cooksonia pertoni Lang. 1937, branching axis and terminal sporangia, from the Cloncannon Formation (Gleedon, Wenlock, Middle Silurian) of County Tipperary, Ireland. The oldest vascular plant. The whole specimen is about 700 μm long. Photograph courtesy of D. E. Edwards.
BRYOPHYTA

D. Edwards

‘Mosses and liverworts have long challenged taxonomists to devise a classification which will be at once reasonably natural and clearly workable’ (Watson, 1964, p. 13). Challenges imposed by their exceedingly inadequate fossil record seem even more insuperable because of the lack of critical information relating to anatomy, sexual reproductive characters or sporophytes. Such uncertainties are reflected in the large numbers of fossils called Muscites, Thallites and Hepaticites in the Palaeozoic and Mesozoic, and also in this analysis, where records during these times are possible only at the ordinal level for hepatics and at subclass level for mosses.

In contrast, the vast majority of bryophytes, particularly mosses, recorded from post-Palaeogene sediments are assigned to extant taxa, and thus to families. In that estimates of moss families range from the forties to over eighty (e.g. Crosby and Magill, 1977), and records in the Neogene (e.g. Miller, 1984) and Quaternary (see Dickson, 1973) are very extensive, treatment at the family level has not been attempted here. This compilation relies heavily on reviews published in Manual of Bryology (1984) by Krassilov and Schuster for the Palaeozoic and Mesozoic, and Miller for the Tertiary.

Kingdom PLANTAE

Division BRYOPHYTA Schimper, 1879

Class HEPATICOPSIDA Rothmaler, 1951

Of the generally accepted major hepatic orders, fossil records are lacking for the Takakiales, Calobryales and Monocleales (Schuster, 1981). The taxonomic position of the Lower Devonian Sporogonites remains uncertain. Hepatic assignment is based on unbranched axes apparently attached to a thalloid gametophyte (Andrews, 1960). Three-dimensional anatomy – essential for the elimination of the possibility of vascular status – has not yet been recorded. Schuster (1966) placed it in its own order, the Sporogonitales. If indeed a hepatic, it would be the oldest representative of the group.

Order METZGERIALES Schuster, ex Schljakov D. (FRS)—Rec. Terr. (Fig. 42.1)

First: Pallavicinites devonicus (Hueber) Schuster, 1966, New York State, USA.

Extant Comments: Schuster (1966) related this taxon to the extant Pallaviciniaceae with closest similarities to Pallavicinia and Symphyogynia. New combinations for Lower Carboniferous taxa, namely Blastites lobatus (Walton) Schuster, 1966, Treubites kidstonii (Walton) Schuster, 1966 and Metzgeriothallus metzgeroides (Walton) Schuster, 1966 are considered representatives of three further families within the Metzgeriales (Krassilov and Schuster, 1984), but these were not named. The Metzgeriales is the only order thought with any confidence to be represented in the Palaeozoic. Earliest fossil assignable to a family is Riccardia palmata (Aneuraceae) from Tertiary amber (Jovet-Ast, 1967).

Order MARCHANTIALES Engler, 1892

Tr. (?CRN)—Rec. Terr.


Extant Comments: Krassilov and Schuster (1984) found no evidence for this group in the Palaeozoic, but document a number of genera from the Triassic into the Eocene. Most are called Marchantites or Thallites. See also list in Schuster (1966) and Jovet-Ast (1967). The earliest record of Marchantia itself is M. lignitica (Ward) Brown, 1962 from the Palaeocene, Fort Union Formation, Yellowstone River, USA.

Order JUNGERMANNIALES Halle, 1913

T. (PRB)—Rec. Terr.

First: Schizolepidella gracilis Halle, 1913, Graham Land, Antarctica.

Extant Comment: A most remarkable Upper Eocene assemblage of Jungermanniales preserved in Baltic amber has been revised recently by Grolle (1980a,b, 1981a,b). It contains the first records of the families Jungermanniaceae (s.s.), Cephalozziellaceae, Lepidoziaceae, Radulaceae, Frullaniaceae and Lejeuneaceae. Most of the representatives are assigned to modern genera. It seems likely that they grew as epiphytes on the trees producing the amber.

Order SPHAEROCARPALES Cavers, 1910

Tr. (RHT)—Rec. Terr.

First: Naiadita lanceolata Buckman, 1850 emend. Harris 1938 (Harris, 1939), Cotham Beds, Avon, England, UK.

Comment: Sporophytic characters place this species in
the Sphaerocarpales, although its gametophyte being erect, radial and isophyllous is calobryalean (see discussion in Krassilov and Schuster, 1984). There are no Cainozoic representatives (Miller, 1984).

**Class** ANTHOCEROTOPSIDA Rothmaler, 1951

**Order** ANTHOCEROTALES Muller, 1940

First: *Phaeoceros* Jarzen (1979: spore forms A–C) Frenchman Formation, Saskatchewan, Canada; Selma Group, Alabama, USA.  
Comment: Earliest records are based on spores (Jarzen, 1979). The first sporophytes are reported (as petrifactions) in the uppermost Cretaceous or Palaeocene Deccan Intratrapan beds of Mahgaonkalan, India (Chitaley and Yawale, 1980).

**Class** BRYOPSIDA Rothmaler, 1951

Unequivocal mosses occur in the Carboniferous, but are not reliably assigned to higher taxa. The earliest is *Muscites plumatus* from the Lower Carboniferous of southern England, tentatively compared with *Grimmia* by Thomas (1972). Upper Carboniferous records include *M. polytrichaceus* Renault and Zeiller and *M. bertrandii* Lignier. Of the five extant subclasses, the Buxbaumiidae has no known fossils.

**Subclass** Sphagnidae Engler et al., 1954

Comment: Neuberg (1956) placed these three genera in a new order, the Protosphagnales, but Krassilov and Schuster (1984) believe that these and the nine genera that she assigned to the Bryales, constitute a single natural group with some similarities to the Isobryales. Ignatov (1990) discussed the relationships of the three protosphagnaleans to each other and to the Sphagnales, and in erecting a new genus *Palaeosphagnum* from Upper Permian strata of the Russian Platform with closest affinity to *Vorcutannularia*, he was convinced of the existence of the
extant order at the end of the Palaeozoic, although he excluded Neuberg's *Protosphagnum* and *Junjagia*. Although there is a record of Sphagnales in the Lower Jurassic of Bavaria (Reissinger, 1950), Miller (1984) does not consider the Sphagnidae to be represented in pre-Cainozoic rocks, and so *Sphagnum?* from a Lower Tertiary/Palaeogene lignite in northern Ellesmere Island becomes the earliest undisputed record of the group.

**Subclass BRYIDAE** Engler et al., 1954


**Comment:** *Muscites plumatus* Thomas (Lower Carboniferous) and *M. bertrandii* (Upper Carboniferous) Lignier are probable Palaeozoic representatives, but cannot be assigned to higher taxa. As mentioned above, most of Neuberg's genera from the Lower Permian and Upper Permian of the Kuznetsk, Pechora and Tunguska Basins, former USSR, may belong here (see *The Fossil Record*, 1967), but although they resemble Mniaceae in certain respects, they show a unique mode of leaf attachment. Ignatov (1990) described nine new taxa from the Upper Permian (upper TAT) Viatsky Suite from the Vologda Province in the northern part of the Russian Platform. On the basis of cell shape and dimensions, on leaf margin characters and on the structure of costa, he compared the fragmentary vegetative fossils with extant genera and families, and in conclusion considered that they included representatives of the extant orders Dicranales, Pottiales, Funariales, Leucodontales and Hypnales. A possible Mesozoic record of this very large subclass is *M. guescelini* Townrow (1959)

![Table Image](image-url)
from the Middle Triassic of Natal, South Africa, thought to be close to the Leucodontaceae (Isobryales). The oldest specimens to be assigned to extant taxa, and hence with confidence to families, are species of Calliergon and Drepanoclados (Amblystegiaceae in the Hypnobryales) from a Lower Tertiary (Palaeogene) lignite on northern Ellesmere Island, Arctic Canada (Kuc, 1973). Most Palaeogene fossils, although clearly belonging to the Bryidae are too badly preserved or incomplete for more precise placement and are named under form genera. In contrast the great majority in Europe and North America are assigned to extant genera. A comprehensive survey is given in Miller (1984).

**Subclass ANDREAEIDAE** Engler et al., 1954
Q. (PLE)-Rec. Terr.
First: Andreaea rothii Weber and Mohr, Riss glacial deposit, Zamszany Poland (Szafran, 1952). Extant

**Subclass POLYTRICHIDAE** Engler et al., 1954
T. (PRB)-Rec. Terr.
First: Polytrichum subseptentrionale Goeppert 1853, Pogonatum suburnigerum (Goeppert and Menge) Dixon, 1927, Catharinea subundulata (Goeppert) Dixon, 1927. Upper Eocene/Early Baltic amber. Comment: The Tertiary record is particularly poor and most records (e.g. Polytrichites) are doubtful, because they are based on few or no structural details. There is no compelling evidence that Upper Carboniferous Muscites polytrichaceus Renault and Zeiller belongs to this subclass.

**REFERENCES**


Harris, T. M. (1939) Naiadita, a fossil bryophyte with reproductive organs. *Annals of Bryology, 12*, 57–70.


In this analysis, I take the Pteridophyta to include all vascular plants which do not bear seeds. It has been argued that the pteridophytes are polyphyletic, but the consensus now seems to be that they probably originated from a single algal ancestor (Stewart, 1983). It is quite clearly a paraphyletic group, however, since the gymnosperms and angiosperms are an offshoot of one of its classes, probably the Progymnospermopsida.

The main pteridophyte classes have become essentially standardized in recent years (Lycopsida, Equisetopsida, Filicopsida and Progymnospermopsida). Details of the palaeontology of these classes can be found in the standard palaeobotany textbooks (Taylor, 1981; Stewart, 1983; Meyen, 1987; Thomas and Spicer, 1987).

The position with the earliest pteridophytes is less stable. At the time of publication of the first edition of The Fossil Record, they were divided into three families of one class, the Psilophytopsida. Banks (1968, 1975) subsequently proposed to raise these families in rank to subdivisions (Rhyniophytina, Zosterophyllophytina, Trimerophytina). Recent work, including critical anatomical investigations, has confirmed the validity of the Zosterophyllphytina, but the limits and content of the Rhyniophytina and Trimerophytina require re-evaluation. Also, new higher taxa need to be erected for plant fossils that have been found to have novel combinations of characters, such as Aglaophyton major (Kidston and Gwynne-Vaughan) D. S. Edwards, 1986, which has a rhyniophyte morphology but moss-like conducting tissues. As far as possible, I have attempted to use Banks' classification, except that I do not use the subdivisional taxa.

There is no recent Treatise-like analysis of the fossil record of plants and it has thus been impossible to use the so-called ‘hierarchical’ approach adopted elsewhere in this volume. This explains what may seem an excessively long list of references given at the end of this chapter. The protologue of a particular taxon is only referenced at the end when the types are the oldest and/or youngest known specimens for the family. In the Zosterophyllaceae, for instance, the reference to Z. myretonianum Penhallow, 1892, is not listed, as the oldest specimens were described by Edwards (1975), while that to S. ornata Hueber, 1971, is given as the types include the youngest known specimens.

Acknowledgements – Thanks go to Josephine Camus (Natural History Museum, London) for advice on fern taxonomic nomenclature, and to Richard Bateman (Smithsonian Institution) for providing unpublished data. I am also grateful to Dianne Edwards (University of Wales, Cardiff), Barry Thomas (National Museum of Wales), Judy Skog (George Mason University, Virginia) and Chris Hill (Natural History Museum, London) for reading early drafts of the manuscript.

Class RHYNIOPSIDA Banks, 1975 (see Fig. 43.1)

Lack of information of xylem from the oldest (Cooksonia) and more complex presumed members (e.g. Renalia hueberi) hampers delineation of this class (Edwards and Edwards, 1986). Most important from an evolutionary standpoint are the small, isomorphously branching forms (e.g. Pertonella, Salopella), usually considered to be the earliest ‘higher’ (i.e. pteridophytic) plants, but in which xylem has not yet been demonstrated. Edwards and Edwards (1986) have used the term ‘rhyniophytoid’ for such fossils and, although it is clearly not a formal taxon, is included in the following analysis.


Last: Taeniocrada lesquereuxii White, 1903, Chemung Formation, Pennsylvania, USA.

Intervening: LDF–EMS.

**Class** ZOSTEROPHYLLOPSIDA Banks, 1975

**Order** ZOSTEROPHYLLALES Banks, 1975

- **F. ZOSTEROPHYLLACEAE** Krause, 1938
  - **D. (LOK-FRS) Terr.**
    - **First:** Zosterophyllum myretonianum Penhallow, 1892, Dundee Formation, Tayside Region, Scotland, UK (Edwards, 1975).
    - **Last:** Sawdonia ornata Hueber, 1971, Onteora Formation, New York, USA.
    - **Intervening:** PRA–EIF.
    - **Comments:** Tims and Chambers (1984) record putative zosterophylls from the LDF? of Victoria, Australia, but they have not yet been described.

Niklas and Banks (1990) emphasize two distinct growth patterns in the fertile axes of the Zosterophyllales, exemplified by Zosterophyllum and Gosslingia. This is probably evidence that two families exist in the order. However, this taxonomic distinction has yet to be established formally.

**F. ZOSTEROPHYLLACEAE** Kräusel, 1938

- **D. (LOK–EMS) Terr.**
  - **First:** Cooksonia pertoni Lang, Ditton Series (micronatus–newportensis) spore biozone), Welsh Borderland, Shropshire, England, UK (Edwards, Davies and Axe, 1992). Older specimens of Cooksonia have not been demonstrated as vascular and hence are included in the rhyniophytoids.
  - **Last:** Hsia robusta Li, 1982, Xujiachong Formation, Yunnan, China.
  - **Comments:** Salopella australis and Hedeia sp. from the LDF? of Victoria, Australia (Tims and Chambers, 1984) may also belong here, but are preserved as impressions showing no evidence of vascular tissue.

**Class** HORNEOPHYTOPSIDA Němejc, 1960

**Order** HORNEOPHYTALES Němejc, 1960

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**Fig. 43.1**

Order RHYNIALES Banks, 1975

F. RHYNIACEAE Kidston and Lang, 1920

D. (LOK–EMS) Terr.

- **First:** Cooksonia pertoni Lang, Ditton Series (micrnatus–newportensis) spore biozone), Welsh Borderland, Shropshire, England, UK (Edwards, Davies and Axe, 1992). Older specimens of Cooksonia have not been demonstrated as vascular and hence are included in the rhyniophytoids.
  - **Last:** Hsia robusta Li, 1982, Xujiachong Formation, Yunnan, China.
  - **Comments:** Salopella australis and Hedeia sp. from the LDF? of Victoria, Australia (Tims and Chambers, 1984) may also belong here, but are preserved as impressions showing no evidence of vascular tissue.
F. HORNEOPHYTACEAE Němejc, 1960
D. (PRA) Terr.

First and Last: Horneophyton lignieri (Kidston and Lang) Barghoorn and Darrah, 1938, Rhynie Chert, Grampian Region, Scotland, UK (El-Saadawy and Lacey, 1979).

Class TRIMEROPHYTOPSIDA Banks, 1975

Order TRIMEROPHYTALES Banks, 1975
F. TRIMEROPHYTACEAE Banks, 1975

First: ?Dawsonites sp., Senni Beds, Powys, Wales, UK (Croft and Lang, 1942). These are fragments of trusses of sporangia, clearly belonging to Psilophyton, but with insufficient characters to assign it to a species. The next oldest, Psilophyton burnotense (=?P. goldschmidtii) is of controversial affinity. The oldest recognized species are Psilophyton forbesii, P. crenulatum and P. princeps from the basal EMS of Belgium (Gerrienne, 1983) and Canada (Gensel and Andrews, 1984).


Intervening: PRA–EMS.

INCERTAE SEDIS

Order BARINOPHYTALES Høeg, 1967
F. BARINOPHYTACEAE Høeg, 1967
D. (PRA)–C. (IVO) Terr.
The classification is based on Thomas and Brack-Hanes (1984), in which only fertile material is definitely included in families. However, mention is also made of isolated sterile specimens (e.g. stems) which may extend the range of particular families (e.g. Lepidodendron for the Flemingitaceae).

**Order DREPANOPHYCALES** Pichi-Sermolli, 1958


Last: Drepanophyceus spineiformis Göppert, 1850, New York State, USA (Stubblefield and Banks, 1978). This is based on sterile axes. The youngest fertile specimens are D. spineiformis from the EMS of the Rhineland, Germany (Kräusel and Weyland, 1930).

Intervening: LOK, PRA, GIV?

Comments: Rayner (1984) places this family in a separate class (Drepanophycopsida), but we have here followed the traditional view and retained it within the lycopsids.

**Order PROTOLEPIDODENDRALES** Pichi-Sermolli, 1958


Last: Brasiliodendron pedraumum Chaloner et al., 1979, Itararé Formation, Paraná Basin, Brazil.

Intervening: EMS–CHD, KSK–ASS?

Comments: In the palæo-equatorial regions, the family is restricted to the Devonian and Lower Carboniferous, but in southern palæolatitudes it extends up into the Permian. Sterile stems occur as high as KAZ? (Lemoigne and Brown, 1980).


First: Eleutherophyllum waldenburgense (Stur) Zimmermann, 1930, Wąbrzych (formerly Waldenburg) Beds, Lower Silesia, Poland.

Last: Eleutherophyllum hamatum Josten, 1983, Hagener Formation, Ruhr, Germany.

**Order LYCOPODIALES** Potonié, 1899

Skog (1986) has recently proposed a new lycopodiaceous family, the Tanydoraceae, based on the Cretaceous Onychiopsis psilotoides (Stokes and Webb) Ward, 1905, traditionally regarded as fern foliage (e.g. Watson, 1969). However, structurally preserved specimens of the latter species described by Fris and Pedersen (1990) have confirmed that it is a fern, probably of the Dicksoniaceae.

F. LYCOPODIACEAE Mirbel, 1802 D. (EIF)–Rec. Terr.

First: Lycopodites oosensis Kräusel and Weyland, 1937, Ooser Plattenkalk, Eifel, Germany.

Intervening: HLK, POD–MYA, RHT–BER.

Comments: Much of the quoted intervening range is based on sterile axes.

F. CYCLOSTIGMACEAE Thomas and Brack-Hanes, 1984


Last: Cyclostigma major (Germar) Brack-Hanes and Thomas, 1983, Blanzy, France (Zeiller, 1906).

Intervening: CHD–KRE.

Comments: This corresponds to the Lepidodendraceae of many authors, and occurs most commonly in the Namurian and Westphalian (KIN–MYA). Records of Lepidodendron stems range up to the Upper Permian in China (e.g. Zhao et al., 1980), but they lack fertile structures.


Intervening: CHD–KRE.

Comments: This family is clearly a natural taxon, which also includes Pectinophyton, Protobarinophyton and Barinos­ trobus. It appears to fall broadly within the concept of the Pteridophyta, as used here. However, it does not appear to be closely related to any of the other pteridophyte classes referred to in this chapter (Brauer, 1981).

F. LEPIDOCARPALES Thomas and Brack-Hanes, 1984

First: Lepidocarpon scoticum Long, 1968a, Cementstone Group, Borders Region, Scotland, UK.

Last: Lepidocarpon scoticum Long, 1968a, Cementstone Group, Borders Region, Scotland, UK.

Comments: This family is clearly a natural taxon, which also includes Pectinophyton, Protobarinophyton and Barinos­ trobus. It appears to fall broadly within the concept of the Pteridophyta, as used here. However, it does not appear to be closely related to any of the other pteridophyte classes referred to in this chapter (Brauer, 1981).

**Order SELAGINELLALES** Potonié, 1899


First: Barinos­ trobus famennensis Fairon-Demaret, 1977, Evieux Formation, Barse, Belgium.

Intervening: HLK–ASB, MEL–DOR, CRN–RHT, BER.

Comments: This corresponds to the Lycopsida, as used here. However, it does not appear to be closely related to any of the other pteridophyte classes referred to in this chapter (Brauer, 1981).

First: Spencerites membranaceus Kubart, 1910, Koksflöz, Ostrava-Karviná Coalfield, Czechoslovakia.

Intervening: MEL, KSK.


First: Diaphorodendron vasculare (Binney) DiMichele, 1985, Hauptflöz, Ruhr Coalfield, Germany (Phillips, 1980).

Intervening: VRK–POD.


First: Caudatocarpus braidwoodense (Arnold) Brack-Hanes 1981, Copland Seam, Illinois, USA.
Last: C. braidwoodense, Carbondale Formation, Illinois, USA (Arnold, 1938).

Intervening: POD–MYA.


First and Last: Pinakodendron ohmannii Weiss, 1893, Veine de l’Olive, Mariemont, Belgium; also Veine 9 Paumes, Anzin, France (Kidston, 1911; Rousseau, 1933).

Comments: Mathieu (1937) records this species from Vendée, France (??PND) but does not state if the specimens are fertile.


Last: Sporangiostrobus feistmantellii (Feistmantel) Němejc, 1931, Seam III, Puertollano, Spain (Wagner, 1983).

Intervening: POD–MYA.


First and Last: Cyclodendron lesii (Seward) Kräusel, 1928, Ecca Group, Hammanskraal, Transvaal, South Africa (Rayner, 1985).

Comments: Sterile stems of this family range from the middle Ecca to lower Beaufort groups (SAK–KUN) (Rayner, 1985).

F. PLEUROMEIACEAE Potonié, 1902 Tr. (GRI–CRN) Terr.

First: Pleuromeia jiaochengensis Wang and Wang, 1982, Luijiaokou Formation, Shanxi, China.
Last: Annalepsis zeilleri Fliche, 1905, Lettenkohle, Lorraine, France (Grauvogel-Stamm and Düringer, 1983).

Intervening: DIE–SPA.

Comments: The chronostratigraphical position of many of the localities yielding this family is in doubt (Wang and Wang, 1982). Other than Annalepsis, however, the family appears to be restricted mainly to the SCY.

Order MIADESMIALES Chaloner, 1967


First and Last: Miadesmia membranacea C. E. Bertrand, 1895, Union Seam, Lancashire, England, UK.

Order ISOETALES Engler, 1924

F. ISOETACEAE Dumortier, 1829 C. (MEL)–Rec. Terr.


Extant Intervening: Tr, VLG–HOL.


First: Polysporia mirabilis Newberry, 1873, No. 1 Coal, Tallmadge, Ohio, USA (Crookall, 1966).
Last: Chaloneria cormosa Pigg and Rothwell, 1983, Duquense Seam, Ohio, USA.

Intervening: VRK–POD.

F. TAKHTAJANODOXACEAE Thomas and Brack-Hanes, 1984 Tr. (SCY) Terr.

First and Last: Takhtajanodoxa mirabilis Snigirevskaya, 1980, Tuntonchansk ‘Suite’, eastern Siberia, former USSR.

Comments: The exact chronostratigraphical position of these strata within the Lower Triassic is uncertain.

Class EQUISETOPSIDA Takhtajan ex Némejc, 1963

This is the Sphenopsida of some authors. The classification is based essentially on Meyer (1987), and relies on the recognition of fertile structures. In contrast to Meyer, however, the Pseudoborniales is retained as a distinct order; the Eviostachyaceae and Cheirostrobaceae are maintained as separate families within the Bowmanitales; the family Calamostachyaceae is included in the Equisetales, rather than being separated into its own order; and the Archaeocalamitaceae (Asterocalamitaceae auct.) is reinserted for the distinctive group of Lower Carboniferous equisetalean taxa.

Order PSEUDOBORNIALES Nathorst, 1902


First: Pseudobornia ursina Nathorst, 1902, Bear Island, Arctic (Schweitzer, 1967).

Order BOWMANITALES Meyen, 1978


First: ?Sphenophyllum subtenuerrimum Nathorst, 1920, Bear Island, Arctic. This is based on sterile foliage. The oldest strobili appear to be Bowmanites tumbana Remy and Spassov, 1959 (associated with S. subtenuerrimum foliage), Tumba, Bulgaria (FAM).

Last: ?Sphenophyllum sinocoreanum Yabe, Lungtan Formation, Jiangxi, China (Mei, 1984). This is based on sterile foliage. The youngest strobili are Bowmanites simonii Remy, 1961, upper Autunian, Thuringia, Germany (ASS).

Intervening: IVO–NOG.
F. EVIOSTACHYACEAE Boureau, 1964
D. (FAM) Terr.

First and Last: Eviostachya hoegii Stockmans, 1948, Evieux Formation, Belgium (Leclercq, 1957).

F. CHEIROSTROBACEAE Scott, 1907
C. (ASB) Terr.

First and Last: Cheirostrobus pettycurensis D. H. Scott, 1898, Pettycur Limestone, Fife Region, Scotland, UK.

Order EQUISITALES Trevisan, 1876
F. ARCHAEOCALAMITACEAE Stur, 1875
C. (IVO–ASB) Terr.

First: Archaeocalamites sp. and Fructification-type A of Scott et al. (1985), Loch Humphrey Burn, Strathclyde Region, Scotland, UK.

Last: Protocalamostachys pettycurensis Chaphekar, 1963, Pettycur Limestone, Fife Region, Scotland, UK.

Intervening: ARU–HLK.

Comments: Distinguishing this family from the Calamostachyaceae is not always easy, particularly with sterile material. Archaeocalamites stems have been found ranging from FAM (Ischenko, 1965) to ARN (Novik, 1968). There is also an unpublished record of stems and foliage from the Clyde Formation (?ART), Texas, USA (R. Bateman, pers. comm.).

F. CALAMOSTACHYACEAE Meyen, 1987
C. (ALP)–P. (KAZ?) Terr.

First: Calamostachys polyodonta (Sternberg) Weiss, 1876, Zone de Sippenaken, Givet-Groyonne, Belgium (Stockmans and Willière, 1953).

Last: ?Calamostachys (?) sp., Ural Mountains, former USSR (Vakhrameev et al., 1978). Better documented are Calamostachys grandeuryi (Renault) Jongmans, 1911, Autun, France (ASS) (Renault, 1876) and C. dumasi (Zeiller) Jongmans, 1911, Sobernheim, Nahe, Germany (ASS) (Kerp, 1984).

Intervening: KIN–NOG.

F. TCHERNOVIACEAE Meyen, 1969
C. (MYA?)–P. (TAT) Terr.

First: ?Phyllotheca deliquescens (Göppert) Schmalhausen, Keregetassker Formation, Priba1chasje, Kazakhstan, former USSR (EMS) has been included by Meyen (1967), Radchenko, 1967). This record is based on sterile foliage of equivocal chronostratigraphical position. Better documented is the fructification Tchernovia ungensis Reinhold, 1962, Alykaevskii Formation (KAS), Kuznetsk, former USSR (Meyen, 1982).

Last: Sendersonia matura Meyen and Menshikova, 1983, Tailuganski Formation, Kuznetsk, former USSR.

Intervening: NOG?–KAZ.

Comments: The Angaran sphenopsids have been reclassified by Meyen (1971) and Meyen and Menshikova (1983) (see also Meyen, 1982, for a review). There is some evidence that the family may range up to the Lower Jurassic based on the distribution of foliage such as Neokoretrophyllites. As pointed out by Meyen (1971), however, assigning such foliage to a particular family without evidence of the fructifications can be suspect, and so this expanded stratigraphical range is not quoted here.

F. GONDWANOSTACHYACEAE Meyen, 1969
P. (KAZ) Terr.

First and Last: Gondwanostachys australis (Brongniart) Meyen, 1969, Newcastle Group, New South Wales, Australia (Townrow, 1956).

Comments: Townrow also mentions foliage from the Raniganj Formation of India, the Beaufort Formation of South Africa, and from Madagascar, Argentina and the Falkland Islands. These are all probably of about the same age.

F. EQUISITACEAE Richard ex De Candolle, 1805
P. (TAT?)–Rec. Terr.

First: ?Neocalamites superpermicus Kon’no, 1973, Toyoma Formation, Kitakami, Japan. This record is based on sterile stems. The oldest fertile structures are Neocalamostachys pedunculatus Kon’no, 1962, Momonoki Formation, Kitakami, Japan (CRN).

Extant Intervening: SPA?–LAD?, RHT–HOL.

F. ECHINOSTACHYACEAE Grauvogel-Stamm, 1978
Tr. (SMI?) Terr.


Class FILICOPSIDA Pichi-Sermolli, 1958

This class has also been called the Pteropsida and Poly-podiopsida. There is little agreement on the classification of the group, or even its taxonomic rank. The scheme used here is based on Meyen (1987), with modifications based on Danzé (1956), Galtier and Scott (1979), Brousmiche (1983) and Scott and Galtier (1985).

Order CLADOXYLALES Hirmer, 1923
F. CLADOXYLACEAE Unger, 1856
D. (EIF)–C. (IVO) Terr.


Last: Cladoxylon waltonii Long, 1968b, Cementstone Group, Borders Region, UK.

Intervening: GIV–HAS.

Comments: Protohyenia janovii Ananiev, 1957, Torgachine, western Siberia, former USSR (EMS) has been included by some authors in this family (e.g. Meyen, 1987), but was described from specimens belonging to more than one species.

