The Sub-Boreal/Boreal ammonite succession at the Oxfordian/Kimmeridgian boundary at Flodigarry, Staffin Bay (Isle of Skye), Scotland

Bronislaw A. Matyja, Andrzej Wierzbowski and John K. Wright

ABSTRACT: This paper describes extensive new collections of ammonites made bed-by-bed across the Oxfordian/Kimmeridgian boundary sequence in the Flodigarry sections at Staffin Bay on the Isle of Skye. The ammonites belong to the Sub-Boreal family Aulacostephanidae and the Boreal family Cardioceratidae, enabling recognition of both the current standard Sub-Boreal and Boreal ammonite zonations. In consequence, it is possible to make a close correlation of these two zonal schemes through the interval studied in Skye. The research has provided new palaeontological data at levels of precision that justify the proposal of the section at Staffin as the site of a potential Global Boundary Stratotype Section and Point (GSSP) for the Oxfordian/Kimmeridgian boundary.

The traditional Oxfordian/Kimmeridgian boundary placed at the Pseudocorda/Baylei zonal boundary of the Sub-Boreal zonal scheme corresponds precisely to the Rosenkrantzii/Bauhini zonal boundary of the Boreal zonal scheme. This level is characterised by the appearance of the first Pictionia (Pictonia flodgariensis sp. nov.) together with first Prorasenia, replacing an older assemblage of Ringsteinia–Microbiopics (Sub-Boreal). It is also characterised by the first occurrence of small-sized Amoeboceras (Plasmaticus) spp., as well as large Amoeboceras schulgi Mesezhnikov (Boreal). An alternative level that may be considered as a potential GSSP is the boundary between the Bauhini Zone and the Kitchini Zone of the Boreal zonal scheme, characterised by first occurrence of Amoeboceras (Amoebites) of the A. bayi group. This level corresponds to the Planula/Galar subzonal boundary of the Sub-Mediterranean zonal scheme, and lies close to the currently accepted Oxfordian/Kimmeridgian boundary in the Sub-Mediterranean Province.

KEY WORDS: ammonites, biostratigraphy, Boreal zonation, correlation, Sub-Boreal zonation

The uppermost Oxfordian–lowermost Kimmeridgian deposits exposed at Staffin Bay in the Trotternish region of northern Skye (western Scotland) are among the stratigraphically most complete and richest in ammonites in Britain. They are developed as dark silty and shaly clays with bands of limestone nodules, and are included in the highest part of the Flodigarry Shale Member of the Staffin Shale Formation (Turner 1966; Sykes 1975; see also Sykes & Callomon 1979; Morton & Hudson 1995; Wright 2001). The deposits yield abundant ammonites belonging to two families, the Aulacostephanidae, typical of the Sub-Boreal Province and the Cardioceratidae, typical of the Boreal Province (Wright 1973, 1989; Sykes & Callomon 1979; Birkelund & Callomon 1985; Matyja et al. 2004). The co-occurrence of ammonites belonging to these two families is of great importance for the detailed biostratigraphical correlation of the Sub-Boreal and Boreal zonal schemes, and for precise recognition of the Oxfordian/Kimmeridgian boundary.

The Kimmeridgian Stage was defined originally within the Sub-Boreal ammonite succession with its base placed at the base of the Baylei Zone–the lowest ammonite zone of the Kimmeridge Clay in Dorset, southern England (Saffeld 1913, see also Arkell 1947b). Subsequent attempts at identifying the base of the Kimmeridgian Stage elsewhere, within the Boreal and Sub-Mediterranean/Mediterranean ammonite successions, were based on this original definition. However, it has since become apparent that some of the correlations were incorrect, resulting in the location of the Oxfordian/Kimmeridgian boundary at different chronostatigraphic horizons in separate ammonite successions. The difference is especially acute between the Sub-Boreal/Boreal, and the Sub-Mediterranean/Mediterranean ammonite successions and their corresponding zonal schemes (Schweigert 1995; Matyja & Wierzbowski 1997; Schweigert & Callomon 1997).

It seemed to the present authors that the first step to clarify the correlation problem would be to study a detailed ammonite succession across the Oxfordian/Kimmeridgian boundary in a continuous succession which combined elements of both the Sub-Boreal and Boreal provinces, preferably in the UK. None of the Dorset sections offers such a possibility due to the existence of a stratigraphical gap at the base of the Kimmeridge Clay in that region (see e.g. Arkell 1956), as well as an almost total lack of Boreal ammonites of the family Cardioceratidae. Of the more complete successions in clay facies, that at South Ferriby, Lincolnshire (Cox 2001a) lacks a really good sequence of Boreal ammonites. The sections at Staffin Bay in the Isle of Skye, and especially the best of them at Flodigarry, showing very complete Boreal and Sub-Boreal ammonite successions, form the best natural link between the Sub-Boreal and Boreal ammonite provinces, and the ammonite subdivisions recognised therein. Moreover, the standard ammonite zonal scheme for the Boreal Upper Oxfordian was largely defined at Staffin, and the position of the Oxfordian/Kimmeridgian boundary inferred there (Sykes & Callomon 1979; Birkelund & Callomon 1985; see also Wierzbowski & Smelror 1993). For these reasons we undertook a detailed study of the Flodigarry section at Staffin Bay, carried out under the remit of the Oxfordian/Kimmeridgian Boundary Working Group of the International Subcommission of Jurassic Stratigraphy of the IUGS. The preliminary results of our study were presented during the 6th International Symposium on the Jurassic System at Mondello, Sicily in
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It seemed to the present authors that the first step to clarify the correlation problem would be to study a detailed ammonite succession across the Oxfordian/Kimmeridgian boundary in a continuous succession which combined elements of both the Sub-Boreal and Boreal provinces, preferably in the UK. None of the Dorset sections offers such a possibility due to the existence of a stratigraphical gap at the base of the Kimmeridge Clay in that region (see e.g. Arkell 1956), as well as an almost total lack of Boreal ammonites of the family Cardiocraniidae. Of the more complete successions in clay facies, that at South Ferriby, Lincolnshire (Cox 2001a) lacks a really good sequence of Boreal ammonites. The sections at Staffin Bay in the Isle of Skye, and especially the best of them at Flodigarry, showing very complete Boreal and Sub-Boreal ammonite successions, form the best natural link between the Sub-Boreal and Boreal ammonite provinces, and the ammonite subdivisions recognised therein. Moreover, the standard ammonite zonal scheme for the Boreal Upper Oxfordian was largely defined at Staffin, and the position of the Oxfordian/Kimmeridgian boundary inferred there (Sykes & Callomon 1979; Birkelund & Callomon 1985; see also Wierzbowski & Smelror 1993). For these reasons we undertook a detailed study of the Flodigarry section at Staffin Bay, carried out under the remit of the Oxfordian/Kimmeridgian Boundary Working Group of the International Subcommission of Jurassic Stratigraphy of the IUGS. The preliminary results of our study were presented during the 6th International Symposium on the Jurassic System at Mondello, Sicily in
1. General details of the sections studied

The Flodigarry Shale Member outcrops in two restricted areas of foreshore at Flodigarry and Digg in Staffin Bay (Fig. 1). These deposits are exposed on the intertidal rock platform, some areas of shale being obscured by a covering of seaweed and basalt and dolerite boulders. The deposits are cut in a few places by dolerite dykes and sills which show very limited thermally altered zones. The strata generally dip steeply to the west, and are cut by small faults which divide the exposures into numerous tectonic blocks showing some differences in dip. The tectonic complexity is related to the Quirang landslip, which originated in the base of the Palaeocene basalt scarp of Trotternish and which affected the Flodigarry Shale Member deposits of the area of Staffin Bay (Anderson & Dunham 1966; see also Wright 1989).

The importance of the Staffin outcrops for studies of the Oxfordian/Kimmeridgian boundary was first noted by Anderson & Dunham (1966), these authors presenting provisional lists of ammonites and maps of the sections. Morris (1968) collected a substantial number of ammonites from the Flodigarry sections. The subsequent work of Wright (1973) and especially the definitive work of Sykes & Callomon (1979) was largely carried out in the Digg sections to the south (Fig. 1). However, the condition of these small outcrops has deteriorated substantially in recent years, and Kimmeridgian exposures are very limited here, so that subsequent work has been concentrated on the much better Flodigarry sections. Wright (1989) provided the first comprehensive description of the Kimmeridgian sequence here, and the work of Sykes & Callomon (1979) and Wright (1989) was synthesised and updated by Morton & Hudson (1995), Cox (2001b) and Wright (2001).

The beach outcrops at Flodigarry were re-surveyed in detail for the present work, and the resulting map (Fig. 2) differs to some extent from those maps published previously (Wright 1973, 1989; Morton & Hudson 1995; Wright 2001; Hesketh & Underhill 2002). The interval of Flodigarry Shale Member studied spans bed SS 33 (upper part) to bed SS 45, according to the standard subdivision of the Staffin Shale Formation between Digg and Flodigarry introduced by Sykes & Callomon (1979), and summarised by Morton & Hudson (1995). The three sections chosen for detailed biostratigraphical study in the present paper are situated close together on the foreshore at Flodigarry, where the deposits show only minor tectonic disturbance and are exposed the most completely. Two of the sections are situated in the northern part of the block F6, about 60 and 25 metres south of the prominent sill marked on Figure 2 (coordinates of the middle part of the sections are: N57°39'39.5", W6°14'43.9"; and N57°39'40.5", W6°14'45.0"), and denoted herein as F6S, and F6N, respectively (Fig. 2). The third section is situated in the middle part of the neighbouring block F5, 26 metres north of the prominent sill (coordinates of the middle part of the section are: N57°39'42.1", W6°14'46.7"), and is denoted as F5. The present work confirms the general sequence of beds and thicknesses given by Sykes & Callomon (1979), Wright (1989), Morton & Hudson (1995), Cox (2001b) and Hesketh & Underhill (2002), although some smaller differences in thicknesses of particular beds can be noticed (Figs 2, 3). The continuous sequence of deposits comprises predominately silty clays (beds SS 33, 35, 37, 39, 41, 42) and shaly clays and clays (beds SS 38, 43, 45) with thin layers (horizons) of calcareous
doggars or nodules (beds SS 34, 36, 40), and a thin, variably
developed, argillaceous sandstone (bed SS 44). The correlation
of particular beds between the three sections does not
present any difficulties, and this enables the recognition of the
complete succession of ammonite faunas in the sequence
studied.

