Revision and New Data of the Ammonite Family Acanthoceratidae de Grossouvre, 1894, from the Lower Turonian of the Iberian Trough, Spain

by

Fernando Barroso-Barcenilla

With 13 plates and 10 text-figures
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Zusammenfassung


Schlüsselwörter: Unteres Turonium – Ammonoidea – Familie Acanthoceratidae – Iberischer Trog – Spanien

Summary

The ammonites assigned to the family Acanthoceratidae de Grossouvre, 1894, from the Wiedmann (Tübingen, Germany) and Goy, Carretero and Meléndez (Madrid, Spain) Collections obtained from the Lower Turonian of the Iberian Trough have been revised. New specimens of the species Spathites (Jeanrogericeras) tavense (Faraud, 1940), S. (J) saenzi (Wiedmann, 1960), S. (J) postsaenzi (Wiedmann, 1960), S. (J) obliquus (Karrenberg, 1935), S. (J) reveliereanus (Courtillier, 1860), S. (J) combesi (Sornay, 1951), S. (Ingridella) malladae (Fallot, 1931), S. (J) depressus (Wiedmann, 1960), S. (Spathites) laevis (Karrenberg, 1935), S. (S) sulcatus (Wiedmann, 1960), Mammites nodosoides (Schütler, 1871), Kamerunoceras ganuzai (Wiedmann, 1960) and K. turoniense (d’Orbigny, 1850) have been also presented. In addition, the specimen of Ammonites inconstans Schütler, 1871, of Mallada (1891, 1892), the holotype of Mammites (Pseudaspidoceras) armatus Pervinquière (1907), and the syntype of variety frachichensis Pervinquière (1907) have been refigured. Studies on the morphologies and the geographical and stratigraphical distributions of all of these species have led to the identification of several phylogenetic relationships between them, and to distinguishing five main phases in the evolution of the family, characterized by the successive dominance of Spathites (Jeanrogericeras) 1, of Spathites (Ingridella), of Spathites (Jeanrogericeras) 2, of Mammites and of Spathites and Mammites.

Key words: Lower Turonian – Ammonoidea – Family Acanthoceratidae – Iberian Trough – Spain
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Introduction

This paper first presents a revision of the Lower Turonian ammonites from the Iberian Trough assigned to the
family Acanthoceratidae that are currently held in the GPIT (Institut und Museum für Geologie und
Palaontologie, Tübingen, Germany) and the UCM (Universidad Complutense de Madrid, Madrid, Spain). These
centres hold the Wiedmann, Goy, Carretero and Melendez collections, which include most of the specimens
of Acanthoceratidae from Spain. Secondly, a detailed taxonomic analysis has been made for the members of this
family obtained during field work carried out for this investigation. The field work focused on the Lower
Turonian outcrops situated in the localities of Puente dey and Soncillo, in the north of the province of Burgos, of
Fuentetoba and Villaciervos, in the centre of Soria, and of Cantalojas, Galve de Sorbe, Condemios and Tamajon,
in the north of Guadalajara, Spain (Text-fig. 1). Thirdly, the obtained information has enabled a discussion of the
taxonomy, distribution and phylogeny of the acanthoceratids.

In order to establish a more precise systematic classification of the taxa being dealt with I have also studied
the original types attributed to this family that are held in the Museu do Instituto Geológico e Mineiro de Lisboa,
Portugal, and in the Musée National d’Histoire Naturelle of Paris, France.
Geological Setting

The Iberian Trough includes the northern, central and southeastern regions of the Iberian Subplate that were temporally or permanently flooded by the Protoatlantic Ocean or by the Tethys Sea during the late Cenomanian and the Early Turonian and that were limited on their west side by the Hesperian Massif and on their east side by the Ebro Massif (Text-fig. 2 A). It was broadly related to the North Cantabrian, Basque, Pyrenean and Levantine basins. Its privileged palaeogeographical location enabled during the Late Cretaceous the arrival of both Boreal fauna coming from the Protoatlantic, as well as Meridional fauna from the Tethys (Text-fig. 2 B). Due to this, cephalopod species with a great variety of origins were recorded in these regions. Likewise, as it constituted a relatively confined marine environment, endemic species arose in these waters as well. The Iberian Trough was divided into different domains, that were, from the north to the southeast, the Outer Navarro-Cantabrian Platform and the Inner Castilian Platform. During relatively high sea level intervals the palaeogeographical region extended from the Inner Castilian Platform to the southeast along the Levantine Platform, from which it received directly Tethyan influence. The Inner Castilian Platform, from where the cephalopods presented in this investigation come from, can be divided into the North-Castilian Sector, with the North-Ebro and South-Ebro areas, and the Central Sector, with the La Demanda and Guadarrama areas (Text-fig. 2 C). All the terms used herein for palaeogeographical regions, in a wide sense, can also be used for the respective geographical regions where their rocks are present.

Nowadays, the materials of the Inner Castilian Platform make up a large northwest-to-southeast orientated belt made up of a thick carbonate sedimentary sequence from the Cretaceous age, with some terrigenous and dolostone intervals. Their main stratigraphical units are the Margas de Puentedey (FLOQUET et al., 1982) and Margas de Picofrentes (FLOQUET et al., 1982) formations, deposited respectively in the marginal and in the internal environments of the inner platform. These formations are remarkable for containing the most complete and characteristic marls of the studied interval in the entire north and centre of Spain, as pointed out by WIEDMANN (1960, 1964, 1975a, 1975b, 1979), WIEDMANN & KAUFFMAN (1978), FLOQUET et al. (1982), FLOQUET (1991), SANTAMARÍA-ZABALA (1991, 1992, 1995) and SEGURA et al. (1993), among others. Further readings on the main aspects of the geological evolution of the Iberian Trough were given by ROSALES et al. (2002), MAS et al. (2002), FLOQUET (2004) and GARCÍA et al. (2004).

Historical Background

From the beginning of the 20th century many ammonites have been collected from the Lower Turonian, not only in the Iberian Trough but in the whole of Spain, and assigned to Acanthoceratidae by several authors. However, only a few detailed taxonomic studies of them have ever been carried out, since only a few of these specimens have been described and illustrated in an appropriate way. Among the first systematic analysis concerning the palaeontology of the upper Cenomanian and Lower Turonian cephalopods in the north of Spain, that of KARRN BERG (1935) was the most noteworthy. He described many new species and mentioned several ammonite taxa, some of which can be attributed to this family. Some years later, BATALLER (1950) published a synopsis about the new species from the Cretaceous of Spain in which many ammonite taxa were mentioned and, among them, several acanthoceratids.

WIEDMANN (1960, 1964) identified numerous ammonite species from the Upper Cretaceous of the Iberian Trough. He described several new taxa from the Celtiberic and Vascogotic Ranges, regions coinciding with the Central Sector and with the North-Castilian Sector and the Outer Navarro-Cantabrian Platform, respectively. Among the obtained specimens, WIEDMANN cited an important number of representatives of the family. Later, WIEDMANN (1975a) described some cephalopods from the La Demanda Area, citing some members of Acanthoceratidae. In the same year, from the ammonite sequences obtained in the Upper Cretaceous of the Central Sector, WIEDMANN (1975b) obtained several acanthoceratids and proposed some new taxa. In the Outer Navarro-Cantabrian Platform, the North Castilian Sector and the La Demanda Area, WIEDMANN & KAUFFMAN (1978) and WIEDMANN (1979) identified a large number of ammonites attributed to the family.

CARRETERO-MORENO (1982) carried out a palaeontological investigation with specimens belonging to various groups of Cretaceous fossils, which were collected from several outcrops of the Levantine Platform and the Guadarrama Area. Cephalopods were included among the invertebrates studied in her work, some of
which were acanthoceratids. Segura & Wiedmann (1982) collected some Acanthoceratidae in Upper Cretaceous outcrops of the Central Sector. Based on a detailed analysis of the ammonites obtained in the Guadarrama Area, Meléndez-Hevia (1984) identified several species of the family. Studying the Turonian biostratigraphy of the Outer Navarro-Cantabrian Platform, Lamolda et al. (1989) reported some acanthoceratids. Floquet (1991) analysed the Upper Cretaceous geology of the northern half of the Iberian Trough and of the Basque Basin, in the north of Spain, and cited a significant number of cephalopods, including some members of Acanthoceratidae, although he did not provide any figures of them.

Santamaría-Zabalá (1991, 1992, 1995) investigated the upper Cenomanian to Santonian ammonites from the North-Castilian Sector, and the Outer Navarro-Cantabrian Platform, and identified several Turonian acanthoceratids. Segura et al. (1993) studied the stratigraphic sequences of the Cenomanian-Turonian transition in some parts of the Central Sector located in the Iberian Ranges. They described some biostratigraphic sections, where members of Acanthoceratidae are mentioned. Taking into account the ammonites studied by Santamaría-Zabalá, Martínez et al. (1996) cited the cephalopod taxa collected from each biozone of the upper Cenomanian to Santonian of the North-Castilian Sector, the Outer Navarro-Cantabrian Platform and the Basque Basin, among them several species of the family.

Lamolda et al. (1997) analysed the fossils and chronostratigraphy of the Cenomanian-Turonian boundary in the Outer Navarro-Cantabrian Platform, where they found some acanthoceratids. In the relatively deep-sea originating series of the Outer Navarro-Cantabrian Platform, Küchler (1998) also recognized some ammonites attributed to the family and presented several biostratigraphic sequences.

Recently, Barroso-Barcenilla (2004) studied the Acanthoceratidae from the upper Cenomanian and Lower Turonian in the northern margin of the North-Castilian Sector, and mentioned several members of this family in the presented biostratigraphic section. The conclusions reached in this work were contrasted with the ones obtained in other regions of the Iberian Trough by Barroso-Barcenilla (2006) and Barroso-Barcenilla, Goy & Segura (manuscript in review), who presented a new ammonite zonation of the upper Cenomanian and Lower Turonian in the Iberian Trough, and identified several species assigned to the Acanthoceratidae.

Furthermore, in the last years several biostratigraphic investigations were carried out in other palaeogeographical regions adjoining to the Iberian Trough, and closely related to it, in which Upper Cretaceous cephalopod sequences were identified. Among these works, those by Wiese (1995, 1996, 1997), Wilmsen (1996, 1997a, 1997b, 2000), Wilmsen & Wiese (1996) and Wiese & Wilmsen (1999) in the North-Cantabrian Basin, and by Martínez (1982) in the Pyrenean Basin, both located in the north of Spain, should be noted.

Revision of Acanthoceratids of the Iberian Trough held in the Collections of the GPIT and the UCM

At the present time, the Wiedmann (JW), Goy (AG), Carretero (CM) and Meléndez (MH) collections of the GPIT and the UCM together contain the largest number of acanthoceratids so far collected from the Lower Turonian of the Iberian Trough. However, it has not been possible to find specimens of all the ammonite taxa cited in the works of Wiedmann (1960, 1964, 1975a, 1975b, 1979), Wiedmann & Kauffman (1978) and Segura & Wiedmann (1982) in the GPIT. The present investigation is therefore based exclusively on specimens that are now curated in the JW Collection, which is why not all the taxa mentioned in the publications of the German investigator have been revised. Likewise, it is important to emphasize that deficiencies in the method by which the fossils of the CM Collection have been numbered and identified has hindered an adequate and individualized tracking of its ammonites. Therefore, the revision of the taxa cited by Carretero-Moreno (1982) has only been partially carried out, and as a result the references to this work in the synonymy of the systematic section are imprecise.

In the present paper the palaeogeographical division (Text-fig. 2 C) and the ammonite zonation (Text-fig. 3) for the upper Cenomanian and Lower Turonian of the Iberian Trough proposed by Barroso-Barcenilla, Goy & Segura (manuscript in review) have been followed. These authors defined several biostratigraphic units, and correlated them with ones previously recognized in the same region by other investigators, and with the standard zones.
Text-fig. 2. The Iberian Trough during the maximum transgression of the late Cenomanian-Early Turonian. A, palaeogeographic situation. Modified from PHILIP & FLOQUET (2000), STAMPFLI et al. (2001) and GELABERT et al. (2002). B, detail of the Iberian Trough showing the facies distribution, the position of the main studied sections and the transect of Text-fig. 2 C. The circles symbolize coastal terrigenous, the horizontal rectangles indicate the position of relatively shallow water carbonate platform sediments, the curved lines stand for the marls deposited in deeper regions of the platform, and the hexagons represent bioclastic limestones located in intermediate bathymetries. C, divisions followed in the Iberian Trough with the approximate location of the studied outcrops and the geographic boundaries between their different palaeogeographic areas.