Order IBYKALES Skog and Banks, 1973
F. IBYKACEAE Skog and Banks, 1973

First: Ibyka amphikoma Skog and Banks, 1973, New York State, USA.

Last: Asteropteris nubloracensis Dawson, 1881, Portage Group, Milo, New York State, USA (Bertrand, 1913).

Comments: The taxonomic position of this order is still in doubt, and some authors have assigned it to the Equisetopsida.

Order COENOPTERIDALES Zimmermann, 1930
F. RHACOPHYTACEAE Barnard and Long, 1975
D. (EIF)–C. (HAS) Terr. (see Fig. 43.2)
Pteridophyta

First: *ProtocephaIopteris praecox* (Haege) Ananiev, 1960, Saian-Alta Mountains, Siberia, former USSR.


Intervening: GIV, FAM.

Comments: The Avon Gorge assemblage has yet to be named or described in detail. However, CCJ has examined the material (in the collection of R. H. Wagner), and it includes fertile structures (see also Wagner, 1984, p. 113).

F. ZYGOPTERIDACEAE Bertrand, 1909

D. (FAM?)–C. (BRI) Terr.

First: ?Clepsydropsis campbellii Read, 1936, New Albany Shale, Kentucky, USA. This species is based on sterile foliage. The oldest fructification appears to be Fructification-type D from Loch Humphrey Burn, Strathclyde Region, Scotland, UK (IVO?) (A. C. Scott *et al.*, 1985).


Intervening: CHD?–HLK?, ASB.

Comments: This family has traditionally been interpreted in a broad sense, for a group of Upper Devonian to Lower Permian fern fossils, typically including stems of the zygopterid type. Following evidence provided by Galtier and Scott (1979), however, we treat it in a more restricted sense, including only those species which are known to have radially arranged sessile sori of elongate exannulate sporangia with inwards-facing dehiscence. Most of the other zygopterids can be assigned to the stratigraphically higher families Corynepteridaceae and Biscalithecaceae (below).

F. STAUNOPTERIDACEAE Hirmer, 1927

D. (FAM)–C. (VRK) Terr.

First: *Gillespie randolphiensis* Erwin and Rothwell, 1989, Hampshire Formation, West Virginia, USA.

Last: *Stauropteris biseriata* Cichan and Taylor, 1982, upper Path Fork Coal, Kentucky, USA.

Intervening: IVO, ASB, MEL.

Comments: Erwin and Rothwell (1989) argue that this is an artificial family, encompassing plant fossils of simple morphology and anatomy, but derived from several independent lineages.

F. CORYNEPTERIDACEAE Cleal, *fam. nov.* C. (IVO?–CHV?) Terr.

First: ?Fructification-type E of Scott *et al.* (1985), Loch Humphrey Burn, Strathclyde Region, Scotland, UK. This record is based on isolated sporangia, which have not yet been fully described. Stockmans and Willière (1955) describe sterile foliage possibly belonging to this family as Alloiopteris quercifolia (Goppert) Potonié, 1897, Zone de Bioul, Belgium (CHO). The oldest record of fertile foliage is Corynepteris stellata Dailly, 1860, ?upper Namurian, County Limerick, Republic of Ireland (MRD?), (Galtier and Scott, 1979).

Last: *Corynepteris angustissima* (Sternberg) Nemejc, Illingen Seam, Saarland, Germany (Brousmiche, 1983).

Intervening: ALP–KRE.

Comments: The circumscription and diagnosis of this family was suggested by Galtier and Scott (1979), but they failed to give it a formal name; I therefore propose the new name here, Corynepteridaceae. It includes those species, previously assigned to the Zygopteridaceae, where sessile sori are attached to laminate pinnules. Each sorus consists of elongate sporangia (1–2.5 mm long) with a V-shaped annulus. The type is the form genus Corynepteris. Reports of corynepterid fronds from higher horizons (Broutn, 1981; Wagner and Sousa, 1983) need to be verified.


First: *Biscalithea musata* Mamay, 1957, Baker Coal Member, Kentucky, USA (Phillips, 1980).


Intervening: KRE–NOG.

Comments: This is the second of the Upper Carboniferous–Permainian groups of zygopterid-like ferns which Galtier and Scott (1979) suggested probably belonged to a separate family, but for which no name was provided. According to Galtier and Scott, it includes those species with long-stalked sori attached directly to the rachis (rather than to the pinnules, as in the Corynepteridaceae). Also, the sporangia are longer (3–4 mm) and have two distinct longitudinal annuli. The type is *Biscalithea* Mamay, 1957. Other form genera included are *Nemejhopteris* Barthel, 1968, and *Schizostachys* Grand’Eury, 1877.

Order BOTYROPTERIDALES Meyen, 1987

F. PSALIXOCHLAENACEAE Holmes, 1981

C. (IVO?–CHV?) Terr.


Last: *Hymenophyllites quadractiactylis* (Gibbier) Kidston, 1923, Wahlshied Seam, Saarland, Germany (Brousmiche, 1983). This record is based on Meyen’s (1987) suggestion that *Hymenophyllites* (Zeiller) Kidston, 1923, may belong to the Psalixochlaenaceae. The youngest recorded unequivocal member of the family is *Norwoodia antiqua* Rothwell, 1976, Cabaniss Formation (POD), Kansas, USA (Good and Rothwell, 1988). Good (1981) argued that *Botryopteris antiqua* Kidston, 1908, belongs to this family, but it differs in details of the vascular anatomy and position of attachment of the sporangia.

F. TEDELEACEAE Eggert and Taylor, 1966

C. (IVO?)–P. (ASS) Terr.

First: ?Fructification-type C of Scott *et al.* (1985), Loch Humphrey Burn, Strathclyde Region, Scotland, UK. This species has yet to be described fully or named. This record is based on isolated sporangia, which have not yet been fully described. Stockmans and Willière (1955) describe sterile foliage possibly belonging to this family as Alloiopteris quercifolia (Goppert) Potonié, 1897, Zone de Bioul, Belgium (CHO). The oldest record of fertile foliage is Corynepteris stellata Dailly, 1860, ?upper Namurian, County Limerick, Republic of Ireland (MRD?), (Galtier and Scott, 1979).


Intervening: ASB–NOG.

Comments: The quoted range assumes that permineralized fructifications known as *Tedelea* Eggert and Taylor, 1966, can be correlated with the compression fructifications *Senftenbergia* Corda, 1845 (Meyen, 1987).
Fig. 43.2

F. BOTRYOPTERIDACEAE Renault, 1883
C. (IVO)–P. (ASS?) Terr.

First: Botryopteris cf. antiqua Kidston, 1908, and Fructification-type F, Loch Humphrey Burn, Strathclyde Region, Scotland, UK (A. C. Scott et al., 1985). This fructification has yet to be fully described, but the structure of the annulus differs slightly from typical Botryopteris antiqua, as described by Galtier (1967). However, its assignment to the family appears to be confirmed by the anatomy of the associated sterile axes.

Last: ?Botryopteris burgkensis (Sterzel) Barthel, 1976, tonstein above Seam 2, Döhlen Formation, Döhlen Basin, Germany. This record is based on adpressions, and Galtier (1986) has expressed doubt as to their attribution. Better documented is Botryopteris forensis Renault, 1875, Rive de Gier Formation, Grand’Croix, France (CHV), (Galtier, 1971).

Intervening: ASB, MEL, POD–CHV.

Comments: The generic taxonomy of this family probably needs to be revised (e.g. Good, 1981), but the species are united at the rank of family by the vascular anatomy and sporangial structure.

F. SERMEYACEAE Eggert and Delevoryas, 1967
C. (VRK)–P. (KAZ) Terr.

First: Oligocarpia brongniartii Stur, 1883, Barnsley Seam, South Yorkshire, England, UK (Kidston, 1923).


Intervening: KSK–DOR.

Comments: The quoted range relies on the correlation between the permineralized Sermeya Eggert and Delevoryas, 1967, and the adpression Oligocarpia Göppert, 1841 (Meyen, 1987), although some still regard the latter as in the Gleicheniaceae (e.g. Galtier and Scott, 1985; Yao and Taylor, 1988). Triassic records of Oligocarpia from Lunz (LAD?) (Vakhrameev et al., 1978) need to be verified. The range of permineralizations is MYA–CHV.

Order URNATOPTERIDALES Danzé, 1956
F. URNATOPTERIDACEAE Danzé, 1956  
C. (ALP)–P. (ASS) Terr.  

First: *Renaultia gracilis* (Brongniart) Zeiller, 1883, Malonne Formation, Lontzen, Belgium (Stockmans and Willière, 1953).  


Intervening: KIN–NOG.  

Order CROSSOTHECALES Danzé, 1956  

F. CROSSOTHECAEAE Danzé, 1956  
C. (VRK–MYA)  

First: *Crossotheca schatzlarensis* Stur, 1885, Fettkohle, Dortmund, Germany (Gothan, 1935).  

Last: *Crossotheca crepinii* Zeiller, 1883, Steinbesch Formation, Lorraine, France (Brousmiche, 1983).  

Intervening: KSK–POD.  

Order MARATTIALES Engler and Prantl, 1902  

There has been considerable disagreement as to the classification of the Marattiales. The view advanced by Hill and Camus (1986) has been adopted here, and just two families recognized. The oldest representative of the order appears to be *Burnitheca pusilla* Meyer-Berthaud and Galtier, 1986, Loch Humphrey Burn, Strathclyde Region, Scotland, UK (IVO?). However, it is based on an isolated sporangial cluster, which does not show the features necessary to assign it to a family.
F. ASTEROTHECACEAE Sporne, 1962
C. (BR?)–P. (UFI)


Last: Gemellitheca saudica Wagner et al., 1985, Unayzah, Saudi Arabia. The taxonomic positions of Asterotheca (?) plusieriata Fefilova, 1973, Pechora Basin, former USSR (KAZ); A. merianii (Brongniart) Stur, 1885, from Lunz and Spitsbergen (CRN); and A. cottonii Zeiller, 1903, from Vietnam (RHT), (Vakhrameev et al., 1978) are uncertain.

Intervening: VRK–ASS.
Comments: This is the same as the Psaroniaceae of many authors. However, the Asterothecaceae is a better name, being based on Asterotheca Presl, 1845, a form genus of sporangia (Psaronius is a form genus for anatomically preserved stems).

F. MARATTIACEAE Berchtold and Presl, 1820
C. (MYA)–Rec. Terr.

First: ‘Radstocka’ kidstonii Taylor, 1967, Mazon Creek, Illinois, USA (a new form-genus name is required for this species – Brousmiche, 1983). The marginally earlier (MYA) Danaeites saraepontanus Stur, 1885, Beust Seam, Saarland, Germany (Corin, 1951) may also belong here (Hill et al., 1985). Extant

Intervening: ASS?, UFI?, RHT–HOL.
Comments: The macrofossil record of this family is discussed by Hill et al. (1985) and Hill and Camus (1986).

Order OSMUNDALES Zimmermann, 1959
F. OSMUNDACEAE Berchtold and Presl, 1820
P. (KAZ)–Rec. Terr.

First: Zalesskaya gracilis (Eichwald) Kidston and Gwynne-Vaughan, 1908, Z. diploxyylon Kidston and Gwynne-Vaughan, 1908, Thamnoperis schlechtendalii (Eichwald) Brongniart, 1849, Bathysipteris rhombidea (Kutorga) Eichwald, 1860, and Anomorrhoea fischi Eichwald, 1860, all from a Kazanian sandstone, Orenburg, former USSR (Kidston and Gwynne-Vaughan, 1908, 1909). Palaeosmunda williamsonii Gould, 1970, and P. playfordii Gould, 1970, Bowan Basin, Queensland, Australia, are quoted as Upper Permian, but it is not stated whether they are older than the Orenburg species. Extant

Intervening: SMIP, CRN–HOL.
Comments: Meyen (1987) has suggested that some of the Permian species may represent an independent family within the Osmundales, but this has yet to be formalized.

Order FILICALES Engler and Prantl, 1902
F. GLEICHENIACEAE (Brown) Presl, 1825
P. (ART?)–Rec. Terr.

First: ?Chansisithea kidstonii Halle, 1927, lower Shihhotse Formation, Shanxi, China. This has gleicheniacean-like sporangia, but atypical vegetative organs. A less equivocal member of the family is Wingataeum plumosa (Daugherty) Ash, 1969, Chinle Formation, New Mexico and Arizona, USA (CRN). Extant

Intervening: UFI?, PLB, BAJ, BER–HOL.
Comments: The Palaeozoic form genus Oligocarpia Göppert, 1841, has been often assigned to the Gleicheniaceae (e.g. Abbott, 1954), but is now more usually referred to the Serameyceae (Botryopteridales). The Gleicheniaceae is rare in the fossil record below the Cretaceous (Arnold, 1964).

F. CYNEPTERIDACEAE Ash, 1969
Tr. (CRN)–Rec. Terr.

First and Last: Cyneperis lasiphora Ash, 1969, Chinle Formation, New Mexico and Arizona, USA.

F. MATONIACEAE Presl, 1847
Tr. (CRN)–Rec. Terr.

First: Phlebopteris smithii (Daugherty) Arnold, 1956 and P. utensis Arnold, 1956, Chinle Formation, Utah, Arizona and New Mexico, USA. Extant

Intervening: RHT–HOL.
Comments: Records of Phlebopteris Brongniart, 1828, from the Kolvuncansker plant fossil assemblage (DIE?) and Tunguska Basin, Siberia, former USSR (Vakhrameev et al. 1978) need to be verified.

F. DIPTERIDACEAE Seward and Dale, 1901
Tr. (CRN?)–Rec. Terr.

First: Clathropteris walker Daugherty, 1941, and Apache arizonica Daugherty, 1941, Chinle Formation, New Mexico and Arizona, USA (Ash, 1969). Other, less well-documented records from CRN localities, such as Lunz, are reviewed by Vakhrameev et al. (1978). Extant

Intervening: NOR–HOL.
Comments: The sudden appearance of this family in such abundance in the Upper Triassic is quite striking, but there is no direct evidence on its origins.

F. POLYPODIACEAE Brown, 1810
Tr. (CRN?)–Rec. Terr.

First: ?Polypodites cladopheboides Brick, 1952, Kurasasajeske Group, Ural Mountains, former USSR. This appears to be based on sterile foliage. The oldest fertile fronds are Aspidites thomasii Harris, 1961, lower Deltaic Group Yorkshire, England, UK (BAJ). Extant

Intervening: BER–HOL.
Comments: This family is treated in the generalized sense used in most palaeontological studies. It includes those groups assigned by some botanists (e.g. Sporne, 1975) to the Dennstaedtiaceae and Adiantaceae.

F. DICKSONIACEAE Bower, 1908
Tr. (RHT)–Rec. Terr.

First: Coniopteris hymenophylloides (Brongniart) Seward 1900, ‘Lower Series’, Karmozd-Zirab, Iran (Klipper, 1964) Extant

Intervening: HET–BER, CMP–HOL.
Comments: See comments on Cyatheaceae.

F. SCHIZAEACEAE Kaulfuss, 1827
J. (BAJ)–Rec. Terr.

First: Stachypteris spicans Pomel, Scabdy Formation, North Yorkshire, England, UK (Harris, 1961). Extant

Intervening: BTH–HOL.
Comments: The Palaeozoic form genus Senftenbergi Corda, 1845, has been widely included in the Schizaeaceae (e.g. Radforth, 1939), but is now more usually referred to the Tedelaceae (Botryopteridales).
F. CYATHEACEAE Kaulfuss, 1827
K. (HAU)–Rec. Terr.

First: Cibotiacaulis taietiae Ogura, 1927 and Cyathocaulis naktongensis Ogura, 1927, North Kyong Sang Province, Korea. Nishida (1989) has recorded a permineralized stem from ‘the Upper Jurassic or Lower Cretaceous’ of Tasmania, which might belong to this family, but the evidence has not yet been published.

Extant

Intervening: BRM–APT, TUR–SAN, DAN.

Comments: Most of the macrofossil evidence for this family comes from stem permineralizations. It is possible that at least some of the records usually attributed to the Dicksoniaceae may in fact be more properly placed here.

F. TEMPSKYACEAE Read and Brown, 1937
K. (BER–SAN) Terr.


Last: Tempskya cretacea Hosius and von der Marck, 1880, Haltern Quartzite, Westfalia, Germany.

Intervening: APT–ALB, CEN.

Comments: There is little direct evidence as to the fronds attached to the Tempskya Corda, 1845, stems, and therefore of the fructifications. The taxonomic rank and position of this taxon is thus uncertain. Records from the Tertiary (Kidston and Gwynne-Vaughan, 1911; Chandler, 1968) appear to be based on reworked fragments of permineralized stems.

F. LOXSOMACEAE Presl, 1875
K. (BER–SAN) Terr.

First: ?Loxsomopteris anasilla Skog, 1976, College Park, Maryland, USA.

Extant

Comments: This is the only reported representative of the family in the macrofossil record, and is based on a fusainized rhizome.

F. LOPHOSORIACEAE Pichi Sermolli, 1970
K. (APT?)–Rec. Terr.


Extant

Comments: This is the only known macrofossil attributed to the family, and shows no evidence of fructifications. The palaeontological background to the family is discussed by Kurmann and Taylor (1987).

Order OPHIOGLOSSALES Engler and Prantl, 1902

F. OPHIOGLOSSACEAE (Brown) Agardh, 1822
T. (DAN)–Rec. Terr.

First: Botrychium wightonii Rothwell and Stockey, 1989, Genesee, Alberta, Canada.

Extant

Comments: This is the only unequivocal representative of the order in the macrofossil record.

Order MARSILEALES Zimmermann, 1959

F. MARSILEACEAE Mirbel, 1802
K. (TUR)–Rec. FW

First: Marsilea vera Jarmolenko, 1935, clay beds of Kysyl­djar Hill, Kara-Tau, Urals, former USSR.

Extant

Intervening: MAA–HOL.

Comments: The fossil record of this family is based mainly on isolated megaspores. A possible relationship with the Schizaceae has been argued by some authors.

Order SALVINIALES Zimmermann, 1959

The fossil record of this order is reviewed by Jain (1971) and Collinson (1980). Its taxonomy is far from settled, some authors recognizing just one family (Salviniaecae) while others recognize three (the two quoted below, plus the Aziniaeae).

F. SALVINIALES Dumortier, 1829
K. (MAA)–Rec. FW

First: Salvinia stewartii Jain, 1971, Edmonton Formation, Genesee, Alberta, Canada.

Intervening: DAN–HOL.

F. AZOLLAECES Wettstein, 1903
K. (MAA)–Rec. FW


Intervening: DAN–HOL.

Class PROGYMNOSPERMOPSIDA Beck, 1960

The following classification has been synthesized mainly from Barnard and Long (1975) and Meyen (1987).

Order ANEUROPHYTALES Kräusel and Weyland, 1941

F. ANEUROPHYTACEAE Kräusel and Weyland, 1941

First: Protopitys thomsonii (Dawson) Kräusel and Weyland, 1933, Sandwick Fish Bed, Orkney, Scotland, UK (Lang, 1926).


Intervening: GIV.

Comments: The taxonomy and stratigraphical distribution of this family are extensively reviewed by Scheckler and Banks (1971).

F. PROTOPITYACEAE Banks, 1968
C. (ARU–ASB?) Terr.


Last: Protopitys buchiana Göppert, 1850, Falkenberg, Germany.

Comments: This species was separated from the Aneurophytales by being heterosporous. A. C. Scott et al., (1984) list it as a pteridosperm, but this is not supported by evidence given by Smith (1962). The chronostatigraphical position of the Falkenberg assemblage is uncertain due to the lack of recent studies (A. C. Scott et al.,...
It is estimated here as ASB?, as it compares well with assemblages of this age from France and the UK.

**Order** ARCHAEOPTERIDAEAS Zimmermann, 1930

F. ARCHAEOPTERIDACEAE Zimmermann, 1930


Last: *Archeopteris hibernica* Forbes, 1853, from Kiltorcan, Republic of Ireland (Chaloner, 1968), and Borders Region, Scotland, UK (Miller, 1857), and Bear Island, Arctic (Kaiser, 1970), all HAS?

Intervening: FRS–FAM.

**Last:**

**Comments:** Meyen (1987) has suggested that 1970), all HAS?

**Order** FOOGERATHIALES Darrah, 1939

F. NOEGGERATHIAECEAE Darrah, 1939

C. (VRK)–P. (ASS) Terr.

First: *Rhacophyton* (?) *Noeggerathia westermannii* Gothan, 1931, Kohlscheider Group, Aachen, Germany. A fragment of foliage without fertile structures. The oldest fertile structures are *Discinites jongmansii* Hirmer, 1941, Limburg, The Netherlands (VRK).

Last: *Noeggerathia zamitoides* Sterzel, 1918, Middle Rotliegend, Saxony, Germany (Hirmer, 1941).

Intervening: KSK–POD, KLA–NOG.

**Comments:** The affinities of this family are still somewhat in doubt, but there is growing consensus that it is progymnospermous (e.g. Meyen, 1987). The taxonomy and distribution are reviewed by Hirmer (1941).

F. TINGIOSTACHYACEAE Gao and Thomas, 1987

C. (KIN?)–P. (TAT?) Terr.

First: **Tingia platea** Tidwell, 1967, Manning Canyon Shale, Utah, USA. This is based on sterile fragments, which occur outside of the normal palaeogeographical range of the form genus (i.e. the Cathaysia paleocontinent). *Tingia* sp., Tongshan Formation, Kaiping, China? (Stockmans and Mathieu, 1939) are the oldest specimens of foliage from Cathaysia (VRK?). *Tingiostachya* sp., Taiyuan Formation, Kaiping, China (Stockmans and Mathieu, 1957) are the oldest strobili, associated with *Tingia triloba* Stockmans are Mathieu, 1939, and T. *partita* Halle, 1927, foliage (CHV?).

Last: **Tingia subcarbonica** Kon’no et al., 1971, Lingin ‘Flora’, Johore, Malaysia and T. *yichuanensis* Feng et al., 1977, Henan, China. These are based on sterile foliage fragments. The youngest known strobili are *Tingiostachya tetracolaris* Kon’no, 1929, lower Shihezi Formation, Shanxi, China (Gao and Thomas, 1987), (UFI? – not Lower Permian, as stated by Gao and Thomas).

Intervening: ROT.

**Comments:** This family has been reviewed by Gao and Thomas (1987), who concluded that it does not belong to the Noeggerathiales, and may not even be a progymnosperm. However, it has many features in common with this order, both in the form of the strobili and the foliage, and so the traditional view as to its taxonomic position has been followed here.

**Order** CECROPSIDALES Stubblefield and Rothwell, 1969


First and Last: *Cecropsis luculentum* Stubblefield and Rothwell, 1989, Duquesne Seam, Ohio, USA.

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GYMNOSPERMOPHYTA

C. J. Cleal

Since the publication of the 1967 edition of *The Fossil Record*, there have been radical changes in gymnosperm taxonomy. For instance, some traditional taxa, such as the Pteridospermopsida, are now thought to be polyphyletic 'grade-groups', and are not given formal taxonomic status, while families established mainly on foliar characters (e.g. Callipteridiaceae Corsin, 1960) are not normally accepted as useful. However, trying to find a coherent alternative classification is far from easy. In many ways the most useful scheme is that of Meyen (1984, 1987), if only because the taxa are formally named and circumscribed. It has, however, been subjected to severe criticism on a variety of fronts (e.g. Beck, 1985; Miller, 1985; Rothwell, 1985; for a reply, see Meyen, 1986), but no alternative formal taxonomy has been proposed. Cladistic analyses (e.g. Hill and Crane, 1982; Crane, 1985; Doyle and Donoghue, 1986) have produced results which partly contradict Meyen's view, although they also disagree to varying extents with each other because of differences in methodology and in the characters analysed. Perhaps the most significant results of these cladistic analyses are:

1. that the seed-bearing plants are a monophyletic group, contrary to some views expressed previously (e.g. Arnold, 1948);
2. that the Cycadales and Bennettitales are not closely related;
3. that the angiosperms seem to be most closely related to the Bennettitales and Gnetales.

In the following analysis, Meyen's scheme has formed the core of the classification adopted, but partly modified to make it compatible with some of the results of the cladistic studies, mentioned above. For instance, the Ginkgoaceae is removed from the group of so-called Mesozoic pteridosperms, and returned to its traditional position in the Pinopsida. Such a compromise scheme will undoubtedly attract more criticism than praise, but it nevertheless provides a reasonably coherent classification on which to base the following analysis.

In virtually all cases, the quoted ranges are based on macrofossil evidence alone. This is mainly because identifying families in the dispersed pollen/spore record is at best very difficult. This factor, combined with the extreme partiality of the plant macrofossil record, must be borne in mind when trying to draw floristic inferences (e.g. diversity analysis) from the results.

For simplicity, the term 'seed' has been used in the following chapter, to refer both to pre-fertilization ovules and post-fertilization seeds.

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Class Lagenostomopsida Cleal, cl. nov.
(see Fig. 44.1)

Meyen (1987) included the Lagenostomes within the Cycadopsida, but analyses by both Crane (1985) and Doyle and Donoghue (1986) point to its being a quite distinct and primitive group of gymnosperms. Therefore it has been placed here in a separate class, the Lagenostomopsida. Following ICBN Article 16, it is automatically typified by the form genus Lagenostoma Oliver and Scott, 1904. The diagnosis is identical to that of its only order, Lagenostomales.

Order Lagenostomales Seward, 1917

The most comprehensive attempt at a family classification of the order is that based on seed structure by Long (1975). This has to be modified by excluding, for instance, Eurystomaceae Long, 1975, which in part belongs to the Calamopityales, and Callamospermaceae Long, 1975, which is synonymous with the Callistophytaceae (Callistophytales).

F. Elkinsiaceae Rothwell et al., 1989
D. (FAM)–C. (ASB?) Terr.
Fig. 44.1

First: *Elkinsia polymorpha* Rothwell et al., 1989, Hampshire Formation, West Virginia, USA.

Last: ??*Megatheca thomasii* Andrews, 1940, Oil Shale Group, Lothian Region, Scotland, UK. This is a compression of a cupule very similar in form to the permineralized *Calathospermum* Walton, 1940, but there is no evidence of the seeds that it contained. The youngest permineralization is *Calathospermum scoticum* Walton 1949b, Loch Humphrey Burn (HLK?), Strathclyde Region, Scotland, UK.

**Intervening:** HAS-ARU.

**Comments:** Rothwell et al. (1989) do not diagnose this family, and include only one form genus (*Elkinsia*). However, they imply a close relationship with a number of other Upper Devonian and Lower Carboniferous fossils, and it is in this wider context that the family is interpreted here. It refers to fossil plants with lagenostomalean seeds borne in multi-ovulate cupules. The seeds have an integument that is free from the nucellus above the plinth and does not form a distinct micropyle. The distal part of the nucellus forms a wide lagenostome with a prominent central plug. Included are seeds of the form genera *Hydra*-

F. GENOMOSPERMACEAE Long, 1975
C. (IVO) Terr.


Comments: Rothwell et al. (1989) compare Genomosperma with Elkinsia (see previous family). It is assigned to a separate family here because it has:

1. a totally free nucellus;
2. a distinctive short, thin lagenostome;
3. was not borne in a cupule.

However, it is recognized that more information is needed on Genomosperma Long, 1959, before this family distinction can be confirmed. Geminitheca scotica Smith, 1959 from Loch Humphrey Burn, Strathclyde Region, Scotland, UK (HLK?) also has a free nucellus, but was borne in a multi-ovulate cupule and has quite a distinct lagenostome (the taxonomic position of this species is uncertain). The
Genomospermaeae is widely regarded as the archetypal primitive gymnosperm family, although it occurs in the fossil record somewhat higher than the Elkinsiaceae.

F. EOSPERMACEAE

Long, 1975
C. (IVO) Terr.


Comments: This family is represented by a series of isolated, apparently non-cupulate seeds that have a highly distinctive, tapered lagensostome, with a conical central plug. Unlike other lagenostomacean, they are platyspermic, and show varying degrees of curvature, from flat (Eosperma Barnard, 1989) to fully campylotropous (Camptosperma Long, 1961). As they have not been found attached to fronds or stems, their position within the Lagenostomaales is provisional.

F. LAGENOSTOMACEAE

Seward, 1917

C. (IVO–KLA?) Terr.


Last: Eusphenopteris rotundiformis Němejc, 1937, Kounov, central Bohemia, Czechoslovakia. This is based on the observation that some lagenostomacean permineralized stems bore eusphenopterid foliage (Shadle and Stidd, 1975). Adpression foliage known as Pseudomariopteris Bangé-Corsin, 1953, which ranges up into the Lower Permian, may have lagenostomacean affinities, but this has yet to be confirmed. The youngest permineralized fructifications are the seeds Gnetopsis elliptica Renault and Zeiller, 1884, and Conostoma sp., Rive de Gier Formation (CHV), Grand’Croix, France (Phillips, 1980).

Intervening: BRI–KRE, DOR?

Comments: This family represents those lagenostomaales with seeds having a fully developed micropyly. Long (1975) also included Stemnostoma Long, 1960, but the lagenostome of these seeds is surrounded by an integumental collar, rather than a true micropyly. The family contains a wide diversity of seeds, including non-cupulate seeds (Conostoma Williamson, 1876), and seeds borne in uniovulate (Lagenostoma Williamson, 1876) and multi-ovulate (Gnetopsis Renault and Zeiller, 1884) capsules. It may thus be further divided as the relationships between the seeds to whole-plant reconstructions become better established.