The ammonites were collected at 66 levels: among them 34
in measured sections in block F6 (15 levels in section F6S; and
19 levels in section F6N), and 32 levels in block F5, in
measured section F5. The position of each level was carefully
measured and checked in relation to characteristic lithological
horizons, such as the thin sandstone (bed SS 44), the band of
limestone nodules (bed SS 36), and the characteristic dark,
shaly clay rich in ammonites of the genus *Pictonia* (bed SS 38).
Additionally, ammonites were collected at six levels directly
below bed SS 36 in the easternmost part in block F7. The
thicknesses of beds, and relative position of the ammonite
assemblages, were measured to the nearest centimetre by
stretching a tape across the steeply inclined beds on the rock
platform; the measurements were reduced according to dip
values: about 70°–78° for section F5, and from 75°, through
about 60°, to about 70° for younger, middle (around bed 37),
and older strata (down to bed 33), respectively, for sections
F6S, and F6N. The position of the particular ammonite
assemblages is given in metres in relation to the positions of
bed SS 36 and bed SS 44 in the sections studied. The
biostratigraphy of the time-diagnostic ammonites is shown in
Figure 3.

2. Genera and species

During latest Oxfordian and earliest Kimmeridgian, the
Aulacostephanidae formed a smoothly evolving lineage from
*Ringsteadia* through *Pictonia* to *Rasenia* (mostly macro-
conchs), and from *Microbilliceps* to *Prorasia* (microconchs)
(see Birkeland & Callomon 1985). The Cardioceratidae
ranged from the *Amoeboceras regulare* group through the
*Amoeboceras rosenkrantzi* group, and then through small-sized
forms of the subgenus *Plasmatites* (the *A. baumii* group) up to
the first *Amoebites* (see Birkeland & Callomon 1985).

Specific names in what follows are used in the sense of
morphospecies, having vertical ranges, as opposed to iso-
chronous 'horizontal' assemblages thought to represent what
had been variable biospecies, phyletic transients in an evolving
lineage (see Callomon 1985). Generic names are used in a
similarly morphogenic sense. The dimorphism strongly
marked in shell morphology within the Aulacostephanidae is
thus similarly expressed morphotaxonomically at the generic
and species levels. Changes of generic name for what were
most probably merely successive segments of a single lineage,
e.g. from *Ringsteadia* to *Pictonia*, may therefore be arbitrary
and reflect merely historical conventions. The dividing
line between particular genus rank taxa are placed commonly at
the level where the new features typical of the forthcoming
taxon become dominant – e.g. the dominance of bullate
ribs, recognised as indicative of the oldest *Rasenia* faunas
(Birkeland & Callomon 1985). A dominance of new features
sometimes appears quite suddenly in the succession. This may
have resulted either from a slow rate of sedimentation or
accelerated evolutionary transformation. Typical examples in
the section studied are the transitions from *Ringsteadia* into
*Pictonia* (macroconchs) and *Microbilliceps* into *Prorasia*
(microconchs).

A review of the genus rank taxa of the Aulacostephanidae
and Cardioceratidae in the Sub-Boreal and Boreal provinces is
given herein in the systematic palaeontology section.

Some 300 aulacostephans and cardioceratids were collected
by the present authors from the Staffin sections. The
collection is housed in the University Museum, Oxford, collec-
tions ST600 to ST926. The following abbreviations are used in
the description of the ammonites: D—diameter of specimen in
mm, Wh—whorl height as percentages of D; Ud—umbilical
diameter as percentages of D; PR—number of primary ribs per
whorl.

3. The standard ammonite chronozones and
chronosubzones of the Sub-Boreal
Oxfordian/Kimmeridgian boundary succession

3.1. Pseudocordata Zone

*Index:* *Ringsteadia pseudocordata* (Blake & Hudleston).
Holotype from the Westbury Ironstone of Wiltshire, figured by
Buckman (1925b, pls 560A, 560B).

*Definition.* Subdivided into Caledonica, Pseudoyo,
Pseudocordata and Evoluta Subzones. The Zone includes all
the British ammonite faunas consisting of *Ringsteadia* and
its microconch counterpart (mostly *Microbilliceps*, also forms
transitional between *Microbilliceps* and *Prorasia*).

*Horizon at Staffin.* This zone is represented in the deposits
outcropping from Flogdarry from 14-72 m below bed 36 (i.e.
down to bed 33) to 1-24 m below bed 36. This means that the
total thickness of the zone is about 13-5 m (or even a little
more).

3.1.1. Caledonica Subzone

*Index:* *Ringsteadia caledonica* Sykes & Callomon.
Holotype from the top of Bed 33 of the Staffin Shale at
Flogdarry, Skye, described and figured by Sykes & Callomon
(1979, p. 890, pl. 121, fig. 8).

*Definition.* Introduced by Sykes & Callomon (1979) as
the *caledonica* horizon of the Boreal Regulate Zone, and
defined as the upper part of the zone at Staffin by Sykes &
Callomon. Used as a formal subzone of the Pseudocordata Zone by
Wright (1980).

*Characteristic fauna and horizon at Staffin.* The oldest
fauna of *Ringsteadia*, consisting of *R. caledonica*, is found
14-72 m below bed 36. The fauna includes small forms of this
genus, representing both macro- and microconchs (75 mm and
30 mm in diameter respectively). Both have irregular, subdued
ornament, with numerous flared ribs preceded in some cases by
possible weak constrictions. Microconchs have a similar style
of ribbing to the macroconchs, but the adults have lappets
(Sykes & Callomon 1979). This same fauna has been placed from
about 9 m to 3-3 m below bed 36 in the Staffin Bay area
by Sykes & Callomon (1979, p. 855, 893, 894). This position in
the sections differs markedly from that stated in the present
paper, and we were unable to find *R. caledonica* at these higher
levels. Moreover, the stratigraphical range of *R. caledonica*
as indicated by Sykes & Callomon (1979) corresponds to the
stratigraphical range of *R. pseudoyo*, and even partly *R.
pseudocordata*, as recognised in the present paper (see Fig. 3).

3.1.2. Pseudoyo Subzone

*Index:* *Ringsteadia pseudoyo* Salfeld. Holotype from the
Marston Ironstone of Woottton Bassett, Wiltshire, described
and figured by Salfeld (1917, p. 74, pl. 8, figs 1a, b).

*Definition.* Introduced by Morris (1968) as the fauna of
the "Upper Calcareous Grit" (=Marston Ironstone) of
Marston, near Swindon, Wiltshire, and included in the formal
correlation table of Sykes & Callomon (1979). *Perispinhinctes,
Euaspidoceras* and *Amoeboceras marstonense* Spath are
characteristic in addition to the distinctively involute platycone *R.
pseudoyo* and *R. spp.*
Characteristic fauna and horizon at Staffin. The oldest ammonites characteristic of this subzone, *Ringsteadia brandesi*, Salfeld and *Microbiplices* sp., were found 13.85 m below bed 36 (i.e. still within bed 33). The *Microbiplices* (Fig. 4a) attain about 40 mm in final diameter, and are moderately evolute (at $D=30-40$ mm, $Wh=32-55$, $ Ud=40-42$%). Up to about $D=25$ mm, they are fairly densely, and somewhat irregularly ribbed, with biplicate, triplicate and intercalary ribs, and the presence of distinct constrictions (PR=34–28). On the last whorl the ribbing becomes regularly biplicate (PR=26). These features show the close similarity of these specimens to *Microbiplices microbiplex* (Quenstedt). A specimen of *Ringsteadia ex gr. pseudoyo* found near the top of the subzone at about 7.5 m below bed 36 (Fig. 4b) is characteristically strongly involute (at $D=62$ mm, $Ud=19-33$, $Wh=42%$), showing typical moderately dense, regular ribbing.

3.1.3. Pseudocordata Subzone

**Index.** as for the Zone.

**Definition.** Introduced by Morris (1968) for the fauna of the Westbury Ironstone, Wiltshire. Sykes & Callomon (1979, p.857) added the fauna of the Sandsfoot Grit of Dorset. *Microbiplices* and *Amoeboceras rosenkrantzii* Spath are also characteristic, in addition to *R. pseudocordata* (Sykes & Callomon 1979; Wright 1998).

Characteristic fauna and horizon at Staffin. *Ringsteadia* cf. *pseudocordata* and *Microbiplices* spp. (including *M. anglicus* Arkell) occur from 7.28 m to 2.34 m below bed 36, i.e. from the uppermost part of bed 33 to the middle part of bed 35. The more evolute *Microbiplices* specimens are generally comparable to the type specimens of *M. anglicus* (see Arkell 1947a, pl. 76, figs 6a, b, 7a, b). Some specimens occurring in this interval still show the dense ribbing and moderately evolute coiling typical of *M. microbiplex* (for instance Sykes & Callomon 1979, pl 121, fig. 15, found about 5 m below bed 36).

3.1.4. Evoluta Subzone

**Index.** *Ringsteadia evoluta* Salfeld. Holotype from the Osmington Mills Ironstone of Osmington Mills, Dorset, described and figured by Salfeld (1917, p.84, pl. 12, figs 1a, b).

**Definition.** Introduced by Morris (1968) for the fauna of the Ringstead Coral Bed of Dorset. Formally defined as such by Sykes & Callomon (1979, p.857). The definition was expanded by Wright (2003) to include the fauna of the Osmington Mills Ironstone, of which the Ringstead Coral Bed is part.
Characteristic fauna and horizon at Staffin. Ringsteadia evoluta Salfeld occurs together with forms transitional between Microbicipites and Prorasesia from 1·8 m to 1·24 m (possibly also 1·1 m) below bed 36. The specimens of Ringsteadia, mostly 60-70 mm in diameter, but also 140 mm and 230 mm, are characterised by fairly evolute coiling (Ud=44%-48%), and fairly strong and distant ribbing (PR=23-26), and compare well with R. evoluta (Fig. 4d, e).

3.1.5. Pseudocorda/Baylee zone boundary

The dividing line between Ringsteadia and Pictonia is discussed in the systematic section of this paper. Based on the choice made there, the boundary between the Pseudocorda Zone and the Baylee Zone, i.e. the boundary between the Sub-Boreal Oxfordian and Kimmeridgian, lies in the 0·16 m thick interval between the highest occurrence of Ringsteadia (1·24 m below bed 36) and the first occurrence of Pictonia (1·08 m below bed 36). Such a position of the Oxfordian/Kimmeridgian boundary as inferred from distribution of the aulacostephanid ammonites is at least 1 m lower than previously assumed (cf. Birkelund & Callomon 1985, pp. 16-17).