Concerning the numeration of WIEDMANN's biostratigraphic units mentioned in the present article, a modification was made between the first and the latter works of this author. WIEDMANN (1960, 1964) considered that the Cenomanian-Turonian boundary was located between the Metoicoceras muelleri and Metoicoceras swallowi zones. Therefore, the latter one was considered as the first biostratigraphic unit of the upper stage. The location of the boundary was subsequently modified by WIEDMANN & KAUFFMAN (1978) and WIEDMANN (1979). They held the opinion that the beginning of the Turonian coincided with the arrival of the genus Vascoceras Choffat, 1898. On the basis of this new premise, the Vascoceras gamai Zone was the oldest Turonian biostratigraphic division, which is why these authors began the enumeration of their zones from this unit. In order to avoid possible confusions, all references made in this paper to WIEDMANN's biostratigraphic zones allude to this author's most recent works.
### Text-fig. 3. Inferred correlation of the biostratigraphic zonation followed in this paper and other Spanish and the standard scales.

#### Watinoceras WARREN, 1930

Two ammonites from the North-Castilian Sector attributed to *Watinoceras* sp. are nowadays held in the GPIT. WIEDMANN (1960, 1964) indicated that these specimens come from the T I zone but *Watinoceras* sp. and *Leoniceras discoidale* (PERVINQUIÈRE, 1907) were subsequently considered by GRAFE & WIEDMANN (1993) as the index taxa of the lowest biostratigraphic unit of the Turonian, equivalent to the T III zone. This second stratigraphical interval seems to be correct.

#### Spathites (Jeanrogericeras) WIEDMANN, 1960

The JW Collection hosts several representatives of *S. (J.) obliquus* (KARRENBERG, 1935) and *S. (J.)* cf. *obliquus* from the T II to T VI zones of WIEDMANN of the Outer Navarro-Cantabrian Platform, the North-Castilian Sector and the La Demanda Area. The numerous specimens of *S. (J.) reveliereanus* (COURTILLER, 1860) and *S. (J.)* cf. *reveliereanus* that are held in this collection have been obtained from the T III to T VI zones of the Outer Navarro-Cantabrian and Inner Castilian platforms. The members of COURTILLER’s taxon of the AG and MH collections come from the *Spathites (Ingridella) malладae* Zone of the Guadarrama Area. The JW Collection has two ammonites from the T V zone of the Outer Navarro-Cantabrian Platform that were assigned by WIEDMANN to *S. (J.) binicostatus* (PETRASCHECK, 1902) and *S. (J.)* cf. *binicostatus*. The CM Collection also contains numerous representatives of PETRASCHECK’s taxon found in the T V zone of the Guadarrama Area. The JW Collection keeps specimens of *S. (J.) combesi* (SORNAY, 1951) and *S. (J.)* cf. *combesi* that, according to WIEDMANN (1960, 1964, 1979), were collected from the T III to T V zones of the Outer Navarro-Cantabrian and Inner Castilian platforms. Nevertheless, SEGURA & WIEDMANN (1982) attributed SORNAY’s species to the T V zone, and considered it a characteristic taxon of this biostratigraphic unit.
Spathites (Ingridella) Wiedmann, 1960

In spite of S. (I.) cf. malladae (Fallot, 1931) is represented in the JW Collection by ammonites obtained from the T III to T V zones of the Inner Castilian Platform, S. (I.) malladae has not been identified by Wiedmann in biostratigraphic levels preceding to the T IV zone. In the same way, the AG and MH collections have specimens of S. (I.) malladae from the eponymous zone of the Guadarrama Area. Carretero-Moreno (1982) assigned three ammonites to S. (I.) malladae but only one has been found in her collection. Nevertheless, this specimen lacks umbilical tubercles and exhibits features that seem close to Vascoceras Choffat, 1898. The JW Collection holds two members of S. (I.) depressus (Wiedmann, 1960) from the T V zone of the La Demanda Area.

Spathites (Spathites) Kummel & Decker, 1954

In the JW Collection there are some specimens of S. (S.) laevis (Karrenberg, 1935) and S. (S.) cf. laevis collected from the T IV and T V zones as well as a specimen of S. (S.) sulcatus (Wiedmann, 1960) from the T V zone of the North-Ebro Area. The same collection also has an ammonite assigned by Wiedmann to S. (S.) chispaensis Kummel & Decker, 1954, coming from undetermined levels of the North-Ebro Area.

?Paramammites Furon, 1935

The JW, AG and CM collections keep some specimens of ?P. saenzi Wiedmann, 1960, from the stratigraphically lower part of the Choffaticeras (Choffaticeras) quaasi Zone of the La Demanda and Guadarrama areas. On the other hand, ?P. postsaenzi Wiedmann, 1960, is represented in the JW and MH collections by ammonites from the upper part of the Choffaticeras (Choffaticeras) quaasi Zone of the La Demanda and Guadarrama areas.

The JW Collection has some specimens classified by Wiedmann as ?P. tuberculatus Barber, 1957, and ?P. cf. tuberculatus, obtained from the T III and, mainly, T IV zones of the South-Ebro and La Demanda Areas; and as ?P. inflatus Barber, 1957, ?P. cf. inflatus, ?P. raricostatus Barber, 1957, and ?P. cf. raricostatus, from the T IV to T VI zones, recorded mainly of the South-Ebro Area and the Central Sector. Nonetheless, all these ammonites are closer to Spathites (Jeanrogericeras) Wiedmann, 1960, mainly to S. (J.) obliquus (Karrenberg, 1935), than to ?P. polymorphum (Pervinquiére, 1907), the type species of the genus ?Paramammites.

Mammites Laube & Bruder, 1887

The JW Collection holds numerous specimens of M. nodosoides (Schlüter, 1871), assigned to the typical, afra, armata and spinosa varieties, and of M. cf. nodosoides, obtained from the T IV and, mainly, T V zones of the Inner Castilian Platform. Likewise, the CM Collection contains members of M. nodosoides from the T V zone of the Guadarrama Area. In the JW Collection there are some ammonites assigned by Wiedmann to M. vielbanci (d'Orbigny, 1850) and M. cf. vielbanci found in the T V zone of the North-Castilian Sector. This taxon and, therefore, these specimens were included by Kennedy et al. (1980a) and Santamaría-Zabala (1991, 1995), among others, in the collignoniceratid species Lecointriceras fleuriussianum (d'Orbigny, 1841). Finally, the Lower Turonian specimen of the CM Collection from the Guadarrama Area attributed by Carretero-Moreno (1982) to M. incertus Douvillé, 1928, shows all the morphological features of Spathites (Jeanrogericeras) subconciliatus (Choffat, 1898).

Kamerunoceras Reyment, 1954

The JW Collection includes a specimen of K. ganuzai (Wiedmann, 1960) from the T IV zone of the Outer Navarro-Cantabrian Platform. This collection also keeps a member of K. inaequicostatus (Wiedmann, 1960) found in the T VI zone of the North-Ebro Area. The CM Collection has two representatives of this species from undetermined Lower Turonian levels of the Guadarrama Area.
New Data for the Acanthoceratidae of the Iberian Trough

This section presents a systematic description of new records of the family Acanthoceratidae from the Iberian Trough, obtained during field work carried out by the author. It also describes previously unpublished members of the group identified in the AG and MH collections.

Conventions

The terminology used to describe the different specimens of this study is based on a glossary of morphological terms applicable to post-Triassic nautiloids and ammonoids, which has been recently completed by Barroso-Barcenilla (2006) and will be published in due time.

Measurements were made with an adjustable caliper, and are given in tenths of millimetre and as percentages of the diameter of the shell. The dimensions used in the analysis are defined as follows: Diameter of the shell (D), maximum distance between two diametrically opposite ventral extremes, measured perpendicularly to the coiling axis; Whorl height (H), maximum distance between the ventral extreme and the most distant point of the dorsal wall, taken parallelly to the plane of bilateral symmetry; Whorl breadth (B), maximum distance between both flanks, measured perpendicularly to the coiling axis (tubercles and ribs have not been taken into account); Umbilical width (U), maximum distance, taken perpendicularly to the coiling axis, separating two diametrically opposite umbilical margins of the same whorl.

To make clear certain taxonomic comments or to indicate the location of several type specimens, the following abbreviations are used throughout the text: BEG, Bureau of Economic Geology, Austin, United States; CS, Château de Saumur, Saumur, France; GPIT, lnstitut und Museum für Geologie und Paläontologie, Tübingen, Germany; HU, Humboldt Universität, Berlin, Germany; MNHN, Musée National d'Histoire Naturelle de Paris, Paris, France; OUM, Oxford University Museum of Natural History, Oxford, United Kingdom; SP, Université de la Sorbonne, Paris, France; SGP, Serviços Geológicos de Portugal, Lisboa, Portugal; UCM, Universidad Complutense de Madrid, Madrid, Spain.

All the specimens presented here are held in the Departamento de Paleontología of the UCM.

Systematic Palaeontology

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Acanthoceratidae de Grossouvre, 1894

[Nom. correct. Hyatt, 1900, p. 585, pro Acanthoceratidés de Grossouvre, 1894, p. 22]

Diagnosis: Members of this family are generally evolute, compressed to very depressed, with robust tubercles, at least umbilical and ventrolateral, and ribs. However, some of its genera can lack ornamentation in late ontogenetic stages. The group's dimorphism only manifests as a change in size. The suture lines are of intermediate complexity yet tends to simplify in later representatives of the family and in descendant groups.

Discussion: As indicated by WRight (1996), the group can be divided into the subfamilies Mantelliceratinae Hyatt, 1903, Acanthoceratinae de Grossouvre, 1894, Euomphaloceratinae Cooper, 1978, and Mammitinae Hyatt, 1900. The family seems to have arisen at the beginning of the Cenomanian as a consequence of the radiation of Lyelliceratidae Spother, 1921.

Distribution: Practically cosmopolitan, from the Lower Cenomanian to the Coniacian.

Subfamily Mammitinae Hyatt, 1900


Diagnosis: A group of ornamented, moderately to highly involute acanthoceratids. Inner whorls are trapezoidal in section, ribbing widely spaced, umbilical tubercles prominent, and inner and outer ventrolateral tubercles more feeble. The siphonal line can show a gentle ridge that quickly disappears during ontogeny. On the
outer whorls, ornamentation can gain in robustness or, on the contrary, it can weaken until it almost vanishes. The suture lines tend to become simpler.

Discussion: HYATT (1900) established the family Mammitidae, including it in his new superfamily Mammitida. Soon after, this author (1903) described the families Buchiceratidae and Metoicoceratidae assigning them, respectively, to the Mammitida and to his new superfamily Mantellicerida. Later on, WRIGHT & WRIGHT (1951) incorporated these two families within the Acanthoceratidae de Grossouvre, 1894, as subfamilies. WIEDMANN (1960, 1964) established the genus Fallotites within his new subfamily Fallotitinae. A few years later, RENZ & ÁlvAREZ (1979) described the genus Mitonia and indicated that to include this group would require recognizing a new subfamily, called Mitoniainae.

I think that the similar appearance of the initial whorls of representatives of Mammitinae and Metoicoceratinae often makes them indistinguishable and justifies, as proposed by KENNEDY et al. (1980b), the integration of the second group in the synonymy of the first one. On the other hand, Fallotites seems to be a mere synonym of Spathites (Jeanragericeras) WIEDMANN, 1960, as explained below, while the morphology and the ornamentation of the small ammonites ascribed to Mitonia fully coincide with those typical of Mammitinae. Thus, a separate subfamily does not seem warranted for them.


Although there is general consensus that the phylogenetic origin of the subfamily can be found in the Acanthoceratinae, it is still not clear which taxon gave rise to the Mammitinae. According to WRIGHT (1996), the group arose from the subgenus Dunveganoceras (Plesiacinthoceras) HAAS, 1964, an evolutionary origin which was implicitly indicated in the study of COBBA & KENNEDY (1991), while COOPER (1998) stated that the subfamily derived from the genus Acanthoceras NEUMAYR, 1875.

Genus Spathites KUmmel & DeCKER, 1954, p. 310

Type species: Spathites chispaensis KUmmel & Decker, 1954, by original designation, synonym of Pseudotissotia coahuilaensis JONES, 1938.

Diagnosis: The members of this group are of intermediate size and have involute to slightly evolute coiling, trapezoidal to subquadrate whorl section, flat or rounded venter and thick umbilical tubercles. From each tubercle, arise one to three ribs that are rounded, radial, low, relatively weak and often separated by shorter intercalated ribs that end on the ventrolateral tubercles. During growth, ornamentation diminishes considerably and may be totally absent in the adult stage. When preserved, the umbilical tubercles usually extend in the coiling direction, and the whorl section becomes rounded. The suture lines are simple and highly variable, and their saddles are large and their first lateral lobes are asymmetrical, bifid and slightly shorter than their ventral lobes. In some species, the suture adopts a pseudoceratitic appearance.

Discussion: KENNEDY et al. (1980b), along with several subsequent authors including WRIGHT & KENNEDY (1990), maintained that this group can be divided into the three subgenera: Spathites (Jeanragericeras) WIEDMANN, 1960, which is the most primitive one; S. (Ingridella) WIEDMANN, 1960, which shows some homomorphism with Vasoceras CHOFFAT, 1898; and S. (Spahites) KUmmel & Decker, 1954, which includes species with the typical features of the genus. On the contrary, COOPER (1998) preferred to raise these three groups to the generic level. In my opinion, their phylogenetic proximity, demonstrated by KENNEDY et al. (1980b) among others, justifies retaining S. (Jeanragericeras), S. (Ingridella) and S. (Spahites) as mere subgenera of Spathites.