F. PHYSOSTOMACEAE

Long, 1975
C. (ASB–POD) Terr.

First: ??Physostoma sp., Pettycur Limestone, Fife, Scotland, UK (Gordon, 1910). This is an unillustrated record of an allegedly poorly preserved specimen. Better documented is Physostoma elegans (Williamson) Oliver, 1909, Upper Foot Seam (MEL), Lancashire, England, UK.

Last: Physostoma calcaratum Leisman, 1964, Cabaniss Subgroup, Kansas, USA.

Comments: This family is in many ways similar to the Elkinsiaceae, except that the seeds were not borne in a cupule. Also, the seeds have a much smaller, thinner lagenostome, which appears to lack a central plug.

Class UNNAMED

Most recent analyses (Crane, 1985; Doyle and Donoghue, 1986; Meyen, 1987) agree that the Mesozoic pteridosperms cluster together with the glossopterids. Meyen referred to them as the Ginkgoopsida, since he included the extant ginkgoales, but the cladistic analyses of Crane, and Doyle and Donoghue support the traditional view that the ginkgos cluster with the conifers. The latter analyses could be used to argue for a single class to encompass conifers, ginkgos, Mesozoic pteridosperms and glossopterids (among others). However, the conifer/ginkgo complex has been retained here as a separate class, and consequently an alternative class name is required for the remainder.

Order CALAMOPITYALES

Taylor, 1981

F. CALAMOPITYACEAE

Solms-Laubach, 1896
C. (HAS–BRI?) Terr.

First: Calamopitys americana Scott and Jeffrey, 1914, C. forrestii Read, 1936, Stenomelone muratum Read, 1936, Dichnia kentuckiensis Read, 1956, and Bostonia perplexa Stein and Beck, 1978, Falling Run Member, New Albany Shales, Kentucky, USA (Read, 1937; Stein and Beck, 1978). The chronostratigraphical position of these fossils has been changed since the first edition of The Fossil Record, following Stein and Beck (1978). An unnamed seed from the Lydienenses Formation (HAS), Hérault, France (Galtier and Rowe, 1989) is the oldest fructification which may belong to the family.


Comments: The taxonomy of this order is problematic because it is not certain what fructifications were attached to calamopityalean stems and vegetation. There is good circumstantial evidence that seeds belonging to the Eurystomaceae pro. parte Long, 1975 (Lyrasperma Long, 1960, Eurystoma Long, 1960, Dolichosperma Long, 1961) may belong here, and it was partly because of this that Meyen (1987) suggested a link with the ‘Mesozoic pteridosperms’. However, evidence of organic connection between these seeds and the calamopityalean plants has never been demonstrated, and neither is there unequivocal proof that the seeds were non-cupulate: both key points if Meyen’s classification is to be accepted (Beck, 1985).

Order CALLISTOPHYTALES

Rothwell, 1981

F. CALLISTOPHYTACEAE

Stidd and Hall, 1970
C. (MEL–P)–P. (ASS?) Terr.

First: ??Callistophyton sp., First Coal, Lancashire, England, UK (Phillips, 1980). This is a questionable example of a fusainized stem. Better documented is the permineralized pollen organ Idanothekion glandulosum Millay and Eggert, 1970, from the Buffaloville Coal (KSK), Indiana, USA (Phillips, 1980).
Last: ?Dicksonites berychii (Weiss) Doubinger, 1956, Lower Rotliegend, Saarland, Germany (Kerp and Fichter, 1985). This assumes that Dicksonites is the adscription analogue of permineralized Callistophyton Delevoryas and Morgan, 1954 fronds. The youngest permineralizations are Callistophyton sp., Redstone Coal (KLA), Ohio, or Pittsburgh Coal, West Virginia, USA (Phillips, 1980).

**Intervening:** POD–DOR, NOG?

**Order PELTASPERMALES Némecj, 1968**

F. PELTASPERMAEAE Thomas ex Harris, 1937 C. (KLA)–Tr. (RHT) Terr.

First: *Autunia conferta* (Sternberg) Kerp and Lodevia nicklessii (Zeiller) Haubold and Kerp, Faiseau de Beaubrun, St Étienne, France (Bouroz and Doubinger, 1977).


**Intervening:** NOG–NOR.

**Comments:** This family is as interpreted by Kerp and Haubold (1988).


**Intervening:** KAZ.

**Comments:** Meyen (1977) originally assigned this family to the conifers (Pinopsida), but subsequently transferred it to the peltasperms (Meyen, 1984).


**First:** *Rhaphidopteris praecursor* Meyen, 1979, Pritimanie Deposits, Komi, former USSR. This record is based on foliage, which is similar to the Mesozoic form genus *Pachypteris*. It is also associated with pollen (*Alisporites*) similar to that found in Jurassic pollen organs belonging to the family (e.g. *Pteroma*), and so has been accepted here as definite evidence of the family.

**Last:** *Rufloria sierra* Archangelsky, 1963 and *Kaltenia circularis* Archangelsky, 1963, Ticó, Santa Cruz Province, Argentina (Taylor and Archangelsky, 1985).

**Intervening:** SMI–HET, AAL, BTH, KIM–HAU.

**Comments:** This is the Corynospermae of some authors. Its taxonomic position is uncertain, and it is argued that it belongs to the Glossopteridales or even its own distinct order.

**Order LEPTOSTROBALES Meyen, 1984**

F. LEPTOSTROBACEAE Meyen, 1984 Tr. (RHT)–K. (CEN?) Terr.

**First:** Leptostrobus longus Harris, 1935, Scoresby Sound, Greenland; and *Irania hermaphrodita* Schweitzer, 1977, Iran.

**Last:** ?Czekanowska ex group rigida Heer, 1876 and *Phoenicopsis steenstrupii* Seward, Koëvunjsker Formation, Anadyr River and Arkagalinskser and Armanjsker formations, Kolyma River, eastern Siberia, former USSR (Vakhrameev, 1966; Samylina, 1973). These records are based on adpressions of foliage. The youngest fructifications are of *Leptostrobus laxiflorus* Heer, 1876, Ilinureksker Formation (BER), Tyl River, eastern Siberia, former USSR (Vakhrameev, in Vakhrameev et al., 1978).

**Intervening:** HET–TTH, VLG?–ALB?.

**Comments:** This has also been called the Czekanowskiaceae. Many authors have regarded it as being closely related to the Ginkgoaceae, but it is now thought to be closer to the Peltaspermales and Callistophytales (Meyen, 1984, 1987; Crane, 1985).

**Order ARBERIALES Meyen, 1984**

F. ARBERIAEAE Meyen, 1984 C. (KLA?)–Tr. (DIE?) Terr.

**First:** *Arberia umbellata* Surange and Lele, 1955, Talchir Formation, India. The detailed correlations between the various Gondwana sequences and how they relate to the internationally recognized chronostratigraphy are still uncertain. The KLA estimate for the position of the Talchir Formation must therefore be regarded as provisional. Furthermore, it may be pre-dated by *Ottokaria* sp., Itarará Subgroup, Paraná Basin, Brazil (Rösler, 1978).


**Intervening:** NOG–KAZ.

**Comments:** This is the Glossopteridaceae of some authors.

F. CAYTONIACEAE Thomas, 1925 Tr. (CRN?)–K. (CEN?) Terr.

**First:** ?*Pramelreuthia halberfelneri* Krasser, 1909, Lettenkohle, Lunz, Austria (Kräusel, 1949). The affinities of this pollen have been queried by Harris (1964), although it should be noted that the typically caytoniacean foliage, *Sagenopteris* sp., has been reported from about the same stratigraphical horizon at Raibl, Austria (Stur, 1885). Better documented, however, are *Caytonanthus kochii* Harris, 1932, *Amphorispernum ellipticum* Harris, 1932, *A. rotundum* Harris, 1932, *A. major* Harris, 1932, and *Sagenopteris hallei* Harris, 1932, Scoresby Sound (RHT), Greenland (Harris, 1932a,b).

**Last:** ?*Sagenopteris variabilis* Velenovsky, Barykovsker
Formation, Ugo’laja Basin, eastern Siberia, former USSR (Vakhrameev, 1966). This record is based on adpressions of foliage. The youngest fructifications are Caytonia nathorstii (Thomas) Harris, 1940, Scalby Formation (BTH), North Yorkshire, England, UK (Harris, 1964).

**Intervening:** RHT–BTH, OXF?, BER?, BRM?, SAN?

**Comments:** Meyen (1987) places this family in a separate order. However, both Crane (1985) and Doyle and Donoghue (1986) found that it clusters with the Arberiaceae.

**Order** GIGANTONOMIALES Meyen, 1987

**F. EMPLECTOPTERIDACEAE** Wagner, 1967

P. (ASS–KAZ?) Terr.

**First:** Emplectopteris triangularis Halle, 1927, Shansi Formation, Taiyuan Coalfield, China (Halle, 1932).

**Last:** ?Gigantopteris taiyuanensis (Asama) Meyen, 1987, upper part of Upper Shihhotse Formation, Taiyuan Coalfield, China (Asama, 1962). This is based on leaf fossils. The youngest fructifications are Gigantonomia fukiensis (Yabe and Oishi) Li and Yao, 1983, and Gigantotheca paradoxa Li and Yao, 1983, lower part of Upper Shihhotse Formation (UFI), Taiyuan Coalfield, China.

**Intervening:** SAK?–KUN?

**Comments:** Wagner (1967) based this family on the ‘Emplectopteris Series’ of Asama (1962). It also corresponds to the Gigantopteridaceae of Li and Yao (1983). Meyen (1987) has argued that the latter name has to be rejected, because some Gigantopithes Schenck, 1883 foliage belongs to the Peltaspermales, and instead proposed the name Gigantonomiaceae. However, it is essentially identical to the Emplectopteridaceae, except in the degree of dissection of the leaf; the seeds of Emplectopteris Halle, 1927 are similar to Gigantonomia Li and Yao, 1983 in both form and position of attachment to the frond (Halle, 1932). Thus there seems little reason for separating the former into a separate family. The family was not included in the analyses of Crane (1985), or Doyle and Donoghue (1986), and it has been placed in its current taxonomic position following Meyen and Eggert, 1967. Meyen (1987) assigned them to the Peltaspermales. The first edition of The Fossil Record included Lescuropteris Schimper, 1869, from the Upper Carboniferous of Europe and North America, but this almost certainly belongs to the Trigonocarpaceae.

**Class** CYCADOPSIDA Barnard and Long, 1975

This class is treated in essentially the same way as Meyen (1987), except that the Lagenostomales and Bennettitales are excluded and placed in separate classes.

**Order** TRIGONOCARPALES Seward, 1917

**F. TRIGONOCARBACEAE** Seward, 1917

C. (BR?)–P. (ASS?) Terr.

**First:** ?Neuropteris antecedens Stur, 1875, and Holcospermum elliptosideum (Göppert) Walton, 1931, upper Black Limestone, Clwyd, Wales, UK (Walton, 1931). This record is based on adpressions yielding little anatomical information. Better documented are Rhynchosperma quinmiss Taylor and Eggert, 1967b, Quaestoria amplecta Mapes and Rothwell, 1980, and Medullosa sp. Taylor and Eggert, 1967a, lower Fayetteville Formation (PND), Arkansas, USA.

**Last:** ?Odontopteris subcrenulata (Rost) Zeiller, 1888, lower Shihhotse Formation, Shanxi, China (Halle, 1927). This is based on adpressions of foliage and can be dated no more accurately than Early Permian (Wagner et al., 1983). More accurately dated are the stem and rachis permineralizations Medullosa stellata Cotta, 1832, M. leucaertii Göppert and Sterzel, 1881, M. porosa Cotta, 1832, M. solmsii Schenck, 1889 and Myeloxylon elegans (Cotta) Brongniart, 1849, associated with the foliage adpressions Neurocallipteris planchardii (Zeiller) Cleal et al., 1990, and Alethopteris schnedieri Sterzel, 1981, Leukersdorf Formation (ASS), Erzgebirge, Germany (Barthel, 1976).

**Intervening:** ARN–NOG, SAK?–KUN?

**Comments:** This is the Medullosaceae of many authors. Attempts to subdivide the Trigonocarpaceae at the family level have not been satisfactory. For instance, the scheme proposed by Corsin (1960), and used in the first edition of The Fossil Record, is too heavily based on frond architecture for it be ‘natural’. Only the Potonieaceae appears to be sufficiently well circumscribed (below). The Trigonocarpaceae is therefore used here to encompass the entire Trigonocarpaceae, exclusive of the Potonieaceae.

**F. POTONIEACEAE** Halle, 1933

C. (PND?)–P. (ASS?) Terr.

**First:** ?Paripertes gigantea (Sternberg) Gothan, 1941, Tseishui Formation, Hunan, China (Yang et al., in Wagner et al., 1983). This refers to foliage adpressions from the upper part of the Lower Carboniferous, in the Chinese classification (its assignment to the PND is tentative). The oldest fructifications are Hexagonocarpus modestae (Bertrand) Seward, 1917 and Potoniea adiantiformis Zeiller, 1899, associated with Paripertes gigantea (Sternberg) Gothan foliage, Zone de Baulet (MRD), Belgium (Stockmans and Willière, 1953).

**Last:** ?Linopteris ganganopteroides (de Stefani) Wagner, 1958 (syn. L. brongniartii Zeiller, 1888, non Gutbier, 1835), Surmoulin and Millery Formations, Autun, France (Bouroz and Doubinger, 1977). This is based on foliage adpressions. The youngest fructifications are permineralized seeds Hexapterospermum pachypterum Brongniart, 1881 and H. stenopterum Brongniart, 1881, Rive de Gier Formation (CHV), Grand’Croix, France (Phillips, 1980).

**Intervening:** CHO–KRE, KLA?–NOG?

**Comments:** This is the only well-circumscribed family within the Trigonocarpaceae, and is based on the connection between Suctillia Scott, 1906 stems, Potoniea Zeiller, 1899 pollen organs, Hexagonocarpus Renault, 1896, Hexapterospermum Brongniart, 1874 seeds and Paripertes Gothan, 1941 and Linopteris Presl, 1838 fronds (Bertrand, 1930; Stidd et al., 1975; Stidd, 1978). It differs from other trigonocarpaceans in producing trilete, rather than monolete, pre-pollen.

**Order** CYCADALES Engler, 1892

The Dirhopalostachyaceae Krassilov, 1975 was proposed as an extinct family of cycads (in its broad sense), which showed a number of characters believed to be ‘proangiospermous’ (Krassilov, 1975, 1977). However, Doludenko and Kostina, in Meyen (1987) have reported evidence suggesting that Krassilov’s fossils are in fact early pinaeacean conifers. The family is thus not included in this analysis.
F. CYCADACEAE Persoon, 1807
C. (KIN?)-Rec. Terr.

First: ??Lesleya cheimarosa Leary and Pefferkorn, 1977, channel-fill immediately below Abbott Formation, Illinois, USA (Leary, 1990). This is a leaf with seeds attached to the axis, found in an extrabasinal ('upland') deposit. It was compared with various other putative early cycads, such as Archaeocycas whitei Mamay, 1973, Belle Plains Formation (ASS), Texas, USA, Phasmatoocycas kansana Mamay, 1973, Wellington Formation (ASS), Kansas, USA, and Soberhemiai jenkeri Kerp, 1983, Wadener Group (ASS), Nahe, Germany (Mamay, 1973, 1976; Kerp, 1983; Gillespie and Pefferkorn, 1986). Crane (1985) initially expressed doubt as to the cycadalean affinities of these Lower Permian fossils, as they had platyspermic seeds, but he later (Crane, 1988) accepted that this was not necessarily a barrier to them belonging to that order. Nevertheless they are quite different morphologically from cycads in the normally accepted sense, and it is perhaps wiser to regard them as cycad precursors, rather than true cycads. The oldest unequivocal cycad remains are Crossozamia chinensis (Zhu and Du) Gao and Thomas, 1989, C. minor Gao and Thomas, 1989, C. spadicea Gao and Thomas, 1989, C. cucullata (Halle) Gao and Thomas, 1989, Tiangbollinia circinais Gao and Thomas, 1989, Yuania chinensis Zhu and Du, 1981 and Taenipteris taiyuanensis Halle, 1927, Tayjuan Formation, Shanxi, China (Gao and Thomas, 1989). At least part of the Tayjuan Formation is Upper Carboniferous (Li and Yao, 1985), but Gao and Thomas claim that the cycadacean fossils originated from the Lower Permian (ASS).

Extant

Intervening: ASS, CRN, RHT–HOL.

Comments: Various other families have been mentioned within the Cycadales, including the Zamiaceae, Stangeriaceae and Nilsoniaceae. However, there has been no coherent attempt to analyse the distribution of these families in the fossil record. Such an analysis is beyond the scope of this report, and so the view of Harris (1961) has been followed, and these groups regarded as subfamilies within the Cycadales. Taylor (1969) suggested that Lasistophus polyasci Taylor, 1969 from the Calhoun Coal, Illinois, might be a Carboniferous pollen cone, but later work (Taylor, 1970) cast doubt on this.

Class GNETOPSIDA Engler, 1954

This class is taken here to have a wider circumscription than in most previous studies. It refers to the gymnospermous families included within the angiosperm/bennettite/pentoxylid/gnetalean clade by Crane (1985) and Doyle and Donoghue (1986).

Order BENNETTITALES Engler, 1892
F. BENNETTITACEAE Engler, 1892
Tr. (CRN?)–K. (MAA?) Terr.


Last: ??Pterophyllum sp., Augustovka River near Boshnaiakovo, Sakhalin Range, Siberia, former USSR (Krassilov, 1978). This is based on foliage without preserved cuticles. Better documented is Monanthesia magnifica Wieland ex Delevoryas, 1959, Mesaverde Formation (CMP), New Mexico, USA, which includes fructifications.

Intervening: RHT–ALB.

Comments: The traditional division of the Bennettitales into the Williamsoniaceae and Cycadeoidaceae (e.g. Taylor, 1981; Stewart, 1983) is regarded by Crane (1985, 1988) as dubious and is not recognized here. Some early authors regarded the Bennettitales as closely related to the Cycadales, due to similarities in the foliage and general habit of the plants (e.g. Chamberlain, 1935). Harris (1969) argued, however, that the phylogenetic relationship is only remote, although he gave no opinion as to the position of the Bennettitales. Recent analyses suggest that the Bennettitales cluster together with the Pentoxylales and Gnetales (Crane, 1985, 1988; Doyle and Donoghue, 1986).

Order PENTOXYLALES Pilger and Melchior, 1954
F. PENTOXYLACEAE Pilger and Melchior, 1954
J. (TOA)–K. (ALB) Terr.

First: Taeniopoteris spatulata McClelland, 1850 and Carnooconites sp., Talbragar Fish Beds, New South Wales, Australia (White, 1981).


Intervening: TTH, HAU, VLG.

Comments: The distribution of this family has been reviewed by Drinnan and Chambers (1985), who conclude that it was a significant element in the mid-Mesozoic floras of Gondwanaland.

Order GNETALES Engler, 1892
F. GNETACEAE Lindley, 1834
Tr. (CRN?)–Rec. Terr.

First: ?Dechellyia gormanii Ash, 1972 and Masculostrobis clathratus Ash, 1972, Chinle Formation, Arizona, USA. The taxonomic position of these enigmatic fossils is still somewhat in doubt. Better documented is Drewnia potomacensis Crane and Upchurch, 1987, Potomac Group (APT), Virginia, USA.

Extant

Intervening: APT.

Comments: Some authors divide the order into three families, one for each of the extant genera. The meagre fossil record of the order is discussed by Crane (1988).

Class PINOPSISIDAE Meyen, 1984

This is the Coniferales of many authors. The classification adopted here is essentially that of Meyen (1987), except that the Ginkgoales have been incorporated. The close relationship of the ginkgos to the conifers is reflected in most traditional classifications (e.g. Chamberlain, 1935) and is supported by cladistic analysis (Crane, 1985; Doyle and Donoghue, 1986). Some expansion of the classification of Palaeozoic conifers has also been included, following Clement-Westervich (1988) and Maps and Rothwell (1991).
Order CORDAITANTHALES Meyen, 1984
F. CORDAITANTHACEAE Meyen, 1984
C. (IVO?)–P. (ASS) Terr.
First: ?Mitrospermum bulbosum Long, 1977, Cementstone Group, Borders Region, Scotland, UK. This is based on an isolated seed, which has many features in common with younger seeds assigned to this family, but there is no evidence of the rest of the plant that produced it. Better documented is Cordaitanthus pitcairnii (Lindley and Hutton) Renault, 1881 and Cordaites palmaeformis (Göppert) Weiss, 1871, Assise de Chokier (KIN), Belgium (Stockmans and Willière, 1954).
Intervening: MRD–NOG.
Comments: This family is known only from palaeo-equatorial assemblages. There are records of Cordaites Unger, 1850 foliage as high as the Upper Permian in Cathaysia (e.g. Mei, 1984) but, in view of the difficulty of separating the foliage of this family from that of other cordaitanthalean families, they are not referred to in the above-quoted range.

F. RUFLORIACEAE Meyen, 1982
C. (KIN?)–P. (TAT?) Terr.
First: ?Rufloria subangusta (Zalessky) Meyen, 1963, Kaezovsky ‘Suite’, Kuznetsk, former USSR (Meyen, 1982). This record is based on foliage adpressions for which there is no epidermal evidence. The oldest fructifications are Krylowsia sibirica Chachlov, 1938, Mazurovsky ‘Suite’ (VRK?), Kemenov and Tom’-Usinsk regions, Kuznetsk, former USSR (Gorelova, in Gorelova et al., 1973).
Intervening: MRD–MEL?, KSK–UFI.
Comments: See comments on the Vojnovskyaceae.

F. VOJNOVSKYACEAE Meyen, 1982
P. (ASS)–P. (TAT) Terr.
First: Vojnovskyaya usjatensis Gorelova, in Gorelova et al., 1973, Promezhutochny ‘Suite’, Kemerov Region, Kuznetsk, former USSR.
Intervening: SAK–KAZ.
Comments: The assignment of this family and the Rufloriciaceae to the Cordaitanthales is following Meyen (1987, 1988), although some doubt has been expressed by Miller (1985) and Rothwell (1988). Cordaites Unger, 1850, leaves, which might belong to the Vojnovskyaceae, are reported as low as the Mazurovsky ‘Suite’ (VRK?) in Angaraland (Vakhrameev et al., 1978). However, their identity has not been confirmed by epidermal evidence, and they are not associated with fructifications.

Order DICRANOPHYLLALES Němejc emend.
Archangelsky and Cúneo, 1990
F. DICRANOPHYLLACEAE Němejc emend.
Archangelsky and Cúneo, 1990
C. (ALP?)–P. (TAT) Terr.
First: ?Dicranophyllum richirii Renier, 1907, Zone de Malonne, Baudour, Belgium (Stockmans and Willière, 1953). This is based on sterile foliage. The oldest fructification is Dicranophyllum gallicum Grand’Eury, 1877, Commentry (KLA?), France (Renault, 1890).
Last: Mostochia sp. with associated fructifications, Kama River, near Ustinov, west of Ural Mountains, former USSR (Meyen and Smoller, 1986); also Sitokovia petschorensis Meyen, 1969, Pechora ‘Series’, Pechora, former USSR.
Intervening: KSK, KLA–ASS, KUN–KAZ.
Comments: Meyen and Smoller (1986) characterize this family mainly on features of the foliage, including epidermal structure. There is very limited evidence available on their fructifications, however, and it is far from certain that it is a homogeneous group.
First: ?Dichophyllum moorei Ellias ex Andrews, 1941, Rock Lake Shale and Ireland Sandstone, Kansas, USA (Cridland and Morris, 1963). This is based on foliage, which Meyen (1987) included in this family. Better documented is Trichopitys heteromorpha Florin, 1949, Lydiennes Formation, Hérault, France (ASS).
Last: Biarmopteris pulchra Zalessky, 1939 and Maurites gracilis Zalessky, 1939, Sylva River, Middle Fore-Urals, former USSR (Meyen, 1982).
Comments: This family has been variously assigned to the Ginkgoales (Andrews, 1941; Florin, 1949) and Peltaspermales (Meyen, 1984). Its presently accepted position in the Dicranophylalles follows Archangelsky and Cúneo (1990).

Order PINALES Meyen, 1984
Fragments of conifer foliage have been widely documented in the Upper Carboniferous, the earliest being Swillingtonia denticulata Scott and Ch-aloner, 1983, Middle Coal Measures, West Yorkshire, England, UK, (VRK: see Lyons and Darrah, 1989 for a review). However, they rarely have fructifications attached, and so cannot be assigned to families.

F. EMPORIACEAE Mapes and Rothwell, 1991
C. (KLA?)–P. (TAT) Terr.
First and Last: Emporia locknrdii (Mapes and Rothwell) Mapes and Rothwell, 1991, Shawnee Group, Hamilton Quarry, Kansas, USA.
F. BURIADIACEAE Pant, 1977
C. (KLA?)–P. (ART) Terr.
First: Buriadia heterophylla (Feistmantel) Seward and Sahni, 1920, Itararé Subgroup, Paraná Basin, Brazil (Rocha Campos and Archangelsky, in Wagner et al., 1985). The chronostatigraphical position of these fossils is not certain, but seems more likely to be Upper Carboniferous than Lower Permian.
Last: Walchia sp. (syn. B. heterophylla – see Florin, 1940), upper Sadong Formation, Pyongyang Coalfield, Korea (Kawasaki, 1934).
Intervening: ASS.
F. UTRECHTIACEAE Mapes and Rothwell, 1991
P. ASS—UFI Terr.


Last: Ortie sia leonardii Florin, 1964, Val Gardena Formation, Dolomites and Vicentinian Alps, Italy (Clement-Westerhof, 1984).

Intervening: SAK—KUN.

Comments: This family is approximately equivalent to the Walchia eae sensu Clement-Westerhof (1984) and Kerp et al. (1990). However, Mapes and Rothwell (1991) gave the family a more rigorous definition based mainly on ovulate cone structure, which required a change of name.


First and Last: Ullmannia bronni Göppert, 1850 and U. frumentaria Göppert, 1850, Kupferschiefer, Lower Rhine, Germany (Schweitzer, 1963); and Marl Slate, Cumbria and Durham, UK (Stoneley, 1958).

Comments: The natural status of this family has still to be confirmed (Clement-Westerhof, 1988). Ullmannia Göppert, 1850 has also been reported from older (SAK?) and slightly younger (KAZ) Angaran assemblages (summarized by Vakhrameev et al., 1978), but their relationship to the European species (and thus to the family) is unclear.

F. VOLTIACEAE Florin, 1951 Tr. (SMI?)—K. (CEN) Terr.

First: Aethophyllum speciosum Schim per, 1869 and Voltzia heterophylla Brongniart, 1835, Upper Buntsandstein, Germany (Mä gdefrua, 1956).

Last: Protodammara speciosa Hollick and Jeffrey, 1909 and Dectyolepis cryptomerioideas Hollick and Jeffery, 1909, Raritan Formation, Staten Island, USA.

Intervening: LAD—BTH.

Comments: Many authors have included within this family a wide variety of Pala eozoic and Mesozoic conifers (e.g. Taylor, 1981; Stewart, 1983). However, Clement-Westerhof (1988) has separated out most of the Pala eozoic taxa into the Majonicaceae and Ullmanniaceae. Whether the remaining Mesozoic members form a 'natural' group, and their relationship to the Taxodiaceae, remain uncertain (Miller, 1982). It includes the Cycadocarpid iaceae, listed separately in the first edition of The Fossil Record, and the Swedenborgiaceae Zimmermann, 1959.

F. PODOCARPACEAE Endlicher, 1847 Tr. (DIE?)—Rec. Terr.

First: ?Voltzia cf. heterophylla Carpentier, 1935 non Brongniart, 1835 (syn. Russikia media (Tennison Woods) Townrow, 1967), Sakoa Group, Madagascar. This record is based on foliage. The oldest frut ications are R. media (Tennison Woods) Townrow, 1967, Burnera WaterFall, Natal, South Africa (SMI?).

Extant Interdivening: NOR, BAJ, BER?, CMP—HOL.

F. PALISSYACEAE Florin, 1958 Tr. (CRN)—J. (BAJ) Terr.

First: Stachyotaxus lipoldii (Stur) Kräusel, 1952, Lettenkohle, Lunz, Austria; and S. sahni i Kräusel, 1952, Lettenkohle, Neuwelt, Switzerland.

Last: Palissy a sp., Saltwick Formation, North Yorkshire, England, UK (Hill and van Konijnenburg van Cittert, 1973). This material has not been described in detail, but is reported to include a female cone.

Extant Interdivening: RHT—HET.

Comments: The validity of this family has recently been questioned (Meyen, 1984; Miller, 1985) but, in the absence of any formal taxonomic changes, the traditional concept has been maintained.

F. ARAUCARIAEAE Henkel and Hochstet tler, 1865 Tr. (CRN?)—Rec. Terr.

First: Araucarites parsorensis Lele, 1954, and A. indica Lele, 1962, Parsora Formation, South Rewa, India. The exact chronostratigraphical position of these fossils is uncertain, but appears to be younger than TAT but older than NOR (Vakhrameev et al., 1978).