3.2. Baylee Zone


Definition. Introduced by Salfeld (1913, p. 423) for the fauna of Pictonia spp. found on the Dorset coast characterising the lowest Zone of the Kimmeridgian Stage. Arkell (1933) noted the presence of the typical species Pictonia in the Inconstans Bed, the basal bed of the Kimmeridge Clay Formation traceable at many localities across England from Dorset to Yorkshire. Most subsequent authors (i.e. Sykes & Callomon 1979, p. 857; Birkelund & Callomon 1985, p. 17; Schweigert & Callomon 1997, p. 43; Cox 2001a, p. 123) have placed the base of the Baylee Zone immediately below the appearance of Pictonia densicostata (Salfeld MS) Buckman, the characteristic species of the Inconstans Bed. However, on the Dorset coast, the lower boundary of the Baylee Zone as so defined corresponds to the major non-sequence at the base of the Inconstans Bed (see e.g. Arkell 1956). Below, in the Osmington Mills Ironstone Member (which includes the Ringstead Coral Bed), fairly abundant specimens of Ringsteadia evoluta Salfeld are known to occur indicating the uppermost part of the Pseudocorda Zone: these consist almost exclusively of heavily ribbed forms having nothing in common with Pictonia densicostata. Thus, the acceptance of the Baylee Zone as the lowest subdivision of the Kimmeridgian Stage as recognised on the Dorset coast led to the problem from the very beginning of the location of the precise boundary between Oxfordian and Kimmeridgian, there being a morphological gap between Ringsteadia and Pictonia in Dorset. It should also be remembered that a marked hiatus must occur at the junction of the Pseudocorda and Baylee zones, i.e. at the boundary of the Oxfordian and Kimmeridgian, in many other English sections (see e.g. Wignall 1990; Cox 2001a). At Staffin, the first occurrence of Pictonia is represented by Pictonia flodigarrensis sp. nov. P. densicostata appears at Flodigarry well above P. flodigarrensis, indicating that the sections at Staffin Bay are much more complete than the English sections (see also Matyja et al. 2004). We propose to distinguish the flodigarrensis biohorizon as the lowest level of the Baylee Chronzone. The reason for such a re-definition of the Baylee Zone is that it gives the zone a larger correlation potential, and the Staffin section where the re-definition is made becomes suitable as the candidate for the GSSP.

Two or three informal faunal horizons have been recognised previously in the Baylee Zone (see Birkelund & Callomon 1985; Hantzpergue 1989; Schweigert & Callomon 1997). These are the densicostata, baylei and normandiana horizons (the two latter were often treated together). According to present work, a further horizon is present, at the base of the Baylee Zone – the flodigarrensis horizon. However, a formal subdivision of the Baylee Zone into two Subzones seems now practicable and useful, and the zone is here divided as follows: the Densicostata Subzone below, and the Normandiana Subzone above (Fig. 3).

Characteristic fauna and horizon at Staffin. The total range of the Baylee Zone as marked by occurrence of ammonites of the genus Pictonia in the sections at Flodigarry is from 1·08 m below bed 36 (i.e. from uppermost part of bed 35) to 3·73 m below bed 44 (i.e. to the lowermost part of bed 43), which indicates that the zone is about 10 metres thick.

3.2.1. Densicostata Subzone

Index: Pictonia densicostata (Salfeld MS) Buckman. Holotype from the Inconstans Bed of Ringstead Bay, Dorset, figured by Buckman (1924, pl. 533).

Definition. Type locality Flodigarry, upper part of bed 35, 1·08 m below bed 36, to bed 39, between 0·2 and 1·8 m below bed 40. The Densicostata Subzone is characterised by occurrence of the macroconch species Pictonia flodigarrensis and P. densicostata associated with microconchs resembling Prorasesia bowerbankii Spáth.

Characteristic fauna at Staffin. The oldest typical representatives of the genus Pictonia occurring from 1·08 m below bed 36 to 0·2 m above bed 36 are distinguished herein as a new species Pictonia flodigarrensis, described more fully in the systematic section (see Fig. 5a-c). Morphologically, the species occupies an intermediate position between the last representatives of Ringsteadia and the previous oldest known species of Pictonia, P. densicostata, being especially close to the latter, and thus placed in the genus Pictonia.

An assemblage of microconchs collected from the same sections and levels as P. flodigarrensis corresponds generally to Prorasesia bowerbankii (see Spáth 1935, p. 43, pl. 14, figs 3a, b (holotype), pl. 13, figs 3a, b; see Fig. 4i). They attain a final diameter ranging from about 30 mm to 40 mm, and show the aperture with lappets. Coiling is markedly evolute. Their innermost whorls up to 5·6 mm diameter are smooth. Thin, dense ribs then appear which show a high point of furcation covered by the younger whorls. At 8–10 mm diameter or slightly later, the ribbing becomes more distant (PR=17-20). The ribs are bipectate and triplicate, becoming heavier and more pointed, with the point of division lowering to below the mid flank of the whorl. The last stage of ornamentation, sometimes preceded by a poorly marked constriction, consists of bipectate ribs showing a similar low point of furcation. This ribbing occupies the last whorl or half-whorl up to the aperture (PR=30).

Abundant specimens of Pictonia densicostata were collected from about 0·9 m above bed 36 to the tough, shaly clay of bed 38. The specimens may exceed 120 mm in diameter, and show densely ribbed inner and middle whorls (PR=36-40 at about 40 mm diameter) with about two secondaries per primary, and flared ribs following constrictions. The ribbing fades on the outer whorl (Fig. 5d). In their character, these specimens agree closely with specimens of P. densicostata from southern England; the holotype and specimens usually attributed to that species (see e.g. Spáth 1935, pl. 8, figs 4a, b; see also Birkelund & Callomon 1985, p. 32; Schweigert & Callomon 1997, p. 39). The microconchs present in this stratigraphic interval are all of the Prorasesia type, about 30 mm in diameter, smooth up to 5 mm diameter, followed by ribbing which soon becomes distant and coarse (at D=15-20 mm, PR=15-20). The
specimens are, however, badly crushed and flattened (Fig. 5e), precluding their precise identification (Prorasenia cf. bowerbanki Spath).

3.2.2. Normandiana Subzone

Index: Pictonia normandiana Tornquist. Lectotype, designated by Schweigert & Callomon 1997, p. 40) from the
Lower Kimmeridgian Calcaires coquilliers of Normandy, described and refigured (as *P. thurmanni* (Contejean)) by Hantzpergue (1989, p. 224, pl. 25d).

**Definition.** Type locality Flodigarry, from bed 39, between 0·2 and 1·8 m below bed 40, to bed 43, between 3·73 and 2·25 m below bed 44. The Normandiana Subzone is characterised by occurrence of the macroconchs *Pictonia bavletnormandiana* showing more distant ribbing, already at fairly small diameters, and sometimes more strongly flared ribs. The characteristic microconchs are less well known, but seem related, at least partly, to *Praorasaenia hardyi*.  

**Characteristic fauna at Staffin.** The youngest specimens of *Pictonia* come from section F5 – from 6·6 to 3·73 m below bed 44 (i.e. from the upper part of bed 39 to the lowermost part of bed 43). The specimens are smooth up to 5 mm diameter, followed by dense biplicate ribbing continuing to about 12–18 mm, rarely 25 mm, diameter. Thereafter, the primary ribs become more distant (PR=about 20). The secondary ribs are as strongly developed as the primaries, with about three secondary ribs per primary. Strong flared ribs with well marked ventral collars follow constrictions. Most *Pictonia* from this interval are small and incomplete, not exceeding 45 mm diameter. Figure 5f shows a specimen about 40 mm in diameter, with half a whorl of body chamber. At the end of the specimen three successive flared ribs are much more closely spaced than the flared ribs occurring on the inner whorls. This does not mean, however, that the specimen is fully grown (see e.g. a large specimen of *Pictonia baylei* illustrated by Hantzpergue 1989, pl. 23b which shows irregularly spaced flared ribs on the inner and middle whorls).

These youngest specimens of *Pictonia* from the Flodigarry sections (see also Fig. 5h–i) may be compared with the inner whorls of *Pictonia baylei* and *P. normandiana*. These two species are very close each other, differing mostly in the persistence of secondary ribs to larger diameters in *P. normandiana*, as well as in more involute coiling of the latter. Hantzpergue (1989) preferred to allocate such specimens to *P. thurmanni* (Contejean), but Schweigert & Callomon (1997) preferred to retain *P. normandiana* formally mainly to distinguish it from *P. thurmanni* on biostratigraphic grounds, designating the lectotype referred to above, and the present authors agree with this proposal. However, the small, incomplete specimens of *Pictonia* from the Flodigarry sections cannot be assigned unequivocally to either of the two species, and they are referred herein to as *Pictonia bavletnormandiana*.

Two larger specimens of *Pictonia*, collected in section F5 from a limestone concretion of bed 40, and from bed 41, about 5·8 m below bed 44 (Fig. 5g), are closely comparable with the lectotype of *Pictonia normandiana*. They show marked collars and flared ribs in the inner whorls (from about 18–20 mm diameter), but these are not present at diameters greater than 45 mm. The bold primary ribs (PR=25–26 at D=50–85 mm) regularly divide into three secondary ribs with occasional intercalaries. This style of ribbing continues to the maximum diameter preserved (80–95 mm), at which point a third to about half of a whorl of body chamber is preserved. Coiling is strongly evolute on the inner whorls, and weakly evolute on the outer whorls.

Four microconchs occurring from the middle part of bed 41 to the lowermost part of bed 43 attain from 35 mm to 43 mm in diameter and show the aperture with lappets. The innermost whorls are smooth. Dense ribbing occurs between 5 mm and about 8 mm, but soon thereafter coarse, distant, triplicate ribs appear. The secondary ribs are clearly visible beneath the overlapping whorl. Between 20 to 30 mm diameter the ribbing becomes biplicate, and the point of furcation is still low. The best preserved specimens (5·70 m (Fig. 4i) and about 4·2 m below bed 44) show markedly prorsiradial ribbing, which becomes dense at the end of the last whorl, with a fairly high whorl section. These features are typical of *Praorasaenia hardyi* (see Spath 1935, p. 40, pl. 15, figs 5a, b).

### 3.3. Cymodoce Zone

**Index:** *Rasenia cymodoce* (d'Orbigny). Lectotype indicated by Tornquist (1896, p. 11), and figured by Arkell (1933, pl. 39, figs 4a, b), from Dompierre sur Mer (Charante-Maritime), Aquitaine (see Hantzpergue 1989).

**Definition.** Formal definition of the base of the zone is yet to be established. The most complete section so far described in England is in the banks of the Fleet lagoon, Weymouth, extending from the Wyke Siltstone upwards (Birkeland et al. 1978). The lowest part of the zone is marked by the *inconstans* horizon which was first identified in East Greenland (Birkeland & Callomon 1985). This horizon is the lowest one showing the dominance of ammonites with bullate ribs typical of the genus *Rasenia*.  