As their main differential characters, it can be mentioned that S. (Jeanragericeras) preserves its ornamentation in the adult state, as opposed to S. (Spahites). On the other hand, S. (Ingridella) loses its ornamentation early on
with the exception of its robust and characteristic umbilical tubercles, which in many specimens are preserved in the adult living chamber.

As indicated by Kennedy et al. (1980b) and Berthou et al. (1985), the genus seems to have evolved from Metoicoceras. Although with some exceptions, along the phylogenetic line linking Metoicoceras, S. (Jeanrogericeras) and S. (Spathites), it can be observed a trend towards more globose and involute forms, generally giving rise to species with wider whorl sections and smaller umbilici, presumably adapted to shallower environments.

**Distribution:** Specimens of the group have been identified in the UK, France, Spain, Portugal, southern Germany, former Czechoslovakia, Romania, North Africa, Tadzhikistan, southern India, the USA, and northern Mexico, from the top of the upper Cenomanian to the upper Turonian.

**Subgenus Spathites (Jeanrogericeras) Wiedmann, 1960, p. 740**

*Fallotites* Wiedmann, 1960, p. 741, type species by original designation Vascoceras subconciliatum Choffat, 1898, p. 64.

**Type species:** Ammonites reveliereanus Courtillier, 1860, by original designation.

**Diagnosis:** Small to medium sized taxonomic group without siphonal tubercles, and with depressed subrectangular or suboval whorl section and typical of the genus suture lines. Throughout ontogeny, ribs become relatively distant and the whorl section rounds.

**Discussion:** Wiedmann (1960, 1964) erected the genus Fallotites, including it in his new subfamily Fallottitinae, which was incorporated in the family Vascoceratidae Douville, 1912. However, Kennedy et al. (1980b) disputed this taxonomic proposal. These authors admitted that, owing to the adult living chamber essentially without ornamentation and the involute coiling of Wiedmann’s group, it maintains a certain morphological similarity to the vascoceratids. Nevertheless, on the basis of the umbilical and ventrolateral tubercles lengthened in the direction of the ribs, the interruption of the ribs at the siphonal line, and the subtrapezoidal section with flat or slightly convex flanks and venter, they recommended referring Fallotites to Spathites (Jeanrogericeras) Wiedmann, 1960, a subgenus assigned to the subfamily Mammitinae Hyatt, 1900. I think that these arguments provided by Kennedy et al. (1980b) support the idea that Fallotites is a subjective synonym of S. (Jeanrogericeras). This view is accepted by almost all current authors.

The subgenus has historically included several highly variable and similar taxa, especially in juvenile stages, whose complex systematic relationships have not been fully resolved. Among these, I could mention Vascoceras subconciliatum Choffat, 1898, characterized by a rounded section and a globose appearance; Fallotites (Fallotites) robustus Wiedmann, 1960, practically without ribs and with a more rounded whorl section and conical umbilical tubercles; Mammites subconciliatum var. obliqua Karrenberg, 1935, which, during ontogeny, undergoes a marked increase in ornamentation and, in adult stage, shows a conspicuous coronate contour; Ammonites reveliereanus Courtillier, 1860, which has a characteristic compressed trapezoidal whorl which is broadest close to the umbilici; Mammites binicostatus Petrascheck, 1902, without intercalated ribs and with narrower, more concave ventral region and wider umbilici than the previous taxon; and Ammonites combesi Sornay, 1951, a poorly known form that could be a synonym of one of the preceding taxa. However, in the last years it has been suggested that M. binicostatus, and F. (F.) robustus and M. subconciliatum var. obliqua could be synonyms, respectively, of A. reveliereanus, and of V. subconciliatum. Similarly, Szász (1986) and Summesberger (1992) assigned to the group their respective new species S. (J.) toroiagenensis and S. (J.) pachycostatus, while Kennedy (1994) proposed the inclusion of the rare taxon Vascoceras tavense Faraud, 1940, in S. (Jeanrogericeras).

The subgenus displays an intermediate morphology between those of Metoicoceras Hyatt, 1903, and the characteristic of Spathites Kummel & Decker, 1954. Its ornamentation resembles that of Metoicoceras during the first ontogenetic stages, but becomes markedly different to the same during the last ones. Nevertheless, S. (Jeanrogericeras) preserves its ribs and its tubercles on the outer whorls, whilst S. (Spathites) does not.

**Distribution:** The subgenus has been cited from the top of the upper Cenomanian to the middle Turonian of eastern Europe, Romania, North Africa, Tadzhikistan and southern India.

According to Kennedy et al. (1980b), the subgenus appears to have arisen from Metoicoceras by increasing of the relative whorl width and the degree of involution, and by slight modifications in the suture line.
Spathites (Jeanrogericeras) tavense (FARAUD, 1940)

Plate 1, Figs. A-B

1934 Vascoceras cf. amiereensis CHOUFFAT – FARAUD, p. 9, fig. 7.
1940 Vascoceras tavense FARAUD, p. 43 (6), pl. 1, fig. 1; pl. 5, fig. 1; pl. 8, fig. 2.
1969 Paravascoceras tavense (FARAUD) – FREUND & RAAB, p. 23, pl. 2, fig. 9; text-figs. 5 e-g (? = V. cauvini).
1985 “Vascoceras” tavense FARAUD – BERTHOU et al., p. 69, pl. 3, figs. 11–12.
1994 Spathites (Jeanrogericeras) tavense (FARAUD) – KENNEDY, p. 259, pl. 4, figs. 1–3; pl. 5, figs. 1–6; pl. 7, fig. 5.
2005 Spathites (Jeanrogericeras) tavense (FARAUD) – MEISTER & ABDALLAH, p. 132, pl. 12, fig. 2; text-fig. 21.

Type: By monotypy the holotype is the original specimen of FARAUD (1940), from the Lower Turonian of Bernon, France.

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<td>873</td>
<td>426 (49)</td>
<td>362 (41)</td>
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Description: Involute and compressed ammonite, with a subrectangular to suboval whorl section that reaches its greatest breadth close to the middle part of the flanks. Its venter, from subtabulate to concave, is limited by approximately twenty-five outer ventrolateral tubercles per whorl, which are marked and elongated in the direction of growth. It also bears several faint inner ventrolateral tubercles that quickly disappear. Its flanks are flat or slightly convex and end in abrupt umbilical shoulders joined to low vertical walls. Apart from the ventrolateral tubercles, its ornamentation includes weak rectiradiate ribs and almost unappreciable umbilical tubercles. Throughout ontogeny, the whorl section increases in relative width and the ornamentation diffuses, such that the body chamber becomes almost smooth showing only a gentle ventral groove. The suture lines are relatively complex.

Discussion: Based on the suture lines of his specimen, FARAUD (1940) assigned his new species to the genus Vascoceras CHOUFFAT, 1898. Years later, however, FREUND & RAAB (1969, ps. 23–24) highlighted the flaws in the original description of Vascoceras tavense, proposing it as a nomen dubium, and assigned FARAUD’s taxon to the group Paravascoceras FURON, 1935. BERTHOU et al. (1985) provided the first photographs of the holotype, which up until then had only been known through drawings, revealing the great similarity of its ventral region to that of Spathites (Jeanrogericeras) WIEDMANN, 1960. These authors referred the specimens of FREUND & RAAB to Vascoceras cauvini CHUDEAU, 1909. Finally, KENNEDY (1994) refigured FARAUD’s original specimen and examined new examples with inner and outer ventrolateral tubercles, assigning this species to WIEDMANN’s subgenus, as did MEISTER & ABDALLAH (2005). The new species presented here also shows remains of inner ventrolateral tubercles, and suture lines that, although faint since it corresponds to a slightly worn marl mould, resemble the typicals of Spathites (Jeanrogericeras) reveliereanus (COURTILLER, 1860). I have therefore included the species in S. (Jeanrogericeras).

The representatives of this taxon show a clear resemblance to the most compressed specimens of S. (J.) reveliereanus. However, members of S. (J.) tavense show more involute coiling and narrower umbilici, and early on during ontogeny they lose their ornamentation. These characteristics allow to separate the two species. Also of note is the morphological similarity of S. (J.) tavense to the subspecies Pseudotissotia (Bauchioceras) nigeriensis bicarinata BARBER, 1957, although their suture lines substantially differ since they are characteristic of different families.

With respect to the phylogeny of FARAUD’s species, it can be mentioned its considerable resemblance to certain forms of Metoicoceras HYATT, 1903, the genus from which Spathites KUMMEL & DECKER, 1954, seems to be derived, and to S. (J.) reveliereanus. This is especially true for the holotype of Metoicoceras stoliczkai SASTRY & MATSUMOTO, 1967, a taxon considered initially by KENNEDY et al. (1981) as a mere synonym of COURTILLER’S species. In general, S. (J.) tavense is one of the least ornate, most compressed, and with most sutural complexity species of the genus, which in my opinion would seem to indicate its adaptation to relatively open and deep ocean waters. Hence, as already mentioned, it is morphologically similar to Metoicoceras and S. (J.) reveliereanus, and occupies a temporal position between these two taxa. These findings prompt the hypothesis that it is a conservative form of S. (Jeanrogericeras) that directly descended from Metoicoceras and developed in a setting of relatively high bathymetry, which, as the result of an adaptation process to shallower waters, with time gave rise to somewhat more ornate and depressed morphologies attributable to S. (J.) reveliereanus. This evolutionary
development would be similar to that experienced by *Spathites (Jeanrogericeras) subconciliatus* (Choffat, 1898), in that its first representatives are compressed and discretely ornate and show characteristics close to those of the genus *Metaioceras*, from which they arose, while its more evolved forms are more ornate, have wider shells and show high morphological variability.

**Distribution**: Prior to the present study, the species had only been obtained from the Lower Turonian of France and Tunisia. Specimen CB-R-546 is the first reported from Spain and has been collected from the *Choffaticeras (Choffaticeras) quaasi* Zone of Condemios, in the Guadarrama Sector of the Iberian Trough.

*Spathites (Jeanrogericeras) saenzi* (Wiedmann, 1960)

Plate 1, Figs. C–H; Plate 2, Figs. A–E; Text-fig. 5 A

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<td>670</td>
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Description: Specimens with usually broader than high whorl section, flattened or mildly concave venter and six or more very marked conical umbilical tubercles per coil. From each tubercle, three fairly marked ribs emerge, which become slightly prorsiradiate on the flanks. Towards the middle part of the flanks, up to two accessory ribs may be intercalated between each pair of main ribs. The last whorl in mature specimens bears around twenty-two ribs. Each one of the ribs presents a rounded inner ventrolateral tubercle per flank, positioned a third of the distance from the ventral region, and another prolonged outer tubercle, located not far from the siphonal line. Sutures have two massive lobes on the flank and a shorter one on the umbilical wall. They also exhibit a wide umbilical saddle.

Discussion: WIEDMANN (1960, 1964), with some doubt, assigned his new species to the genus ?Paramammites Furon, 1935, on the basis of a set of adult characteristics that he considered proper to this taxonomic group. Notwithstanding, he observed that the inner whorls were similar to those of the representatives of his new genus Fallotites, and suggested that ?Paramammites saenzi was derived from these. In addition, he considered that the ammonite classified as Ammonites inconstans Schlüter, 1871, by Mallada (1891, 1892), obtained from the same locality as the holotype of ?P. saenzi, was a possible synonym of this taxon. In France, Thomel (1969) described the subspecies cassissianum to include globose specimens with approximately ten umbilical tubercles per whorl, maintaining Wiedmann's taxon within Furon's group. This generic assignment was also the one taken by Chancellor (1982) in his discussion of ?Paramammites mohovanensis (Böse, 1920) when referring to ?P. saenzi and to ?Paramammites postsaenzi Wiedmann, 1960. However, the correct generic assignment of these two species was again placed in doubt by Chancellor et al. (1994) who, as Wiedmann (1960, 1964) did indirectly, found that they showed certain similarities to several members of Spathites Kummel & Decker, 1954.

During this investigation, I have obtained new specimens of S. (J.) saenzi and I have noted that the number of umbilical tubercles can increase during ontogeny to more than the six per whorl shown by the holotype. Furthermore, I have observed that the inner whorls of its representatives show all the typical features of Spathites (Jeanrogericeras) Wiedmann, 1960, and thus this species has been ascribed to this subgenus. The specimen of A. inconstans described by Mallada (1891, 1892) displays the ventral region and whorl section of S. (J.) saenzi, and the umbilical width and prorsiradiate ribs of S. (J.) postsaenzi. Although its morphology seems to be closer to that of the first of these two species, it may be interpreted as a transitional specimen.