Extant Interdivening: RHT—HOL.

Comments: The fossil record of this family is reviewed by Stockey (1982).

F. PINACEAE Lindley, 1836 Tr. (CRN)—Rec. Terr.

First: Compos trobus neoteric us Delevoyas and Hope, 1973 and Millerostrobus pekinensis Taylor et al., 1987, Pekin Formation, North Carolina, USA.

Extant Interdivening: RHT—HET, BAJ—BTH, BER—HOL.

Comments: Compos trobus Delevoyas and Hope, 1973, was originally placed in a separate family (Compos tro baceae Delevoyas and Hope, 1973), but most authors now include it in the Pinaceae. The pollen cone Millerostrobus Taylor et al., 1987, has features indicative of both the Pinaceae and the Podocarpaceae.

F. CHEIROLEPIDIACEAE Takhtajan, 1963 Tr. (CRN?)—K. (CMP?) Terr.

First: ??Frenelopsis hoheneggeri (Ettingshausen) Carpentier, 1937, Sainte Baume, France. This is based on incompletely described and poorly preserved specimens. Better documented is Frenelopsis oligostomata Romariz, 1946, Esigueira (TUR), Beira Littorale, Portugal (Alvin, 1977).
Its circumscription has become considerably enlarged to the Jurassic. They are similar to both the Pinaceae and the Cheirolepidae. Comments: The confused nomenclature for this family encompass taxa originally included in the Cupressaceae and suggest a close phylogenetic relationship with the Cheirolepidae. Intervening: RHT—ALB.


Comments: The confused nomenclature for this family has been discussed and stabilized by Watson (1982, 1988). Its circumscription has become considerably enlarged to encompass taxa originally included in the Cupressaceae (e.g. in the first edition of *The Fossil Record*).

F. PARARAUCARIACEAE Stockey, 1977 J. (?m./u.)—Rec. Terr. First and Last: *Pararaucaria patagonica* Wieland, 1929, Cerro Cuadrado fossil forest, Patagonia, Argentina (Stockey, 1977). Comments: The exact chronostratigraphical position of these fossils cannot be fixed beyond Middle to Upper Jurassic. They are similar to both the Pinaceae and Taxodiaceae, and suggest a close phylogenetic relationship between these families.


F. ARCTOPTYCAEAE Manum and Bose, 1989 J. (OXF)—K. (TUR) Terr. First: *Sciadopitys persulcata* (Johansson) Sveshnikova, 1981 and *S. nathorstii* (Halle) Sveshnikova, 1981, Ramsa Formation, Andeya, Norway (Manum, 1987). Last: *Sciadopitys uralesis* (Dorofeev and Sveshnikova) Sveshnikova, 1981, Ural Mountains, former USSR. Intervening: KIM—ALB. Comments: This family was proposed for a variety of leafy shoots from mainly Arctic regions, which were traditionally included in the Sciadopityaceae (Manum and Bose, 1989). However, full details of the proposal have still to be published. No fructifications are known.

F. SCIADOPITYACEAE Seward, 1919 J. (OXF)—Rec. Terr. First: *Sciadopitys macrophylla* (Florin) Manum, 1987, *S. lagerheimii* (Johansson) Manum, 1987 and *Sciadopitys*-like cone scales. Ramsa Formation, Andeya, Norway (Bose, 1955; Manum, 1987). Extant Intervening: DAN—HOL. Comments: Virtually all macrofossils assigned to this family are foliage fragments, although there is good palynological evidence for the existence of this family in the Lower Tertiary (Manum and Bose, 1988). Many authors have included *Sciadopitys* Siebold and Zuccarini, 1870 and its allies within the Taxodiaceae (e.g. Taylor, 1981). However, Christophel (1976) has argued cogently for the separation of the Sciadopityaceae, a view which has been adopted here. Florin (1958) assigned foliage fragments (*Elatocladus* sp.) from the Scalby Formation (BAJ), North Yorkshire, England, UK, to this family, an opinion which has been disputed by Harris (1979). The inclusion of *Sciadopitys scania* Florin, 1922 from the Rhaetic (RHT) of Sweden has also been rejected (Bose, 1955).

F. CEPHALOTAXACEAE Neger, 1907 J. (BAJ?)—Rec. Terr. First: *Elatocladus zamoides* (Leckenby) Seward, 1919, Cloughton Formation, North Yorkshire, England, UK (Harris, 1979). This record is based on foliage alone. Extant Intervening: BTH—HOL. Comments: Foliage regarded as typical of this family occurs reasonably commonly in the fossil record, but records of fructifications are equivocal. For instance, some of the seeds identified as *Cephalotaxoxspermum* Berry, 1910 might in fact belong to the Podocarpaceae or Taxaceae (Miller, 1977).

F. CUPRESSACEAE Bartling, 1830 T. (DAN)—Rec. Terr. First: *Cupressinoxia interruptus* (Newberry) Schweitzer, 1974, Volcanic Tuff, Smoky Tower, Alberta, Canada (Christophel, 1976). Extant Comments: Many authors have extended the range of this family back to the Triassic. However, this is based on fossils which, at least in part, probably belong to the Cheirolepidae (Watson, 1977, 1988).

Order GINKGOALES Engler, 1897 F. GINKGOACEAE Engler, 1897 Tr. (CRN?)—Rec. Terr. First: *Ginkgoites lunzensis* (Stur) Florin, 1936, Lettenkohle, Lunz, Austria (Kräusel, 1943). This record is based on foliage adpressions. The oldest fertile material is *Allicospermum xystrum* Harris, 1935, Scoresby Sound, Greenland (RHT). Extant Intervening: RHT, HET, BAJ—BTH, BER, CEN—HOL. Comments: Meyen (1987) classified the Ginkgoales with the so-called 'Mesozoic pteridosperms'. However, Crane (1985) and Doyle and Donoghue (1986) show that they are more closely aligned with the Pinales. Many of the putative ginkgoaleans from the Palaeozoic mentioned in the first edition of *The Fossil Record* probably belong to the Peltaspermpidosida (Meyen, 1987). Attempts to classify the Ginkgoales into families have tended to rely on vegetative structures and have not been widely followed.

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MAGNOLIOPHYTA ('ANGIOSPERMAE')

M. E. Collinson, M. C. Boulter and P. L. Holmes

We consider that the angiosperms are a special case, requiring a format which differs from other chapters in this volume. Our reasons are explained below.

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COMMENETS ON THE 1967 LIST

The presentation of stratigraphical ranges of angiosperm families in the first edition of The Fossil Record (Chesters et al., 1967) was based on the wisdom of those three authors. It provided valuable suggestions about the likely current consensus for about 150 angiosperm families. The influence of the late Marjorie Chandler was not insignificant in the judgements (N. F. Hughes, pers. comm.). There was no attempt to justify the taxonomic composition of the family names, or to caution the users of uncertainties involving taxonomy, migration and evolution. Many users of these data may have accepted the records unaware of the subjective evidence upon which they were based.

PROBLEMS OF THE ANGIOSPERM RECORD

We are anxious to avoid these pitfalls and to stress the limitations of what we understand from present knowledge. Most importantly, we are anxious that the data presented here are not seen as accurate expressions of the stratigraphical ranges of any angiosperm taxa; although the most well-researched examples (noted under 'comments') should indicate minimum ages. The differences between the first and second editions of the angiosperm chapter in The Fossil Record may seem to be a regression, especially in comparison to the way in which other fossil groups are treated in this volume. This is because we believe the angiosperms require special treatment.

Angiosperms are generally represented in the fossil record by individual organs like pollen, flowers, fruits, seeds, leaves and wood. Each organ provides a different set of characters and to the extent to which these are diagnostic of modern taxa (or can be used to diagnose extinct taxa) varies considerably, both within and between organs. These problems have been exacerbated in the past by a common tendency to include fossils in modern taxa based on superficial similarity rather than upon in-depth analysis. Although the latter is now the rule rather than the exception, many older determinations have not yet been revised. The diversity of many modern angiosperm taxa renders these revisions time-consuming and often beyond the scope of an individual or even a small group of researchers. Angiosperm organs also vary in their preservation potential which is further influenced by the habitat, growth habit and functional biology of the plant on which they are borne. The Cretaceous (Lidgard and Crane, 1990) and early Tertiary (Collinson, 1990) are periods of rapid diversification with novel character combinations on individual organs and reconstructed plants. These partly influence, and are influenced by, co-adaptation with insects and mammals. Combined, these phenomena make the angiosperms an exceptionally complex taxon for which to present a synthesis of family groupings. A stratigraphical range chart for angiosperm families is thus unobtainable at present, and has not been produced to accompany this chapter.

PROCEDURE FOR THE CURRENT LIST

We base our primary occurrence data on two defined authoritative sources; Muller (1981, with occasional reference to Muller, 1985) for pollen, and Holmes et al. (1991) for the fossil remains of other plant organs. The age quoted in these documents for the fossil genera within each family is listed below. For the pollen this age ('Muller First') is the first occurrence of type species of fossil angiosperm genera within the families represented and only includes the first appearances of type species of fossil angiosperm genera within the families represented and only includes...
fossil genera described up to the early 1980s. The PFR also includes at least 213 generic names for angiosperms which were not assigned to families by the original authors and thus could not be considered here. Both PFR and Muller (1981, 1985) include untested and therefore doubtful indications of family affinity.

The taxonomic system utilized is believed to be most widely accepted, that of Cronquist (1981) and, where possible, the time ranges are set against the matching stratigraphical scheme of Harland et al. (1990). All the established angiosperm families (except Priscaceae) have modern representatives and so we only record the first appearances of the generic types. Extinct groups, e.g. Czekanowskiales and Dirhopalostachyaceae, which are considered to be ‘proangiosperms’ (see Krassilov, pp. 7–10, in Douglas and Christophel, 1990) have been excluded (covered in Chapter 44, this volume).

**EXTINCT ANGIOSPERM FAMILIES**

Some palaeobotanical researchers try to fit fossil genera into a modern family, even when they may actually fall between division assignment for these ‘intermediates’. Workers are reluctant to form a new intermediary family for extinct angiosperms; some are even reluctant to entertain the concept that high-ranking groups during the early times of two such families. Others give only an ordinal, class or reluctant to form a new intermediary family for extinct angiosperms; some are even reluctant to entertain the concept that high-ranking groups during the early times of ‘angiosperm’ evolution may have been very different from the modern families and orders. At its most extreme, this part of our argument means that the Magnoliophyta, a group based on modern plants, is a name that has less and less meaning back in time; the earliest plants of the lineage, taken on their own, might have had a very different definition and probably should be named accordingly and differently.

These difficult taxonomic problems were made easier through the Montreal–Leningrad editions of the ICBN by the concept of the ‘organ-genus’. This confusingly named taxon allowed ‘some genera of fossil plants not to be assigned to a family’. The organ-genus taxon was removed from the Code at the Melbourne congress, leaving fossil plant genera to be either modern genera or form genera. The latter ‘may or may not be assigned to a family’. The Code does not distinguish between taxa of family rank and higher, being based on modern or on fossil material. Nevertheless, we are aware of only one extinct angiosperm taxon at a higher rank than that of genus.

The major reason that hardly any extinct angiosperm families or orders have been established by palaeobotanists is that plant fossils are found as separate organs. To diagnose any large group, extinct or living, requires evidence from as many organs as possible. Usually the evidence of such associations is lacking for fossil angiosperms. Exceptions are for the modern families Betulaceae, Cercidiphyllaceae, Fagaceae, Platanaceae, Juglandaceae, Ulmaceae and to some extent Trochodendraceae, Salicaceae, Aceraceae and the extinct Priscaceae (comments herein and review by Collinson, 1990). This detailed knowledge is largely the result of intensive research over the last ten or so years. More frequently, there is detail available for individual organs such as pollen, leaves, woods and fructifications, but their links are rarely clear. It is generally considered inadequate to establish families from the evidence of just one organ.

The palynological evidence, taken on its own, does show evidence of some large groups of extinct angiosperms. Muller (1985) summarized the widely held view that the normapolles and triploprojectate pollen forms are from plants of two distinct and extinct families. Also, small, clavate pollen from the Cretaceous may be from a third, even older, group of family rank. Several palaeobotanists are working hard to show details of other organs that were associated with these fossils: other extinct angiosperm families may soon be described. In this present work the palynological record of these three most ancient groups is recognized within the Juglandales (see ‘Comments’, Juglandaceae), the Santalales (see ‘Comments’, Loranthaceae) and the Laurales (see ‘Comments’, Chloranthaceae) respectively.

Of course, these limitations in palaeobotanical taxonomy are highlighted when a compendium such as this is prepared. If nothing else, a major result of this chapter is to demonstrate these theoretical constraints in a much more practical way using the fossils themselves. The primary data presented here, although authoritative, give a very clouded view of angiosperm evolution, which can only be partially improved by our ‘Comments’ additions. This may encourage more consideration of the high-ranking extinct angiosperm taxa that are, so far, largely not established (but see Priscaceae Retallack and Dilcher, 1981; Kvaček, 1992), and which might guide a scientific re-assessment of Cretaceous and early Tertiary angiosperm evolution. We hope that this chapter will initiate production of a more intelligent and informed set of data in the (hopefully) computerised third edition of *The Fossil Record*.

**STANDARDS AND PRINCIPLES FOR OUR COMMENTS**

For each of the family listings we have extracted the earliest occurrence of the family which is cited in the PFR (Plant Fossil Record) database (Holmes et al., 1991). Where several examples are cited with a broad age range (e.g. Tertiary) but one is more focused (e.g. Eocene), we have taken that more accurate example. This means that an earlier record may have been excluded, but this cannot be corrected without a complete revision of all the stratigraphical citations in PFR. We have excluded tentative family assignments, except where these were the only examples cited in PFR. One of us (MEC) has commented on the megafossil record (following each PFR entry) and MCB has commented on the pollen records (Muller, 1981) after each Muller entry. The use of the words ‘pending’ and ‘rejected’ is explained by Muller (1981).

Comments on megafossils are given only when they are based on additional information not included within the entire PFR, and they reflect only personal knowledge rather than a substantive search of the entire literature on fossil angiosperms. While such a detailed search would have been preferable, it is impossible within the time-scale of two months available for this project, ever since the PFR database became available for use. Furthermore, comments on all the specific PFR citations are impossible at this time as they would require major world travel; consultation with many specialists world-wide and numerous searches of museum collections for old and forgotten specimens, some of which might well have deteriorated or even have been lost. The comments are restricted to the pre-Pleistocene
fossil record. We hope that this publication will stimulate the necessary revisions both of the PFR database and of the evidence cited in our comments.

Comments on megafossils follow the philosophy of Collinson (1986b) whereby an isolated organ can be assigned to a modern genus, and hence family, provided that it exhibits a suite of diagnostic characters which fall within the range of variation of the organ in the modern representatives of the family and which are unique to that family. Obviously, additional information from multiple organs, especially in organic connection, strengthens the proposed relationship (Collinson, 1990). It is widely accepted that many early determinations of leaves to modern genera and families were incorrect (see discussion in Taylor, 1990, p. 281). In the Cretaceous, recent studies of both leaves and woods have shown that these organs often possess some characteristics of several modern families or have a generalized form perhaps for an order or subclass (e.g. Page, 1981; Crabtree, 1987; Wheeler et al., 1987; Upchurch and Dilcher, 1990). For these reasons, we have not accepted records from older literature unless they have been accepted as part of a more recent study.

F. ACANTHACEAE de Jussieu, 1789

PFR: No record.
Comments: A single seed from the uppermost Eocene of England was identified to modern Acanthus by Reid and Chandler (1926). The original has deteriorated and no new specimens have been found. This record should be considered as unconfirmed. We are not aware of any well-substantiated megafossil record for the family.

Muller First: Multiarolites formosus (form taxon) Pares Regali et al., 1974a, Lower Miocene, Brazil. Multimarginites vanderhammeni (form taxon) Germeraad et al., 1968, Lower Miocene, northern South America.

Comments: Unchallenged. See also list in Taylor (1990) for possible records from the Middle Eocene to Lower Oligocene of North America.

F. ACERACEAE de Jussieu, 1789

Comments: The modern genus Acer is recorded from the latest Palaeocene onwards and the related 'Acer articum' complex occurs in the upper Maastrichtian (Wolfe and Tanai, 1987). These records are based on fruits and associated foliage.

Comments: Unchallenged.

F. ACTINIDIAEAE Hutchinson, 1926

Comments: Seeds like those of modern Saurauia were recorded from the Maastrichtian onwards in Europe (Knobloch and Mai, 1986). Seeds like those of modern Actinidia are known from the Upper Eocene onwards in Europe (Fris, 1985a). Leaves like those of Saurauia occur in the Middle Eocene of North America (Taylor, 1990).

Pollen: No record.

F. AGAVACEAE Endlicher, 1841

PFR First: Asteliaephusphylum italicum Squinabol, 1892. Leaf. Tertiary, Italy: Santa Guistina.
Comments: Tidwell and Parker (1990) described stems of Protoyucca (an arborescent monocotyledon with secondary growth), but although they noted similarity to modern Yucca, they did not make a family assignment for the fossils. We know of no well-substantiated megafossil record of the family (Daghlian, 1981).

Comments: Too early; no supporting evidence available of this modern genus in the Eocene.

F. AKANIIACEAE Stapf, 1912

PFR: No record.
Comments: Romero and Hickey (1976) described a single leaf impression from the Palaeocene of Argentina as Akania americana Romero and Hickey, which they included in the family Akaniaceae, although expressing caution in the discussion regarding the determination to the family based on such limited material.

Pollen: No record.

F. ALANGIACEAE de Candolle, 1828

Comments: Leaves and fruits like those of modern Alangium are recorded from the Middle Eocene of North America (Taylor, 1990) and the Lower (Chandler, 1964), Middle (Mai, 1976), and Upper (Mai and Walther, 1985) Eocene of Europe.

Comments: Unchallenged.

F. ALISMATACEAE Ventenat, 1799

Comments: Erwin and Stockey (1989) assigned a permineralized petiole from the Middler Eocene of Canada to the family. Collinson (1983) documented fruits from the uppermost Eocene/Lower Oligocene of England, UK, but the majority of the records are Oligocene or younger (Mai, 1985a; Collinson, 1988a; Erwin and Stockey, 1989).
Muller First: Pending.

F. AMARANTHACEAE de Jussieu, 1789

PFR: No record.
Comments: Negru (1979) recorded seeds like those of modern Amaranthus in the uppermost Miocene (Pontian) of Moldavia, former USSR. Friis (pers. comm., 1991) has unpublished seeds from the Santonian/Campanian of Sweden.

Muller First: see Chenopodiaceae.
Comments: It is not possible to distinguish the pollen of these two families.

F. ANACARDIACEAE Lindley, 1830

Comments: Fruits are diverse in the Lower Eocene of England (Chandler, 1964) and fruits, leaves and woods are reported from the Middle Eocene of North America (Taylor,
Plants

1990). Mai (1987a) lists an Upper Palaeocene fruit, and Knobloch and Mai (1986, p. 170) refer to Upper Cretaceous foliage from several areas, but all these pre-Eocene records are in need of revision. Romero (1986a) cites one Coniacian record followed by a Lower Tertiary diversification of the family in South America.

**Muller First:** *Rhus* type = *Tricolporopollenites cingulum* (form taxon). Gruas-Cavagnetto, 1976a, Palaeocene, France.

**Comments:** Possible.

**F. ANNONACEAE** de Jussieu, 1789


**Comments:** Seeds are widespread in the Eocene; the earliest record is from the Maastrichtian of Nigeria and one foliage from several areas, but all these pre-Eocene records followed by a Lower Tertiary diversification of the family in South America.

**Muller First:** *Tricolporopollenites cingulum* (form taxon). Gruas-Cavagnetto, 1976a, Palaeocene, France.

**Comments:** Possible.

**F. APIACEAE** Lindley, 1846

**PFR First:** *Peucedanites specabilis* Heer, post-October 1859. Fruit. Tertiary, Miocene, Switzerland: Oeningen.

**Comments:** Seeds are widespread in the Eocene; the earliest record is from the Maastrichtian of Nigeria and one species is recorded in the Middle Palaeocene of Pakistan (Tiffney and McClammer, pp. 13–20, in Collinson, 1988c). Leaves are recorded in the Middle Eocene of North America (Taylor, 1990).

**Muller First:** *Foveomorphomonocolpites humberoides* (form taxon). Sole de Porta, 1971: Maastrichtian, Colombia.

**Comments:** Unchallenged.

**F. AQUIFOLIACEAE** Bartling, 1830


**Comments:** Fruits like those of modern *Ilex* are recorded from the Maastrichtian onwards in Europe (Knobloch and Mai, 1986; Mai, 1987a) although there is only one doubtful record from the well-known Tertiary floras of England, UK (Chandler, 1964). Two Eocene and one Upper Palaeocene records of *Ilex* leaves are cited by Taylor (1990). The latter may need revision.

**Muller First:** *Ilex pollenites* (form genus). H. A. Martin, 1977. Turonian, Australia.

**Comments:** Well-supported for family.

**F. ARECACEAE** de Jussieu, 1789

**PFR First:** *Limnophyllum primaevum* Hosius and Marck, April 1880. Leaf. Cretaceous, Senonian, Germany, Westfalen.

**Comments:** Fruits and seeds occur in the Middle Eocene of North America and seeds have a widespread occurrence in younger strata (Cevallos-Ferriz and Stockey, 1988a). Leaves are recorded from the Middle Eocene of Europe (Wilde, 1989) and Lower and Middle Eocene of North America (Taylor, 1990).

**Muller First:** *Spathiphyllum* type: Graham, 1976. Lower Miocene, Mexico. Leopold, 1969; Miocene, Palau, West Pacific.

**Comments:** Unchallenged.

**F. ARALEACEAE** de Jussieu, 1789

**PFR First:** *Araliopsis breviliba* Berry, 1916. Leaf. Upper Cretaceous, USA: Maryland, Cecil County, Bull Mountain.

**Comments:** Knobloch and Mai (1986) recorded fruits like those of modern *Aralia* and *Acanthopanax* in the Maastrichtian of Europe, while fruits like modern *Aralia*, *Pentapanax* and *Schefflera* are recorded from the Upper Eocene onwards (Mai and Walther, 1985; Palamarov, pp. 97–106, in Collinson, 1988c). Araliaceae leaves (especially like modern *Dendropanax* and *Orepanax*) are listed from the Palaeocene and Middle Eocene onwards in North America (Taylor, 1990). Leaves from the Middle Eocene of Europe, reported by Wilde (1989), were not determined to modern genera.

**Muller First:** *Tricolporopollenites armatus* (form taxon). Gruas-Cavagnetto and Bui, 1976. Upper Palaeocene, France.

**Comments:** Unchallenged.

**F. APOCYNACEAE** de Jussieu, 1789


**Comments:** The fossil record for this family is sporadic, but we see no reason to reject fruits and seeds recorded in the Lower Eocene of England, UK (Chandler, 1964) and foliage in the Middle Eocene of Germany (Wilde, 1989). Cretaceous woods included in the family by Taylor (1990) were described only as ‘woods with characteristics of Apocynaceae’ by Wheeler et al. (1987) who also noted similarity to Simaroubaceae and other families.

**Muller First:** *Alyxia* type Muller, 1968, Palaeocene, Borneo. *Diporites isokassenzygogrii* (form taxon). Gruas-Cavagnetto, 1976, Lower Eocene, France.

**Comments:** Well-supported by other records of pollen and megafossils.

**F. APONOGETONACEAE** Agardh, 1858

**PFR:** No record.

**Comments:** Zhilin (1974a,b, 1989) and Pneva (1988) have described leaves like those of modern *Aponogeton* from the Oligocene of the former USSR.

**Pollen:** No record.
Comments: See review by Gee (pp. 315–19, in Knobloch and Kvacek, 1990). Maastrichtian, South America, Africa and Malaysia.


Comments: All unchallenged.

F. ARISTOLOCHIACEAE de Jussieu, 1789


Comments: Leaves assigned to modern Aristolochia are listed by Taylor (1990) from North America and reported from the Tertiary, Eocene, USA: California, Nevada County, You Bet (sic.).

Pollen: No record.

F. ASCLEPIADACEAE Brown, 1810

PFR First: Asclepiadites laterita MacGinitie, 15 November 1941. Leaf, Tertiary, Eocene, USA: California, Nevada County, You Bet (sic.).

Comments: Seeds from the uppermost Eocene of England were assigned to modern Phyllanthera and Tylorapha by Reid and Chandler (1926). The former was represented by six specimens, the latter by a single specimen. The originals are in poor condition, and no new material has been found. Palamarev (1968) assigned a Miocene seed from Bulgaria to the family. We consider all these records to be unconfirmed, and we know of no well-substantiated mega-fossil record for this family.


Comments: Unchallenged.

F. ASTERACEAE Dumortier, 1822


Comments: A Lower Eocene fruit described by Chandler (1978, p. 30) was tentatively compared with this family. The fruit record seems otherwise to be restricted to the Miocene onwards in Europe (e.g. Mai, 1985a; Szafer, 1954).

Muller First: Tricolporopollenites microechinatus (form taxon) Hochuli, 1978, Oligocene, Austria. Tubulifloridites antipodica (form taxon) Kemp and Harris, 1975, Oligocene, Indian Ocean. Tubiflorae type Kruzsch, 1970d, Oligocene, Germany; Leopold and Macginitie, 1972, Oligocene, USA.

Comments: More ultrastructural examination required.

F. BALANOPHORACEAE L. C. and A. Richard, 1822

PFR: No record.

Comments: We know of no well-substantiated mega-fossil record for this family.


Comments: Unchallenged.

F. BERBERIDACEAE de Jussieu, 1789

PFR First: Winchellia triphylla Lesquerreux, October 1893. Leaf: Cretaceous, USA: Yellowstone River, near mouth of Powder River.

Comments: Leaves like those of modern Mahonia are listed from the Middle Eocene and commonly from the Oligocene of North America (Taylor, 1990). Lower and Upper Oligocene examples (the former Mahonia, the latter Mahonia and Berberis) were accepted by Wolfe and Schorn (1989) and Manchester and Meyer (1987). The single Maastrichtian record, of a leaf assigned to the family listed by Taylor (1990), may need reassessment. Wolfe (pers. comm., 1991) considers that the Middle Eocene Mahonia as the earliest reliable records. Tertiary records (Oligocene onwards) from the former USSR are documented in Takhtajan (1974). Fruits like those of modern Achlys were described from the Lower Palaeocene of Europe by Mai (1987a).

Muller First: Records rejected; no proven evidence.

F. BETULACEAE Gray, 1821


Comments: Crane (chapter 6, vol. 2, in Crane and Blackmore, 1989) reviewed the fossil record. He recognized modern Alnus and modern Betula (Betuleae) as well defined by the Middle Eocene, based upon multiple organ evidence. The earliest reproductive structures of Alnus are late Palaeocene in age and foliage from the Maastrichtian onwards may represent Betuleae. Coryloaceae are represented in the Upper Palaeocene by nuts like those of Corylus, and by the extinct genus Palaeocarpinus with associated foliage.


Comments: May be too early for the family due to confusion with extinct groups yielding porate pollen.

F. BIGNONIACEAE de Jussieu, 1789


Comments: One leaf, assigned to modern Chilopsis, from the Upper Oligocene of North America is listed by Taylor (1990), but this was rejected as indeterminate by Wolfe and Schorn (1989). However, Wolfe and Schorn (1989) did list a leaf assigned to modern Catalpa from the Upper Oligocene of North America (for details see Wolfe and Schorn, 1990). Gregor (1982) lists Catalpa leaves from the European Miocene. Seeds from the Uppermost Eocene of England were assigned to modern Catalpa, Radermachera and Incavellia, each based on a single specimen. The originals are in poor condition and no new material has been found (Reid and Chandler, 1926). We consider these seed records to be unconfirmed.

Muller First: Albertipollenites araneosus (form taxon) Frederiksen, 1973, Middle Eocene, south-east USA.

Comments: Unchallenged.

F. BIXACEAE Link, 1831
Comments: Many of the original identifications made by bacaceoxylon, Berry are incorrect (see discussion in Taylor, 1990, p. 281).

Puryear, p. 90) to be 'not intended to imply affinities with only the family, was specifically stated by Wheeler (1983).

Muller First: Pending.

F. BRUNELLIAEAE Engler, in Engler and Prantl, 1897

PFR: No record.

Comments: We know of no claims for a megafossil record for this family.

Muller First: Pending.

F. BURMANNIAEAE Blume, 1827

PFR: No record.

Comments: We know of no claims for a megafossil record for this family.

Muller First: Pollen record rejected.

F. BURSERACEAE Kunth, 1824


Comments: These fruit records reflect the diversity of the family in the Lower Eocene of England. Leaves and fruits occur in the Middle Eocene (one tentative assignment in the Upper Palaeocene) of North America listed by Taylor (1990).

Muller First: Pending.

F. BUTOMACEAE Richard, 1815


Comments: We know of no well-substantiated leaf fossils for this family. Seeds like those of modern Butomus occur in the Oligocene onwards in Europe (Mai, 1985a). Kovach and Dilcher (1988) noted suggestions of similarity between Cretaceous seed-like cuticles named Costathea and Butomaceae seeds, but they rejected an assignment to the family without further comparative surveys and in the absence of an intervening fossil record. Seeds of this form, borne on wetland plants, have high fossilization and recovery potential, so intervening examples should not have passed unreported.