**Characteristic fauna and horizon at Staffin.** Specimens found in the highest part of the Flodigarry sections include three representatives of the genus *Rasenia*, occurring in the middle and upper part of bed 43, 2·25 m, and 0·59 m below bed 44, as well as in bed 44. The specimens show the finely ribbed inner whorls and bullate ribs appearing thereafter (from about 20 mm diameter) typical of *Rasenia*. The secondaries are usually hidden by the overlapping whorl. The larger two specimens (0·59 m below bed 44, and from bed 44 – see Fig. 5j), although fragmentarily preserved, are about 80–100 mm in diameter, and still show the presence of nearly straight, rather weakly bullate primary ribs. The character of ribbing and the coiling of these specimens indicate their close similarity to *Rasenia inconstans* Spath (see Birkeland & Callomon 1985, pp. 33–35, pl. 12, figs 1–4; pl. 13, figs 1–5; pl. 14, figs 1–4; see also specimens illustrated by Spath 1935) and put into synonymy of the species by Birkeland & Callomon (1985). The microconchs found in the Flodigarry sections associated with *R. inconstans* are represented by two specimens of *Prorasaenia* found 2·25 m below bed 44.

The boundary between the Baylei and Cymodoce zones must lie lower than the occurrences of these specimens of *Rasenia*, and above the last occurrence of *Pictonia* (3·73 m below bed 44). This means that the boundary in question lies within the 1·48 m thick interval between 3·73 m and 2·25 m below bed 44, i.e. in lower part of bed 43. The overlying part of bed 43, and bed 44, are thus assigned to the *inconstans* horizon of the Cymodoce Zone. The occurrence of *Rasenia cf. evoluta* Spath in bed 43 at Flodigarry, as indicated by Wright (1989, 2001), seems rather unlikely, as *R. evoluta* is indicative of the upper part of the Cymodoce Zone (see Birkeland et al. 1983).

### 4. The standard ammonite chronozones and chronosubzones of the Boreal Oxfordian/Kimmeridgian boundary succession

#### 4.1. Regulare Zone

**Index:** *Amoeboceras regulare* Spath. Holotype from Novaya Zemlaya refigured by Sykes & Callomon (1979, pl. 118, fig. 2).

**Definition.** The Regulare Zone of the Upper Oxfordian in the Boreal zonal scheme is characterised by the occurrence of evolute, densely and regularly ribbed *Amoeboceras* of the *A. regulare* group (Sykes & Surlyk 1976; Sykes & Callomon 1979).
Characteristic fauna and horizon at Staffin. This zone has yielded typical representatives of *A. regulare* from 13-85 m (close to the base of the sections studied) to 9-93 m below bed 36 (Fig. 3). These specimens are between 40 and 50 mm in diameter, and bear fine, wiry, rectiradiate ribs which are non-tuberculate. Sykes & Callomon (1979) noted the presence of more strongly ribbed and even mildly tuberculate forms at this level, referring these to *A. freboldi* Spath, *A. cf. leucum* Spath and *A. cf. schulginae* Mesezhnikov. All these may be taken as representatives of the *A. regulare* group.

Sykes & Callomon (1979, pl. 119, fig. 5) record “*A. cf. regulare* Spath (m) – late form transitional to *A. marstonense* Spath” 8-2 m below bed 36. The first specimens of *A. marstonense*, indicative of the lower part of the overlying Roskenranti Zone, have been found by the present authors between about 7-50 m and 7-28 m below bed 36. Thus both their records and those of Sykes & Callomon (1979) agree in placing the boundary between the Regulare and Roskenranti zones through the interval from 9-93 m to 7-50 m below bed 36, i.e. in the upper part of bed 33. However, it is clear that the position of the boundary between these zones as drawn at the base of bed 35 in the Staffin Bay area by Sykes & Callomon (1979, p. 855, text-fig. 3) and by Wright (2001, fig. 5.15) is drawn too high when compared with data presented herein.

4.2. Roskenranti Zone

**Index:** *Amoeboceras rosenkrantzi* Spath. The holotype, from Wollaston Foreland, Greenland, was refigured by Sykes & Callomon (1979, pl. 120, fig. 3).

**Definition:** Subdivided into the Marstonense and Roskenranti Subzones. The Roskenranti Zone was defined originally by Sykes & Suryk (1976) as the range zone of the index-species. Sykes & Callomon (1979) divided it into two subzones, a lower Marstonense Subzone defined by the co-occurrence of *A. marstonense* Spath and *A. rosenkrantzi*, and an upper Bauhini Subzone with *A. rosenkrantzi* and *A. (Plasmatites) bauhini* (Oppel). Subsequently, the latter was treated as an independent Zone corresponding to the lowermost zone of the Boreal Kimmeridgian (see the description of the Bauhini Zone below). There then appeared the problem of the classification of the stratigraphical interval characterised by the occurrence of *A. rosenkrantzi* well above the upper range of *A. marstonense* and below the appearance of representatives of the *A. bauhini* group. This interval was distinguished as the Roskenranti Subzone by Wright (2003) (see also Matyja et al., 2004).

Characteristic fauna and horizon at Staffin. The lower part of the zone is characterised by profuse *A. marstonense*. The middle part of the zone is characterised by the occurrence of *A. cf. leucum* Spath. This occurs 6-34 m below bed 36, in the upper part of the Marstonense Subzone, and it possibly continues upwards to about 3-5 m below bed 36 – i.e. into the lower part of the Roskenranti Subzone. At a level 1-17 m below bed 36, *A. rosenkrantzi* co-occurs already with the first representatives of the subgenus *Plasmatites*, indicating the presence of the Bauhini Zone (see below). The total thickness of the Roskenranti Zone in the Flodigarry sections is thus about 6-35-6-85 m, extending from 7-5 m to 1-2 m below bed 36.

4.2.1. Marstonense Subzone

**Index:** *Amoeboceras marstonense* Spath. Holotype from the Marston Ironstone of South Marston, Wiltshire, described and figured by Spath (1935, p. 20, pl. 4, figs 5a, b).

**Definition:** Introduced by Sykes & Callomon (1979) for the *Amoeboceras* fauna of bed 35 of the Staffin Shale at Staffin. Re-defined by Wright (2003) as that part of the Roskenranti Zone containing abundant *A. marstonense* ranging from about 8 m to about 5 m below bed 36. The stratigraphical range of *A. marstonense* as recognised here is from about 7-50 m below bed 36 (i.e. the uppermost part of bed 33) to 5-25 m below bed 36 (i.e. lowermost part of bed 35). Thus, the Marstonense Subzone is at minimum 3 m thick.

4.2.2. Roskenranti Subzone

**Index:** as for the zone.

**Definition:** Introduced by Wright (2003) for the upper part of the Roskenranti Zone containing an abundance of *A. rosenkrantzi* without *A. marstonense* and/or ammonites of the *Amoeboceras* (*Plasmatites*) group. This specific fauna ranges from about 3-5 m below bed 36 (see Sykes & Callomon 1979, pl. 119, fig. 10; pl. 120, figs 2a, b) to 1-65 m below bed 36. The minimum thickness of the Roskenranti Subzone is thus 1-85 m.

**Characteristic fauna at Staffin.** The most typical forms of *A. rosenkrantzi*, being close to its lectotype (Spath 1935, pl. 12, fig. 4; see also Sykes & Callomon 1979, p. 888), make their appearance in the Marstonense Subzone (see above), and continue through the Roskenranti Subzone into the overlying Bauhini Zone (see below). The specimens show moderately dense ribbing (PR is about 30–35) consisting of weakly prorsiradiate or reeadiatate primaries terminating in a feeble tubercle at about the mid-height of the whorl. The secondaries show a more or less pronounced backward curve, and are accentuated at the ventrolateral margin. The keel is distinctly crenulated, and bordered by smooth bands. The more complete specimens may be divided into macroconchs (showing a weakly ornamented outer whorl from about 85 mm in diameter), and microconchs (strongly ornamented and showing a more loosely coiled outer whorl), e.g. a specimen, about 50 mm in diameter, found together with a macroconch in section F6/S at 1-65 below bed 36.
Figure 6 Cardioceratid ammonites from the Rosenkrantzi, Bauhini and Kitchini zones (all specimens actual size). (a) Amoeboceras marstonense Spath: ST846; Flodigarry, bed 33, about 7.5 m below bed 36; Rosenkrantzi Zone, Marstonense Subzone. (b) Amoeboceras leucum Spath emend. Mesezhnikov: ST846; Flodigarry, section F6N, uppermost part of bed 33, 6.34 m below bed 36; Rosenkrantzi Zone, Marstonense Subzone. (c, e) Amoeboceras rosenkrantzi Spath; Flodigarry, (c) ST848, basal part of bed 37, Bauhini Zone; (e) ST850, section F6N, uppermost part of bed 35; 1.17 m below bed 36; Bauhini Zone. (d) Amoeboceras schulginiae Mesezhnikov: ST849; Flodigarry, section F6S, basal part of bed 37, 0.17 m above bed 36; Bauhini Zone. (f) Amoeboceras (Plasmatites) praebauhini (Safied): ST851; Flodigarry, section F6N, uppermost part of bed 35, 1.17 m below bed 36; Bauhini Zone. (g) Amoeboceras (Plasmatites) aff. baehini (Oppel): ST852; Flodigarry, section F6S, uppermost part of bed 35, 0.6 m below bed 36; Bauhini Zone. (h, i, q) Amoeboceras (Plasmatites) baehini (Oppel); Flodigarry, (h) ST853, section F5, uppermost part of bed 37, 9.02 m below bed 44; Bauhini Zone; (i) ST854; upper part of bed 37; Bauhini Zone; (q) ST861; section F5, bed 41, 5.7 m below bed 44; Bauhini Zone. (j, o-p) Amoeboceras (Plasmatites) lineatum (Quenstedt); Flodigarry, section 5: (j) ST855; upper part of bed 37, 9.80 m below bed 44; Bauhini Zone; (o) ST859; bed 41, 5.66 m below bed 44; Bauhini Zone; (p) ST860; bed 41, 5.7 m below bed 44; Bauhini Zone. (k-n) Amoeboceras aff. Schulginiae Mesezhnikov: (k-l) ST856; fragments of the same specimen, Flodigarry, section F5, lower part of bed 39, 7.96 m below bed 44; Bauhini Zone; (m) ST857; Flodigarry, section F5, lower part of bed 39, 7.96 m below bed 44; Bauhini Zone; (n) ST858; Digg, the same level as specimens k-n. (r) form transitional between Amoeboceras baehini (Oppel) and Amoeboceras bayi Birkeland and Callomon: ST862; Flodigarry, section F5, bed 42, 4.79 m below bed 44; Kitchini Zone, Subkitchini Subzone, bayi horizon. (s) Amoeboceras (Amoebites) bayi Birkeland and Callomon: ST863; Flodigarry, section F5, bed 42, 4.79 m below bed 44. Kitchini Zone, Subkitchini Subzone, bayi horizon.
4.3. Bauhini Zone

Index: *Amoeboceras* (Plasmattites) bauhini (Oppel). Holotype from Handsrück, Swabia, White Jura Beta; cast figured by Sykes & Callomon 1979, pl. 121, fig. 3.