With regard to possible misinterpretations, S. (J.) saenzi differs in the juvenile ornamentation and in some aspects of the adult one, and in that its suture lines bear an additional lobe on the flanks than that of ?Paramammites polymorphum (Pervinquiére, 1907). As observed by Chancellor (1982), S. (J.) saenzi possesses larger living chamber and broader umbilici than ?P. mohovanensis. However, it is very similar to Spathites (Jeanrogericeras) subconciliatus (Chooffat, 1898), a species from which it may be distinguished on the basis of its more robust ornamentation and its less rounded whorl section.

Phylogenetically, its morphological resemblance to S. (J.) subconciliatus and its stratigraphical distribution seem to indicate that Chooffat's species gave rise to S. (J.) saenzi through certain modifications in whorl section and ornamentation.

Distribution: Lower Turonian of Spain and France. In the Iberian Trough it has been identified in the lower part of the Choffaticeras (Choffaticeras) quaasi Zone of the Central Sector. The oldest S. (J.) saenzi specimens have been obtained very close to the base of this biostratigraphic unit, in which the Cenomanian-Turonian boundary has been established.

Spathites (Jeanrogericeras) postsaenzi (Wiedmann, 1960)

Plate 3, Figs. A–F

1960 ?Paramammites postsaenzi Wiedmann, p. 754, pl. 5, figs. 7–8.

Type: The holotype is specimen CE 1162/3 of the JW Collection of the GPIT, figured by Wiedmann (1960, pl. 5, figs. 7–8) and obtained from the Choffaticeras (Choffaticeras) quaasi Zone of Picofrentes, Spain.
**Material and dimensions:**

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<td>~ 300 (48)</td>
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<td>1258</td>
<td>530 (42)</td>
<td>545 (43)</td>
<td>367 (29)</td>
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</table>

**Description:** Specimens mainly depressed with strongly concave venter and broad umbilici. From the umbilical shoulders some ten umbilical tubercles per whorl arise, each of which giving rise to two markedly prorsiradiate primary ribs, coinciding on the ventrolateral margin with oblique tubercles and disappearing as they approach the ventral region. However, on the inner whorls, the ribs may bifurcate or even trifurcate such that a considerable number of secondary ribs arise, which rarely are intercalated. Ornamentation in general tends to weaken throughout ontogeny. Sutures resemble those of *Spathites (Jeanrogericeras) saenzi* Wiedmann, 1960.

**Discussion:** When Wiedmann described the species (1960, 1964) he assigned it, with some doubts, to ?*Paramammites* Furon, 1935. Years later, Chancellor (1982) retained it in the same group, indicating a certain similarity between his ammonites and specimen 20826 of the BEG, collected by Kummel & Decker (1954) and classified by him as a probable ?*Paramammites mohovanensis* (Böse, 1920). However, as recognised by Chancellor (1982), Kummel & Decker’s ammonite is smaller and lacks the characteristic ventral concavity of *Spathites (Jeanrogericeras) postsaenzi* Wiedmann, 1960.

In my opinion, this poorly known species has certain peculiarities that make it difficult to ascribe it to a particular genus. Its morphological features are closer to *S. (J.) reveliereanus* than to ?*P. polymorphum*. Furthermore, *S. (J.) saenzi* and *S. (J.) pachycostatus* Summesberger, 1992, from which I examined a cast of the holotype at the OUM, seem to be the closest forms. Hence, I have found it more appropriate to ascribe *S. (J.) postsaenzi* to the subgenus *Spathites (Jeanrogericeras)* Wiedmann, 1960.

*S. (J.) saenzi* and *S. (J.) pachycostatus* can be distinguished from *S. (J.) postsaenzi* by their considerably wider umbilici, intensely projected ribs, and larger number of umbilical tubercles per whorl.

The above mentioned morphological proximity between *S. (J.) saenzi* and *S. (J.) postsaenzi* and their respective stratigraphical distributions appear to indicate a phylogenetic relationship, as indicated by Thomel (1969), and that the former may have given rise to the latter. In this regard, the *Ammonites inconstans* Schlüter, 1871, of Mallada (1891, 1892), refigured here (Text-fig. 4), is especially revealing, as its morphological characteristics are intermediate to those of Wiedmann’s two taxa.

**Distribution:** The species *S. (J.) postsaenzi* has only been identified in the Lower Turonian of Spain, since has only been found in the upper part of the *Choffaticeras (Choffaticeras) quaasi* Zone of the Central Sector of the Iberian Trough.

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**Text-fig. 5. Suture lines. A, Spathites (Jeanrogericeras) saenzi (Wiedmann, 1960), TA-S-118, from the Choffaticeras (Choffaticeras) quaasi Zone of Tamajón. B, Spathites (Jeanrogericeras) obliquus (Karrenberg, 1935), PU-S-310, from the Mammites nodosoides Zone of Puentedey. Both are × 3/2.**
Spathites (Jeanrogericeras) obliquus (Karrenberg, 1935)

Plate 4, Figs. A–F; Text-fig. 5 B

Description: Involute ammonites with very depressed section, which whorl width can double whorl height, and narrow and deep umbilici with subvertical walls and rounded shoulders. The contour of the specimens adopts a coronate appearance. The ornamentation of the inner involutions consists of several robust, conical and prominent tubercles located on the umbilical shoulder, where the whorls reach their greatest breadth. From the umbilical tubercles pairs of wide, straight, elevated and prorsiradiate to rursiradiate ribs arise, each one bearing two slightly elongated and relatively widely spaced ventrolateral tubercles. Throughout ontogeny, ribbing becomes more prominent, increasing in density as intercalated ribs emerge, and the distance separating the inner from the outer ventrolateral tubercles increases. Each last whorl may have up to twenty-two ribs and between seven and eight umbilical tubercles.

Discussion: In their revision of the Portuguese specimens described and assigned by Chouffat (1898) to his new genus Vascoceras, Berthou et al. (1985) considered that this species, like S. (J.) robustus (Wiedmann, 1960), could be a mere synonym of S. (J.) subconciliatus (Chouffat, 1898). However, they admitted that they had not yet examined the types from Spain. Notwithstanding, Santamaría-Zabala (1991, 1995) emphasized that the very depressed whorls with characteristic coronate sections, the robust umbilical tubercles throughout ontogeny and the wide separation of the inner ventrolateral tubercles, considerably greater than in the remaining close species of Spathites (Jeanrogericeras) Wiedmann, 1960, facilitate their differentiation and supports the validity of the species.

S. (J.) obliquus and S. (J.) subconciliatus are without doubt two close taxa, as indicated by the marked similarity of their initial whorls. This means that juvenile representatives of both species are difficult to distinguish, and implies the existence of several doubtful specimens, among which I find the neotype of Mammites subconciliatum proposed by Karrenberg (1935) which, despite having been originally assigned to Chouffat's species, has a subsemicircular, depressed and ornate whorl section that seems very close to that of S. (J.) obliquus, as noted by Wiedmann (1960, 1964). Nevertheless, during ontogeny, the morphologies of both species gradually differentiate and adult forms are easily discernable, as argued by Santamaría-Zabala (1991, 1995).
During the present investigation, I have also observed that *S. (J.) obliquus* shows a higher stratigraphical distribution than *S. (J.) subconciliatus*, and thus I have opted for maintaining the separation of the two species.

The above presented data seem to suggest that *S. (J.) obliquus* arose from *S. (J.) subconciliatus* by a pronounced increasing in the depression of the whorl section and the robustness of the ornamentation.

Specimen CB-R-23 exhibits an appearance relatively close to *Paramammites polymorphum* (PERVINQUIÈRE, 1907). Nevertheless, this ammonite has a notably involute and depressed whorl, with semicircular section, and a reduction of the originally strong tubercles and ribs.

Distribution: The species seems to be exclusive to the Lower Turonian of Spain. During the present study, I have only identified it with relatively feeble ornamentation by erosional reduction of the originally strong tubercles and ribs.

*Spathites (Jeanrogericeras) reveliereanus* (COURTILLER, 1860)

Plate 4, Fig. G; Plate 5, Figs. A–D; Text-figs. 6 A–B

1860 *Ammonites reveliereanus / reveliereanus* COURTILLER, p. 249, pl. 2, figs. 5–8.
1935 *Mammites revelierei* (COURTILLER) – FARAUD, p. 18, fig. 3.
1935 *Mammites revelierei* (COURTILLER) – KARRENBERG, p. 131, pl. 30, figs. 2–4; pl. 33, figs. 2–3; text-fig. 2 [included the quadrata, globosa and lata varieties].
1950 *Mammites reveliereanus* (COURTILLER) var. *globosa* KARRENBERG – BATALLER, p. 104 [included an un-numbered figure].

1960 *Jeanrogericeras binicostatum* (PETRASCHECK) – WIEDMANN, p. 741, pl. 2, figs. 7–9; text-fig. 5.
1964 *Jeanrogericeras binicostatum* (PETRASCHECK) – WIEDMANN, p. 126, figs. 10 a–c, 11.
1975c *Jeanrogericeras cf. binicostatum* (PETRASCHECK) – WIEDMANN & KAUFFMAN, pl. 9, fig. 1.
1979 *Jeanrogericeras cf. binicostatum* (PETRASCHECK) – WIEDMANN, pl. 9, fig. 1.

1979 *Jeanrogericeras reveliereanus* (COURTILLER) – WIEDMANN, ps. 189, 193.
1980b *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – KENNEDY et al., p. 826, pl. 105, figs. 1–12; pl. 106, figs. 1–2; text-figs. 3–6 [with additional synonymy].
1981 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – WRIGHT & KENNEDY, text-fig. 22.
1982 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – ROBASZYNISKI et al., pl. 3, figs. 1 a–b.
1984 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – MELÉNDEZ-HEVIA, p. 75, pl. 21, fig. 3 a–b.
1984 *Spathites (Jeanrogericeras) sp.* MELÉNDEZ-HEVIA, p. 79, pl. 20, figs. 1 a–b.
1985 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – AMÉDRO & HANCOCK, figs. 8 a–b.
1986 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – SÁSZ, p. 124, pl. 5, figs. 1–2; pl. 7, figs. 2–3.
1989 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – LAMOLDA et al., text-fig. 3, figs. 5 a–b.
1991 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – SANTAMARÍA-ZABALA, p. 135, pl. 7, fig. 4.

1992 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – THOMEL, p. 223, pl. 118, figs. 3–4; pl. 119, fig. 1.
1995 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – SANTAMARÍA-ZABALA, p. 41, pl. 3, fig. 2.
1996 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – WRIGHT, p. 173, text-figs. 132/2 a–c.
? 1996 *Spathites (Jeanrogericeras) aff. reveliereanus* (COURTILLER) – MEISTER & ABDALLAH, p. 10, pl. 14, fig. 2.
1997 *Spathites reveliereanus* (COURTILLER) – WISE, pl. 2, figs. 5–6.
1998 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – KÜCHLER, pl. 6, figs. 4 a–b, 6; pl. 10, fig. 5.

cf. 1998 *Spathites cf. reveliereanus* (COURTILLER) – KÜCHLER, pl. 9, fig. 7.
2001 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – CECCA, p. 219, figs. 3/1 a–b.
2004 *Spathites (Jeanrogericeras) reveliereanus* (COURTILLER) – BÁRROSO-BARCELONA, p. 100.
? 2005 *Spathites (Jeanrogericeras) gr. reveliereanus* (COURTILLER) – MEISTER & ABDALLAH, p. 130, pl. 9, figs. 1–2; text-fig. 19.
aff. 2005 *Spathites (Jeanrogericeras) aff. reveliereanus* (COURTILLER) – MEISTER & ABDALLAH, p. 133, pl. 10, figs. 1 a–d; text-fig. 23.
Type: The lectotype, designated by Kennedy et al. (1980b), is Courtiller's original (1860, pl. 2, figs. 5–6), refigured by Pervinquière (1903a, figs. 7 a–b), which was formerly preserved in the CS and whose present whereabouts are unknown.

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Description: Involute ammonites with an unusually high and compressed whorl section that is broadest close to the deep and narrow umbilici, which have subvertical walls and rounded shoulders. The inner half of the flanks appears gently convex, while their outer part becomes straight and converges towards the narrow and flat, or slightly concave, ventral region. Initial whorls show wide morphological variation. During ontogeny, whorl section become trapezoidal and slightly depressed, reaching its greatest breadth close to the conical and prominent umbilical tubercles. From each tubercle, up to seven pairs of prorsiradiate and not very robust ribs per whorl emerge. Commonly, intercalated ribs arise near the middle part of the flanks. Final whorls may have up to twenty-two ribs, each one bearing a feeble and conical inner ventrolateral tubercle and another somewhat more marked outer ventrolateral tubercle, elongated parallelly to the axis of growth, per flank. Their suture lines are not excessively complex, with external lobes bifid and asymmetrical.