Pollen: No record.

F. BUXACEAE Dumortier, 1822

PFR: No record.

Comments: Mai and Walther (1985) described seeds like those of modern Pachysandra (as P. ascidiiformis Mai) from the Upper Eocene as the first megafossil record in Europe. Kvacék et al. (1982) reviewed the fossil record of leaves and fruits like those of modern Buxus from the Early Miocene onwards in Eurasia. Uemura (1979) described leaves like those of modern Buxus from the Miocene of Japan. Taylor (1990) lists no megafossils of the family in North America. Flowers very similar to those in modern Buxaceae have been recorded in the Albian of North America (Drinnan et al., 1991).


Comments: Unchallenged.
F. CABOMBACEAE Richard, 1828

Comments: The fossil history is reviewed by Mai (1985a), Cevallos-Ferriz and Stockey (1989), and Collinson (1980). Several fossil seed forms (including those cited above) are intermediate in character between genera now segregated in Cabombaceae and Nymphaeaceae sensu stricto. However, seeds identical with those of modern Brachycarpa (Cabombaceae) occur in the Upper Eocene of England, UK (Collinson, 1980 and in prep.).
Pollen: No record.

F. CACTACEAE de Jussieu, 1789

PFR First: Eupuntia douglasii Chaney, 7 November 1944. Tertiary, Middle Eocene.
Comments: The material of Eupuntia was re-examined by MacGinitie (1969, p. 91) who stated that ‘the objects cannot be assigned to the Cactaceae’. They were thought to be possible monocotyledonous tubers. We know of no well-substantiated megafossil record for this family.
Pollen: No record.

F. CAESALPINIACEAE R. Brown, in Flinders, 1814

Comments: In their revisions of fossil legumes, Herendeen and Dilcher (1990b, 1991) document pods and leaves of several genera in this family (as Caesalpinioideae) from the Eocene, especially Middle Eocene, of North America. They note that most records of the family in the older literature still await revision.
Muller First: Sindorapolli (form genus) Krutzsch, 1969b, Maastrichtian, Siberia, former USSR.
Comments: Unchallenged.

F. CALLITRICHACEAE Link, 1821

PFR: No record.
Comments: Fruits are recorded from the Pliocene in Europe (Mai, 1985a).
Muller First: Pending.

F. CALYCANHTHACEAE Lindley, 1819

PFR: No record.
Comments: Fruits like those of modern Calycanthus were recorded by Mai (1987b) from the Middle Miocene of Siberia, former USSR.
Pollen: No record.

F. CAMPANULACEAE de Jussieu, 1789

PFR: No record.
Comments: Seeds are recorded in the Upper Miocene of Poland (Lancucka-Środoniowa, 1979).
Muller First: Pending.

F. CANELLACEAE Martius, 1832

PFR: No record.

Comments: We know of no claims for a megafossil record of this family.
Muller First: Pending.

F. CANNABACEAE Endlicher, 1837

PFR: No record.
Comments: The fossil record was reviewed by Collinson (Chapter 18, vol. 2, in Crane and Blackmore, 1989) who accepted fruits like those of modern Humulus (and a related extinct genus) from the Oligocene of the former USSR and Bulgaria.
Pollen: No record.

F. CANNACEAE de Jussieu, 1789

Comments: Leaves previously assigned to Cannaceae were considered to be ‘not well understood’ by Daghlian (1981).
Pollen: No record.

F. CAPRARACEAE de Jussieu, 1789

PFR First: Cappartes cymphyloides, 1919. Leaf. Upper Cretaceous, USA: Alabama, Fayette County, Shirley Mill.
Comments: Fruits and seeds were recorded by Chandler (1964) in the Lower Eocene of England, UK. This is an isolated record for the family, but we know of no reason to reject it. Taylor (1990) noted a wood assigned to the family from the Middle Eocene of North America. We know of no well-substantiated leaf fossils for the family.
Muller First: van Campo, 1976, Upper Miocene, Spain.
Comments: Unchallenged.

F. CARIFOLIACEAE de Jussieu, 1789

PFR: No record.
Comments: Seeds identical with those of modern Sambucus occur from the Early Eocene onwards (Chandler, 1964) and fruits of Abelia occur in the uppermost Eocene/Lower Oligocene (Crane, in Collinson, 1988c, pp. 21–30) of England, UK. Sambucus also occurs in the Middle Eocene of Messel, Germany (Collinson, 1988b). Several Palaeocene records for modern Viburnum listed by Taylor (1990) may require revision. According to Hickey (1977) some represent ‘only plausible generic assignments retained pending further study’.
Muller First: Tricolporopollenites viburnoides (form taxon) Grunas-Cavagnetto, 1978. Middle Eocene, France.
Comments: The associated megafossil record does support the family identity.

F. CARYOCARACEAE Szyszylowicz, in Engler and Prantl, 1893

PFR: No record.
Comments: We know of no claims for megafossils of this family.
Muller First: Retisyncolporites angularis (form taxon). Gonzalez-Guzman, 1967; Muller, 1970, Middle Eocene, Venezuela.
Comments: Very characteristic parasyncolpate pollen.

F. CARYOPHYLLACEAE de Jussieu, 1789

Comments: There are several records of this and another species in the Middle and lower Upper Eocene of England, UK (Chandler, 1964). These are isolated records, but we know of no reason to reject them. Van der Burgh (1987) records seeds like those of modern Stellaria from the Upper Miocene of Europe.


Comments: Unchallenged.

F. CASUARINACEAE Brown, in Flinders, 1814

PFR First: Casuaroxylon anglica Goepert and Stache, 15 May 1855. Wood? No age is given for this genus in PFR, there is one Upper Triassic taxon assigned tentatively to the Casuarinaceae.

Comments: The family is well documented in Australasia by reproductive structures and leafy stems. The earliest examples belong to modern Gymnostoma, and this is common and well defined in the Middle Eocene onwards (Scriven and Christophel, in Douglas and Christophel, 1990, pp. 137-47); the record from Mt. Hotham cited by these authors is probably Palaeocene (Greenwood, pers. comm., 1991). The fossil record is also summarized by Johnson and Wilson (Chapter 9, vol. 2, in Crane and Blackmore, 1989) who note one megafossil of Gymnostoma in Patagonia. This is stated (as Casuaria) by Romero (1986a) to be Palaeocene.


Comments: Well supported in the Southern Hemisphere.

F. CELASTRACEAE Brown, in Flinders, 1814


Comments: Fruits and seeds are recorded in the Lower Eocene of England, UK (Chandler, 1964) and leaves are listed from the Middle Eocene of North America (Taylor, 1990).


Comments: Unchallenged.

F. CENTROLEPIDACEAE Endlicher, 1836


Comments: Unconfirmed. We know of no well-substantiated megafossil record of this family.


Comments: Possible; indistinguishable from Restionaceae.

F. CERATOPHYLLACEAE Gray, 1821

PFR: No record.

Comments: Herendeen et al. (1990) review the fossil record in North America and document the earliest fruits Ceratophyllum furcatispinum Herendeen et al. in the Upper Palaeocene of North America. Mai (1985a) reviewed the European record which extends from the Oligocene onwards.

Pollen: No record.

F. CERCIDIPHYLLACEAE Engler, 1909


Comments: Extinct partially reconstructed whole plants (the Joffrea and Nyssodium 'plants' being most thoroughly reconstructed), are widespread in uppermost Cretaceous and Palaeocene floras of the mid to high latitudes of the Northern Hemisphere (see review in Friis and Crane, in Crane and Blackmore, 1989). These were included in Ceridiphyllaceae by Crane and Stockey (1985, p. 363; 1986) and Crane et al. (1990) and they are more closely related to Ceridiphyllum than to any other extant genus (Crane and Stockey, 1985, Friis and Crane, in Crane and Blackmore, 1989). Fossil plants similar to modern Ceridiphyllum do not occur until the Oligocene (Crane and Stockey, 1985).

Muller First: Ceridiphyllites brevicolpatus (form taxon). Jarzen and Norris, 1975, Campanian, Canada.

Comments: Unchallenged.

F. CHENOPODIACEAE Ventenat, 1799


Comments: Seeds like those of modern Chenopodium were described from the Middle and Upper Miocene of Europe (Gregor, 1982; Van der Burgh, 1987).

Muller First: Polyoporina cribraria (form taxon) Srivastava, 1969a, Maastrichtian, Canada.

Comments: Difficult to distinguish from Liquidambar type and some Amarantaceae pollen and some dinoflagellate cysts.

F. CHLORANTHACEAE Brown ex Lindley, 1821

PFR: No record.

Comments: Androecia of Chloranthaceae were described by Crane et al. (1989) from the Upper Cretaceous (Upper Santonian/Lower Campanian) of Sweden. These are very similar to modern Chloranthus but contain spiraperturate pollen not found in the family today although similar in exine structure to grains of modern Sarcandra and some species of Chloranthus. Crane et al. (1989) also describe a single Lower Cretaceous chloranthoid androecium which contains tricole plate pollen, but they do not assign it to Chloranthaceae. They note that several Lower Cretaceous dispersed pollen forms (especially Clavatipollenites and Asteropollis), are considered to be very similar to grains of modern Chloranthaceae (Ascarina and Hedysosum, respectively) and that abundance of these pollen indicates wind-pollinated parent plants; in contrast to the two fossil androecia which suggest insect pollination. Leaf fossils from the Lower Cretaceous resemble Chloranthaceae but are not sufficiently diagnostic to assign to the family (Crane et al., 1989). Crepet et al. (1991) draw attention to differences between Lower Cretaceous chloranthoid flowers and those of modern Chloranthaceae.

Muller First: Clavatipollenites—Ascarkin complex, in Muller, 1981, Aptian, Central Africa, South America, North and Central America, Europe, Australia.

Comments: Well-supported records may be assignable to an extinct and related family.
F. CHRYSOBALANACEAE Brown, in Tuckey, 1818

**PFR:** No record.

**Comments:** Fruits tentatively assigned to modern *Parinari* were recorded in the Pliocene of Colombia (Wijninga and Kuhry, 1990).

**Pollen:** No record.

**F. CISTACEAE** de Jussieu, 1789

**PFR First:** *Cistinocarpum roemeri* Conwentz, 1886. Fruit. Lower Tertiary, Germany: West Prussia.

**Comments:** Gottwald (1992) assigned an Upper Eocene wood to this family.

**Muller First:** *Cistacearumpollenites* (form genus) Konzalova, 1976a. Lower Miocene, Czechoslovakia.

**Comments:** Possible.

**F. CLETHRACEAE** Klotzsch, 1851

**PFR First:** *Clethracarpum asepalum* Menzel, 1914. Fruit. Tertiary (Braunkohle), Germany: Herzogenrath.

**Comments:** Possible. The material was noted to show features of *Clethraceae*. Seeds assigned to *Cyrillaceae* have a record more consistent with that of these pollen types. (See also our discussion under *Cyrillaceae*.)

**Muller First:** *Clethra* type Chmura, 1973. Maastrichtian, California, USA.

**Comments:** Too early; difficult to distinguish tricolporate pollen and from that of the *Cyrillaceae*. According to Taylor (1990), pollen of *Cyrillaceae* cannot be distinguished from that of *Clethraceae*. Seeds assigned to *Cyrillaceae* have a record more consistent with that of these pollen types.

**F. CLUSIACEAE** Lindley, 1826


**Comments:** Seeds like those of modern *Hypericum* occur in the Oligocene onwards in Europe (Frisi, 1985a). *Muller First:* *Kielmeyerapollenites* *eocenicus* (form taxon) Sah and Kar, 1974. Lower Eocene, India.

**Comments:** Unchallenged.

**F. COMBRETACEAE** Brown, 1810


**Comments:** Fruits once assigned to *Terminalia*, the only megafossils of the family reported by Taylor (1990) from the Upper Oligocene of North America. They were considered to be in need of revision (Manchester and Meyer, 1987) being similar to fruits of several modern families. Fruits very similar to those of modern *Combretum* and *Terminalia* are abundant in the Lower Miocene of Kenya (Chesters, 1957; Collinson, in prep.). Woods assigned to Combretaceae are common in the Oligocene and Neogene of Africa and south-east Asia (Bande and Prakash, 1986, Bourreau *et al.*, 1983). Gregor (1978) documented fruits like those of modern *Quisqualis* from the Middle Miocene onwards in Europe.


**Comments:** Unconfirmed. Fruits like those of modern *Cnestis* are recorded from the Lower Miocene of Kenya (Chesters, 1957).

**Pollen:** No record.

**F. CONVOLVULACEAE** de Jussieu, 1789

**PFR First:** *Palaeopomoea fukuiensis* Matsuo Mai, 1956. Leaf. Tertiary: Middle Miocene, Japan, Fukui Prefecture.

**Comments:** We know of no well-substantiated megafossil record for this family. See discussion under *Verbenaceae* for comments on *Porana* cited by Chesters *et al.* (1967) as *Convolvulaceae*.

**Muller First:** *Calystegiapolpis microechinatus* (form taxon) Salard-Cheboldaeff, 1975a, Lower Eocene, Cameroon.

**Comments:** Unchallenged.

**F. CORIARIACEAE** de Candolle, 1824

**PFR:** No record.

**Comments:** The fossil record was reviewed by Gregor (1980) who described new material of seeds assigned to *Coriaria* from the Lower Miocene of Germany.

**Muller First:** *Coriaria*. Van Campo, in Muller, 1981. Upper Miocene, Spain.

**Comments:** Unchallenged.

**F. CORNACEAE** Dumortier, 1829


**Comments:** Knobloch and Mai (1986) recorded fruits of four extinct genera of *Mastixioideae* (as *Mastixiaceae*) from the Maastrichtian of Europe, and the fossil record is widespread and diverse from then onwards. The fossil record of *Cornoxyloidea* was reviewed in detail by Eyde (1988), who accepted fruits of blue-line *Cornus* in the Middle Eocene and of red-line *Cornus* in the Lower Eocene. Eyde (1988) noted problems in identifying fossil leaves and woods to the family, but accepted leaves from the Lower Eocene as ‘vestiges of early dogwoods’ (p. 269). These and other leaves are listed as *Cornus* by Taylor (1990).

**Muller First:** Pending (the pending status is reaffirmed by Eyde (1988, pp. 269–70) who discussed problems in identifying pollen to this family with certainty).

**F. CRASSULACEAE** de Candolle, in Lamarck and de Candolle, 1805

**PFR:** No record.

**Comments:** According to Friis and Skarby (1982) all mega-
fossils assigned to this family are questionable and require revision.

Pollen: No record.

F. CRYPTEROONIAEAE de Candolle, 1868

PFR: No record.

Comments: We know of no claims for megafossils of this family.

Muller First: Dactylocladus type. Anderson and Muller, 1975. Upper Miocene, Borneo.

Comments: There is no evidence to distinguish from pollen of Combretaceae and Melastomataceae.

F. CUCURBITACEAE de Jussieu, 1789


Comments: Unchallenged.

F. CUNONIAEAE Brown, in Flinders, 1814


Comments: Leaves similar to those of modern Weinmannia and Cunonia are reported from the Oligocene of Tasmania (Hill, in Douglas and Christophel, 1990, pp. 31–42). Palaeocene leaves from Europe and Greenland have also been assigned to Weinmannia based upon morphological and epidermal characters, but these should be regarded with caution in view of the largely Southern Hemisphere distribution of the modern genus (Friis and Skarby, 1982; Friis, 1990). Wolfe (pers. comm., 1991) does not accept any Northern Hemisphere records for the family. Lower Eocene leaves from North America, identified as Lamanonia by Hickey (1977), are now known to be Platyacara of the Juglandaceae (see citations in Manchester, 1987). Gottwald (1992) assigned an Upper Eocene wood to this family.


Comments: Unchallenged.

F. CYCLANTHACEAE Dumortier, 1829


Comments: This taxon was revised by Biradar and Bonde (in Douglas and Christophel, 1990, pp. 51–7), who concluded that this was an underground rhizomatous stem which continued into an aerial, woody pseudostem (named Musocaunon), bearing strap-like leaves with sheathing based (of which petioles when found isolated had been named Helicomiates). Anatomical evidence suggested that fruits named Triocridites were borne on this plant. The reconstructed plant was considered to combine characters of Musaceae and Strelitziaceae, and hence cannot be assigned to Cyclanthaceae. Collinson (1988b) reported fruiting cycles very similar to those of modern Cyclanthus, in the Middle Eocene of Messel, but did not assign these to Cyclanthaceae.

Pollen: No record.

F. CYMODOCEACEAE N. Taylor, 1909

PFR: No record.

Comments: Daghlian (1981) rejected previously published records of the family. Recently described Upper Middle Eocene material from Florida (USA) includes leaves and rhizomes of species assigned to modern Thalassodendron and Cymodocea (and leaves tentatively assigned to Halodule), representing a seagrass bed in which characteristic epibionts and an associated fauna are also preserved (Ivary et al., 1990).

Pollen: No record.

F. CYPERACEAE de Jussieu, 1789


Comments: The family is well represented by a diversity of fruits from the Middle Palaeocene onwards in Europe (Chandler, 1964; Mai and Walther, 1985; Mai, 1987). Fruiting heads (of Caricoides) similar to those of modern Mapaniaeae are found in the Middle Eocene of Germany (Collinson, 1988b). We know of no well-substantiated leaf fossils of the family.

Muller First: Cyperaceopsis (form genus) Krutzsch, 1970a, Middle Eocene, Germany.

Comments: Well supported.

F. CYRILLACEAE Endlicher, 1841


Comments: Fruits and seeds, assigned to three extinct genera and forms referable to modern Cyrilla, are recorded from the Maastrichtian to Miocene in Europe (Knobloch and Mai, 1986; Mai and Walther, 1978, 1985). The extinct Epacridicarpum Chandler occurs commonly in the Maastrichtian to Miocene strata, however, Friis (1985a) questioned its inclusion in Cyrillaceae, suggesting that some species might belong in Ericaceae. Fruits of Valvacearpus Knobloch and Mai were stated to show features of Cyrillaceae and Clethraceae. Friis (1985b) described Upper Cretaceous (Santonian/Campanian) flowers, fruits and seeds of Ericales which showed similarities with members of the Cyrillaceae, Clethraceae, Ericaceae, Epacridaceae and Diapensaceae (perhaps being most similar to the latter). In view of this complex character mixing, we consider all records of these families provisional unless the fossils can be matched exactly in one modern genus (see also comments on Clethraceae). Fruits like those of modern Cyrilla are only known from one Upper Eocene locality (Mai and Walther, 1985).

Muller First: Clethra type Chmura, 1973. Maastrichtian, California, USA.

Comments: Too early; difficult to distinguish tricolpate pollen and especially Clethraceae (see comments on Clethraceae).

F. DAPHNIPHYLLACEAE Muell.-Arg. in de Candolle, 1869

PFR: No record.

Comments: Leaves of Daphniphyllum protonematum Murai were described by Uemura (1988) from the Upper
Miocene of Japan.

Pollen: No record.

F. DATISCACEAE Lindley, 1830


Comments: We are unable to comment on this wood record. We know of no other megafossil record for this family.

Pollen: No record.

F. DIAPENSIACEAE Lindley, 1836

PFR: No record.

Comments: No megafossils can be assigned to the family but many characteristics of the family are seen in Upper Cretaceous flowers, fruits and seeds (see discussion under Cyrillaceae).

Pollen: No record.

F. DICAPTELACEAE Baillon, in Martius, 1886

PFR: No record.

Comments: We know of no claims for megafossils of this family.

Muller First: Tapura ivorensis type. Medus, 1975b, Miocene, Senegal.

Comments: Well-supported evidence of characteristic pollen morphology but no megafossil data.

F. DIDYMELACEAE Leandri, 1937

PFR: No record.

Comments: We know of no claims for megafossils of this family.

Muller First: Didymelites = Schizolusus martinensis. Harris, 1974, Palaeocene, Indian Ocean and New Zealand.

Comments: Well supported by pollen morphology, but there is no support from the megafossil record.

F. DILLENIAEACEAE Salisbury, 1807


Comments: Seeds like those of modern Tetracera and Hibbertia were recorded in the Lower Eocene of England, UK (Chandler, 1964). Dilleniid leaves are common in Upper Cretaceous floras but they are not diagnostic of modern Dilleniaceae (e.g. Crabtree, 1987; Taylor, 1990).

Muller First: Curatella type Wymstra, 1971. Middle Miocene, Guyana.

Comments: Unchallenged.

F. DIOCOREACEAE Brown, 1810


Comments: Daghiian (1981) considered all records of the family questionable and in need of revision. A Lower Oligocene record from Hungary (Andrásnszky, 1959) was apparently not included in Daghiian's work, but we can find no reason to treat this as more reliable.

Muller First: Pending.

F. DIPSACEAE de Jussieu, 1789

PFR: No record.

Comments: Rare fruits of Scabiosa cf. columbaria L. were described by Szafer (1954) from the Pliocene of Poland.


Comments: Unchallenged.

F. DIPTEROCARPACEAE Blume, 1825


Comments: The material on which this PFR record is based is considered to be of questionable derivation and has no attached matrix from which this might be reassessed. Wolfe et al. (1975, p. 819) felt that further consideration of Woburnia was valueless. We agree that this record must not be cited as evidence for Cretaceous Dipterocarpaceae. Wolfe (1977) described leaves of Parasroduced from the Middle Eocene of North America, and noted the rarity of the family in the Palaeogene. This observation is confirmed by the tabulated review of fossil Dipterocarpaceae leaves provided by Lakhanpal and Guleria (1986) who recognized Dipterocarpus leaves in the Neogene of India. Woods assigned to Dipertocarpyxylon are common in the Neogene of south-east Asia (Bande and Prakash, 1986).


Comments: Unchallenged.

F. DROSERACEAE Salisbury, 1808

PFR: No record.

Comments: Seeds like those of modern Aldrovanda are documented from the Upper Eocene onwards in Europe (Mai, 1985a; Chandler, 1964). Seeds from the Maastrichtian of Europe were assigned to Palaeoaldrovanda by Knobloch and Mai (1986). This early record should be treated with caution in view of the absence of intervening examples.


Comments: Unchallenged.

F. EBENACEAE Gürke, in Engler and Prantl, 1891


Comments: Basinger and Christophel (1985) described Ebenaceae flowers and leaves from the Middle Eocene of Australia.


Comments: Supported.

F. ELAEAGNACEAE de Jussieu, 1789


Comments: Taylor (1990) lists two records of leaves assigned to modern Shepherdia in the Oligocene of North America. One was rejected as indeterminate by Wolfe and Schorn (1989) and Wolfe (pers. comm., 1991) does not accept the other. Wolfe (1964) described leaves of Elaeagnus from the Middle Miocene of North America. These should
now be included in Shepherdia and represent the earliest record of the family in North America (Wolfe, pers. comm., 1991).

**Muller First:** *Slowakipollis hippocladoidea* (form taxon). Krutzsch, 1962, Oligocene, Germany.

**Comments:** Possible. Bohlenisipollis hohti has now been recorded from many Oligocene sediments in north-west Europe (Vinken, 1988), and according to lists in Taylor (1990), from the Middle and Upper Eocene of North America. It has demisyncolpate apertures, not present in modern Elaeagnus pollen, and may be from extinct groups of this family.

**F. ELAEOCARPACEAE** de Candolle, 1824


**Comments:** Rozefelds *(in Douglas and Christopenh, 1990, pp. 123–6) described Lower Oligocene fruits like those of modern *Elaeocarpus*, and Christophe and Greenwood (1987) recorded leaves similar to those of modern *Sloanea* and *Elaeocarpus* from the Middle Eocene – both in Australia. Chan德尔 (1964) recorded fruits like those of modern *Echinoecarpus* in the Lower Eocene of England, UK.


**Comments:** Unchallenged.

**F. ELATINACEAE** Dumortier, 1829

**PFR:** No record.

**Comments:** Seeds like those of modern *Elatine* were documented by Mai (1985a) from the Miocene of Europe.

**Pollen:** No record.

**F. EMPETRACEAE** Gray, 1821

**PFR First:** *Empetrum* sp. Boulter, 1971, Upper Miocene, England, UK.

**F. EPACRIDACEAE** Brown, 1810


**Comments:** The genus *Epacridarpum* Chandler has been included in Cyrilaceae. We know of no well-substantiated megafossils of this family. (See discussion under Cyrilaceae.)

**Pollen:** No record.

**F. ERICACEAE** de Jussieu, 1789


**Comments:** Dilcher and Manchester *(in Collinson, 1988c, pp. 45–58) considered Cretaceous records inconclusive. They document flowers and fruits of tribe Hippomaneae in the Middle Eocene. Lower Eocene fruits are found in England, UK (Chandler, 1964) and leaves referred to as ‘euphors’ are recorded by Wolfe and Upchurch (1986) in the Upper Maastrichtian of North America. Tanai (1990) also reviewed the fossil history of the family and treated the PFR wood record as euphorbioid. He documented leaves of four modern genera from the Middle and Upper Eocene of Japan.


**Comments:** Unchallenged.
F. EUPOMATIACEAE Endlicher, 1841

PFR: No record.
Comments: We know of no megafossil record of this family.
Muller First: Pending.

F. EUPTETACEAE Wilhelm, 1910

PFR: No record.
Comments: Leaves assigned to Euptelea orientalis (Sanborn) Wolfe were documented by Wolfe (1977, p. 89) from the Upper Eocene of North America. A wood from the Middle Eocene of Oregon is the only record of the family listed by Taylor (1990). This wood record seems acceptable, although no associated fruits or foliation have been found in Oregon (Manchester, pers. comm., 1991).
Muller First: Eupteleapolpis (form taxon). Krutzsch, 1966c, Upper Eocene, Germany.
Comments: Unchallenged.

F. FABACEAE Lindley, 1836

PFR First: Palaeocassia augustinolia Ettingshausen, 1867. Leaf. Cretaceous: Cenomanian, Germany, Saxony.
Comments: Fruits like those of modern Diplotropis are recorded (under Leguminosae, Papilionoideae) in the Middle Eocene and papillionoid flowers from the Palaeocene/Eocene both in North America (Herendeen and Dilcher, 1990b).
Comments: Unchallenged.

F. FAGACEAE Dumortier, 1829

Comments: Crepet (in Crane and Blackmore, 1989) considered castaneous and trigonobalanoid inflorescences with pollen, fruits and associated foliation in the Palaeocene/Eocene of North America as the earliest unequivocal Fagaceae. He suggested an uppermost Cretaceous origin for the family based upon this simultaneous appearance of multiple organ fossils comparable with both modern tribes. Fagaceae fossils in Europe from the Eocene onwards are reviewed by Kvaek and Walther (1989). Nothofagus (Nothofagaceae of some authors) fossils were reviewed by Hill (1991a) who noted that Cretaceous and many Lower Tertiary fossils need to be revised. Evidence from fossil cupules and leaves shows that all extant subgenera were established as distinct entities (with no intermediates) by the Oligocene. Fossil wood, named Nothofagoxylon, from the Upper Cretaceous of South America may be the earliest megafossil of the family (noted in Hill, 1991a; Romero, 1986b).
Comments: Unchallenged without in situ evidence for this small and varied tricolp(or)ate morphology.

F. FLACOURTIACEAE de Candolle, 1824


F. FLAGELLARIACEAE Dumortier, 1829

PFR: No record.
Comments: We are not aware of any claims for megafossils of this family.
Comments: Unchallenged.

F. FOUQUIRIACEAE de Candolle, 1828

PFR: No record.
Comments: We are not aware of any claims for megafossils of this family.
Muller First: Earlier records rejected.

F. FUMARIACEAE de Candolle, 1821

PFR: No record.
Comments: Cronquist (1981) refers to leaves, seeds and inflorescences like those of modern Garrya from the Miocene of the western United States. Wolfe (1964) described the leaves from the Middle Miocene of North America and he considers these to be the oldest examples (Wolfe, pers. comm., 1991).
Pollen: No record.

F. GARRYACEAE Lindley, 1834

PFR: No record.
Comments: Flowers from the Lower Eocene of North America were assigned to this family (Crepet and Daghlian, 1981). These contain Pistillipollenites pollen but this is also found in other flowers which are not Gentianaceae (Stockey and Manchester, 1988). The inclusion of all records of Pistillipollenites in this family (e.g. Taylor, 1990), implying a Maastrichtian to Eocene fossil record, is therefore incorrect.
Muller First: Pending.

F. GENTIANACEAE de Jussieu, 1789

PFR: No record.
Comments: Flowers from the Lower Eocene of North America were assigned to this family (Crepet and Daghlian, 1981). These contain Pistillipollenites pollen but this is also found in other flowers which are not Gentianaceae (Stockey and Manchester, 1988). The inclusion of all records of Pistillipollenites in this family (e.g. Taylor, 1990), implying a Maastrichtian to Eocene fossil record, is therefore incorrect.
Muller First: Pending.

F. GERANIIDACEAE de Jussieu, 1789

PFR: No record.
Comments: A possible Upper Pliocene Geranium or Erodium is described by Strauss (1969). We know of no well-substantiated megafossils of this family.
Comments: Unsupported Spanish records are based on only one and 14 specimens respectively with no evidence from other organs.
F. GOODENIACEAE Brown, 1810

PFR: No record.
Comments: We know of no claims for megafossils of this family.
Comments: Unchallenged.