**Definition.** The base of this zone is defined in the present paper by the appearance of small-sized *Amoeboceras* of the subgenus *Plasmattites*. This definition of the base of the Bauhini Zone, and thus the base of the Boreal Kimmeridgian, as presented herein, differs a little from that given by Wierzbowski & Smelror (1993, pp. 233, 242). These authors placed an interval of co-occurrence of the last *A. rosenkrantzi* together with the first *A. (Plasmattites)*, such as *A. praebauhini* Saffeld, still in the Rosenkrantzi Zone. The Bauhini Zone was restricted to the total range of *A. bauhini* together with small-sized *A. schulginiae* (= *A. aff. schulginiae* as treated herein). On the other hand, the definition of the base of the Bauhini Zone accepted here is close to that given originally by Sykes & Callomon (1979, p. 856) who defined the Bauhini Subzone as “characterised by incoming of diminutive species of the group of *A. bauhini*”. They indicated overlapping of the range of the group with that of *A. rosenkrantzi* (see also Matyja et al. 2004).

The Bauhini Zone as defined herein thus may be informally subdivided into two parts: (1) the lowermost part characterised by appearance of first *A. (Plasmattites)* such as *A. praebauhini*, and with the occurrence of typical large *A. schulginiae* and the last representatives of *A. rosenkrantzi*; (2) the major part of the zone characterised by the occurrence of various *A. (Plasmattites)*, including *A. bauhini*, and a form similar to *A. schulginiae*, but differing in its smaller final size, and referred to as *A. aff. schulginiae*, which occurs in a thin faunal horizon in the lower part of bed 39.

The major part of the Bauhini Zone in the Flodigarry sections corresponds to the range of closely allied forms of the subgenus *Plasmattites* including *A. bauhini*, *A. praebauhini* and *A. lineatum* (Quenstedt). These are recognised from the lower/middle parts of bed 37 (from about 2 m (?possibly even 0-88 m) above bed 36) to the lower and middle parts of bed 41 (from about 1 m above its base). The range of the Bauhini Zone is from 1-17 m below bed 36 to 5-5 m below bed 44, indicating a thickness for the zone of at least 9 m.

**Characteristic fauna and horizon at Staffin.** At Flodigarry, the sole initial microconch representative is *A. (Plasmattites) praebauhini*, which first appears in the uppermost part of bed 35, from 1-17 m to 1-04 m below bed 36. The specimens are 20-30 mm in diameter, moderately densely ribbed (at D=25 mm, PR=33—see Fig. 6f). The secondary ribs are curved backwards and accentuated at the ventro-lateral edge, from where they continue onto the crenulated keel. The specimens are very similar to the lectotype of *A. (P.) praebauhini*—see Saffeld (1915, pl. 17, figs 5a,b). Another specimen of *Plasmattites* found in section F6S about 0-60 m below bed 36 is more coarsely ribbed (PR≈25). It is about 25 mm in diameter and shows rectiradiate primaries and markedly rursiradiate secondaries (Fig. 6g). Some uncoiling observed at the end of the shell suggests the specimen was fully grown. The specimen is referred to as *A. (P.) aff. bauhini* (Oppel) as it differs from typical representatives of *A. bauhini* in the somewhat lower point of division of the ribs, the lack of a smooth lateral band, and in somewhat more involute coiling.

Abundant representatives of the *Plasmattites* group occur in the upper part of bed 37 (9-8 m to 9-02 m below bed 44) through bed 38 up to the lower and middle parts of bed 41, 5-5 m below bed 44. The specimens are 25-35 mm in diameter, except the youngest ones which are 15-25 mm in diameter. Most common are specimens of *A. bauhini*, recognised in all the faunas listed above (Fig. 6h, i and q). The specimens compare well with the holotype (Saffeld 1915, pl. 17, fig. 5), as well as with other specimens of this species (see e.g. Schweigert 1995, text-figs 1F-g; Schweigert & Callomon 1997, pl. 1, figs 1-26). They show coarse ribbing, with the primary ribs accentuated or bearing small tubercles above the mid-height of the whorl, and separated by a smooth spiral band from the short secondaries.

Another group of microconch specimens is less strongly ribbed, showing more numerous and less differentiated ribs. It comprises *A. (P.) praebauhini* and *A. (P.) lineatum*, forms which are indistinctly separated from *A. bauhini*—see Matyja & Wierzbowski (1988, pp. 424-427, pl. 2; 1997, p. 99, pl. 5, figs 1-4). These specimens are well represented in the Flodigarry sections (Fig. 6j, o-p) covering nearly the whole interval of occurrence of *A. bauhini* from 9-8 m to 5-66 m below bed 44. To the same group of more densely ribbed *Plasmattites* could be attributed specimens referred to as *Amoeboceras* cf. *bayi* Birkeland & Callomon by Wright (1989, figs 4G-J) from bed 39 at Flodigarry. These specimens show the projected secondary ribs continuing up to the keel characteristic of *A. (P.) lineatum*. Hence, this assemblage ranges from the lower part of bed 37 to the lower part of bed 41, taking into account the records of *A. bauhini* about 2 m above the base of bed 37 by Birkeland & Callomon (1983, p. 17).

The lowermost part of the Bauhini Zone in the Flodigarry sections yields two additional macroconch species. It contains the last representatives of *A. rosenkrantzi*, which ranges up into the lowest part of bed 37 (Fig. 6c, e). In addition, the first typical large representatives of *A. (Amoeboceras) schulginiae*, are present possibly occurring already at 1-44 m below bed 36 (cf. *A. schulginiae*), but well recognised from 1-04 m and 0-61 m below bed 36 and 0-17 m above bed 36. A similar, small, incomplete specimen, found at the base of bed 37 in the Staffin Bay area, was referred to as *Amoeboceras* cf. *tuberculatoalternans* (Nikitin) by Sykes & Callomon (1979, pp. 889-890, pl. 121, fig. 7). These more coarsely ribbed and trituberculate *Amoeboceras* (see Fig. 6d) are discussed further under systematic palaeontology below, as are smaller specimens referred to here as *A. aff. schulginiae* occurring in bed 39 (Fig. 6k-n).

4.4. Kitchini Zone

Index: *Amoeboceras kitchini* Saffeld, from the Kimmeridgian Clay of Eathie, Cromarty, Scotland. Lectotype designated and figured by Birkeland & Callomon (1985, p. 21, fig. 6).

**Definition.** Characterised by a wide variety of *Amoebitites* species listed by Birkeland & Callomon (1985, p. 20) and Wierzbowski & Smelror (1993, p. 247), including *A. bayi* Birkeland & Callomon and *A. subkitchini* Spath.

**Characteristic fauna and horizon at Staffin.** *A. (Amoebites) bayi* and *A. (A.) cricki* Saffeld appear in the upper part of bed 41 and in bed 42, from 4-99 m below bed 44 upwards. The largest of the specimens are about 30-40 mm in diameter (without aperture preserved) and show on the outer whorl the presence of looped ribs (Fig. 6s). They may be referred to easily as *A. (Amoebites) bayi*, being very close to the specimens of the type-series of that species (Birkeland & Callomon 1985, pl. 1, figs 1-12). Smaller specimens show dense ribbing and poorly marked ventral sulci along the keel, and may be compared with *A. (Amoebites) cricki*, well characterised by its lectotype (Saffeld 1915, pl. 19, figs 2a-c; see also Birkeland & Callomon 1985, p. 16). It seems that the two forms in question are very close each other, and may even appear conspecific (see Atrops et al. 1993, p. 221). Similar specimens from the Flodigarry sections attributed to *A. bayi* and *A. cricki*, from beds 41-42, were illustrated by Wright (1989, figs 4A-B, and 4C-F).
The boundary between the Boreal Bauhini and Kitchini zones runs through the 0.8 m interval between the last occurrence of the A. bauhini group and the first occurrence of A. bayi. However, specimens transitional in character between A. (Amoebites) bayi and A. (Plasmatis) bauhini are also known from the immediately overlying interval 4.99 to 4.6 m below bed 44. The specimens in question are two small-sized ammonites – one attaining 18 mm in final diameter found 4.99 m below bed 44, and another 28 mm in final diameter found 4.79 m below bed 44 (Fig. 6r). They show rather distant and coarse ribbing which becomes much more dense and weaker at the aperture. The small size of the specimens, and the slightly backward course of the secondary ribs, show the affinity of these specimens with the A. bauhini group, whereas weakening of the secondary ribs at the keel indicates affinity with A. bayi (see Birkelund & Callomon 1985, p. 15; Atrops et al. 1993, pp. 220–222; Schweigert 2000, p. 205). Thus, it may be suggested that the boundary in question could run rather in the upper part of the 0.8 m interval indicated.

The occurrence of A. bayi and A. cricki from 4.99 m to 3.81 m below bed 44 characterises the lowermost part of the Kitchini Zone. This corresponds to the bayi horizon of the lower part of the Subkitchini Subzone (see Wierzbskiowski et al. 2002; see also Wierzbskiowski & Smelror 1993). The youngest specimens found in the lowermost part of bed 43, from 4.21 m to 3.81 m below bed 44, are either moderately to coarsely ribbed showing the presence of looped ribs, and thus referred to as A. (Amoebites) cf. bayi, or more densely ribbed, and compared with A. (A.) cf. cricki. A single indeterminate specimen of Amoebites was found 2.86 m below bed 44.

Beginning from bed 44 upwards, ammonites become “disappointingly few and badly preserved” (Wright 1989, p. 270). A single fragmentarily preserved specimen showing the development of ventrolateral nodes typical of A. (Amoebites) subkitchini found 1.37 m above bed 44 is indicative of the higher part of the Subkitchini Subzone of the Kitchini Zone (Wierzbskiowski & Smelror 1993, p. 247) (see also specimens illustrated by Birkelund & Callomon (1985, pl. 2, figs 1–7; pl. 3, figs 1–11).

5. Correlation between the Boreal, Sub-Boreal and Sub-Mediterranean zonal schemes

5.1. Correlation of the Boreal and Sub-Boreal zonal schemes

The ammonite succession in the Flodigarry sections on the Isle of Skye is possibly the most complete and fossiliferous of all the sections available through the Boreal and Sub-Boreal uppermost Oxfordian and lowermost Kimmeridgian, thus making possible close correlation of the Boreal and Sub-Boreal zonal schemes. The numbers of specimens of the families Cardioecreatidae and Aulaostephanidae are nearly equal, comprising for the uppermost Oxfordian, 40 specimens of Cardioecreatidae and 49 of Aulaostephanidae; for the Bauhini Zone plus the corresponding part of the Baylei Zone, 81 and 88 specimens respectively; and for the Kitchini Zone plus the corresponding parts of the Baylei and Cymodoce zones, 22 and 20 specimens respectively. These data differ markedly from those calculated for corresponding stratigraphical intervals in other areas of the Sub-Boreal and Boreal provinces. In southern England most of the ammonites belong to the Aulacostephanidae, whereas the Cardioecreatidae are rare (see Sykes & Callomon 1979). In central East Greenland (see Birkelund & Callomon 1985) and in cores from the Norwegian Sea offshore Norway (Wierzbskiowski et al. 2002) there is a marked dominance of the Cardioecreatidae over the Aulacostephanidae (in cores from the latter the ratio of specimens is 3:1). In Spitsbergen and in cores from the Barents Sea almost all specimens belong to the Cardioecreatidae (see Yershova 1983; Wierzbskiowski & Smelror 1993), but there is a single level in the Cymodoce Zone where the Aulacostephanidae occur commonly (Wierzbskiowski 1989).