Discussion: When first describing the species, Courtiller (1860) underscored its high morphological variation. Some years later, Peron (1896) accepted the nominal priority of Ammonites rochebrunnei Coquand, 1858, over Ammonites reveliereanus, which has not yet been confirmed owing to the disappearance of Coquand's types and to the fact that his original work was unillustrated. Within the ample morphological diversity of the species, Karrenberg (1935) distinguished four forms: the typical and those he denoted as the varieties quadrata, globosa and lata. Wiedmann (1960, 1964) attributed A. reveliereanus to his new group Jeanrogericeras and emphasized that Mammites binicostatus Petrascheck, 1902, could be distinguished from Courtiller's species on the basis of its lack of intercalated ribs, its narrower and more concave ventral region, its greater umbilical width and, mainly, on the basis of its eight, rather than four, umbilical tubercles per whorl. In a subsequent revision of the genus Spathites Kummel & Decker, 1954, Kennedy et al. (1980b), based on a detailed analysis of the characteristics of A. reveliereanus, ascribed it to S. (Jeanrogericeras), underscoring its broad morphological diversity. These authors also briefly compared the species with other taxa of this genus, and observed the presence of seven, or even eight, umbilical tubercles per whorl in some of the smallest specimens of S. (J.) reveliereanus, and thus had insufficient grounds to maintain the specific separation of M. binicostatus. In addition, they interpreted Metoicoceras stoliczkai Sastry & Matsumoto, 1967, closely resembling the lectotype of Petrascheck's taxon, as a synonym of Courtiller's species. Later on, several authors followed the synonymy of Kennedy et al. (1980b).

In the material presented herein, two forms can be discerned corresponding to A. reveliereanus and M. binicostatus, respectively, collected from the same Lower Turonian levels, such that it has been unable to establish any geographical or stratigraphical differences between them. However, no intermediate forms have been found so far that I have decided to consider Petrascheck's taxon as a synonym of Courtiller's one, recognizing within this taxon the morphotypes reveliereanus (Plate 5, Figs. C–D; Text-fig. 6 B) and binicostatum (Plate 4, Fig. G; Plate 5, Figs. A–B; Text-fig. 6 A). It should not be, however, ruled out the possibility that the two morphotypes are sexual dimorphs, an idea that was indirectly suggested by Courtiller (1860). Although with a less rounded whorl section, the holotype of M. stoliczkai is practically indistinguishable from the original specimens of Petrascheck, and thus I have considered Sastry & Matsumoto's taxon a synonym of S. (J.) reveliereanus.
Specimens classified as *S. (f.) aff. reveliereanus* by Meiester & Abdallah (1996) and as *S. (f.) gr. reveliereanus* by Meiester & Abdallah (2005), which were illustrated as *gr. reveliereanus* and *cf. reveliereanus* by the latter authors, are variably close to Courtiller's type but it is very difficult to establish a precise systematic classification of these ammonites.

As mentioned above, the species seems to be phylogenetically very close to *Spathites (Ingridella) tavense* (Faraud, 1940), from which it probably arose.

**Distribution:** Lower and middle Turonian of France, Germany, Spain, southern India, Romania and, possibly, Tunisia. Kennedy et al. (1980b) pointed out that, in the French Touraine, the species occurs together with *Kamerunoceras turoniense* (d'Orbigny, 1850) and *Collignoniceras woolgari* (Mantell, 1822), while, in the rest of Europe, it may also be found in somewhat lower levels. In the present work *S. (f.) reveliereanus* has been identified in the *Spathites (Ingridella) malladae* and *Mammites nodosoides* zones, although it has also been cited in the underlying *Choffaticeras (Choffaticeras) quaasi* Zone and in middle Turonian levels of the Outer Navarro-Cantabrian and Inner Castilian platforms. Furthermore, some of the oldest records of the species have been obtained in this palaeogeographical region by Floquet (1991) in the *Mammites nodosoides* Zone of the Ebro Reservoir, and by Santamaria-Zabala (1991, 1992, 1995) together with representatives of *Choffaticeras (Choffaticeras) quaasi* (Peron, 1904) in Navarra. This extended vertical distribution decreases the biostratigraphic value of *S. (f.) reveliereanus*.

**Spathites (Jeanrogericeras) combesi** (Sornay, 1951)

Plate 5, Figs. E–F; Plate 6, Figs. A–B

1951 *Ammonites combesi* d'Orbigny in litt. – Sornay, p. 627, text-figs. 1 a–d.
1955 *Ammonites (Mammites) combesi* d'Orbigny in coll. – Sornay, fisch. 9, figs. 1–2.
1960 *Jeanrogericeras combesi* (Sornay) – Wiedmann, ps. 716, 721.
1979 *Jeanrogericeras combesi* (Sornay) – Wiedmann, p. 176.
1979 *Jeanrogericeras cf. combesi* (Sornay) – Wiedmann, p. 189.
1982 *Jeanrogericeras combesi* (Sornay) – Segura & Wiedmann, p. 296, pl. 1, figs. 7–8; pl. 2, fig. 1.
1994 *Spathites (Jeanrogericeras) combesi* (Sornay) – Kennedy, p. 258, pl. 1, figs. 1–6; pl. 3, figs. 1–4; pl. 4, figs. 4–6; pl. 6, figs. 1–3, 6–8; pl. 8, figs. 1–3.
2005 *Spathites (Jeanrogericeras) combesi* (Sornay) – Meiester & Abdallah, p. 132, pl. 11, figs. 2–3; text-fig. 22.

**Type:** The lectotype, designated by Sornay (1955), is original 6125 of the d'Orbigny Collection figured by Sornay (1951, figs. 1 a–d) and currently hosted at the MNHN, from the Lower Turonian of Fumel, France.

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**Description:** Depressed and evolute specimens with embracing whorls of subtrapezoidal or subreniform section that attain their greatest width close to the umbilical shoulders. Their strong ornamentation, with ribs and
umbilical and inner and outer ventrolateral tubercles, confer these ammonites a robust appearance. They have twenty to twenty-five ribs, and approximately six strong and conical umbilical tubercles per whorl. From each umbilical tubercle, about two straight and slightly prorsiradiate main ribs emerge, and, between these, secondary ribs often occur. Their ventral region and flanks are discretely arched, and the umbilici are deep. Suture lines have wide and rounded first lateral saddles.

Discussion: Kennedy (1994) noted a marked resemblance between the adult body chambers of Spathites (Jeanrogericeras) combesi (Sornay, 1951) and S. (Ingridella) malladae (Fallot, 1931). However, even in mature specimens, the robust, globose and ornate appearance of Sornay's species allows its easy distinction from that of Fallot, whose evolute shell is practically smooth. Greatest similarities are shared with S. (J.) subconciliatus (Choffat, 1898), S. (J.) robustus (Wiedmann, 1960) and S. (J.) obliquus (Karrenberg, 1935). The first of these is more evolute and somewhat less depressed, and shows shallower umbilici limited by fainter umbilical tubercles than S. (J.) combesi. On the other hand, Wiedmann's species shows a much weaker and scarce ornamentation, while that of Karrenberg develops notably more depressed whorls and longer umbilical tubercles. In addition, the stratigraphical distribution of S. (J.) combesi is appreciably higher than that of S. (J.) subconciliatus and S. (J.) robustus.

From the perspective of phylogeny, S. (J.) combesi seems to have arisen from S. (J.) reveliereanus by an increased relative width of the whorl and certain modifications to its ornamentation.

Distribution: To date, the species has only been identified in the Lower Turonian of France, Spain and Tunisia. Specimens from the Iberian Trough occur in the Wrightoceras munieri Subzone of the Outer Navarro-Cantabrian and Inner Castilian platforms.

Subgenus Spathites (Ingridella) Wiedmann, 1960, p. 749

Type species: Vascoceras malladae Fallot, 1931, by original designation.

Diagnosis: Evolute subgenus with regular coiling, in which the first whorls bear faintly marked ribs. It shows wide, rounded and very characteristic umbilical and small inner and outer ventrolateral tubercles, and subquadrate whorl section. Throughout ontogeny ornamentation disappears, with the only exception of the robust umbilical tubercles that may persist in the adult body chamber. The last whorl, entirely smooth and rounded, shows a certain resemblance to that of Vascoceras Choffat, 1898. The suture lines have two lobes on the flanks, second lateral saddles that are wide and ventral lobes higher than lateral lobes.

Discussion: When he described this group, Wiedmann (1960, 1964) considered it very close to his new genus Fallotites. Thus, he included Ingridella in Fallotites as a subgenus grouping the species Vascoceras malladae Fallot, 1931, with rounded and slightly depressed whorl section and wide umbilici of vertical walls, and Fallotites (Ingridella) depressus Wiedmann, 1960, with more discoid and depressed morphology and somewhat more simple suture lines. This author also indicated that the phylogenetic origin of Ingridella seemed to be found in the subgenus Fallotites (Fallotites) Wiedmann, 1960. Kennedy et al. (1980b) were in agreement with this possible evolutionary origin of Ingridella, yet ascribed the group to Spathtes Kummel & Decker, 1954, maintaining its subgenus category. Kennedy (1994) also found great similarity between the characteristic ornamentation of Wiedmann's subgenus and that of Spathites (Jeanrogericeras) combesi (Sornay, 1951). Nevertheless, Cooper (1998) preferred to consider Ingridella, along with Jeanrogericeras Wiedmann, 1960, and Spathites, as a differentiated genus. Although the final whorls of S. (Ingridella) resemble those of Vascoceras Choffat, 1898, its initial volutions, as indicated by Kennedy et al. (1980b), suggest that this group is a specialized subgenus of Spathites.

In differentiating S. (Ingridella) from the remaining members of Spathites, I could add the simplified trace of its suture, which is notably simpler than that of S. (Jeanrogericeras). However, if the morphology and distribution of specimens from the Iberian Trough are examined, it can be seen that representatives of S. (Jeanrogericeras) and S. (Ingridella) are highly similar during initial ontogenetic stages. Furthermore, S. (Jeanrogericeras) appeared earlier than S. (Ingridella), suggesting that the latter subgenus was derived from the former. This phylogenetic origin is consistent with that suggested by Wiedmann (1960, 1964), since F. (Fallotites) is currently accepted as a synonym of S. (Jeanrogericeras).

Distribution: To date, the subgenus has only been identified in the Lower Turonian of Spain and, possibly, France.
Spathites (Ingridella) malladae (FALLOT, 1931)
Plate 6, Figs. C–E; Plate 7, Figs. A–G; Plate 8, Figs. A–B; Text-fig. 7 A

1891 Ammonites peramplus MANTELL – MALLADA, pl. 7, figs. 1–2.
1892 Ammonites peramplus MANTELL – MALLADA, p. 184.
1931 Vascoceras malladae FALLOT, p. 216.
1950 Vascoceras malladae FALLOT – BATAILLER, p. 106 (included an un-numbered figure).

1960 Fallotites (Ingridella) malladae (FALLOT) – WIEDMANN, p. 749, pl. 6, figs. 1–6; text-fig. 9.
1975b Fallotites (Ingridella) malladae (FALLOT) – WIEDMANN, ps. 140, 143.

1979 Ingridella cf. malladae (FALLOT) – WIEDMANN, ps. 193, 205.
1984 Spathites (Ingridella) malladae (FALLOT) – MELÉNDEZ-HEVIA, p. 80, pl. 22, figs. 2 a–b, 3 a–c, 4 a–b.
1984 Spathites (Ingridella) cf. depressus (WIEDMANN) – MELÉNDEZ-HEVIA, p. 82, pl. 22, fig. 1.
1996 Spathites (Ingridella) malladae (FALLOT) – WRIGHT, p. 173, text-figs. 133/2 a–b.
1998 Spathites (Ingridella) malladae (FALLOT) – KÜCHLER, pl. 5, figs. 8 a–b.
1998 Ingridella malladae (FALLOT) – COOPER, fig. 2.
? 2001 Spathites (Ingridella) malladae (FALLOT) – JOLET et al., p. 228.
2004 Spathites (Ingridella) malladae (FALLOT) – BARROSO-BARCÉNILLA, p. 103, pl. 2, fig. 4.

Type: The lost original specimens of MALLADA (1891) were not adequately identified such that WIEDMANN (1960, p. 749, pl. 6, figs. 3–6; text-fig. 9) designated and figured as neotype an ammonite of the CHUDEAU Collection of the SP from the Spathites (Ingridella) malladae Zone of Picoferentes, Spain.

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Descriptive: Evolute specimens with subcircular and slightly wider than high whorl section. Inner whorls may have two sets of gentle ventrolateral tubercles that quickly disappear, and faint ribs that do not reach the venter. Their umbilici are extremely wide and have abrupt walls. Adult living chambers show about ten highly characteristic umbilical tubercles per whorl, which are wide and rounded. Their suture lines have fairly long umbilical saddles.