F. GROSSULARIACEAE de Candolle, in Lamarck and de Candolle, 1805

PFR: No record.
Comments: Leaves like those of modern *Quintinia* are recorded (as Escalloniaceae) from the Middle Eocene of Australia (Christophel et al., 1987; Christophel and Greenwood, 1988). Friis (1990) described Upper Cretaceous (Santonian/Campanian) flowers of Saxifragales (with associated leaves) which showed close correlation of characters with modern Escalloniaceae, especially *Quintinia*, but also showed similarity with other woody Saxifragales. Several records of leaves like those of modern *Ribes* are listed by Taylor (1990) from Upper Eocene onwards in North America. Upper Oligocene examples are accepted by Wolfe and Schorn (1989). Mai (1985b) recorded fruits like those of modern *Itea* (Iteaceae of some authors) from the Miocene and Pliocene in Europe. A flower from the Baltic amber is similar to *Iteaceae* (Friis and Skarby, 1982). Leaves like those of modern *Itea* are recorded in the Middle Eocene of North America (Taylor, 1990).

Comments: All unchallenged.

F. GUNNERACEAE Meissner, 1841

PFR: No record.
Comments: No megafossil record is known to us for *Gunnera*, the only genus Cronquist includes in the family.
Comments: Unchallenged.

F. HALORAGACEAE Brown, in Flinders, 1814

Comments: Fruits like those of modern *Proserpinaca* and *Myriophyllum* are recorded from the Oligocene onwards in Europe (Mai, 1985a).
Comments: Unchallenged.

F. HAMAMELIDACEAE Brown, in Abel, 1818

Comments: Seeds are recorded from the Upper Cretaceous onwards (Chandler, 1964; Knobloch and Mai, 1986; Mai, 1987a) and flowers very similar to those of modern *Hamamelis*, subfamily Hamamelidoideae, occur in the Santonian/Campanian of Sweden; subfamily Liquidambaroideae may also be distinct in the Upper Cretaceous (Fris and Crane, in Crane and Blackmore, 1989; Endress and Friis, 1991). Leaves of Hamamelidaceae also occur in the Campanian (Crabtree, 1987).

Comments: Unchallenged.

F. HELICONIACEAE Nakai, 1941 (see comments under MUSACEAE)

F. HERNANDIACEAE Blume, 1826

PFR: No record.
Comments: Berry (1937) described fruits of *Gyrocarpus* from the Upper Miocene of Venezuela. We know of no other megafossils from this family, and consider that this record requires confirmation.

Pollen: No record.

F. HIPPOCASTANACEAE de Candolle, 1824

PFR: No record.
Comments: Fruits like those of modern *Aesculus* are recorded in the Upper Miocene and Pliocene of Europe (Szafer, 1961) with tentative records in the Middle Miocene (Gregor, 1982). Upper Eocene leaf records from North America were considered questionable by Taylor (1990).

Muller First: *Aesculus*. Smiley et al., 1975, Miocene, Idaho, USA.
Comments: Unchallenged.

F. HIPPOCRATEACEAE de Jussieu, 1811

PFR: No record.
Comments: We know of no megafossil record for this family.

Muller First: See Celastraceae.

F. HIPPURIDACEAE Link, 1821

PFR: No record.
Comments: Fruits like those of modern *Hippuris* are recorded from the Oligocene of Europe (Mai, 1985a).

Pollen: No record.

F. HUGONIACEAE Arnott, 1834

PFR: No record.
Comments: We know of no megafossil record for this family.

Comments: Unchallenged.

F. HUMIRIACEAE de Jussieu, in St-Hilaire, 1829

PFR: No record.
Comments: Romero (1986a) refers to work by Berry documenting fruit casts and leaf impressions of *Humiria* in the Maastrichtian and Lower Eocene of Colombia. The material was originally thought to be Miocene, but the sections were redated palynologically. These records should probably be considered as unconfirmed and requiring re-examination. Endocarps like those of modern *Sarcoglyttis* and others tentatively assigned to modern *Humiriastrum* were reported in the Pliocene of Colombia (Wijninga and Kuhry, 1990).

Muller First: *Humiria* type, van de Hammen et al., 1973, Pliocene, Colombia.
Comments: Unchallenged.
F. HYDRANGEACEAE Dumortier, 1829

PFR: No record.

Comments: Flowers of Hydrangea are documented from the Middle Eocene of North America (Manchester and Meyer, 1987; Manchester, in Knobloch and Kvacek, 1990, pp. 183–7) and the Middle Eocene to Pliocene of Europe (Mai, 1985b). Fruits and seeds like those of modern Hydrangea, Dichroa and Schizophragma are also reported from the Middle Oligocene and later in Europe (Mai, 1985b). Wolfe and Schorn (1989) accepted the determination of leaves of modern Jamesia in the Upper Oligocene of North America. Various Cretaceous and Palaeocene leaf records, assigned to Hydrangea and Philadelphus, should probably be considered in need of revision (Taylor, 1990; Friis and Skarby, 1982; Mai, 1985b). Wolfe (pers. comm., 1991) considers that there are no reliable pre-Eocene records.

Pollen: No record.

F. HYDROCHARITACEAE de Jussieu, 1789


Comments: The family is represented by seeds of Stratiotes from the Upper Palaeocene upwards in England, UK (Collinson, 1986a, 1990) and by foliage of other freshwater genera in the Middle and Upper Eocene of Europe (Wilde, 1989; Mai and Walther, 1978, 1985). Seagrass beds from the Upper Middle Eocene of North America (see Cymodoceaceae) include representatives of modern Thalassia (Ivany et al., 1990).

Pollen: No record.

F. ICACINACEAE Miers, 1851


Comments: Eocene fruits of the family are diverse, but rarer examples occur in the Upper Palaeocene (Crane et al., 1990; Collinson, 1986a; Mai, 1987a) and possibly Upper Cretaceous (Tanai, 1990) of Europe, Africa and North America. Leaves are known in the Lower and Middle Eocene of North America (Taylor, 1990), Middle and Upper Eocene of Japan (Tanai, 1990) and tentatively in the Middle Eocene of Europe (Wilde, 1989). Maastrichtian woods named Icacinoyxylon listed by Taylor (1990) are not conclusively included in the family (e.g. Wheeler et al., 1987).


Comments: Well supported.

F. ILLICIACEAE Smith, 1947

PFR: No record.

Comments: Leaves like those of modern Illicium are recorded from the Middle Eocene of Germany (Wilde, 1989) and North America (Taylor, 1990). Fruits are documented in the Oligocene of North America (Tiffney and Barghoorn, 1979).

Muller First: Illicium Chmura, 1973. Maastrichtian, California, USA.

Comments: No supporting evidence.

F. IRIDACEAE de Jussieu, 1789


Comments: We know of no well-substantiated early megafossil record for this family, although Pleistocene seeds are known from Europe and Japan (Miki, 1961; Mai, 1985a).

Muller First: Pending.

F. JUGLANDACEAE Richard ex Kunth, 1824


Comments: The major diversification of this family occurred in the Palaeocene and is documented from a range of organs, including inflorescences, fruits and foliage (Manchester, 1987; Stone in Crane and Blackmore, 1989). Cretaceous flowers (Friis, 1983), some of which contain Normapolles pollen (Manninigia containing Trudapolis and Caryanthus containing Placopollis), are sometimes assigned to the family (Knobloch and Mai, 1986). These are best considered either as Juglandales or intermediates between Juglandales and Myricales. They differ from Juglandaceae in the small size of the fruits, bisexual flowers and undivided locule (Friis and Crane, in Crane and Blackmore, 1989).

Muller First: Momipites fragilis type. Nichols, in Muller, 1981. Lower Campanian, USA.

Comments: Current megafossil evidence (above) suggests that Muller's four pollen groups (Engelhardia–Alfaroa, Carya, Platycarya and Juglans–Pterocarya) developed in the Tertiary from earlier groups closely related to the Juglandales and the Myricales, which produced Nichols' Momipites and the extinct Normapolles.

F. JULIANTIACEAE Hemslay, 1906

PFR: No record.

Comments: Wolfe (pers. comm., 1991) considers that the leaf material which he described in 1964 as a species of Schinus may in fact belong in this family.

Pollen: No record.

F. JUNCACEAE de Jussieu, 1789

PFR: No record.

Comments: Seeds like those of modern Juncus are recorded in the Upper Eocene/Lower Oligocene of England, UK (Collinson, 1983) and from the Miocene onwards elsewhere in Europe (Mai, 1985a). Kovach and Dilcher (1988) noted the suggestions that Cretaceous seed-like cuticles named Spermellites might have some relationship with Juncaceae, but considered these suggestions to be unconfirmed in the absence of detailed comparative studies and in view of the absence of intervening records. Seeds like those of Juncus, if borne on wetland species, would have high fossilization and recovery potential, and intervening examples should not have passed unreported.

Pollen: No record.

F. JUNCAGINACEAE Richard, 1808


Comments: Neither Mai (1985a) nor Collinson (1988a)
recorded this family in their reviews of fossils of wetland plants.

**Pollen:** No record.

**F. LACTORIDACEAE** Engler, in Engler and Prantl, 1888

**PFR First:** No record.

**Comments:** We know of no claims for megafossils of this family.


**Comments:** The first report of this family in the fossil record, is from Turonian–Campanian sediments off the south-west coast of South Africa. The permanent tetrahedral tetrads consist of anasulate pollen which is primitive in structure and ancestry.

**F. LAMIACEAE** Lindley, 1836


**Comments:** We know of no megafossils assigned to this family.

**Pollen:** No record.

**F. LARDIZABALACEAE** Decaisne, 1838


**Comments:** We are unable to comment on this wood record. Mai (1980) recorded seeds like those of modern *Lycopus* from the Oligocene onwards in Europe.

**Muller First:** *Salvia* Emboden, 1964. Upper Miocene, USA: Alaska.

**Comments:** Unchallenged.

**F. LARICACEAE** Lindley, 1836


**Comments:** Unchallenged.

**F. LATELLARIEAE** Gruas-Cavagnetto, 1978


**Comments:** We know of no megafossils assigned to this family.

**Pollen:** No record.

**F. LAVOYACEAE** Delevoryas and Emigh, 1979

**PFR First:** *Lavoyna* Delevoryas and Emigh, 1979. Wood. Tertiary, Pliocene? or Miocene, former USSR.

**Comments:** We are unable to comment on this wood record. Shallom, 1960. Seed. Tertiary, Pliocene? or Miocene, former USSR.

**F. LAVOYACEAE** Delevoryas and Emigh, 1979

**PFR First:** *Lavoyna* Delevoryas and Emigh, 1979. Wood. Tertiary, Pliocene? or Miocene, former USSR.

**Comments:** We are unable to comment on this wood record. Shallom, 1960. Seed. Tertiary, Pliocene? or Miocene, former USSR.

**F. LAVOYACEAE** Delevoryas and Emigh, 1979

**PFR First:** *Lavoyna* Delevoryas and Emigh, 1979. Wood. Tertiary, Pliocene? or Miocene, former USSR.

**Comments:** We are unable to comment on this wood record. Shallom, 1960. Seed. Tertiary, Pliocene? or Miocene, former USSR.

**F. LEMNACEAE** Gray, 1821


**Comments:** Seeds like those of modern *Lemna* are recorded by Dorofeev (1988), Mai (1985a), and Mai and Walther (1978) from the Oligocene onwards in Europe and Asia. *Lemnospermum* was placed *incertae sedis* by Mai and Walther, 1978. Leaves assigned to modern *Spirodella* are reported from the Palaeocene and Eocene of Canada (Taylor, 1990).

**Pollen:** No record.

**F. LENTIBULARIACEAE** Richard, in Poiteau and Turpin, 1808

**PFR:** No record.

**Comments:** *Utricularia* is known only in the Quaternary (Mai, 1985a; Collinson, 1988a).

**Muller First:** *Utricularia minor* type. Graham, 1976, Upper Miocene, Mexico; Miocene, Senegal.

**Comments:** Unchallenged.

**F. LILIACEAE** de Jussieu, 1789


**Comments:** Pollen of this family has little sporopollenin in the exine and thus low preservation potential (Drinnan et al., 1990; Lidgard and Crane, 1990). The flowers noted above failed to yield pollen in spite of their excellent preservation.

**F. LECYTHIDACEAE** Poiteau, 1825


**Comments:** Other Tertiary woods assigned to the family are from south-east Asia (Band and Prakash, 1986). Seeds from the South American Upper Oligocene were described as *Lecythidospermum* by Pons (1983), who reviewed the fossil record from the area, including a fruit from the Maastrichtian assigned to the family. One Middle Eocene leaf form, requiring confirmation, is noted by Taylor (1990) from North America.

**Muller First:** *Marginipollis concinns* (form taxon). Venkatachala and Rawat, 1972. Lower Eocene, India.

**Comments:** Unchallenged.

**F. LEEACEAE** Dumortier, 1829

**PFR:** No record.

**Comments:** We know of no megafossils assigned to *Lea*, in this monotypic family often included in Vitaceae.

**Muller First:** Previous record rejected.

**F. LEITNERIACEAE** Bentham, in Bentham and Hooker, 1880

**PFR:** No record.

**Comments:** Chesters *et al.* (1967) cited a Miocene record, and Cronquist (1981) refers to Miocene and possible Oligocene records of the single modern genus *Leitneria*.

**F. LEMNACEAE** Gray, 1821


**Comments:** Seeds like those of modern *Lemna* are recorded by Dorofeev (1988), Mai (1985a), and Mai and Walther (1978) from the Oligocene onwards in Europe and Asia. *Lemnospermum* was placed *incertae sedis* by Mai and Walther, 1978. Leaves assigned to modern *Spirodella* are reported from the Palaeocene and Eocene of Canada (Taylor, 1990).

**Pollen:** No record.

**F. LENTIBULARIACEAE** Richard, in Poiteau and Turpin, 1808

**PFR:** No record.

**Comments:** *Utricularia* is known only in the Quaternary (Mai, 1985a; Collinson, 1988a).

**Muller First:** *Urticularia minor* type. Graham, 1976, Upper Miocene, Mexico; Miocene, Senegal.

**Comments:** Unchallenged.

**F. LILIACEAE** de Jussieu, 1789

**PFR First:** *Cretovarium* M. Stopes and Fujii, March 1910. Upper Cretaceous, Japan: Hokkaido.

**Comments:** We know of no well-substantiated megafossil record for this family (Daghlian, 1981).


**Comments:** Unchallenged.

**F. LIMNANTHACEAE** Brown, 1833

**PFR:** No record.

**Comments:** One tentative and unconfirmed leaf fossil from the Oligocene of North America is noted by Taylor (1990).

**F. LINACEAE** Gray, 1821

**PFR First:** *Wetherellia variabilis* Bowerbank, post-24 March
Magnoliophyta ('Angiospermae')

825

Comments: This genus probably belongs in Euphorbiaceae (Dilcher and Manchester, in Collinson, 1988c, pp. 45–58). We are not aware of other megafossils except Decaplatyspernum Reid and Chandler which was only tentatively assigned to the family (Chandler, 1964).

Comments: Unchallenged.

F. LOASACEAE Dumortier, 1822
PFR: No record.
Comments: Chesters et al. (1967) cited a Miocene record of Mentzelia. Wolfe (pers. comm., 1991) considers that this record needs re-examination. We know of no well-substantiated megafossils of this family.

F. LOGANIACEAE Martius, 1827
PFR: No record.
Comments: Mai (1968) assigned fruits and seeds named Saxifragaceaeecarpum Menzel from the Middle and Upper Miocene of Europe to this family.

F. LORANTHACEAE de Jussieu, 1808
Comments: Leaves of the family occur in the Middle and Upper Eocene of Germany (Wilde, 1989; Mai and Walther, 1978) and also in the Middle Eocene of Anglesea, Australia (D. C. Christophel, pers. comm., 1991).


Comments: These two taxa by Krutzsch are now supported with megafossil evidence of the family from Germany. Muller (1985) places the Aquilapollenites complex in the Santalales 'as an extinct family, with closest affinity to Loranthaceae, its exact phylogenetic relationship within the order remains to be discovered.' However, Muller refrained from actually creating or naming the extinct family. Muller's views were stimulated by the work of Wiggins (1982) who suggested that Expressipollis stratus from the Campanian of Alaska can be assigned to the Loranthaceae, and this species could form part of a transitional series.

F. LYTHRACEAE Jaume St-Hilaire, 1805
Comments: The family is diverse in the Eocene with several Lower Eocene fruits from England (Chandler, 1964). Seeds similar to those of modern Decodon occur in the Upper Paleocene in England (Collinson, 1986a) and are common in the Eocene in Europe and North America (Eyde, 1972; Cevallos-Ferriz and Stockey, 1988b).

Comments: Unchallenged.

F. MAGNOLIACEAE de Jussieu, 1789
Comments: Unchallenged.

Comments: Seeds from the Upper Cretaceous and Palaeocene of Europe are assigned to the family (Knobloch and Mai, 1986; Mai, 1987a). Flowers named Archaeanthus from the Cenomanian of North America are said to be 'probably closely related to extant Magnoliaceae' (Crane et al., 1989). Magnoliacean foliage is common in the Upper Cretaceous, but this often possesses generalized features, combining the characters of two or more modern families (e.g. Crabtree, 1987; Upchurch and Dilcher, 1990). Cevallos-Ferriz and Stockey (1990a) summarize the fossil record and note that by the Eocene widespread seeds provide clear evidence for several modern genera. Magnolia-like leaves are listed by Taylor (1990) from the Palaeocene onwards in North America. Upper Cretaceous to Eocene woods can be compared with the family, but are not identical to woods of any extant genera (Cevallos-Ferriz and Stockey, 1990a).

Muller First: Magnolipollis gracilexinus and M. megafiquaturus (form taxa). Krutzsch, 1970a, Middle Eocene, Germany.
Comments: Supported by megafossil evidence.

F. MALPIGHIACEAE de Jussieu, 1789
Comments: Specialized, bee-pollinated flowers of the family (named Eoglindudulosa) occur in the Middle Eocene of North America (Taylor and Crepet, 1987). Fossil fruits like those of modern Tetrameris have recently been revised, and most North American records removed from this genus and family (Manchester, 1991).

Muller First: Persisyncolporites pokornyi (form taxon). Pares Regali et al., 1974a. Middle Eocene, Brazil.
Comments: Unchallenged.

F. MALVACEAE de Jussieu, 1789
Comments: We know of no recent revision of megafossils of this family. No megafossils are cited for North America by Taylor (1990). However, Rasky (1956) reported Kydia from the Upper Eocene/Lower Oligocene of Hungary and Iljiniskaia (1986) reported Eocene leaves of the family in the former USSR. Seeds of Kosteletzkya were recorded in the Miocene of the former USSR by Dobrofeev (1959, 1988).

Comments: Unchallenged.

F. MARANTACEAE Petersen, in Engler and Prentl, 1888
PFR: No record.
Comments: Although a possible record is cited by Chesters et al. (1967), Daghiian (1981) did not accept a fossil record for the family.

F. MARCGRAVIACEAE Choisy, in de Candolle, 1824
Comments: We are unable to comment on this wood
record. We know of no other megafossil record for this family.

**Muller First:** Pending.

**F. MELASTOMATACEAE** de Jussieu, 1789

**PFR First:** *Melastomites druidum* Unger, January–April 1850. Leaf. Tertiary: Eocene, Austria: Styria, Sotzka.

**Comments:** Seeds occur in the Miocene of Europe (Dorofeev, 1988; Collinson and Pingen, 1992; material previously misidentified as Portulacaceae). Hickey (1977) described Lower Eocene leaves as *Acrovena*, noting that all features could be matched only in this family. One other record is given for this genus in Taylor (1990). Other leaf records either require revision or have been rejected (Pingen and Collinson, in prep.).

**Muller First:** Pending.

**F. MELIACEAE** de Jussieu, 1789


**Comments:** Fruits occur in the Lower Eocene of England, UK (Chandler, 1964). Leaves similar to *Cedrela* are listed by Taylor (1990) from the Middle Eocene onwards in North America; in one Lower Oligocene example, leaves and seeds occur in association (Manchester and Meyer, 1987). Fruits like those of *Guarea* are also listed by Taylor (1990) from the Maastrichtian and Palaeocene. These may need revision.


**Comments:** Possible.

**F. MENISPERMAECEAE** de Jussieu, 1789


**Comments:** Endocarps diagnostic of the family are recorded in the Maastrichtian and Palaeocene of Europe (Collinson, 1986a; Knobloch and Mai, 1986; Mai, 1987a), although they are much more diverse in the Lower and Middle Eocene (Chandler, 1964; Collinson, 1988b), where leaves are also recorded (Wilde, 1989; Takhtajan, 1974). Endocarps are also diverse in the Middle Eocene of North America (Manchester *in* Knobloch and Kvacek, 1990, pp. 183–8), and one form is recorded in the Upper Palaeocene (Crane et al., 1990). Taylor (1990) lists numerous Eocene records with four Palaeocene examples. Crabtree (1987) states that an early Campanian leaf is 'entirely consistent with the leaf morphology of extant Menispermaeae'.

**Pollen:** No record.

**F. MENYANTHACEAE** Dumortier, 1829

**PFR:** No record.

**Comments:** Seeds like those of modern *Menyanthes* are recorded from the Oligocene onwards in Europe (Mai, 1985a). No record.

**F. MIMOSACEAE** Brown in Flinders, 1814

**PFR First:** *Accaciaphyllites grevilleoides* E. W. Berry, 1914. Leaf. Upper Cretaceous, USA: South Carolina: Chesterfield County, Middendorf.

**Comments:** Herendeen and Dilcher (1990c) documented leaves and fruits in association with *Eomimosoidea* in-florescences, and suggested these were all derived from a single plant species which shared several features with extant *Dinizia*. Isolated flowers from the Palaeocene/Eocene boundary were also assigned to this family (as Mimosoideae), although they shared certain characters with Caesalpinioideae (Crepet and Taylor, 1986).


**Comments:** Mutually supported by PFR and Muller. Records from the Lower Eocene are reviewed in Herendeen and Dilcher (1990c).

**F. MONIMIACEAE** de Jussieu, 1809


**PFR First:** *Protohedycarya ilicoides* (O. Heer) L. Ruffle, January 1965. Leaf. Cretaceous: Lower Senonian, Germany, Quedlinburg.

**Comments:** We find no evidence to confirm these early records, although Knappe and Ruffe (1975) also described European Santonian leaves. Leaves with some similarity to those of modern *Doryphora* occur in the Middle Eocene of Anglesea, Australia (Christophel and Greenwood, pers. comm., 1991). Gottwald (1992) assigned Upper Eocene Woods to two genera of Monimiaceae. Leaves like those of modern *Atherosperma* were reported from the Pliocene/ Pleistocene of Australia (Hill and Macphail, 1985) which is now considered to be Lower Middle Pleistocene (Hill, pers. comm., 1991).

**Muller First:** *Laurelia* type. Muller, 1970, Oligocene, New Zealand.

**Comments:** Muller, 1970; pending: may be too early.

**F. MORACEAE** Link, 1831

**PFR First:** *Arthmiocarpus hesperus* (Wieland) Delevoryas, 1964. Fruit. Upper Cretaceous, USA, South Dakota, Grand River valley, slightly west of its junction with Cottonwood Creek (Wieland, 1908).


**Comments:** The fossil record was reviewed by Collinson *in* Crané and Blackmore, 1989, who accepted several genera (including forms like those of modern *Ficus* and *Morus*) based on endocarps and achenes from the Lower Eocene of Eurasia. All earlier records were considered in need of critical revision and many leaf fossils and putative fleshy fruits, previously assigned to the family, were rejected.

**Muller First:** *Ficus* type, Potter, 1976. Middle Eocene, Tennessee, USA.

**Comments:** Unchallenged.

**F. MORINGACEAE** Dumortier, 1829

**PFR:** No record.

**Comments:** We know of no claims for megafossils of this family.

**Muller First:** Pollen record rejected.

**F. MUSACEAE** de Jussieu, 1789

**PFR First:** *Haastia speciosa* Ettingshausen, 1887. Leaf.
Upper Cretaceous, New Zealand: Pakawau, Nelson. This use of the genus is nomenclaturally invalid as it is a junior homonym of Haastia J. D. Hooker, 1864.

Comments: Large Musa-like leaves, including Musophyllum and Musocaulon (see comments on Cycanthaceae, and Boyd, 1990) should not be considered to belong in Musaceae, but may combine characters of Heliconiaceae and Strelitziaceae with those of Musaceae, or simply may not be diagnostic of any single family. One record of Musa fruits from the Eocene of the Deccan was noted by Daghlian (1981) and Manchester (in Knobloch and Kvacek, 1990, pp. 183–8) lists Musa as a component of the Middle Eocene Clarno flora.

Pollen: No record.

F. MYRICACEAE Blume, 1829

PFR First: Myricophyllum longepetiolatum C. von Ettingshausen, 1893 (post-13 April). Leaf. Cretaceous, Australia: Queensland, between Warragh and Oxley. This use of the genus is nomenclaturally invalid as it is a junior homonym of Myricophyllum G. Saporta, 1862, assigned to the Proteaceae.

Comments: Hill (1988) listed all Australian leaf fossils of Myricaceae as incorrectly identified. Macdonald (in Crane and Blackmore, 1989) reviewed the literature on fossil history for this family and concluded that megafossils diagnostic of Myricaceae could not be identified earlier than the Eocene. In Europe endocarps like those of Myrica occur in the Lower Eocene but are much more abundant from the Upper Eocene onwards (Chandler, 1964; Mai and Walther, 1978), Friis, 1985a). Comptonia foliage and endocarps also occur in the Oligocene onwards of Europe (Mai and Walther, 1978) and Middle Eocene leaves of Comptonia are reported in North America (Taylor, 1990). (See also discussion under Juglandaceae.)

Muller First: aff. Triatriopollenites sp. (form genus) Doyle and Robbins, 1977, Santonian, eastern USA.

Comments: May be too early: poor support from megafossils.

F. MYRISTICACEAE Brown, 1810

PFR First: Myristicoxylon princeps E. Boureau, 10 October 1950. Wood. Tertiary: Palaeocene of North America, while leaves assigned to modern Eugenia are listed by Taylor (1990) from the Middle Eocene. Myrtus seeds were described by Friis (1985a) from the Lower Miocene of Denmark. Leaves of Rhodomyrtophyllum are common in the Middle and Upper Eocene of Europe (Mai and Walther, 1985; Wilde, 1989; Walther, in Knobloch and Kvacek, 1990, pp. 149–58). Myrtaceae foliage is common in the Middle Eocene of Australia (Christophel and Greenwood 1987, 1988; Christophel et al., 1987). Leaves and fruits of Eucalyptus have also recently been reported from the Middle Eocene Nelly Creek flora (Greenwood, pers. comm., 1991).


Comments: Unchallenged.

F. NAJADACEAE de Jussieu, 1789


Comments: Seeds like those of modern Najas are common from the Oligocene onwards in Europe (Mai, 1985a; Collinson, 1988a).

Pollen: No record.

F. NELUMBONACEAE Dumortier, 1828

PRE: No record.

Comments: Leaves assigned to Nelumbo occur in the Lower Eocene of North America and Nelumbo is recorded from the Eocene onwards in Europe (listed by Mai, 1985a; Taylor, 1990). Nymphaealian leaves occur in the Upper Cretaceous (e.g. Crabtree, 1987), but these are generally not determinable to a modern family.

Muller First: Buraviocolpites venustus (form taxon) Bratzeva, 1976, Eocene, Siberia, former USSR.

Comments: Unchallenged.

F. NEPENTHACEAE Dumortier, 1829

PFR: No record.

Comments: We know of no claims for megafossils of this family.

Muller First: Nepenthes. Anderson and Muller, 1975. Lower Miocene, Borneo.

Comments: Unchallenged.

F. NYCTAGINACEAE de Jussieu, 1789

Comments: Berger (1954) referred to a Miocene record for Abronia, and Wolfe and Upchurch (1986) cited a possible Palaeocene record of the family. However, we know of no well-substantiated megafossils for this family.

**Muller First:** *Lymingtonia* (form genus) Muller, 1970. Lower Eocene, England, UK.

**Comments:** Supported.

**F. NYMPHAEACEAE** Salisbury, 1805

**PFR First:** *Brasenioptis venulosa* G. Saporta, June 1893. Leaf. Cretaceous: Albion, Portugal: Buarcos.

**Comments:** Nymphaealean leaves are common in the Upper Cretaceous, but generally cannot be assigned to a modern family (e.g. Crabtree, 1987). Palaeocene leaves are listed by Taylor (1990), but their exact family affinities are equally unclear. Seeds (Sabrenia and *Palaeonymphaea*) occur in the Upper Palaeocene (Collinson, 1980, 1986a), but many more forms occur from the Middle Eocene onwards in Europe, with one record in North America (Collinson, 1980; Mai, 1985a; Cevallos-Ferriz and Stockey, 1989). Collinson (1980) considered that certain extinct genera like *Sabrenia* were intermediate in characters between Cabombaceae and Nymphaeaceae s. s., whereas Cevallos-Ferriz and Stockey (1989) concluded that these two families were probably distinguishable by the Middle Eocene.