Detailed analysis of the Boreal and Sub-Boreal ammonites in the sections studied at Flodigarry indicates that the Sub-Boreal Pseudocordata Zone corresponds to a part of the Boreal Regulare Zone plus the whole Rosenkrantzi Zone (as defined herein). The Caledonia Subzone plus a part of the Pseudojo Subzone of the Pseudocordata Zone corresponds to the upper part of the Regulare Zone. This is shown by the co-occurrence of ammonites typical of these Sub-Boreal subzones with Amoeboceras regulare indicative of the Regulare Zone (Figs 3, 7).

The rest of the Pseudojo Subzone, and possibly at least a part of the Pseudocordata Subzone, is equivalent to the Marstonense Subzone of the Rosenkrantzi Zone. Such a correlation results from co-occurrence of ammonites such as Ringsteadia ex gr. pseudojo, R. cf. pseudocordata and Microbiplices anglicus together with Amoeboceras marstonense. In the Flodigarry sections, these occur from the upper part of bed 33, about 1.5 m below its top, to the lowermost part of bed 35, about 0.75 m above its base. This corresponds well with data from southern England where the stratigraphical ranges of Ringsteadia pseudojo, R. pseudocordata, and Amoeboceras marstonense partly overlap (see e.g. Wright 1998, 2003). Also, in the South Ferrriby section in northern England, R. pseudocordata, A. cf. marstonense and A. rosenkrantzi are recorded together from the stratigraphical interval corresponding to the Pseudocordata Subzone (Schweigert & Callomon 1997, text-fig. 9; Cox 2001a, p. 123).

Some of the upper part of the Pseudocordata Subzone, plus the Evoluta Subzone of the Pseudocordata Zone (Sub-Boreal) may be correlated with the Rosenkrantzi Subzone of the Rosenkrantzi Zone (Boreal). This is shown by the co-occurrence of Ringsteadia evoluta, Microbiplices anglicus, and forms that are transitional between Microbiplices and Prorasenia, together with Amoeboceras rosenkrantzi in the upper part of bed 35, from 2.34 m to 1.24 m below bed 36.

In the Sub-Boreal zonal scheme, the boundary between the Oxfordian and Kimmeridgian corresponds to the boundary between the Evoluta Subzone of the Pseudocordata Zone and the Densicostrata Subzone of the Baylei Zone as re-defined in the present study (see section 3.2). This is placed between 1.24 m and 1.08 m below bed 36 at Flodigarry. In the Boreal zonal scheme, the Oxfordian/Kimmeridgian boundary corresponds also to the boundary between the Rosenkrantzi Subzone of the Rosenkrantzi Zone and the Bauhini Zone as defined herein (see section 4.3) (Fig. 7). This is placed 1.17 m below bed 36 at Flodigarry. It appears, thus, that the Oxfordian/Kimmeridgian boundary both in Sub-Boreal and the Boreal zonal schemes is placed exactly (or almost exactly) at the same level in the Flodigarry sections (Fig. 3).

The lower part of the Sub-Boreal Baylei Zone, distinguished herein as the Densicostrata Subzone, plus the lower part of an upper subzone, the Normandiana Subzone, corresponds to the Boreal Bauhini Zone. This is shown by co-occurrence from the uppermost part of bed 35, 1.17 m below bed 36, to the middle part of bed 41 of the A. bauhini group, with ammonites of the genus Pictonia typifying the Baylei Zone (see also Birkelund & Callomon 1985). The lowermost part of the Densicostrata Subzone, newly designated as the flodigarryensis horizon (uppermost part of bed 35, 1.08 m below its top, to the lowermost
part of bed 37, 0.2 m above its base), is nearly an exact equivalent of the lowermost part of the Bauhini Zone characterised by the co-occurrence of the first Amoeboceras (Plasmatisites), the last A. rosenkrantzii, as well as by the appearance of large A. schulginae (from 1.17 m below bed 36 to the lowermost part of bed 37).

The upper part of the Normandiana Subzone of the Baylei Zone contains the bayi horizon of the lowermost part of the Boreal Kitchini Zone. This is shown by the co-occurrence of the last representatives of the genus Pictonia with A. bayi/A. cricki in the uppermost part of the interval corresponding to beds 41 and 42 (from 4.99 m below bed 44) to the lowermost part of bed 43 (3.91 m below bed 44). However, the still younger Sub-Boreal biostatigraphical unit recognised in the sections studied (the inconstans horizon of the lowermost Cymodoce Zone) cannot be precisely compared with its Boreal equivalent. The inconstans horizon is recognised in the upper part of bed 43, from 2.25 m to 0.59 m below bed 44, up to bed 44. It thus occurs between the last occurrence of A. bayi (3.91 m below bed 44) indicative of the bayi horizon of the lowermost Boreal Kitchini Zone, and the first occurrence of A. subkitchini (1.37 m above bed 44) indicative of the upper part of the Subkitchini Subzone of the Kitchini Zone.

The highest Oxfordian zone of the Boreal subdivision of this stage in Siberia is the Amoeboceras ravnii Zone (see Mesezhnikov 1967, 1984, 1988; Sachs et al. 1969a, b). It contains at its base Amoeboceras regularae, followed by A. freboldi, A. leuctum Spath emend. Mesezhnikov, A. schulginae="A. ravnii Spath" and A. pectinatum Mesezhnikov. This assemblage is typical of the Regulare Zone plus the Rosenkrantzii Zone of the standard Boreal subdivision, and possibly also of the lowermost part of the Bauhini Zone, based on the ammonites studied at Flodigarry. Mesezhnikov et al. (1989, pp. 40–42) later placed in the Amoeboceras ravnii Zone a fauna consisting of ammonites of the Amoeboceras bauhini group described from the Russian Platform, indicating that the whole of the Bauhini Zone could correspond to the lower and middle parts of the Amoeboceras ravnii Zone. It should be remembered that the ammonites of the subgenus Plasmatisites (=the A. bauhini group) are widely distributed in the Boreal Province, in the Norwegian Sea (Århus et al. 1989; Wierzbowski et al. 2002), and Barents Sea areas (Wierzbowski & Århus 1990; Wierzbowski & Smelror 1993), making everywhere a clear distinction of the standard Bauhini Zone of the lowermost Boreal Kimmeridgian.

5.2. Correlation with the Sub-Mediterranean zonal scheme
The correlation of the Boreal and Sub-Boreal zonal schemes with the Sub-Mediterranean one is more difficult and still not clear in many details, although much progress has been made in recent years (see e.g. Matyja & Wierzbowski 1997, 2002, 2003, Schweigert & Callomon 1997, and older papers cited therein).

Amoeboceras rosenkrantzii occurs together with ammonites of the genus Ringsteadia (some similar to R. caledonica) and Microbiplices microbiplex in the semimammatum horizon in Central Poland (Matyja & Wierzbowski 1994, pl. 1, figs 11–13). This horizon is situated in the lower part of the Hypselum Subzone of the Bimammatum Zone in the Sub-Mediterranean zonal scheme. The ammonites recorded indicate that this horizon is equivalent to a lower part of the Sub-Boreal Pseudocordata Zone and the corresponding lower part of the Boreal Rosenkrantzii Zone. Still older deposits belonging to the Sub-Mediterranean Grossouvre Subzone, and thus representing the upper part of the Bifurcatus Zone, have yielded Boreal ammonites in Central Poland comparable with late representatives of the A. regularae group (Matyja & Wierzbowski 1994, pl. 1, figs 4–10). An unquestionable representative of the Sub-Boreal genus Ringsteadia has been found in deposits of the upper part of the Bifurcatus Zone in southern Germany (Schairer 1989, pl. 3, fig. 6). This suggests that the lowermost part of the Sub-Boreal Pseudocordata Zone, and the corresponding upper part of the Boreal Regulare Zone, correlate with some upper part of the Sub-Mediterranean Bifurcatus Zone (Fig. 7).

The correlation of still younger Sub-Mediterranean biostatigraphical units of the Bimammatum Zone (such as the upper part of the Hypselum Subzone (i.e. the berrense horizon), and the Bimammatum Subzone) with the Boreal/Sub-Boreal succession is less clear. The problems are partly related to the scarcity of Boreal/Sub-Boreal ammonites in this part of
the Sub-Mediterranean succession when compared with their common occurrence in the lowermost part of the Bimammatus Zone, but they also result from the generally poor knowledge of ammonite distribution in this Sub-Mediterranean stratigraphical interval (see Schweigert & Callomon 1997, pp. 35-36). However, it should be remembered that the occurrence of the first representatives of Amoeboceras (Plasmatites), such as A. prachbushini, A. lineatum, and even forms similar to A. baumii, as well as the first representatives of Prorasenia, are reported from the Bimammatus Subzone in northern Poland and southern Germany (see Matyja & Wierzbowski 1998, p. 40, pl. 1, figs 9–10; Schweigert 2000, p. 205, pl. 1, fig. 8). This indicates that at least part of the Bimammatus Subzone of the Sub-Mediterranean succession correlates with the lowermost part of the Bauhini and Bayeli zones, i.e. with the lowermost Boreal/Sub-Boreal Kimmeridgian (Matyja & Wierzbowski 2003).

In Central Poland and southern Germany the upper part of the Sub-Mediterranean Bimammatus Zone, i.e. the Hauffianum Subzone, has yielded fairly abundant ammonites of Boreal and Sub-Boreal affinity – such as Amoeboceras baumii, A. aff. schultginae, Pictonia densiscosta and Prorasenia bowserbankii. These specimens have been found in the middle part of the subzone (Matyja & Wierzbowski 1997, pp. 99–100, pl. 5, figs 1–13; Schweigert & Callomon 1997, pl. 1, figs 1–26, pl. 2, figs 1–2, pl. 5, fig. 2). This allows correlation of the middle part of the Hauffianum Subzone with the lowermost Boreal/Sub-Boreal Kimmeridgian, i.e. with some parts of the Bauhini Zone and the Densiscosta Subzone of the Bayeli Zone (except their lowermost parts).