Discussion: The evolute coiling, gentle truncation of the venter and, in some juvenile specimens, the presence of small ventrolateral tubercles help to distinguish this species from the taxa proper to Vascoceras Choffat, 1898. Although Spathites (Ingridella) malladae (FALLOT, 1931) can show some degree of morphological variation, possible confusions with other representatives of Spathites KUMMEL & DECKER, 1954, can be avoided by noting the rapid disappearance of the ventrolateral tubercles, the more evolute coiling and the simplified suture lines.

From a phylogenetic viewpoint, the species seems to have arisen from poorly ornate representatives of S. (Jeanrogericeras) WIEDMANN, 1960. However, there are several species, such as S. (J.) subconciliatus (Choffat, 1898), S. (J.) robustus (Wiedmann, 1960) and S. (J.) saenzi (Wiedmann, 1960), whose stratigraphical distribution is immediately lower and whose morphology resembles, in a more or less evident manner, that of S. (J.) malladae. Because of this, it is very difficult to determine the taxon of the subgenus S. (Jeanrogericeras) that gave rise to FALLOT's species.

Distribution: The species is practically restricted to the Lower Turonian of Spain, since outside this country, S. (J.) malladae was only cited by JOLET et al. (2001, p. 228) from levels probably corresponding to the Mammites nodosoides Zone of Bédoue, southeast France. In the Iberian Trough, the FALLOT's species has been identified in the eponymous biostratigraphic zone of the Outer Navarro-Cantabrian and Inner Castilian platforms, although some possible records from the Mammites nodosoides Zone have been obtained.

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Text-fig. 7. Suture lines. A, Spathites (Ingridella) malladae (FALLOT, 1931), CA-R-605, from the Spathites (Ingridella) malladae Subzone of Condemios. B, Spathites (Ingridella) depressus (Wiedmann, 1960), CA-R-184, from an unknown level of Condemios. Both are × 3/2.
**Spathites (Ingridella) depressus** (Wiedmann, 1960)
Plate 8, Figs. C–D; Plate 9, Figs. A–G; Text-fig. 7 B

1960 *Fallotites (Ingridella) depressus* Wiedmann, p. 752, pl. 6, figs. 7–8; pl. 7, figs. 5–6.
1964 *Fallotites (Ingridella) depressus* Wiedmann – Wiedmann, p. 136, figs. 22 a–b, 23 a–b.
1975b *Fallotites (Ingridella) depressus* Wiedmann – Wiedmann, p. 140.
1984 *Spathites (Ingridella) cf. depressus* (Wiedmann) – Mélénède-Hévia, p. 82, pl. 22, fig. 1.

**Type**: The holotype is specimen CE 1162/10 of the JW Collection of the GPIT, obtained from the *Wrightoceras munieri* Subzone of Picofrentes, Spain, and originally figured by Wiedmann (1960, pl. 7, figs. 5–6). As paratype, this author designated specimen CE 1162/11 of the same collection and source.

**Material and dimensions**: D H (%) E (%) O (%)

<table>
<thead>
<tr>
<th>Specimen</th>
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<th>O (%)</th>
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<td>250 (34)</td>
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<td>358 (38)</td>
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<td>FT-R-717</td>
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<td>~ 275 (36)</td>
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<td>FT-R-729</td>
<td>762</td>
<td>~ 324 (43)</td>
<td>~ 318 (42)</td>
<td>~ 300 (39)</td>
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<td>FT-R-833</td>
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<td>FT-S-762</td>
<td>1202</td>
<td>387 (32)</td>
<td>~ 380 (32)</td>
<td>420 (35)</td>
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<td>TA-R-758</td>
<td>699</td>
<td>~ 275 (39)</td>
<td>~ 270 (39)</td>
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**Description**: Discoidal specimens that show slightly compressed whorl section and umbilical shoulders with about five, rounded and very characteristic tubercles per whorl. In juvenile stages, the ventral region is flat and the surface has wide gentle ribs that carry inner and outer ventrolateral tubercles. During ontogeny, the whorl section rounds and ventrolateral tubercles rapidly disappear. Suture lines are very simple.

**Discussion**: The species is clearly very close to *Spathites (Ingridella) malladae* (Fallot, 1931) from which, as pointed out by Wiedmann (1960, 1964) in his original description, it can be distinguished by its higher than wide whorl section, its proportionally narrower umbilicus and its only five umbilical tubercles per whorl. There are, however, some specimens with intermediate characteristics that are difficult to assign to one of these taxa.

By comparing the respective morphologies and distributions of *S. (I.) malladae* and *Spathites (Ingridella) depressus* (Wiedmann, 1960), it appears that the latter was originated from the former.

**Distribution**: *S. (I.) depressus* has been collected from Lower Turonian of Spain, specifically from the *Wrightoceras munieri* Subzone of the Central Sector of the Iberian Trough.

**Subgenus Spathites (Spathites)** Kummel & Decker, 1954, p. 310

[†*Amblydiscus* Adkins, 1933, p. 238, nom. nud. *Neoptychites (Spathitoides)* Wiedmann, 1960, p. 754, type species by original designation *Neoptychites (Spathitoides) sulcatus* Wiedmann, 1960.]

**Type species**: *Spathites chispaensis* Kummel & Decker, 1954, by original designation, synonym of ?*Pseudotissotia coahuilaensis* Jones, 1938.

**Diagnosis**: Group comprising species showing the most representative characters of the genus. Specimens exhibit a very involute morphology with a subquadrate or subtrapezoidal whorl section, a wide ventral region and an adult living chamber that almost invariably lacks ornamentation.

**Discussion**: Wiedmann (1960, 1964) proposed his new subgenus *Neoptychites (Spathitoides)* to group together specimens with smooth and highly involute shell, subtrapezoidal whorl section, narrow umbilici, and flat or convex ventral region. These features, along with the observations of Kennedy et al. (1980b), who indicated that the constrictions on the body chamber described by Wiedmann seemed simply to be the spaces separating
the ventrolateral tubercles, suggest N. (Spahtitoides) to be a mere synonym of *Spahtites* (Spahtites) Kummel & Decker, 1954. Furthermore, its high stratigraphical distribution and reduced size of the umbilici are in perfect agreement with the tendency to develop more involute forms observed in the phylogenetic line of *Spahtites*. Thus, as pointed out by Wright (1996), the slight differences shown by the body chamber and sutures of *N. (Spahtitoides)* do not seem sufficient to warrant its separation from the genus of Kummel & Decker.

With regard to its phylogeny, Kennedy et al. (1980b), Wright (1996) and Cooper (1998), among others, agreed that the group arose from *Spahtites (Jeanrogericeramus)* Wiedmann, 1960.

**Distribution:** From the top of the Lower to the upper Turonian of the USA, Mexico and Spain.

*Spahtites (Spahtites) laevis* (Karrenberg, 1935)

*Plate 10, Figs. A-B; Text-fig. 8 A*

1935 Mammites laevis Karrenberg, p. 137, pl. 30, figs. 9-9 a; pl. 33, fig. 8.
1950 Mammites laevis Karrenberg – Bataller, p. 103 [included an un-numbered figure].
1964 Spahtites laevis (Karrenberg) – Wiedmann, p. 115.
1979 Spahtites laevis (Karrenberg) – Wiedmann, p. 189.
1991 Spahtites (Spahtites) aff. sulcatus (Wiedmann) – Santamaria-Zabala, p. 131, pl. 7, fig. 5.
1995 Spahtites (Spahtites) aff. sulcatus (Wiedmann) – Santamaria-Zabala, p. 39, text-fig. 2 k.

**Type:** The holotype by monotypy is the original specimen of Karrenberg (1935), from the top of the Lower Turonian or the base of the middle Turonian of Soncillo, Spain.

**Material and dimensions:**

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<td>659 (51)</td>
<td>583 (45)</td>
<td>189 (15)</td>
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<td>CA-R-522</td>
<td>1204</td>
<td>609 (51)</td>
<td>500 (42)</td>
<td>138 (11)</td>
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<td>CA-R-537</td>
<td>1123</td>
<td>641 (57)</td>
<td>~ 497 (44)</td>
<td>190 (17)</td>
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</table>

**Description:** Intermediate sized and involute specimens with a subrectangular or subtrapezoidal compressed whorl section, whose maximum width occurs close to the umbilical margins. Their ventral region is tabulate or slightly convex, the flanks are flat and convergent or gently arched, and the umbilici are narrow and deeply incised with vertical walls and rounded shoulders. During initial ontogenetic stages, they exhibit faint ribs and inner and outer ventrolateral tubercles. Throughout ontogeny, ornamentation is quickly lost to generate a completely smooth adult body chamber. Suture lines are relatively simple, each one with three major elements, narrow and deep lobes, and wide and discretely bifid saddles.

**Discussion:** The early disappearance of the ribs and umbilical and inner and outer ventrolateral tubercles, the tabulate trend shown by the venter, the umbilici of reduced size and the simple suture lines approximate *Mammites laevis* Karrenberg, 1935, to the type of *Spahtites* (Spahtites) Kummel & Decker, 1954. It therefore seems that Karrenberg’s species should be assigned to the subgenus of Kummel & Decker.

*S. (S.) laevis* lacks the conspicuous concave venter that characterizes *Spahtites* (Spahtites) sulcatus (Wiedmann, 1960) and has less pronounced secondary sutural elements. The taxon also has less rounded appearance and more compressed whorls than the species of Wiedmann or than *Spahtites* (Spahtites) coahuilaensis (Jones, 1938). *Spahtites (Jeanrogericeramus) tavense* (Faraud, 1940) has relatively more rounded whorls that reach their maximum width close to the middle part of the flanks, wider umbilici and more complex suture lines. The morphology of some specimens of *S. (S.) laevis* is also vaguely similar to that of *Pseudotissotia nigeriensis* (Woods, 1911), but the former species shows a higher stratigraphical distribution and its suture lines have less major sutural elements.

Moreover, although Santamaria-Zabala (1991, 1995) only provided a lateral view and a suture line of his specimen, its dimensions and morphological characteristics are perfectly consistent with those of *S. (S.) laevis*.

**Distribution:** This rare species has only been identified in the upper part of the Lower Turonian and the base of the middle Turonian of Spain. Karrenberg (1935) attributed the holotype to his interval 4, which he named of *Mammites reveliereanus*. This historic and long-ranged biostratigraphic division of the North-Ebro Area is difficult to correlate with subsequent units, and probably corresponds to a large part of the Lower and middle Turonian. The same range includes the interval assigned by Wiedmann (1960, 1964, 1979) to this species.

Santamaría-Zabala (1991, 1995) obtained his specimen from undetermined levels in Soncillo, while those presented here have been collected from the Wrightoceras munieri Subzone of the North-Ebro and Guadarrama areas of the Iberian Trough.

*Spathites (Spathites) sulcatus* (Wiedmann, 1960)

*Plate I*0, Figs. C-H; Text-fig. 8 B

1960 Neoptychites (Spathitoides) sulcatus Wiedmann, p. 756, pl. 7, figs. 7–8; text-figs. 11–12.

1964 Neoptychites (Spathitoides) sulcatus Wiedmann – Wiedmann, p. 139, figs. 27 a–b, 28–29.

1978 Neoptychites (Spathitoides) sulcatus Wiedmann – Wiedmann & Kauffman, pl. 9, fig. 6.

1979 Neoptychites (Spathitoides) sulcatus Wiedmann – Wiedmann, pl. 9, fig. 6.

1980b Spathites (Spathites) sulcatus (Wiedmann) – Kennedy et al., text-figs. 2 a–c.

non aff. 1991 Spathites (Spathites) aff. sulcatus (Wiedmann) – Santamaría-Zabala, p. 131, pl. 7, fig. 5 (= S. (S.) laevis).

non aff. 1992 Spathites sulcatus (Wiedmann) – Thomel, p. 224, pl. 130, figs. 1–2.

non aff. 1995 Spathites (Spathites) aff. sulcatus (Wiedmann) – Santamaría-Zabala, p. 39, text-fig. 2 k (= S. (S.) laevis).

**Type:** The holotype is specimen CE 1162/4 of the JW Collection of the GPIT, figured by Wiedmann (1960, pl. 7, figs. 7–8; text-figs. 11–12), from the Wrightoceras munieri Subzone of Pedrosa, Spain.

**Material and dimensions:**

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<td>FT-R-743</td>
<td>602</td>
<td>318 (53)</td>
<td>371 (62)</td>
<td>117 (19)</td>
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**Description:** Involute small to medium sized specimens with subtrapezoidal whorl section, and convex and convergent flanks. Their ventral region is wide and slightly concave, and their umbilici are small with gently arched and practically vertical walls, and narrow and abrupt umbilical shoulders. Inner whorls show rounded umbilical tubercles from which smooth and widely distant sets of ribs arise, crossing the flanks, ventrolateral margins and venter. These ammonites also bear inner and outer ventrolateral tubercles, elongated along the axis of growth. During ontogeny, the flanks progressively arch, ventral region sinks and ornamentation is lost leaving some totally smooth outer whorls. The suture lines have narrow lobes and wide rounded saddles.