**Muller First:** Zonosulcites scollardensis and *Z. parvus* (form taxa) Srivastava, 1969b, Maastrichtian, Canada.

**Comments:** Unchallenged.

**F. NYSSACEAE** Dumortier, 1829


**Comments:** These Lower Eocene fruits of the family are highly diagnostic. *Protosynta* was later included in *Nyssa* and Mai and Walthier (1978) reported the *N. bilocularis* in the Lower, Middle and Upper Eocene of Europe. Middle Oligocene fruits are reported from North America (Taylor, 1990).

**Muller First:** Tricolporopollenites krusi (form taxon). Haseldonckx, 1973, Palaeocene, Spain; Gruas-Cavagnetto, 1978, Palaeocene, France.

**Comments:** Possible.

**F. OCHNACEAE** de Candolle, 1811

**PFR:** No record.

**Comments:** Chesters et al. (1967) cited a North American Eocene record of *Ouratea*, but this was not listed by Taylor (1990).

**Muller First:** Pending.

**F. OLACACEAE** Mirble ex de Candolle, 1824

**PFR:** No record.

**Comments:** The record for this family is sporadic. Fruits like those of modern *Olax* and *Erythrophllum* occur in the Lower Eocene of England, UK (Chandler, 1964). Leaves assigned to *Schoepfia* occur in the Middle Eocene of North America (Taylor, 1990). The *Olax* fruit listed by Taylor (1990) was not listed by Manchester (in Knobloch and Kvacek, 1990, pp. 183–8) in his summary of the Clarno flora, and Manchester (pers. comm., 1991) has confirmed that Olacaceae are not represented in the Clarno Flora; the supposed *Olax* fruits being *Musa* seeds.


**Comments:** Well supported palynologically.

**F. OLEACEAE** Hoffmannsegg and Link, 1813–1820

**PFR First:** *Oleiphylum boreale* Convenzt, 1886. Leaf. Lower Tertiary, Germany: Western Prussia.

**Comments:** Many examples of leaves and fruits assigned to *Fraxinus* are listed by Taylor (1990) from the Palaeocene onwards in North America. However, we are not aware of any recent revision of this record. Wolfe (pers. comm., 1991) accepts Middle Eocene and later records. Endocarps like those of modern *Olea* are recorded in the Upper Eocene of England, UK (Chandler, 1964), and seeds like those of modern *Jasminium* occur in the Miocene and Pliocene of Europe (Szafer, 1961).

**Muller First:** Retticorbitipes oleoides (form taxon). Roche and Schuler, 1976. Oligocene, Belgium.

**Comments:** Unchallenged.

**F. ONAGRACEAE** de Jussieu, 1789


**Comments:** This is an isolated record, but we know of no reason to reject it. Seeds like those of modern *Ludwigia* are common from the Middle Oligocene onwards, especially in the Miocene, of Europe (Friis, 1985a; Mai, 1985a).


**Comments:** Unchallenged.

**F. OPILIAEAE** Valeton; 1886


**Comments:** We are unable to comment on this wood record. We know of no other megafossil record for this family.

**Pollen:** No record.

**F. ORCHIDACEAE** de Jussieu, 1789


**Comments:** Schmid and Schmid (1973) concluded that the family had no reliable fossil record, but considered a Pliocene example (Strauss, 1969) as most plausible. Friis (1985a) described a Lower Miocene seed which was tentatively compared with Orchidaceae.

**Muller First:** Pending.

**F. OROBANCHACEAE** Ventenat, 1799

**PFR:** No record.
Comments: We know of no claims for megafossils of this family.
Comments: Unchallenged.

F. OXALIDACEAE Brown, in Tuckey, 1817
Comments: Seeds like those of modern Oxalis were recorded by Mai and Walther (1988) in the Pliocene of Germany. Leaves (Averrhoites Hickey) described by Hickey (1977) were morphologically similar to leaves of this family, but this was not considered to indicate a close relationship.
Pollen: No record.

F. PANDANACEAE Rudolphi, 1830 (see RANUNCULACEAE)

F. PANDANACEAE Brown, 1810
Comments: Daghlian (1981) stated that the Pandanaceae have no reliable fossil record, although it is not clear if he considered and rejected all possible records such as the Oligocene to Miocene material from Europe summarized in Beucher, 1975, Pliocene, Sahara.
Comments: Unchallenged.

F. PAEONIACEAE Rudolphi, 1830 (see RANUNCULACEAE)

F. PAEONIACEAE Brown, 1810
PFR First: Ref. F. Brown, 1848, 1836 (post-30 May). Fruit. Jurassic, UK, England was assigned to modern Papaver. Myers (1926) listed the family as having been assigned to the family. We know of no other fossil record for this family.
Comments: This PFR record was only tentatively assigned to the family. We know of no well-substantiated megafossils of this family.
Pollen: No record.

F. PAPAVERACEAE de Jussieu, 1789
PFR: No record.
Comments: A single seed from the Uppermost Eocene of England was assigned to modern Papaver by Reid and Chandler (1926). The original has deteriorated and no new specimens have been found. Dorofeev (1969) recorded seeds like those of modern Macleaya from the Middle Miocene. We consider these isolated records to be unconfirmed.

F. PASSIFLORACEAE de Jussieu ex Kunth, 1817
Comments: Seeds like those of modern Passiflora were described from the Middle Miocene of Europe by Mai (1964) and Gregor (1978, 1982). We know of no well-substantiated leaf record of this family.
Muller First: Pending.

F. PEDALIACEAE Brown, 1810
PFR: No record.
Comments: Fruits of Trapella (Trapelliaceae of many authors) occur in the Miocene onwards in Europe (Mai, 1985a; Collinson, 1988a).

F. PELLICIERACEAE Beauvisage, 1920
PFR: No record.
Comments: Fruits from the Upper Cretaceous of Europe were described as two species of a new genus Allericarpus Knobloch and Mai; others were included in an extinct species of the modern genus Pentaphylyx (Knobloch and Mai, 1986). We know of no other fossil record for this family and thus consider that these isolated records should be treated with caution.
Pollen: No record.

F. PHYTOLACACEAE Brown, in Tuckey, 1819
PFR First: Stachycarpus eocenica Meunier, 1898. Fruit. Tertiary: Eocene, France: Béthune, Beuvry. This use of the genus is nomenclaturally invalid as it is a junior homonym of Stachycarpus (Endlicher) Van Tieghem, 1891.
Comments: This PFR record was only tentatively assigned to the family. We know of no well-substantiated megafossils of the family.
Pollen: No record.

F. PIPERACEAE Agardh, 1825
Comments: Seeds like those of modern Peperomia were recorded by Dorofeev (1988) from the Miocene of Siberia and Tambov, former USSR.
Pollen: No record.

F. PITOSPORACEAE Brown, in Flinders, 1814
Comments: This was the only megafossil noted by Friis and Skarby (1982) as having been assigned to the family. The determination should be considered unconfirmed.
Comments: Unchallenged.

F. PLANTAGINACEAE de Jussieu, 1789
PFR: No record.
Comments: Seeds like those of modern Plantago are recorded in the Pliocene of Poland (Szafer, 1954).
Comments: Unchallenged.
F. PLATANACEAE Dumontier, 1829

Muller First: *Gilia filififormis* type Muller, 1970. Upper Miocene, USA

Comments: Unchallenged.

F. POLYGALACEAE Brown, in Flinders, 1814

PFR: No record.

Comments: We know of no published megafossils of this family, but Wolfe (pers. comm., 1991) has an unpublished leaf of *Securidaca* from the Lower Miocene of Oregon.

Muller First: *Psilasterphancoecolitrites fissilis* (form taxon). Doubinger and Chotin, 1975, Palaeocene, Chile.

Comments: Unchallenged.

F. POLYGONACEAE de Jussieu, 1789

PFR: No record.

Comments: We know of no claims for megafossils of this family.


Comments: Unchallenged.

F. POACEAE Barnhart, 1895

PFR: No record.

Comments: We know of no claims for megafossils of this family.


Comments: Unchallenged.

F. POLEMONIACEAE de Jussieu, 1829

PFR: No record.

Comments: We know of no claims for megafossils of this family.

Muller First: *Potamogeton.* Upper Miocene: Van Campo.

Comments: No record.

F. POSIDONIACEAE Lotsy, 1911

PFR: No record.

Comments: Daghlian (1981) considered that this family did not have a megafossil record inspite of several claims in the literature.

Muller First: *Potamogeton.* Upper Miocene: Van Campo.

Comments: No record.

F. POTAMOGETONACEAE Dumontier, 1829


Comments: Fruits like those of modern *Potamogeton* are widespread from the lower Middle Eocene onwards in Europe and Asia (Collinson, 1982, 1988a; Mai, 1985a) and leaves assigned to *Potamogeton* are listed by Taylor (1990) from the Middle Eocene of North America. Fruits named *Limnocarpus* (and related fossil genera), often assigned to this family, are considered intermediate between those of this family and Ruppiaceae (Collinson, 1982). (See comments on Ruppiaceae.)

Muller First: *Potamogeton.* Upper Miocene: Van Campo.
Comments: Unchallenged.

F. PRIMULACEAE Ventenat, 1799

PFR: No record.

Comments: Seeds like those of modern Lysimachia are recorded from the Upper Oligocene onwards in Europe and Asia (Friis, 1985a).


Comments: Unchallenged.

F. PRISCACEAE Retallack and Dilcher, 1981

Upper Cretaceous only

PFR: No record.

First: Prisca reynoldsii Retallack and Dilcher, 1981. Fruiting axis with associated leaves. Lower Cenomanian, Dakota Formation, central Kansas, USA.

Comments: Kvacek (1992) proposes that other material of leaves and reproductive structures from the European Upper Cretaceous should be included in the family. The family is closely related to Lauraceae, within Laurales (Kvacek, 1992) and the reproductive structures are similar to the lower Cenomanian material from Maryland included in Lauraceae by Drinnan et al. (1990). (See comments on Lauraceae.)

Pollon: No record. No pollen is preserved in any of the reproductive structures mentioned by the above authors.

F. PROTEACEAE de Jussieu, 1789


PFR First: Rogersia sp. 1889. L Cretaceous, Potomac Group, USA.

Comments: Proteaceae are now well documented in the Middle Eocene onwards in Australia. Records include foliage similar to modern Banksia and Dryandra of tribe Banksieae (Banksiaephyllum Cookson and Duigan, 1950 – Hill and Christophel, 1988); foliage similar to modern Lomatia (Carpenter and Hill, 1988) and inflorescences of Mussgraveanthes alcoensis Christophel (1984) also of tribe Banksieae. Leaves and fruits assigned to Lomatia from the Middle Eocene onwards in North America are listed by Taylor (1990), but these require confirmation.


Comments: There is no evidence from megafossils for such an early origin.

F. PUNICACEAE Horaninow, 1834

PFR First: Punicites hesperidum C. O. Weber, December 1855. Flower. Tertiary, Germany, Rott. This genus was only tentatively assigned to this family.

Comments: Friis (1985a) rejected the earlier assignment by Gregor of Carpolithes natans Niktin ex Dorofeev to modern Punicia citing differences such as the absence of a heteropyle and presence of a raphal chamber on the opposite side of the seed to the germination valve in the fossils. The species occurs in the Middle Oligocene to Upper Miocene in Europe. Gregor (1978) recorded fruits and seeds of another species, which he assigned to Punica, from the Middle Miocene of Germany.

Pollen: No record.

F. RANUNCULACEAE de Jussieu, 1789


Comments: The PFR record may perhaps belong in Paeoniaceae sensu Cronquist (1981). Fruits of Myosurus were recorded in the Upper Oligocene of Germany and England, UK (Mai and Walther, 1978). Fruits like those of Ranunculus are recorded from the Oligocene onwards in Europe and former USSR (Mai, 1985a; Lancucka-Srodoniowa, 1979; Takhtajan, 1974).

Muller First: Punctioratipollis ludwigi (form taxon). Krutzsch, 1966c, Lower Miocene, Germany.

Comments: According to megafossils this record is too late.

F. RESEDACEAE Gray, 1821

PFR: No record.

Comments: We know of no claims for megafossils of this family.


Comments: Unchallenged.

F. RESTIONACEAE Brown, 1810


Comments: This PFR record was only tentatively assigned to the family. No megafossil record was accepted for this family by Daghlian (1981).


Comments: See Milfordia within Centrolepidaceae; possibly from an extinct family.

F. RHAMNACEAE de Jussieu, 1789


Comments: Leaves from the Middle Eocene onwards are listed for North America by Taylor (1990). Wolfe (pers. comm., 1991) considers that Maastrichtian and Palaeocene leaves from North America may be assigned to the family. Fruits and seeds like those of modern Paliurus occur in the Middle Miocene of Denmark (Friis, 1985a) and like those of modern Zizyphus in the Lower Miocene of Kenya (Chesters, 1957).


Comments: Unchallenged.

F. RHIZOPHORACEAE Brown, in Flinders, 1814


Comments: Viviparous embryos of Ceriops have also been reported from the Lower Eocene of England (Wilkinson, 1981). Leaves assigned to Kandelia from the Middle Eocene of North America are listed by Taylor (1990).

**Comments:** Unchallenged.

F. *RHOIPTLEACEAE* Handel-Mazzetti, 1932

**PFR:** No record.

**Comments:** Fruits assigned to *Rhoiptelea pontwallensis* (Vangerow) Knobloch and Mai, 1986 were recorded from the Maastrichtian of Europe. We know of no other mega-fossil record for this family and, in view of the complexity of Upper Cretaceous Juglandales/Myricales (discussed under 'Juglandaceae'), feel that this record should be considered as unconfirmed.

**Muller First:** Pending.

F. *ROSACEAE* de Jussieu, 1789


**Comments:** Numerous examples are listed by Taylor (1990) from North America, which include several well-substantiated Middle Eocene leaves (of Spiraeoideae and Rosoideae) and one flower. One citation is from the Maastrichtian, and leaves and fruits named *Prunus* (Prunoideae) are listed in the Palaeocene. Woods of Prunoideae are known from the Lower Eocene onwards (Cevallos-Ferriz and Stockey, 1990c). The record of *Prunus* fruits in Europe (from the Eocene onwards) was reviewed in detail by Mai (1984). Foliage of Rosaceae is recorded in the Middle Eocene of Europe (Wilde, 1989).


**Comments:** Unchallenged.

F. *RUBIACEAE* de Jussieu, 1789


**PFR First:** *Paleorubusceaphyllum ecenicum* (E. W. Berry) J. L. Roth and D. L. Dilcher, 10 December 1979. Leaf. Tertiary: Eocene, USA.


**Comments:** Taylor (1990) lists foliage from the Middle Eocene onwards in North America. Vauudos-Mieja (1976) documented fruits from the Lower Eocene of France. *Cephalanthus* fruits are widespread from the Upper Eocene onwards in Europe (Friis, 1985a; Mai and Walther, 1985).

**Muller First:** *Tripotretidites natcherstedtensis* (form taxon). Krutzsch, 1970b. Oupper Eocene, Germany.

**Comments:** Unchallenged.

F. *RUPPIACEAE* Hutchinson, 1934

**PFR:** No record.

**Comments:** Fruits of the extinct *Limmocarpus* and related genera were considered to be intermediate in character between Ruppiaceae and Potamogetonaceae (Collinson, 1982). These occur from the Upper Palaeocene onwards in Europe and former USSR. Fruits identical with those of modern *Ruppia* were only recognized in the Pleistocene by Collinson (1982), who considered that Miocene fossil fruits (*Midratula* Collinson, *Medardus* Collinson and a grouping of ‘fossil Ruppia’) were closest to modern *Ruppia* but somewhat intermediate between that genus and Potamogetonaceae.

**Muller First:** Pending.

F. *RUTACEAE* de Jussieu, 1789


**Comments:** Rutaceae are well documented from seeds from the Eocene onwards in North America, Europe and Asia (e.g. Collinson and Gregor, pp. 67–80, in Collinson, 1988c; Gregor, 1989), and seeds were also reported from the Maastrichtian (Knobloch and Mai, 1986) and Palaeocene (Mai, 1987a). Leaves occur in the Middle Eocene of Europe (Wilde, 1989) and North America (Taylor, 1990).


**Comments:** Possible.

F. *SABIACEAE* Blume, 1851

**PFR First:** *Sabioeaulis sakuraiii* M. C. Stopes and K. Fuji, 14 February 1910. Stem, Upper Cretaceous, Japan, Hokkaido.

**Comments:** Endocarps like those of modern *Sabella* and *Meliosma*, as well as an extinct form *Institiocarpus* Knobloch and Mai, were recorded by Knobloch and Mai (1986) in the Maastrichtian of Europe. Palaeocene examples are reported by Crane *et al.* (1990) and Mai (1987a) from North America and Europe, respectively. Leaves assigned to *Meliosma* are listed by Taylor (1990) from the Palaeocene onwards in North America.

**Pollen:** No record.

F. *SALICACEAE* Mirbel, 1815

**PFR First:** *Credneria integerrima* Zenker, 1833. Leaf. Upper Cretaceous, Germany: Blankenburg.

**PFR First:** *Dryoxylon jenense* Schleiden, 1853. Wood. Middle Triassic, Germany: near Jena.

**Comments:** Well-substantiated Salicaceae occur in the uppermost Palaeocene (*Populus*) and Lower Eocene (*Salix*) of North America. Middle Eocene examples of both genera are based on connected foliage and reproductive organs (Manchester *et al.*, 1986).

**Muller First:** *Salix*. Graham and Jarzen, 1969, Oligocene, Puerto Rico.

**Comments:** Unchallenged.

F. *SANTALACEAE* Brown, 1810

**PFR First:** *Thesianthium inclusum* Conwentz, 1886. Flower. Lower Tertiary, Germany: West Prussia.

**Comments:** Mai (1976) described seeds assigned to modern *Santalum* from the Middle Eocene of Germany. Chesters *et al.* (1967) cited a North American Cenomanian leaf, but this is not listed by Taylor (1990).

**Muller First:** *Santalumidites canosicius* (form taxon). Cookson and Pike, 1954, Eocene, Australia.

**Comments:** Unchallenged.

F. *SAPINDACEAE* de Jussieu, 1789

**PFR First:** *Sapindopsis cordata* Fontaine, 1889. Leaf fragment. L Cretaceous.

**Comments:** The fossil record for Sapindaceae is rather sporadic. Seeds (assigned to *Sapindospermum* Reid and Chandler) occur in Europe in the Maastrichtian (Knobloch and Mai, 1986). A variety of fruit and seed forms and twigs
occur in the Lower Eocene of England, UK (Chandler, 1964, Wilkinson, in Collinson, 1988c, pp. 81–6). In a review of the fossil record for Sapindaceae, Erwin and Stockey (1990) do not accept any Cretaceous megafossils from North America, but note various Palaeocene and Eocene leaf forms (see also list in Taylor, 1990). Erwin and Stockey (1990) described flowers from the Middle Eocene of Canada as *Wehrwoofea* Erwin and Stockey which they assign to Sapindaceae. Wolfe and Tanai (1987) discuss the extinct forms (see also list in Taylor, 1990). Erwin and Stockey (1990) described flowers from the Middle Eocene of Canada as *Wehrwoofea* Erwin and Stockey which they assign to Sapindaceae. Wolfe and Tanai (1987) discuss the extinct fruit *Bohienia*, which is somewhat intermediate between Aceraceae and Sapindaceae. Fruits of *Pteleacarpus*, which range from the Eocene to Miocene in Europe, Asia and North America, were assigned to Sapindaceae (Buzek et al., 1989). However, this assignment was incorrect (Manchester, pers. comm., 1991).

**Muller First:** *Tricolporites* sp. (form genus). Kemp, 1976. Middle Eocene, central Australia.

**Comments:** Tricolporate pollens are notoriously difficult to name and to assign to modern taxa.

**F. SAPOTACEAE de Jussieu, 1789**


**Comments:** The fossil record of the Sapotaceae is scant, but we have no reason to reject these Lower Eocene fruit and seed records. Foliage also occurs in the Middle Eocene of Europe (Wilde, 1989).

**Muller First:** *Sapotaceoidae pollenites robustus* (form taxon). Muller, 1970, Senonian, Borneo.

**Comments:** Unchallenged.

**F. SARGENTODOXACEAE Stapf, ex Hutchinson, 1926**

**PFR:** No record.

**Comments:** Tiffney (pers. comm., 1992) has recognized seeds of this family in the Oligocene Brandon lignite, Vermont, USA. Details of the locality may be found in Tiffney and Barghoorn (1979).

**Pollen:** No record.

**F. SAURURACEAE Meyer, 1827**

**PFR First:** *Saururopsis nipponensis* M. Stopes and Fujii, March 1910. Stem. Upper Cretaceous, Japan: Hokkaido. This use of the genus is nomenclaturally invalid as it is a junior homonym of *Saururopsis* Turczaninow, 1848.

**Comments:** Seeds like those of modern *Saururus* range from the Upper Eocene to the Pliocene in Europe (Friis, 1985a).

**Pollen:** No record.

**F. SAXIFRAGACEAE de Jussieu, 1789**


**Comments:** This fruit was reassigned to Flacourtiaeaceae (Chandler, 1964). *Saxifragaceaecarpum* was reassigned to Loganiaceae (Mai, 1968). Several Upper Cretaceous Saxifragalean flowers have been reported (Friis, 1990), but these combine features of modern Saxifragaceae with those of Hydrangeaceae and Escalloniaceae (= Grossulariaceae *sensu* Cronquist), perhaps being most similar to the latter.

Leaves listed as Saxifragaceae in the Upper Oligocene of North America (Taylor, 1990, p. 302) are Hydrangeaceae *sensu* Cronquist (*Philadelphus, Jamesia* and *Fendlera*). Flowers from the Baltic amber previously included in Saxifragaceae should not be included in the family, due to lack of information on the androecium (Friis and Skarby, 1982). Seeds like those of modern *Chrysosplenium* and *Mitella* have been recorded in the Pliocene of Europe (noted in Friis and Skarby, 1982).

**Pollen:** No record.

**F. SCHEUCHZERIACEAE Rudolphi, 1830**

**PFR:** No record.

**Comments:** Chesters et al. (1967) cite a Pliocene record. We know of no well-substantiated megafossil record for this family.

**Pollen:** No record.

**F. SCHISANDRACEAE Blume, 1830**

**PFR:** No record.

**Comments:** Leaves like those of modern *Schisandra* are recorded in the Upper Eocene of Europe (Mai and Walther, 1985; Wilde, 1989) and fruits of *Schisandra* are listed by Manchester (in Knobloch and Kvacek, 1990, pp. 183–8) from the Middle Eocene of North America.

**Muller First:** *Schisandra* type. Chmura, 1973, Maastrichtian, California, USA.

**Comments:** Unchallenged.

**F. SCROPHULARIACEAE de Jussieu, 1789**

**PFR First:** *Paulownioxyylon hondoense* S. Watar, 1948. Wood. Tertiary, Lower Miocene, Japan, Hanenisi, Simane Prefecture, Kute Toun, Anno District.

**Comments:** Seeds like those of modern *Limosella* are recorded from the Upper Eocene onwards in Europe (Mai and Walther, 1985). Seeds of *Gratiola* are recorded from the Upper Miocene of Poland (Lancucka-Srodoniowa, 1979).

**Muller First:** Pending.

**F. SIMAROUBACEAE de Candolle, 1811**


**Comments:** Fruits like those of modern *Ailanthus* occur from the Middle Eocene onwards in North America (Taylor, 1990) and they are also recorded in the Middle Eocene of Europe (Collinson, 1988b).

**Muller First:** Pending.

**F. SMILACACEAE Ventenat, 1799**


**Comments:** Several leaf forms with morphology and cuticular details similar to those of modern *Smilax* are assigned to Smilacaceae (as Smilacoideae) from the Middle Eocene of Messel, Germany; other examples occur in the Oligocene and Miocene in Europe (Mai and Walther, 1978; Wilde, 1989). One leaf of this type was noted in the Oligocene of North America (Taylor, 1990).

**Muller First:** *Smilax*. Graham, 1976. Upper Miocene, Mexico.

**Comments:** Unchallenged.
F. SOLANACEAE de Jussieu, 1789

Comments: This is an isolated record, but we have no reason to reject it. Seeds like those of modern Physalis are recorded in the Middle Miocene and Pliocene of Europe (Zsafer, 1961) and seeds like those of modern Solanum are reported from the European Middle to Upper Miocene (Gregor, 1982; Van der Burgh, 1987).

Pollen: No record.

F. SONNERATIACEAE Engler and Gilg, 1924

Comments: Mehrotta (1988) described a wood from the Lower Tertiary, Deccan Intertrappean Beds as a species of Sonneratia and critically reviewed other records.

Comments: Unchallenged.

F. SPARGANIACEAE Rudolphi, 1830

Comments: Fruits like those of modern Sparganium are known from the Upper Eocene onwards in Europe (Chandler, 1964; Mai and Walther, 1978; Mai, 1985a; Friis, 1985a).

Comments: These monoporate pollens may be from an extinct group with ecological, facies or systematic connections to the Typhaceae, Centrolepidaceae and Restionaceae.

F. STACHYURACEAE Agardh, 1858

PFR: No record.
Comments: Seeds like those of modern Stachyurus were described from the Middle Miocene of Germany (Mai, 1964).
Pollen: No record.

F. STAPHYLEACEAE Lindley, 1829

PFR: No record.
Comments: Fruits like those of modern Tapiscia occur in the Lower and Middle Eocene of Europe and North America (Manchester, in Collinson, 1988c, pp. 59–66). Leaves, seeds and woods assigned to Staphylea and Turpinia are listed by Taylor (1990) from the Upper Palaeocene onwards in North America.

Comments: Unchallenged.

F. STEMONACEAE Engler, in Engler and Prantl, 1887

PFR: No record.
Comments: Numerous species of Spirella Knobloch and Mai were described from the Upper Cretaceous of Europe (Knobloch and Mai, 1986). Two of these (Maastrichtian to Lower Palaeocene) were tentatively assigned to Stemonaeeae by Mai (1987a). This is an isolated fossil record of the family and requires confirmation.

Pollen: No record.

F. STERCULIACEAE Bartling, 1830

Comments: These woods are critically documented Middle Eocene examples of the family. Leaves, some similar to modern Sterculia, others to modern Dombeya, are recorded from the Lower, Middle and Upper Eocene of Europe and North America (Wilde, 1989; Taylor, 1990). The Palaeocene leaves listed by Taylor (1990) as ‘Pterospermites’ Penosphyllum’ were not considered as members of the Sterculiaceae by Manchester (1980).

Muller First: Reveisapollenites spp. (form genus), Krutzsch, 1970f, Palaeocene, Germany.
Comments: Unchallenged.

F. STRELITZIACEAE Hutchinson, 1934

PFR: No record.
Comments: Zhilin (1974b) assigned an Upper Oligocene/Lower Miocene leaf to Strelitzia sp., but this was not mentioned by Daghlan (1981). Zhilin (1989, p. 258) included other Upper Oligocene leaves in Strelitzia. (See also comments under ‘Musaceae’ and ‘Cyclanthaceae’.)
Pollen: No record.

F. STYRACACEAE Dumortier, 1829

PFR: No record.
Comments: Leaves assigned to Styrax are listed by Taylor (1990) from the Middle Eocene of North America, but these may require revision. Fruits like those of modern Pterostyrax were recorded by Mai and Walther (1985) in the Upper Eocene of Europe, and fruits like those of modern Rehderodendron have been recorded in the Lower Eocene of England, UK, and France (Vaudois-Mieja, 1983).
Pollen: No record.

F. SURIANACEAE Arnott, in Wight and Arnott, 1834

PFR: No record.
Comments: Taylor (1990) noted a wood from the Eocene of North America assigned to this family, but indicated that the record required confirmation or reinvestigation.
Pollen: No record.

F. SYMPLOCACEAE Desfontaines, 1820

Comments: Fruits like those of modern Symphloes occur in the Lower Eocene onwards in Europe (Mai and Walther, 1985; Chandler, 1964) and leaves like those of Symphloes occur in the Middle Eocene of Europe (Wilde, 1989) and North America (Taylor, 1990).

Comments: Too early.
Pollen: No record.
F. TACCACEAE Dumortier, 1829

PFR: No record.
Comments: Seeds like those of modern Taca were recorded by Gregor (1983) from the Oligocene of Czechoslovakia.
Pollen: No record.

F. TAMARICACEAE Link, 1821

PFR First: Tamarixylon africanum (Kräusel) Bourbeau, 1951. Quaternary, Somaliland.
Comments: Gokhtuni and Takhtajan (1988) have recorded shoots like those of modern Tamarix from the uppermost Miocene of the former USSR.
Pollen: No record.

F. TETRACENTRACEAE Van Tieghem, 1900

PFR: No record.
Comments: Leaves assigned to Tetracentron (the only modern genus in the family) are recorded from the Upper Cretaceous and Lower Tertiary of North America, Europe and the former USSR (Takhtajan, 1974; Wolfe, 1977). However, some of these leaves are associated with (or very similar to those associated with) the partially reconstructed plants assigned to Cercidiphyllaceae and Trochodendraceae (see discussion on these families). Confirmation of a fossil record for Tetracentraceae must await complete revision of all the leaf fossils and recovery of appropriate reproductive material.
Muller First: See comments on Trochodendraceae.