In the Planula Zone of the Sub-Mediterranean zonal scheme, ammonites of Boreal/Sub-Boreal affinity are known to occur in the upper part of the Planula Subzone, and in the overlying Galar Subzone. The ammonites from the Planula Subzone, known from southern Germany and northern Poland, represent various forms of the Amoeboceras baumii group (Schweigert 2000, p. 205, pl. 1, fig. 12; Matyja & Wierzbowski 2002, pl. 1, fig. 2), and "Sub-Mediterranean" species of the genus Pictonia. The latter, such as Pictonia perispheinctoides (Wegele), are similar to the Sub-Boreal species Pictonia normandiana – see Hantzpergue (1989, pp. 224, 229) and Schweigert & Callomon (1997, pp. 40, 45, pl. 7, figs 13–14). Thus, they are still indicative of the Boreal Bauhini Zone (of its upper part), and an upper part of the Sub-Boreal Bayeli Zone (markedly below its top). On the other hand, Boreal ammonites occurring at the base of the Sub-Mediterranean Galar Subzone, and continuing up through this subzone, in northern Poland and southern Germany, include Amoebites baiyi and allied forms (Matyja & Wierzbowski 2002, pl. 1, figs 1, 3a, b; Schweigert 2000, p. 206, pl. 1, fig. 13). These indicate that this Sub-Mediterranean subzone correlates already with the lowermost part of the Boreal Kitchimi Zone.

In the Galar Subzone in northern Poland the last representatives of the Sub-Boreal genus Pictonia have been found, distinguished as the new species Pictonia kuiaviensis Matyja & Wierzbowski. The species has ransend-like appearance and represents a form phylogenetically close to the earliest members of the genus Rasenia. Thus, it may be treated as indicative of the uppermost part of the Sub-Boreal Bayeli Zone (Matyja & Wierzbowski 2002, pp. 416–417, 419–420, pl. 1, figs 4–11, 12). Hence, the boundary between the Planula Subzone and the Galar Subzone of the Sub-Mediterranean zonal scheme is very close to the boundary between the Boreal Bauhini and Kitchimi zones (Schweigert & Callomon 1997, text-fig. 12; Matyja & Wierzbowski 2002, text-fig. 5), but it still runs within the uppermost part of the Sub-Boreal Bayeli Zone (Matyja & Wierzbowski 2002, text-fig. 5). This boundary, well recognised both in the Boreal and in the Sub-Mediterranean succession, and lying fairly close to the currently accepted Oxfordian/Kimmeridgian boundary in the Sub-Mediterranean succession, has a large correlation potential and it may be considered as a candidate level for the Oxfordian/Kimmeridgian boundary (Matyja & Wierzbowski 2002, 2003; Matyja et al. 2004).

The occurrence in the lowermost part of the Sub-Mediterranean Platynota Zone in southern Germany, Switzerland, and southern France of the ammonites of the genus Amoeboceras grouped around the species Amoeboceras (Amoebites) baiyi (see Atrops et al. 1993, pl. 2, figs 1–6), may be treated as indicative of the lower part of the Boreal Kitchimi Zone, and possibly still of the upper part of the Sub-Boreal Bayeli Zone (see e.g. Matyja & Wierzbowski 2002, 2003).

6. Systematic palaeontology

Superfamily Stephanoceratoidea Neumayr, 1875
Family Cardioceratidae Siemiradzki, 1891
Subfamily Cardioceratinae Siemiradzki, 1891
Genus Amoeboceras Hyatt, 1900

Type species. Ammonites alternans von Buch, 1831. The oldest members of the genus Amoeboceras Hyatt, 1900 include representatives of the nominative subgenus Amoeboceras based originally on small strongly-ribbed microconchs, and also representatives of the subgenus Prionodoceras (type species Prionodoceras priodes Buckman = Amoeboceras serratum Planerby) comprising large macroconchs with a smooth body chamber (see Sykes & Callomon 1979). The common features of all these Upper Oxfordian forms comprise "tabulate venter, and minutely serrated keel flanked by smooth bands or shallow sulci" (Arkell et al. 1957, p. L 306). These features are recognised in representatives of the nominative subgenus, as well as on the inner whorls of large macroconchs. As there exists a considerable variability of the dimorphs within the Upper Oxfordian representatives of Amoeboceras, and as the general affiliation of corresponding micro- and macroconchs to a single species does not present serious difficulties (see Sykes & Callomon 1979), the distinction between the subgenera Amoeboceras and Prionodoceras seems unnecessary. Thus, all the Upper Oxfordian species discussed herein are placed in the nominative subgenus Amoeboceras.

Amoeboceras schultginae Mesezhnikov

Fig. 6d

1967 Amoeboceras (Prionodoceras) schultginae Mesezhnikov, p. 123–8, pl. 1, fig. 4; pl. 3, fig. 1; pl. 4, fig. 1.
non 1979 A. cf. schultginae Mesezhnikov. Sykes & Callomon, p. 884, pl. 118, fig. 5.

Material. Four specimens (ST722, ST725, ST849, ST902) from the top of bed 35 and the base of bed 37 at Flodigarry.

Description. These specimens are large, attaining up to about 110 mm in their final diameter. The primary ribs are strong and distant from the inner whors up to the first half of the last whorl (PR is about 20). They are markedly accentuated and curved at the umbilical margin, and then recciradate or weakly prorsistrate up to a strong lateral tubercle situated somewhat above the mid-height of the whorl. The secondary ribs are partly placed independently of the primaries. They are
short, almost rectiradiate, and strongly tuberculate at the ventro-lateral shoulders. The keel is coarsely crenulated. On the last half of the outer whorl the ribbing becomes much more dense and weaker, with strongly projected secondaries.

Discussion. These specimens co-occur in the Flodgarry sections with other specimens showing the normal ornamentation of *A. rosenkrantzi*, and the two may be treated possibly in horizontal classification as members of a uniform faunal assemblage. On the other hand, in a more typological approach, the more heavy ribbed forms may be readily compared with *Amoeboceras schulginae* Mesezhnikov. This latter interpretation is accepted herein. The type specimens of *A. schulginae* as interpreted by Mesezhnikov (1967), together with specimens of the very close "Amoeboceras (Prionomoceras) rami Spath" sensu Mesezhnikov (1967, pp. 116-117, pl. 1, fig. 1; see also Mesezhnikov 1988, pl. 9, fig. 14), constitute members of a well defined assemblage occurring in the Levaya Boyarka section of North Siberia. This assemblage occurs directly above one containing *Amoeboceras regulare* (see Sachs et al. 1969a, p. 24; 1969b, p. 72).

The name *A. schulginae* has been used in the geological literature as a specific name for *Amoeboceras* of a variety of different ages and differing somewhat in their appearance. These attributions are mostly not accepted here: (1) the specimens referred to as *A. schulginae* A. cf. *schulginiae* co-occurring with ammonites of the much older *A. regulare* group (see Sykes & Callomon 1979, p. 884, pl. 118, fig. 5) differ mostly from typical representatives of *A. schulginae* in their weaker ornamentation; (2) the specimens referred to as *Amoeboceras (Amoebites)* aff. *A. schulginae* by Birkelund & Callomon (1985, p. 18, pl. 4, figs 1-3) found together with *Pictonia cf. normandiana*, may represent extremely coarsely ribbed end-members of *Amoeboceras bayi*; (3) the specimens referred to as *Amoeboceras schulginae* by Wierzbowski & Smelror (1993, pl. 1, fig. 6), as well as by Schweigert (1995, pp. 178-180, figs 1a-e; see also Schweigert & Callomon 1997, p. 6, pl. 2, fig. 1; pl. 5, fig. 3) co-occurring with *Plasmattites of the A. baumhini group, seem the most similar to typical representatives of *A. schulginae*, but differ mostly in their much smaller end-size (see below).

*Amoeboceras aff. schulginae* Mesezhnikov

Fig. 6-k-n

1993 *Amoeboceras schulginae* Mesezhnikov; Wierzbowski & Smelror, pl. 1, fig. 6.
1995 *Amoeboceras schulginae* Mesezhnikov; Schweigert, pp. 178-180, figs 1a-e.
1997 *Amoeboceras schulginae* Mesezhnikov; Schweigert & Callomon, p. 6, pl. 2 fig. 1; pl. 5, fig. 3.

Material. Three specimens (ST856, ST857, ST858) from Bed 39 at Digg and Flodgarry.

Description. The specimens attain from 45 mm to 60 mm in final diameter. Coiling is from weakly evolute to weakly involute. The ribbing of the inner and middle whorls, sometimes up to a part of the last whorl, is coarse and distant to moderately dense (PR = 25-33 at D ≤ 36 mm). The primaries are slightly flexuous, accentuated at the umbilicus, and terminate in a feeble lateral tubercle above the mid-height of the whorl. The secondary ribs are short, rursiradiate in their course, with the development of ventrolateral tubercles. The keel is markedly crenulate. On the outer whorl (or sometimes on its end-part only) the ribs become more densely spaced, without clear differentiation into primaries and secondaries. The ribs here are slightly flexuous, and show the presence of elongated ventrolateral tubercles. There is marked projection of the ribs on the side of the venter, and they may continue with some weakening onto the crenulated keel.

Discussion. These specimens are very similar in their ornamentation to *A. schulginae*, showing the typical tri-tuberculation before the final stage of ribbing. They differ, however, from that species in the much smaller final size of the shell, and are referred to herein as *A. aff. schulginae*. The specimens from the Staffin sections are very similar, and possibly conspecific, with the specimens from the Barents Sea and southern Germany listed in the synonymy above. They co-occur at these localities with *A. (P.) baumhini* (Oppel). At Staffin, *A. aff. schulginae* occurs at a single level in the lower part of bed 39 at Flodgarry (Fig. 6-k-m) and at Digg (Fig. 6-n).

Subgenus *Plasmattites* Buckman, 1925

Type species. *Plasmattites crenulatus* Buckman, 1925c (almost surely a younger synonym of *Amoeboceras (Plasmattites) praebauhinii* (Saffeld 1915)). Included here are small forms "with dense straight wiry ribbing of the group of *A. baumhini* (Oppel)" – see Sykes & Callomon (1979, p. 858). The ribbing is falcial. In some specimens there is poor differentiation of primary and secondary ribs. In other specimens there is strong differentiation of primaries and secondaries with feeble tubercles at the end of the primary ribs and a smooth spiral band between primary and secondary ribs. The secondary ribs, raised if not tuberculate on the shoulders, run up onto the coarsely crenulated keel. Ribbing on the outer whorl may be very dense in contrast to the inner whorls where ribbing is usually much more distant. The whorl section varies from lenticulate to oval and even subquadrate/subrectangular (see Saffeld 1915, pp. 178-9; Matyja & Wierzbowski 1988, pp. 425-6, pl. 2: Atrops et al. 1993, pp. 219-20, text fig. 2.11).

Small-sized *Plasmattites* attaining 15-40 mm in final diameter have been usually recognised as microconchs (e.g. Sykes & Callomon 1979; Matyja & Wierzbowski 1988) although there always remained the problem of their dimorphic counterpart. Somewhat larger specimens, attaining 40-50 mm in final diameter, referred here to *Amoeboceras aff. schulginae* (see above) may be considered as potential macroconchs of *A. (P.) baumhini*. Detailed analysis of representatives of Sub-Mediterranean *Plasmattites* by Matyja & Wierzbowski (2000) has shown that their small end-sizes were related to early attainment and long time duration of the mature stage (as shown by crowding of the septae in most or all of the last whorl of the phragmocone).