**Discussion:** Besides refiguring the holotype of *Spathites (Spathites) sulcatus* Wiedmann, 1960, Kennedy et al. (1980b) compared it to the type species of the genus, *S. (S.) coahuilaensis* (Jones, 1938), and came to the conclusion that the differences between the two specimens were scarce. Really, only the typical concavity of the venter and the subtrapezoidal section of the whorl of the species of Wiedmann enable its distinction from that of Jones. These small differences are perhaps insufficient to justify the specific status of *S. (S.) sulcatus*. Thus, I cannot rule out that *S. (S.) sulcatus* is only a European geographical variety of *S. (S.) coahuilaensis*. So far, however, only a few specimens of Wiedmann’s taxon have been identified and until further specimens can be compared with the holotype of *S. (S.) coahuilaensis*, I would prefer not to relegate *S. (S.) sulcatus* to the subspecific status. It should be noted that the specimen of *S. sulcatus* of Thomel (1992, pl. 130, figs. 1–2), besides a slightly compressed
whorl section, has a convex rather than concave ventral region, and therefore lacks the main differential character of this species.

**Distribution:** S. (S.) *sulcatus* has been identified in the Lower Turonian of Spain, specifically in the *Wrightoceras munieri* Subzone of the North-Ebro Area and Central Sector of the Iberian Trough.

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**Genus Mammites LAUBE & BRUDER, 1887, p. 229**

*Schluetericeras* HYATT, 1903, p. 110, type species by original designation *Ammonites nodosoides* SCHLÜTER, 1871.

Type species: *Ammonites nodosoides* SCHLÜTER, 1871, by monotypy, since the three species included in the genus by LAUBE & BRUDER (1887) seem to be synonymous.

**Diagnosis:** Involute group with a typically rectangular, subquadrate or subtrapezoidal whorl section, and a flattened or slightly concave venter, which in some specimens shows a small siphonal keel. Initial whorls are very similar to those of *Manitelliceras* HYATT, 1903, with strong but relatively distant inner and outer ventrolateral tubercles. During ontogeny, the number of tubercles diminishes, the inner and outer ventrolateral tubercles possibly fusing to form spines. The suture lines are moderately incised and similar to that of *Acanthoceras Neumayr, 1875*, and *Calycoceras* HYATT, 1900, being the first lobes narrower than the external saddles.

**Discussion:** Since the description of the genus at the end of the 19th century, most species of the Lower and middle Turonian with subrectangular whorl section and robust ventrolateral tubercles were traditionally assigned to *Mammites LAUBE & BRUDER, 1887*. However, especially during the second half of the 20th century, this simple interpretation of the group was placed in doubt, questioning the systematic position of some of its taxa. In 1965a, COLLIGNON argued that *Ammonites conciliatus* STOLICZKA, 1864, should be attributed to the genus *Pseudaspidoceras* HYATT, 1903, while authors such as MATSUMOTO (1978) and CHANCELLOR (1982), preferred to ascribe this species to *Mammites*. Furthermore, WRIGHT & KENNEDY (1981) claimed that many of the forms attributed until then to LAUBE & BRUDER’s genus, seemed to be synonyms of other forms or could be ascribed to different groups. Among the species morphologically closest to *Mammites nodosoides* (SCHLÜTER, 1871), these authors cited *M. mohovanensis* BÖSE, 1920, with dense ribs, and ventrolateral tubercles elongated in the direction of growth; *M. wingi* MORROW, 1935, with numerous ribs and ventrolateral tubercles projected in the direction perpendicular to the flanks; *M. dixeyi* REYMENT, 1955, and *M. mutabilis* REYMENT, 1955, both with relatively small shells which, according to WRIGHT & KENNEDY (1981), could be interpreted as dimorphs; and *M. depressus* POWELL, 1963, with its widely spaced ornamentation and relatively evolute coiling. Similarly, they indicated that the morphology of *Acanthoceras pseudonodosoides* CHOUFFAT, 1898, was reminiscent of that of *Mammites menabensis* COLLIGNON, 1939, and the aspect of *Mammites laevis* KARRENBERG, 1935, was similar to that of *Spaltites KUMMEL & DECKER, 1954*. CHANCELLOR (1982) affirmed that *Mammites* shows a greater degree of involution than *Pseudaspidoceras*. Furthermore, he added that P. BENGTSON had commented to him that the exaggerated development of the ventrolateral spines observed in some adult specimens of LAUBE & BRUDER’s genus does not occur in representatives of *Pseudaspidoceras*, except rarely in *P. vicentinii* COLLIGNON, 1966.

COBBAN & HOOK (1983) noted that some of the species mainly assigned to *Mammites* show initial ontogenetic stages lacking ornamentation and suture lines with very wide lateral lobes. To group these specimens, these authors proposed their new genus *Morrowites*, including in it the species *M. wingi*, whose characters are diagnostic of the group, *M. dixeyi* and *M. depressus*, among others. KENNEDY et al. (1987) assigned *A. pseudonodosoides* to the genus *Pseudaspidoceras*. Other authors, such as THOMELE (1992), considered that *M. mohovanensis* also shows the characteristics of *Morrowites*. Because of these interpretations, the large number of taxa originally assigned to the species described by LAUBE & BRUDER is currently very reduced.

Among the species included in the genus that could undoubtedly be ascribed to other groups, I find *A. pseudonodosoides*, from Portugal, and *Mammites laevis* KARRENBERG, 1935, from Spain, both poorly understood. After examining two specimens of the former preserved today in the SGP, I think it could be assigned to *Pseudaspidoceras*. The holotype by monotypy of the latter species shows small umbilici with vertical walls and ornamentation comprising small ventrolateral tubercles and smooth ribs that disappear early on during ontogeny and leave behind a completely smooth shell. These characteristics, as already pointed out, coincide fully with those of *S. (Spathites).*
The morphology of the genus is clearly very similar to that of *Metoioceras* Hyatt, 1903, and *Spathites*, from which it can be differentiated mainly by the more quadrate appearance of the whorl section and the increasing robustness of the tubercles during ontogeny. As already mentioned, *Mammites* can with relative ease be confused with some representatives of *Pseudaspidoceras*, despite the fact that the type species of both genera are easily distinguishable. The genus can also show a morphological similarity to *Lecointriceras* Kennedy et al., 1980a, but this Collignoniceratid has umbilical tubercles that persist throughout ontogeny, conferring it a subpentagonal section.

On the basis of the fact that the initial whorls of *Spathites* *(Jeannrogericeras)* Wiedmann, 1960, and *Mammites* are practically indistinguishable, Kennedy et al. (1980b) considered that the latter group arose from the former. This evolutionary relationship was confirmed by Wright (1996) and Cooper (1998), among others.

**Distribution:** Turonian of Europe, North and West Africa, Madagascar, Syria, Israel, Turkistan, southern India, the USA and South America.

*Mammites nodosoides* (Schlüter, 1871)

Plate 11, Figs. A–D

nom. nud. 1829 *Ammonites nodosoides* Schlotheim in von Buch, p. 424.

1871 *Ammonites nodosoides* Schlotheim, p. 19, pl. 8, figs. 1–4.

1902 *Mammites nodosoides* (Schlotheim) – Petrascheck, p. 142.

1902 *Mammites michelobensis* Laube & Bruder – Petrascheck, p. 142, pl. 8, figs. 2 a–b; pl. 9, figs. 2 a–b; pl. 10, fig. 1.

cf. 1935 *Mammites cf. nodosoides* (Schlotheim) – Karrenberg, p. 136, pl. 31, fig. 10; pl. 33, fig. 6.

1935 *Mammites nodosoides* (Schlotheim) var. *armata* Karrenberg, p. 136, pl. 30, fig. 8–8a; pl. 33, fig. 7.

1940 *Mammites nodosoides* (Schlotheim) var. *spinosa* Basse, p. 458, pl. 7, fig. 2; pl. 9, fig. 2.

? 1940 *Mammites tischeri* Laube & Bruder – Basse, p. 458, pl. 7, figs. 3 a–b.

1950 *Mammites nodosoides* (Schlotheim) var. *armata* Karrenberg – Bataller, p. 103 [included an un-numbered fig.].

cf. 1955 *Mammites cf. afer* Pervinquière – Reyment, p. 53, pl. 9, fig. 3.

aff. 1957 *Mammites aff. M. nodosoides* (Schlotheim) – Bürgl, p. 137, pl. 13, figs. 2 a–b.

? 1957 *Pseudaspidoceras* sp. Bürgl, pl. 13, fig. 5.

1957 *Mammites nodosoides* (Schlotheim) – Wright, p. 1416, text-figs. 535/4 a–c.

1960 *Mammites nodosoides* (Schlotheim) – Wiedmann, ps. 712, 714, 720–721, 723 [included the *armatus* and *afer* varieties].


non 1963 *Mammites nodosoides* (Schlotheim) – Powell, p. 316, pl. 33, figs. 1, 3–4, 6, 10–11; text-figs. 3 m–o, t–u (= *Morrowites* sp.).

1966 *Mammites nodosoides* (Schlotheim) – Wiedmann, ps. 111, 115, 116 [included the *armatus* and *afer* varieties].


1966 *Mammites nodosoides* (Schlotheim) – Collignon, p. 39, pl. 20, figs. 11, 11 a–b, 12, 12 a, 13, 13 a; pl. 21, figs. 1, 1 a–b, 2 [included the *spinosa*, *afer*, *tassagdelensis* and *zeibaensis* varieties].


1979 *Mammites nodosoides* (Schlotheim) – Wiedmann, ps. 184, 205.

1981 *Mammites nodosoides* (Schlüter) – Wright & Kennedy, p. 75, pl. 17, fig. 3; pl. 19, fig. 3; pl. 20, fig. 4; pl. 22, fig. 4; pl. 23, figs. 1–3; pl. 24, figs. 2–3; text-figs. 19 b, 23–24 [with additional synonymy].

1982 *Mammites nodosoides* (Schlüter) – Renz, p. 89, pl. 27, figs. 1–7, 9–10.

1982 *Mammites nodosoides* (Schlotheim) – Segura & Wiedmann, p. 296, pl. 2, figs. 2–5.

1983 *Mammites nodosoides* (Schlüter) – Cobban & Hook, p. 8, pl. 1, figs. 14–15; pl. 3, figs. 21–22; pl. 4, figs. 4–9, 17, 18; pl. 5, figs. 1–3; text-fig. 2.

1984 *Mammites cf. nodosoides* (Schlotheim) – Meléndez-Helia, p. 67, pl. 18, fig. 2.

1986 *Mammites nodosoides* (Schlüter) – Kennedy, p. 13, figs. 4–5.

1987 *Mammites nodosoides* (Schlüter) – Zaborski, p. 40, figs. 18–20, 22.

1989 *Mammites nodosoides* (Schlüter) – Cobban et al., p. 41, figs. 42, 90 d–h, m–n.

1990 *Mammites nodosoides* (Schlüter) – Robaszynski et al., p. 265, pl. 19, figs. 2 a–b, 3 a–b, 4 a–b.

1990 *Mammites nodosoides* (Schlüter) – Zaborski, p. 571, figs. 3 e–r, 4 a–b.

1991 *Mammites nodosoides* (Schlüter) – Santamaría-Zabala, p. 147, pl. 9, figs. 2–3.

1992 *Mammites nodosoides* [sic] (Schlüter) – Thomel, p. 214, pls. 107–111; pl. 112, figs. 1–3; pl. 113; text-fig. 71.

1994 *Mammites nodosoides* (Schlüter) – Chancellor et al., p. 44, pl. 1, figs. 4–5; text-figs. 10, 11 b–d, f, 15.

1994 *Mammites nodosoides* (Schlüter) – Kennedy, p. 260, pl. 1, figs. 7–11; pl. 2, figs. 3–5.

1995 *Mammites nodosoides* (Schlüter) – Santamaría-Zabala, p. 47, pl. 1, figs. 6, 8.

1996 *Mammites nodosoides* (Schlüter) – Wright, p. 175, text-figs. 134/2 a–d.
robust than that of the members of Schütter's species, and these specimens should be referred to the suture lines. Moreover, Schütter's species. The scarce morphological peculiarities of the varieties might constitute a new species. In contrast, Cobb & Hook (1983) preferred to assign W. Wright & Kennedy (1981) interpreted the mentioned taxa of Laube & Bruder (1887) and Hyatt (1903) underscored the particular robustness of the tubercles and ribs of the Mammites nodosoides of Laube & Bruder (1887), selecting this ammonite as the holotype of Schluetericeras laubei. Years later, De Oliveira & Brito (1969) and Beurlen (1970) chose certain Brazilian specimens to propose their respective new species Mammites sergipensis and Mammites beurleni. Taking as the type a juvenile specimen morphologically extremely close to M. nodosoides, Etayo-Serna (1979) described his new species Mammites nodosoidesappelatus. In their exhaustive revision, Wright & Kennedy (1981) interpreted the mentioned taxa of Laube & Bruder (1887) and Hyatt (1903) as conspecific morphologies of M. nodosoides, a decision followed by several subsequent authors such as Wright (1996). Similarly, although they expressed their uncertainty about M. nodosoides var. spinosa Basse, 1940, and M. nodosoides var. zeibaensis Collignon, 1966, Wright & Kennedy (1981) recognized that the different varieties of Schütter's species described to date seemed to remain within its range of morphological variation. They also included M. sergipensis, M. beurleni and, with some uncertainty, M. nodosoidesappelatus in the synonymy of M. nodosoides. Finally, these authors added that the peculiar ammonites assigned to M. nodosoides by Powell (1963) could constitute a new species. In contrast, Cobb & Hook (1983) preferred to assign M. michelobensis to their new genus Morrowites.