F. THEACEAE Don, 1825

Comments: In their review of fossil Theaceae, Grote and Diller (1989) considered all North American Cretaceous and Palaeocene leaf records as needing revision. They cited unpublished Gordania-like fruits from the Middle Eocene and described new Middle Eocene fruit material of subfamily Camellioideae. Seeds like those of modern genera in the family) are recorded from the Upper Cretaceous and Lower Tertiary of North America.
Comments: Unchallenged.

F. THEOPRISTACEAE Link, 1829

Comments: We know of no well-substantiated mega-fossils of this family.
Pollen: No record.

F. THYMELAEACEAE de Jussieu, 1789

PFR First: Daphnites goepperi Ettingshausen, post-7 February 1867. Leaf. Cretaceous, Austria: Aigen. This use of the genus is considered by some to be nomenclaturally invalid as a junior homonym of Daphnites K. P. J. Sprengel, 1824.
Comments: Taylor (1990) lists an unpublished flower of this family from the Upper Palaeocene of North America. Mai and Walther (1978, 1985) recorded fruits like those of modern Agulila from the Lower Eocene to Middle Oligocene and seeds of Thymelaeaspermum from the Middle Eocene to Miocene in Europe.
Muller First: Pseudospinaepollis pseudospinosus (form taxon) Krutzsch, 1966a, Germany; Gruas-Cavagnetto, 1976a, England, UK.
Comments: Unchallenged.

F. TILIACEAE de Jussieu, 1789

Comments: Leaves like those of modern Tilia and Willisia are recorded from the Middle Eocene of North America (Taylor, 1990). Several fruits are recorded in the Lower Eocene of Europe (Chandler, 1964; Vaudois-Miéja, in Collinson, 1988c, pp. 31–44).
Comments: Unchallenged.

F. TRAPACEAE Dumortier, 1828

Comments: Mai (1985a, fig. 485) gives an elegant diagrammatic representation of the fossil record of this family, which is represented by fruits assigned to Hemitropa in the Upper Oligocene and to modern Trapa in the Miocene onwards in Europe. Fruits or seeds superficially similar (and previously assigned to Hemitropa) from the Lower Cretaceous of Australia were rejected as not angiospermous (Drinnan and Chambers, 1986).
Muller First: Sporotropoidites illingensis (form taxon) Konzaloa, 1976a, Lower Miocene, Czechoslovakia.
Comments: Unchallenged.

F. TROCHODENDRACEAE Prantl, in Engler and Prantl, 1888

PFR First: Trochodendroides rhomboides (Lesquereux) E. W. Berry, 23 March 1922. Leaf. Upper Cretaceous, Arthur's Bluff, Texas, USA.
Comments: The extinct, partially reconstructed Nordenskioeldiabplant, represented by associated infructescences and leaves (Crane et al., 1990, 1991) is assigned to this family. It was widespread from the Palaeocene onwards in the Northern Hemisphere and ranges into the Miocene (Crane et al., 1991; Manchester et al., 1991). Trochodendron is first known in the Miocene (Manchester et al., 1991). Upper Cretaceous material may also represent Nordenskioldia (Friis and Crane, in Crane and Blackmore, 1989), but this has not been confirmed. (See also comments on Tetragynaceae.)
Muller First: Rejected; no record.

F. TRIMENIACEAE Gibbs, 1917

PFR: No record.
Comments: We know of no claims for mega-fossils of this family.
Muller First: Pending.

F. TURNERACEAE de Candolle, 1828

PFR: No record.
Comments: We know of no claims for megafossils of this family.

Muller First: Pending.

F. TYPHACEAE de Jussieu, 1789


Comments: Fruits and seeds like those of modern Typha are widespread in the Upper Cretaceous onwards in Europe (Mai, 1985a; Knobloch and Mai, 1986; Collinson, 1988a). Grande (1984, p. 265) figures a striking example of a complete spike of Typha sp., probably in the fruiting condition, from the Lower Eocene of North America.

Muller First: Typha latifolipites Wilson and Webster, 1946. Palaeocene, Montana, USA.

Comments: Pollen may be difficult to distinguish from that of the Sparganiaceae.

F. ULMACEAE Mirbel, 1815


Comments: Manchester (in Crane and Blackmore, 1989) reviewed the fossil history of the family and, while accepting Upper Cretaceous (Santonian–Campanian) and Palaeocene foliage as examples of Ulmoideae, noted that no well-substantiated fruits of the subfamily were known until the Eocene. In the Eocene, leafy shoots with attached fruits are known for Ulmus, Zeikova and an extinct genus Cedrello spernum. The fossil record of Celtidaceae includes foliage, fruit and flowers, with the earliest examples being fruits from the Maastrichtian of Europe and Palaeocene of North America.

Muller First: Triorites minutipora (form taxon) Muller, 1968. Turonian, Sarawak.

Comments: Unchallenged.

F. URTICACEAE de Jussieu, 1789


Comments: The PFR record was only tentatively assigned to the family. Collinson (in Crane and Blackmore, 1989) reviewed the fossil history and was unable to confirm any records prior to the Upper Cretaceous. Cretaceous fruits assigned to the family were dissimilar to modern examples. Fiis and Crane (in Crane and Blackmore, 1989) suggested that some of these might be similar to Carpinusus a genus of Cretaceous Juglandales/Myricales. Fruits like those of modern Pllea and Lapoeta occur in the Oligocene onwards in Europe and Asia.

Muller First: Pending.

F. VALERIANACEAE Batsch, 1802


Comments: The PFR record was only tentatively assigned to the family. Fruits like those of modern Patrinia occur in the Miocene to Pliocene of Europe and the former USSR (Lańcucka-Środoniowa, 1979; Dorofeev, 1988) and Mai (1985a) lists Valeriana from the Miocene onwards in Europe.

Muller First: Pending.

F. VERBENACEAE Jaume St-Hilaire, 1805


Comments: Taylor (1990) lists several occurrences of a flower said to be similar to Holmkioldia, but notes that revision is required. Manchester and Meyer (1987) note that flowers given this name are the same as those of Florissantia physalis Knowlton (and others termed Porana spiri). They possess a large, fused, five-lobed perianth, five-carpedell ovary with a single style. They are considered to represent an extinct plant, possibly within Malvales, and are thus unlikely to represent Verbenaceae (Lamiales). The only other fossils listed for this family by Taylor (1990) are Middle Eocene leaves assigned to modern Clerodendrum. Bande (1986) recorded wood like that of modern Gmelina from the Lower Tertiary Decan Intertrappean Beds of India.


Comments: Unchallenged.

F. VIOLACEAE Batsch, 1802

PFR First: No record.

Comments: Several species of Viola are represented by seeds in the Oligocene to Pliocene of Europe (Lańcucka-Środoniowa, 1979).

Muller First: Pending.

F. VISCACEAE Miers, 1851

PFR First: Viscoxylon huastoria from within Pinus wood from the Upper Miocene of Germany. Although originally assigned to Loranthaceae, a close comparison was indicated with Viscum which is placed in Viscaceae sensu Cronquist (1981). Flowers and fruits like those of modern Arceuthobium occur in the Upper Miocene of Poland (Lańcucka-Środoniowa, 1980).

Comments: Unchallenged.

F. VITACEAE de Jussieu, 1789


Comments: Vitaceae are well represented by seeds from the Upper Cretaceous onwards in Europe (Chandler, 1964; Mai and Walther, 1979, 1985; Collinson, 1986a; Mai, 1987a). Foliage is recorded from the Middle Eocene (Wilde, 1989) and Upper Eocene to Oligocene (Mai and Walther, 1985) of Europe. Notably, the strongly diagnostic seeds are not recorded in the Upper Cretaceous material of Knobloch and Mai (1986). Seeds are also well represented in the Middle Eocene of North America (Manchester, in Knobloch and Kvacek, 1990, pp. 183–8; Cevallos-Ferriz and Stockey, 1990b) and foliage is listed by Taylor (1990) from the Palaeocene onwards in North America.


Comments: Unchallenged.

F. VOCHYSIACEAE St-Hilaire, 1820

PFR First: Qualeoxylon itaquaquacutubense K. Suguio and

Comments: We know of no earlier claims for megafossils of this family.

Pollen: No record.

F. WINTERACEAE Lindley, 1820

PFR: No record.

Comments: The one example of fossil leaves included in Winteraceae (Takhtajan, 1974) had been revised and included in Magnoliaceae by Kirchheimer (1957). Hill and Macphail (1985) described Tasmannia seeds from the Pliocene of Australia, but this material is now considered to be early middle Pleistocene in age (Hill, pers. comm., 1991). Hill (pers. comm., 1991) may have Winteraceae seeds in the Australian Oligocene. Gottwald (1992) assigned an Upper Eocene wood to this family.


Comments: Doyle et al. (1990) described ulcerate pollen tetrads from the Upper Barremian–Lower Aptian of Gabon as Walkeriopus gabonensis, which resemble pollen of this family.

F. XYRIDACEAE Agardh, 1823

PFR: No record.

Comments: Mai (1985a) lists Xyris in the Miocene of Europe.

Pollen: No record.

F. ZANNICHELLIACEAE Dumortier, 1829

PFR: No record.

Comments: Fruits like those of modern Zannichellia are recorded from the Miocene and Pleocenes in Europe (Szafer, 1961).

Pollen: No record.

F. ZINGIBERACEAE Lindley, 1835


Comments: Spirematospermum is now known from the Santonian/Campanian of North America and Maastrichtian of Europe (Goth, 1986; Knobloch and Mai, 1986; Friis, in Collins, 1988c, pp. 7–12). This seed record is supported by leaves of Zingiberopsis also in the Upper Cretaceous of North America (Friis, in Collins, 1988c, pp. 7–12; Taylor, 1990). Subsequent seed records occur throughout the Tertiary (Friis, in Collins, 1988c, pp. 7–12) and leaves at least in the Middle and Upper Eocene (Wilde, 1989; Taylor, 1990).

Pollen: No record.

F. ZOSTERACEAE Dumortier, 1829

PFR: No record.

Comments: Daghlian (1981) considered all megafossil records to be unreliable.

Pollen: No record.

F. ZYGOPHYLLACEAE Brown in Flinders, 1814


Comments: We know of no well-substantiated megafossils for this family.

Müller First: Pending.

Comments: See Oxalidaceae.

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Friis, E. M. (1985a) Angiosperm fruits and seeds from the Middle Miocene of Jutland, Denmark. *Biologiske Skrifter, 24*, 1–165.


<table>
<thead>
<tr>
<th>Category</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acanthodians</td>
<td>589–91</td>
</tr>
<tr>
<td>Acritarchs</td>
<td>33–4</td>
</tr>
<tr>
<td>Actinopterygians</td>
<td>611–53</td>
</tr>
<tr>
<td>Aglaspids</td>
<td>297</td>
</tr>
<tr>
<td>Agnathans</td>
<td>573–80</td>
</tr>
<tr>
<td>cyclostome</td>
<td></td>
</tr>
<tr>
<td>Albatrosses</td>
<td>721</td>
</tr>
<tr>
<td>Algae</td>
<td>15–37</td>
</tr>
<tr>
<td>blue-green</td>
<td></td>
</tr>
<tr>
<td>calcified</td>
<td></td>
</tr>
<tr>
<td>green</td>
<td>16–18, 24–5</td>
</tr>
<tr>
<td>Ammonites</td>
<td>213–23</td>
</tr>
<tr>
<td>Ammonoids</td>
<td>189–227</td>
</tr>
<tr>
<td>Amniosites</td>
<td>681–771</td>
</tr>
<tr>
<td>Amphibians</td>
<td>665–77</td>
</tr>
<tr>
<td>Amphineurans</td>
<td>125–9</td>
</tr>
<tr>
<td>Amphipods</td>
<td>332–3</td>
</tr>
<tr>
<td>Angiosperms</td>
<td>809–37</td>
</tr>
<tr>
<td>Animals</td>
<td>41–771</td>
</tr>
<tr>
<td>Annelids</td>
<td>676–7</td>
</tr>
<tr>
<td>Anthracosaurians</td>
<td>676–7</td>
</tr>
<tr>
<td>Ants</td>
<td>408–13</td>
</tr>
<tr>
<td>Apodans</td>
<td>672</td>
</tr>
<tr>
<td>Archaeocyathids</td>
<td>92–8</td>
</tr>
<tr>
<td>Archaeogastropods</td>
<td>134–42</td>
</tr>
<tr>
<td>Archosauromorphs</td>
<td>693–707</td>
</tr>
<tr>
<td>Archosaurs</td>
<td>693–706</td>
</tr>
<tr>
<td>Arthropods</td>
<td>279–42</td>
</tr>
<tr>
<td>Artiodactyls</td>
<td>758–61</td>
</tr>
<tr>
<td>Asteroids</td>
<td>506–9</td>
</tr>
<tr>
<td>Astrapotheres</td>
<td>763–4</td>
</tr>
<tr>
<td>Bacteria</td>
<td>3–6</td>
</tr>
<tr>
<td>Barnacles</td>
<td>337–40</td>
</tr>
<tr>
<td>Bats</td>
<td>755–6</td>
</tr>
<tr>
<td>Bears</td>
<td>753</td>
</tr>
<tr>
<td>Bees</td>
<td>408–13</td>
</tr>
<tr>
<td>Beetles</td>
<td>395–400</td>
</tr>
<tr>
<td>Belemmites</td>
<td>229–33</td>
</tr>
<tr>
<td>Birds</td>
<td>717–34</td>
</tr>
<tr>
<td>Bivalves</td>
<td>239–61</td>
</tr>
<tr>
<td>anomalodesmatan</td>
<td>258–60</td>
</tr>
<tr>
<td>heterocornc</td>
<td>253–8</td>
</tr>
<tr>
<td>isofibranch</td>
<td>241–3</td>
</tr>
<tr>
<td>lucinate</td>
<td>252–3</td>
</tr>
<tr>
<td>palaeotaxodont</td>
<td>239–40</td>
</tr>
<tr>
<td>pteryomorph</td>
<td>243–52</td>
</tr>
<tr>
<td>rudist</td>
<td>258</td>
</tr>
<tr>
<td>Blastoids</td>
<td>494–5</td>
</tr>
<tr>
<td>Bocklice</td>
<td>393–4</td>
</tr>
<tr>
<td>Bowfins</td>
<td>619</td>
</tr>
<tr>
<td>Brachiopods</td>
<td>427–54</td>
</tr>
<tr>
<td>articulate</td>
<td>431–54</td>
</tr>
<tr>
<td>atrypid</td>
<td>446–7</td>
</tr>
<tr>
<td>inarticulate</td>
<td>427–31</td>
</tr>
<tr>
<td>orthid</td>
<td>431–5</td>
</tr>
<tr>
<td>rhychonellid</td>
<td>442–6</td>
</tr>
<tr>
<td>spiriferid</td>
<td>447–52</td>
</tr>
<tr>
<td>strophomenid</td>
<td>435–42</td>
</tr>
<tr>
<td>terebratulid</td>
<td>452–4</td>
</tr>
<tr>
<td>Brittle stars</td>
<td>525–6</td>
</tr>
<tr>
<td>Bryophytes</td>
<td>775–8</td>
</tr>
<tr>
<td>Bryozoans</td>
<td>465–86</td>
</tr>
<tr>
<td>cheilostome</td>
<td>468–76</td>
</tr>
<tr>
<td>cryptostome</td>
<td>482–3</td>
</tr>
<tr>
<td>ctenostome</td>
<td>465–8</td>
</tr>
<tr>
<td>cyclostome</td>
<td>476–8</td>
</tr>
<tr>
<td>cystopore</td>
<td>478–9</td>
</tr>
<tr>
<td>fenestrat</td>
<td>483–6</td>
</tr>
<tr>
<td>phylactolaemate</td>
<td>465</td>
</tr>
<tr>
<td>trepostome</td>
<td>479–82</td>
</tr>
<tr>
<td>Bugs</td>
<td>385–93</td>
</tr>
<tr>
<td>Butterflies</td>
<td>413–14</td>
</tr>
<tr>
<td>Caddis flies</td>
<td>419–20</td>
</tr>
<tr>
<td>Caecilians</td>
<td>672</td>
</tr>
<tr>
<td>Caenogastropods</td>
<td>142–53</td>
</tr>
<tr>
<td>Calcarea</td>
<td>84–5</td>
</tr>
<tr>
<td>Calcihordates</td>
<td>531–4</td>
</tr>
<tr>
<td>Calcispheres</td>
<td>69–70</td>
</tr>
<tr>
<td>Camels</td>
<td>758</td>
</tr>
<tr>
<td>Carnivores</td>
<td>752–4</td>
</tr>
<tr>
<td>Carp</td>
<td>628–30</td>
</tr>
<tr>
<td>Cats</td>
<td>753</td>
</tr>
<tr>
<td>Cattle</td>
<td>758</td>
</tr>
<tr>
<td>Centipedes</td>
<td>360–1</td>
</tr>
<tr>
<td>Cephalochordates</td>
<td>533</td>
</tr>
<tr>
<td>Cephalopods</td>
<td>169–236</td>
</tr>
<tr>
<td>Ceratitids</td>
<td>199–208</td>
</tr>
<tr>
<td>Chaetetids</td>
<td>89–90</td>
</tr>
<tr>
<td>Chaetognaths</td>
<td>529</td>
</tr>
<tr>
<td>Charophytes</td>
<td>18–19</td>
</tr>
<tr>
<td>Chelicerates</td>
<td>297–319</td>
</tr>
<tr>
<td>Cheloniens</td>
<td>683–6</td>
</tr>
<tr>
<td>Chimaeras</td>
<td>605–7</td>
</tr>
<tr>
<td>Chitons</td>
<td>125–9</td>
</tr>
<tr>
<td>Chondrichthians</td>
<td>593–607</td>
</tr>
<tr>
<td>Chondrostеans</td>
<td>611–15</td>
</tr>
<tr>
<td>Chordates</td>
<td>533–771</td>
</tr>
<tr>
<td>Ciliates</td>
<td>69–70</td>
</tr>
<tr>
<td>Cimolestans</td>
<td>750–2</td>
</tr>
<tr>
<td>Cladocerans</td>
<td>335</td>
</tr>
<tr>
<td>Clams</td>
<td>239–61</td>
</tr>
<tr>
<td>Coccoliths</td>
<td>19–22, 69</td>
</tr>
<tr>
<td>Cockroaches</td>
<td>373–5</td>
</tr>
<tr>
<td>Cod</td>
<td>637</td>
</tr>
<tr>
<td>Coelancanthus</td>
<td>660–1</td>
</tr>
<tr>
<td>Coelenterates</td>
<td>101–22</td>
</tr>
<tr>
<td>Coleoids</td>
<td>229–34</td>
</tr>
<tr>
<td>Collembois</td>
<td>364–5</td>
</tr>
<tr>
<td>Conchostracans</td>
<td>335</td>
</tr>
<tr>
<td>Condylarths</td>
<td>764–5</td>
</tr>
<tr>
<td>Conifers</td>
<td>801–4</td>
</tr>
<tr>
<td>Conodonts(?)</td>
<td>559, 565–70</td>
</tr>
<tr>
<td>Conularids</td>
<td>104</td>
</tr>
<tr>
<td>Corals</td>
<td>107–22</td>
</tr>
<tr>
<td>rugose</td>
<td>116–22</td>
</tr>
<tr>
<td>scleractinian</td>
<td>108–11</td>
</tr>
<tr>
<td>tabulate</td>
<td>111–16</td>
</tr>
<tr>
<td>zoantharian</td>
<td>108–22</td>
</tr>
<tr>
<td>Cornutes</td>
<td>532–3</td>
</tr>
<tr>
<td>Crabs</td>
<td>324–32</td>
</tr>
<tr>
<td>king</td>
<td>298–300</td>
</tr>
<tr>
<td>Cranes</td>
<td>724–6</td>
</tr>
<tr>
<td>Craniates</td>
<td>533–771</td>
</tr>
<tr>
<td>Creodonts</td>
<td>752</td>
</tr>
<tr>
<td>Cribricthyadids</td>
<td>546</td>
</tr>
<tr>
<td>Criconarids</td>
<td>265–7</td>
</tr>
<tr>
<td>Crinoids</td>
<td>498–505</td>
</tr>
<tr>
<td>Crocodiles</td>
<td>694–8</td>
</tr>
<tr>
<td>Crustaceans</td>
<td>321–55</td>
</tr>
<tr>
<td>Ctenophores</td>
<td>122</td>
</tr>
<tr>
<td>Cynads</td>
<td>800–1</td>
</tr>
<tr>
<td>Cystoids</td>
<td>491–3, 495–8</td>
</tr>
<tr>
<td>Deer</td>
<td>758</td>
</tr>
<tr>
<td>Demosponges</td>
<td>71–9, 88–92</td>
</tr>
<tr>
<td>Diatoms</td>
<td>22–4</td>
</tr>
<tr>
<td>Dinoflagellates</td>
<td>25–32, 69</td>
</tr>
<tr>
<td>Dinosaurs</td>
<td>701–6</td>
</tr>
<tr>
<td>Dipnoans</td>
<td>657–60</td>
</tr>
<tr>
<td>Divers</td>
<td>721</td>
</tr>
<tr>
<td>Dogs</td>
<td>752–3</td>
</tr>
<tr>
<td>Dragonflies</td>
<td>369–73</td>
</tr>
<tr>
<td>Ducks</td>
<td>723–4</td>
</tr>
<tr>
<td>Earwigs</td>
<td>376–7</td>
</tr>
<tr>
<td>Echinoderms</td>
<td>491–526</td>
</tr>
<tr>
<td>Echinoids</td>
<td>513–25</td>
</tr>
<tr>
<td>Echiurids</td>
<td>558</td>
</tr>
<tr>
<td>Edentates</td>
<td>745–6</td>
</tr>
<tr>
<td>Edrioasteroids</td>
<td>505–6</td>
</tr>
<tr>
<td>Eels</td>
<td>625–8</td>
</tr>
<tr>
<td>Elasmobranchs</td>
<td>593–605</td>
</tr>
<tr>
<td>Elephants</td>
<td>765</td>
</tr>
<tr>
<td>Entoprocts</td>
<td>558</td>
</tr>
<tr>
<td>Equisetaleans</td>
<td>783–7</td>
</tr>
<tr>
<td>Eurypterids</td>
<td>300–2</td>
</tr>
<tr>
<td>Falcons</td>
<td>723</td>
</tr>
<tr>
<td>Ferns</td>
<td>787–90</td>
</tr>
<tr>
<td>Fishes</td>
<td>573–661</td>
</tr>
<tr>
<td>bony</td>
<td>611–61</td>
</tr>
<tr>
<td>flat-fishes</td>
<td>652</td>
</tr>
<tr>
<td>lobe-finned</td>
<td>557–61</td>
</tr>
<tr>
<td>Flatworms</td>
<td>555</td>
</tr>
<tr>
<td>Flies</td>
<td>400–8</td>
</tr>
<tr>
<td>Flying lemurs</td>
<td>755</td>
</tr>
<tr>
<td>Foraminifera</td>
<td>44–66</td>
</tr>
</tbody>
</table>
Index

Frogs 673-4
Fungi 9-12
Galeaspid 579-80
Gars 618
Gastropods 131-63
opisthobranch 154-6
pulmonate 156-63
Ginkgos 804
Goniati 194-8
Graptolites 537-41
Grasshoppers 378-9
Grebes 721
Gulls 726-7
Gymnosperms 795-804
Hag fishes 580
Hedgehogs 754
Hemichordates 529-31, 537-41
Herrings 628
Heterocorals 122
Heterostracans 573-6
Hexactinellids 79-84
Holocephalans 579-80
Holocephalans 573-6
Holosteans 615-19
Holothurians 509-13
Horses 766
Horse-tails 783-7
Humans 757
Hummingbirds 729
Hydroids 105-6
Hyoliths 267-70
Hyaxes 766-7
Ichthyosaurs 687-8
Insectivores 754
Insects 363-426
apterygote (flightless) 365
pterygote (winged) 365-426
Invertebrates 41-560
Isopods 332
Jellyfishes 101-2, 104-5
Kingfishers 729-30
Labyrinthodonts 668-72, 676-7
Lacewings 417-18
Lamellibranchs 239-61
Lampeyo 580
Lepidosauros 688-93
Lepidosaurus 688-93
Lissamphibians 672-6
Litopterns 762-3
Liverworts 775-8
Lizards 689-92
Lobsters 324-32
Locusts 378-9
Lungfishes 657-60
Lycophytes 782-3
Lycopsides 782-3
Machaeridians 547
Magnoliophytes 809-37
Malacostracans 321-35
Mammals 739-68
marsupial 742-5
monotreme 740
placental 745-68
Mantises 378
Mayflies 366-7
Medusoids 101-5
Microsaur 667-8
Millepedes 357-60
Mites 307-11
Mitrates 533-4
Molluscs 125-270
Monkeys 757
Monoplacophorans 129
Moles 413-14
Multi-tuberculates 741-2
Mussels 243
Myriapods 357-61
Nautiloids 169-85
Nectrideans 667
Nematoids 555-7
Nematomorphs 557
Nemerteans 555
Neogastropods 153
Neopterygians 615-53
Neoselachians 598-602
Nightjars 729
Nothosaurs 706
Nothosarcs 334-5
Notoungulates 763
Octocorals 107-8
Octopus 234
Oligochaetae 277-8
Onychophorans 558-9
Ophiuroids 525-6
Osteichthys 611-61
Osteostracans 577-9
Ostracods 343-55
Owls 727-8
Oystes 250-2
Paddle-fishes 615
Palaeonisciforms 611-15
Paratrilobits 544-5
Parrots 727
Pelecyopods 239-61
Pelicans 721
Pelecans 707
Penguins 721
Perch 642-52
Perissodactyli 765-6
Phorists 463
Phyllopods 333-4
Pigeons 727
Pikes 628
Placoderms 583-7
Placodonts 706
Plathyhelinths 555
Plesiosaurs 706-7
Pogonophorans 558
Polychaetae 271-7
Priapulids 557-8
Primates 756-7
Problematica 543-51
Proboscideaens 765
Protists 15-70
Protozoans 43-70
Pteridophytes 779-90
Pycnogonids 297
Rabbits 747
Radiolaria 66-9
Rat fishes 605-7
Ratites 720-1
Rays 602-5
Reptiles 681-711
anapsid 681-6
diapsid 686-707
synapsid 707-11
Rhinoceroses 766
Rhipidistians 661
Rodents 747-50
Rostroconchs 238-9
Rotifers 555
Salamanders 674-6
Salmon 632
Sauropterygians 671-65
Sarcopterygians 706-7
Scaphopods 239
Scorpion flies 414-16
Scorpions 302-5
Sea cucumbers 509-13
Sea urchins 513-25
Seals 753
Sharks 593-602
Shorebirds 726-7
Shrews 754
Shrimps 321-4
Silicoflagellates 69
Sipunculids 558
Sirensians 767-8
Skates 602-5
Snails 156-63
Snakes 692-3
Solutes 531-2
Solutes 531-2
Songbirds 730-3
Sphinctozoa 85-8
Spiders 311-19
Sponges 71-98
Springtails 364-5
Squames 689-93
Squid 233
Star-fishes 506-9
Stenothecoids 546-7
Sternoclad 507-6
Sternopods 90-2
Sturgeons 615
Tardigrades 558
Teleosts 621-53
Temnospondyls 668-72
Tentaculites 265
<table>
<thead>
<tr>
<th>Termite</th>
<th>378</th>
<th>Tomotids</th>
<th>545–6</th>
<th>Vendiamorphans</th>
<th>544</th>
</tr>
</thead>
<tbody>
<tr>
<td>Terosurs</td>
<td>698–700</td>
<td>Tree-shrews</td>
<td>754–5</td>
<td>Vertebrates</td>
<td>561–771</td>
</tr>
<tr>
<td>Testudinates</td>
<td>683–6</td>
<td>Trilobites</td>
<td>279–91</td>
<td>Vultures</td>
<td>722</td>
</tr>
<tr>
<td>Tethytheres</td>
<td>765–8</td>
<td>Trilobozoans</td>
<td>543–4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetrapods</td>
<td>665–771</td>
<td>Tuatara</td>
<td>688–9</td>
<td>Wasp</td>
<td>408–13</td>
</tr>
<tr>
<td>Thecodontians</td>
<td>693–4, 698</td>
<td>Tunicates</td>
<td>533</td>
<td>Whales</td>
<td>761–2</td>
</tr>
<tr>
<td>Thelodonts</td>
<td>576–7</td>
<td>Turtles</td>
<td>683–6</td>
<td>Woodpeckers</td>
<td>730</td>
</tr>
<tr>
<td>Therapsids</td>
<td>707–11</td>
<td></td>
<td></td>
<td>Worms</td>
<td>271–8</td>
</tr>
<tr>
<td>Thrips</td>
<td>394–5</td>
<td>Ungulates</td>
<td>758–67</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Toads</td>
<td>673–4</td>
<td>Urochordates</td>
<td>533</td>
<td>Xiphosurans</td>
<td>298–300</td>
</tr>
</tbody>
</table>
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Michael Benton is a Reader in the Department of Geology at the University of Bristol, UK.

The cover illustration shows an unnamed fossil bird from the Green River Formation (Early Eocene) of Wyoming, nicknamed 'Speedy Gonzales'. It is specimen 336284 in the United States National Museum, Washington, DC. Photograph courtesy of Paul Davis (Bristol).

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