Subgenus *Amoebites* Buckman, 1925

Type species. *A. akanthophorus* Buckman. 1925a [= *A. kitchini* (Saffeld 1915) sub-j.]. *Amoebites* "differs from *Amoeboceras s.s.* in abandoning mid-lateral tuberculation of primary ribbing and developing instead strongly accentuated secondary ribbing" (Birkelund & Callomon 1985, p. 12). It differs also in the presence of looped ribs on the outer whorl. This type of ornamentation tends to appear already in some more coarsely ribbed forms related to *A. rosenkrantzi*, such as *A. leucum* and *A. schulginae*. Strongly accentuated secondaries are also common in coarsely ribbed *A. (Plasmattites) baumhini*, which show the presence of a smooth spiral band separating long primary and short secondary ribs (see also Mesezhnikov 1967, p. 123; Birkelund & Callomon 1985, p. 12). The general succession of the species of *Amoeboceras* was largely established by Birkelund & Callomon (1985), and discussed by other authors (e.g. Wierzbowski & Smelror 1993). It begins with the small-sized *A. (Amoebites) bayi* and continues into generally
larger-sized *A. (Amoebites) subkitchini*, and finishes with the smaller-sized forms of *A. (Amoebites) kitchini* and its allies.

Superfamily Perisphinctoidea Steinmann, 1890
Family Aulacostephanidae Spath, 1924

The ammonite faunas of the family Aulacostephanidae consist of successive members from *Ringsteadia* through *Pictonia* to *Rasenia* (mostly macroconchs) and *Microbiplices* to *Prorasenia* (microconchs) which formed during the latest Oxfordian and earliest Kimmeridgian a smoothly evolving lineage (see Birkelund & Callomon 1985). Crucial for the stratigraphical problems discussed here is the nature of the transition from *Ringsteadia to Pictonia*, and the distinction of the oldest species with the dominant features of *Pictonia, Pictonia flodigarriensis* sp. nov. It is also necessary to discuss the transition from *Microbiplices to Prorasenia*, and the occurrence of forms transitional between *Microbiplices* and *Prorasenia*.

Genus *Ringsteadia* Salfeld, 1913

**Type species.** *Ammonites pseudocordatus* Blake & Hudleston, 1877. *Ringsteadia* has long, distinct primary ribs on the innermost whorls, most ribs splitting above the mid-height of the whorl, but with some long intercalated secondary ribs. Primary and secondary ribs are equally strong. Deeply incised and relatively wide constrictions may be present. The main stage of ornamentation consists of more loosely spaced and stronger primary ribs, weakening at about the mid-height of the whorl at the point of division. The secondary ribs are more numerous (two to five for each primary), and thinner than the primary ribs. Constrictions are poorly marked, wide and shallow. In specimens retaining large sizes (400 mm+) the ornamentation completely disappears on the outer whorl. The whorl section of the innermost whorls is rounded, that of the middle and outer whorls oval, usually tapering towards the ventral side.

The transition between *Ringsteadia* and *Pictonia* is marked by the retention in some specimens of *Ringsteadia* of dense ‘perisphinctoidal’ ornament up to somewhat larger diameters compared with the bulk of *Ringsteadia* at the same level. Thus Figure 4c, collected from the uppermost *Pseudocordata* Subzone 2-34 m below bed 36, reveals *Pictonia*-like ornament up to about 17 mm in diameter, when other specimens from this level show similar ornament up to a few millimetres in diameter only. The same phenomenon is even more visible in a younger fauna of *R. evoluta* (F6S, 1-65 m below 36) where irregular ribbing resembling that of *Pictonia* occurs to about 20-30 mm diameter in some specimens.

Genus *Pictonia* Bayle, 1878

**Type species.** *Pictonia baylei* Salfeld, 1913 [ICZN Opinion 426; = *Pictonia cymodocae* Bayle, 1878 (non d’Orbigny, 1850)]. *Pictonia* differs from *Ringsteadia* in being generally more evolute and planulate. Ribbing on the inner whorls of *Pictonia* is of the ‘perisphinctoidal’ type, generally densely ribbed, with mostly biplicate secondaries and sometimes single intercalated ribs. On the middle whorls the ribbing often becomes more distant, biplicate and polyplete. At larger diameters ornamentation fades, and in most species it is reduced to only dense strie occurring on the body chamber. The principal characteristic feature of the genus is irregularity of ribbing expressed by the periodical occurrence of swollen ribs (flared ribs) bordering deep constrictions, especially strongly developed on the middle whorls (cf. Birkelund & Callomon 1985; Hantzpergue 1989).

The first specimens which show predominantly the characteristic features of *Pictonia* appear in large numbers in the *P. flodigarriensis* faunal horizon distinguished herein as the lowest level of the Baylei Zone.

*Pictonia flodigarriensis* sp. nov.

(Fig. 5a–c)

![Image](https://example.com/image)

?1985. *Pictonia*? sp. indet B; Birkelund & Callomon, p. 32, pl. 11, fig. 4.

**Diagnosis.** *Pictonia* having the dense ribbing, constrictions and flared ribs characteristic of the genus, with a more regularly ribbed body chamber resembling that of *Ringsteadia*.

**Material.** The holotype (ST383, Fig. 5c), paratypes (ST386 and ST387, Fig. 5a, b) and seven other specimens (ST683, ST697, ST699, ST701, ST702, ST710, ST721) from the Staffin Shale Formation, uppermost part of bed SS35 to lowermost part of bed SS37 (from 1-08 below bed 36 to 0-2 m above bed 36); lowermost part of the Baylei Zone, *flodigarriensis* horizon.

**Derivation of name.** From the hamlet of Flodigarich which adjoins the beach section where the type specimens were collected.

**Description.** The inner whorls show dense ribbing (PR is about 35–45) consisting mostly of biplicate ribs; the point of furcation is located high on the whorl side; stronger accentuated ribs with the character of flared ribs appear at narrow constrictions. Such ornamentation may continue to 15 mm, but often it exists at larger diameters – commonly 20–30 mm, sometimes even 50 mm. On the middle whorls the primary ribs become more distant. The ribbing is mostly triplicate with a number of intercalatory ribs appearing above the mid flank. Flared ribs occur at the well marked constrictions. This ornamentation usually continues up to 50–80 mm diameter. On the last whorl ribbing becomes much more regular, consisting of fairly strong and distant primary ribs, and similarly developed (or somewhat weaker) secondary ribs; the number of secondaries per primary is two to three. The constrictions, if present, are poorly marked here, becoming wide and shallow. This final ornamentation may begin in some specimens a little earlier than in others, i.e. already on the penultimate whorl where it may partly replace the distant and irregular ornamentation of the former stage normally occurring there. The largest specimens attaining about 130–140 mm diameter carry the same type of final ornamentation to the end of the whorl.

The coiling of the inner and middle whors (phragmocone), showing the irregular *Pictonia*-type ornamentation described above, is strongly evolute. On the other hand, the more regularly ribbed outer whor correspond mostly to the body chamber (at least two thirds of it) is much less evolute – from weakly evolute to even weakly involute (at D=70–90 mm, Wh=34–39%, Ud=36–42%). and resembles that of *Ringsteadia*.

**Discussion.** The species described herein is the oldest species of the genus *Pictonia*. It differs mostly from the closely allied *Pictonia densicostata*, Buckman in having regular strong ornamentation of the outer whorl, and its weakly evolute to weakly involute coiling. Closely similar to *Pictonia flodigarriensis* sp. nov. is a single specimen referred to as *Pictonia*? sp.indet. B by Birkelund & Callomon (1985, p. 32, pl. 11, fig. 4). This specimen reveals an involute body chamber with regular ornamentation, but its inner whorls are not preserved, which precludes unequivocal interpretation.

Genus *Microbiplices* Arkell, 1936

**Type species.** *Ammonites microbiplices* Quenstedt, 1887–8. According to the original definition (Arkell 1936, p. xli),
Microbiloces comprises forms "with a few coarse, rounded, bifurcating ribs with widely-splayed strong secondaries". However, this type of ornamentation is characteristic, only of the last whorl up to the aperture as marked by presence of lappets. Several specimens of this type species, M. microbiloces, show a different type of ornamentation in the preceding whorl (as well as at the beginning of the last whorl). This consists of fairly thin triplicate, as well as biplicate ribs, with some long intercalary ribs (see e.g. Arkell 1936, pl. C, figs 6a–c; Enay 1962, pl. 2, figs 4a–d).

Genus Prorasenia Schindewolf, 1925

Type species. Prorasenia quenstedti Schindewolf, 1925. A change in ornamentation from triplicate ribbing of the inner whorls to biplicate ribbing of the last whorl similar to that seen in earlier Microbiloces occurs in representatives of Prorasenia. According to some authors (Schweigert & Callomon 1997) this justifies treatment of the name Microbiloces as a junior synonym of Prorasenia. However, in contrast to the similarity in ornamentation of the last whorl, there are marked differences in ornamentation of the penultimate stage. In Microbiloces the ribbing is thin, and the point of rib division lies at, or even somewhat above, the mid-height of whorl. In Prorasenia the primary ribs are much thicker, and the point of division lies below the mid-height of the whorl. Thus, in the present paper the two taxa are treated separately.

The transition from Microbiloces to Prorasenia is best observed in the upper part of the Pseudocordata Zone where the microconchs occurring here reveal a newer type of ornament. There are three growth stages in Microbiloces and Prorasenia: (1) a stage of smooth whorls up to about 4.5–5.5 mm diameter; (2) a stage with biplicate and intercalary ribs, later changing in ornamentation to triplicate ribs, with deep constrictions and strongly accentuated bordering ribs; (3) a stage with coarse, regularly furcating, biplicate, though sometimes single ribs, occupying a major part of the last whorl up to the aperture. The evolutionary changes appear mostly at the second stage. The primary ribs, initially at the end of the stage, become thicker, and the point of division of the ribs lowers on the whorl side, resulting in the exposure of secondaries of the penultimate whorl at the umbilical margin. Such a style of ribbing appears at the end of the penultimate and at the beginning of the last whorl (from 15–20 mm diameter), and is typical of the genus Prorasenia. However, it follows 'normal' thin ribbing of the Microbiloces type in the inner whorls. The remainder of the last whorl bears coarse biplicate and single ribs, showing a somewhat lower point of rib furcation than in the outer whorl of typical Microbiloces. These specimens are thus intermediate in character between Microbiloces and Prorasenia (Fig. 4F–h; see also Sykes & Callomon 1979, pl. 121, fig. 14).

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7. References