In my opinion, the descriptions of M. tischeri and M. michelobensis seem to be based on specimens of M. nodosoides which, as a consequence of crushing, show falsely tricarinate venters and some minor modifications to the suture lines. Moreover, S. laubei, M. sergipensis and M. beurleni appear to be indistinguishable from Schütter's species. The scarce morphological peculiarities of the varieties indicate that Powell (1963) characterized M. nodosoides as a less robust than that of the members of Schütter's species, and these specimens should be referred to Morrowites.

### Table: Material and dimensions

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**Description**: Involute ammonites of subquadrat or rectangular whorl section, with wide tabulate or gently convex venter, flat, parallel or discretely convergent flanks, and small round-shouldered umbilici. Their ornamentation is characterized by prominent umbilical and ventrolateral tubercles that standout on the ribs. Around the umbilici appear about six robust and conical umbilical tubercles per whorl that may increase their relative width during ontogeny. From each of these tubercles one to three feeble and straight or slightly prosiradiate ribs arise which, after crossing the ventrolateral tubercles, reach the wide ventral region and disappear before reaching the plane of symmetry.

**Discussion**: Based on specimens with seemingly tricarinate venters, Laube & Bruder (1887) proposed their new species Mammites tischeri and Mammites michelobensis, including among the type of the latter, one of the original specimens of Ammonites woollgari var. lupulina Fritsch, 1872. Hyatt (1903) chose certain Brazilian specimens to propose their respective new species Mammites sergipensis and Mammites beurleni. The juvenile specimen morphologically extremely close to M. nodosoides, Etayo-Serna (1979) described his new species Mammites nodosoidesappelatus. In their exhaustive revision, Wright & Kennedy (1981) interpreted the mentioned taxa of Laube & Bruder (1887) and Hyatt (1903) as conspecific morphologies of M. nodosoides, a decision followed by several subsequent authors such as Wright (1996). Similarly, although they expressed their uncertainty about M. nodosoides var. spinosa Basse, 1940, and M. nodosoides var. zeibaensis Collignon, 1966, Wright & Kennedy (1981) recognized that the different varieties of Schütter's species described to date seemed to remain within its range of morphological variation. They also included M. sergipensis, M. beurleni and, with some uncertainty, M. nodosoidesappelatus in the synonymy of M. nodosoides. Finally, these authors added that the peculiar ammonites assigned to M. nodosoides by Powell (1963) could constitute a new species. In contrast, Cobb & Hook (1983) preferred to assign M. michelobensis to their new genus Morrowites.
The type of _M. nodosoides appelatus_ is very small and could correspond to this or to another coarsely tuberculate acanthoceratid species.

In its characteristic ornamentation, substantially more robust than that of the members of _Spathites Kummel_ & _Decker_, 1954, the tubercles lie conspicuously on the ribs, facilitating the identification of the species. However, as argued by _Kennedy_ et al. (1980b), juvenile individuals can become very similar to those of _Spathites (Jeanrogericeras) Wiedmann_, 1960, whose representatives could have given rise to the genus _Mammites Laube_ & _BRUDER_, 1887. On the other hand, _M. nodosoides_ lacks the siphonal tubercles proper to _Lecoine triceras fleuriaussianum_ (d’ _Orbigny_, 1841).

**Distribution:** Practically cosmopolitan, the species has been cited in the _Mammites nodosoides_ Zone of the Lower Turonian of former Czechoslovakia, Germany, the UK, Tunisia, France, Turkestan, Spain, Syria, Peru, Madagascar, Morocco, Brazil, the USA, Venezuela, Nigeria and, with doubts, Colombia. Within the Iberian Trough, it has been identified across the entire Inner Castilian Platform.

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**Subfamily Euomphaloceratinae COOPER, 1978**

**Diagnosis:** Taxonomic group showing abundant tubercles and constrictions at all ontogenetic stages. The suture lines have very narrow first lateral saddles and broad lateral lobes.

**Discussion:** Shortly after this group was described by _COOPER_ (1978), _Wright & Kennedy_ (1981) considered that _Euomphaloceras Spath_, 1923, _Kamerunoceras Reymert_, 1954, _Yubariceras Matsumoto_ et al., 1957, _Shuparoceras Matsumoto_, 1975, _Obiraceras Matsumoto_, 1975, _Romaniceras Spath_, 1923, and, probably, _Hourcqiceras Collignon_, 1939, could be assigned to it. _Wright_ et al. (1983) ascribed to _Euomphaloceratinae_ the genera _Euomphaloceras_ and _Kanabiceras Reeside & Weymouth_, 1931, of the upper Cenomanian, _Romaniceras, Yubariceras, Shuparoceras_ and _Obiraceras_, of the Turonian, and _Codazziceras Etayo-Serna_, 1979, of the Coniacian, thus extending the stratigraphical distribution of the group. Some years later, after elevating it to the generic status, _Wright & Kennedy_ (1990) ascribed _Lotzeites Wiedmann_, 1960, to _COOPER’s_ subfamily. Among the subsequent works that examined the genera attributable to the _Euomphaloceratinae_, I should mention that of _Wright_ (1996), who included _Lotzeites, Euomphaloceras, Paraburroceras COBBAN_ et al., 1989, _Morrowites COBBAN_ & _Hook_, 1983, _Kamerunoceras, Pseudaspidoceras Hyatt_, 1903, _?Paramammites Furon_, 1935, _Romaniceras_, and _Codazziceras_ in the subfamily. In the same treatise, _Kanabiceras_, and _Yubariceras, Shuparoceras_ and _Obiraceras_ remained in the group, the former as a synonym of _Euomphaloceras_, and the remaining three as subgenera of _Romaniceras_. In contrast, _COOPER_ (1997) preferred to elevate the group to the family rank and divided it into _Euomphaloceratinae_ and his new _Romaniceratinae_. According to this author, the first subfamily grouped _Euomphaloceras_ ( _Euomphaloceras_), _Euomphaloceras_ ( _Kanabiceras_), _Burroceras COBBAN_ et al., 1989, _Paraburroceras_, _Paraburroceras_ ( _Pseudaspidoceras_), _Paraburroceras_ ( _Ampakabites_ ) _Collignon_, 1965a, and _Morrowites_, and the second one joined _Schindewolfites Wiedmann_, 1960, _Kamerunoceras, Codazziceras, Proromaniceras (Proromaniceras) Wiedmann_, 1960, _P. (Obiraceras), Neomphaloceras Matsumoto & Obata_, 1982, _Yubariceras_ and _Romaniceras_.

According to its origins, _COOPER_ (1978) proposed the _Euomphaloceratinae_ to group the multituberculate species derived from _Acanthoceras Neumayr_, 1875. This is a phylogenetic root in line with that suggested by _WRIGHT_ et al. (1983), among others. However, _WRIGHT & Kennedy_ (1990) reported that the origin of the genus _Lotzeites_, which they consider the oldest representative of the group, seemed to be found in _Calycoceras Hyatt_, 1900. In a detailed study of the evolutionary history of the subfamily, these authors identified a phylogenetic line linking it to _Lotzeites, Euomphaloceras, Kamerunoceras_ and _Romaniceras_. _COOPER_ (1997) found that the phylogeny of the group divided early, from _E. (Euomphaloceras)_ determining a different evolutionary line for each resultant subfamily.

**Distribution:** The group may be considered almost cosmopolitan with a range spanning the upper Cenomanian to the Coniacian.

**Genus Kamerunoceras Reymert, 1954, p. 250**

_[Schindewolfites Wiedmann, 1960, p. 736, type species by original designation Schindewolfites inaequicostatus Wiedmann, 1960, p. 736. Possibly, Polyaspidoceras Matsumoto, 1978, p. 18, type species by original designation Polyaspidoceras shimizui._]

_Type species_: _Acanthoceras eschii_ _Solger_, 1904, by original designation.
**Diagnosis:** This highly evolute, small to medium in sized and slightly compressed group has subquadrate or rounded whorl section, which increases its height throughout ontogeny, and wide umbilici. Some of its species sometimes adopt a slightly serpenticonic shape. Initial whorls are usually smooth, but simple ribs rapidly appear, which are straight or sinuous, each with seven clavate tubercles, yet curve backwards on the flanks and umbilical walls. The genus has umbilical tubercles elongated towards the ribs, and inner and outer ventrolateral and siphonal tubercles that gradually stretch out in the direction of growth. Lateral tubercles are absent, although umbilical tubercles can become displaced towards the flanks during ontogeny. The siphuncle appears close to the shell periphery, and in some specimens defines on the ventral region a rounded ridge in the form of a keel. Ribbing usually becomes irregular as the venter is crossed. The suture lines are simple with asymmetric lobes.

**Discussion:** Reyment (1954) described the genus *Kamerunoceras* to group forms with subquadrate whorl section, lateral and inner and outer ventrolateral tubercles, numerous relatively irregular ribs and simple suture lines, designating *Acanthoceras eschii* Solger, 1904, as its type species. He also pointed out that this taxonomic complex was close to the group he denoted “*Acanthoceras* amphibolum Morrow, 1935, and to Collignoniceras Breistroffer, 1947. A few years later, Wiedmann (1960, 1964) proposed his new genus *Schindewolfites*, underscoring that it included ammonites with subquadrate or rounded whorl section, highly irregular ornamentation and acanthoceratid suture lines with high and bifurcated lateral lobes. This author ascribed to his group *Acanthoceras dowvillei* Pervinquère, 1907, and the new species *S. inaequicosatum*, which he considered the generotype, and *S. ganuzai*. Wiedmann (1960, 1964) also reported the presence of *Schindewolfites* in his T IV and T VI zones of the Lower Turonian of North Africa, Madagascar and Spain, and indicated that *Kamerunoceras* should be a synonym of *Pseudaspidoceras* Hyatt, 1903. In addition, Matsumoto (1978) described his new genus *Polyaspidoceras*, highlighting that the group was close to *Pseudaspidoceras* in terms of many morphological features. Shortly after this, Kennedy & Wright (1979) noted that the type species of *Schindewolfites* and *Kamerunoceras* only differed in that the former was smaller in size and showed a predominance of ribbing on the tubercles. These authors also emphasized the great similarity between *S. inaequicosatum* and the juvenile whorls of *Ammonites turoniensis* d’Orbigny, 1850. They therefore interpreted the group of Wiedmann as a synonym of that of Reyment, and suggested that the differences observed between the two taxa could be the result of sexual dimorphism. These ideas were shared by numerous subsequent authors, among whom could be mentioned Kennedy et al. (1980c), who also provided an interesting definition of *Kamerunoceras* by comparing it to *Romaniceras* Spath, 1923. In contrast, Matsumoto & Kawashita (1989) and Cooper (1997) again elevated *Schindewolfites* to the genus rank. More specifically, the latter author highlighted the peculiarities of Wiedmann’s group to which, besides its type species, he referred *Kanabiceras puelboense* Cobban & Scott, 1972, *Acanthoceras calvertense* Powell, 1963, and *Kamerunoceras jacobsoni* Reyment, 1955. Cooper (1997) also added that *Schindewolfites isovokyense* Collignon, 1965a, and *K. jacobsoni* could be synonyms of *K. puelboense* and *S. inaequicosatum*, respectively. More recently several authors, such as Wright (1996), incorporated *Schindewolfites* and, with reservations, *Polyaspidoceras* in the synonymy of *Kamerunoceras*. Apparently, the original descriptions of *Schindewolfites* and *Polyaspidoceras* do not sufficiently separate these groups from *Kamerunoceras*, and should be consequently referred to this genus.

In an exhaustive revision of the group, Kennedy & Wright (1979) assigned to *Kamerunoceras*, the species *A. eschii*, *A. turoniense*, *A. dowvillei*, *Acanthoceras setzi* Riedel, 1932, *Kamerunoceras jacobsoni*, *S. inaequicosatum*, *S. ganuzai*, *Kamerunoceras timbertense* Collignon, 1965b, *Kamerunoceras antsaronese* Collignon, 1965a, *S. isovokyense*, *Schindewolfites schindewolfi* Collignon, 1965a, *Kamerunoceras lecointrei* Collignon, 1966, and *K. puelboense*, although they argued that the latter could be a synonym of *S. isovokyense*. Subsequently to this, Renz (1982) described his new species *Kamerunoceras* (“*Schindewolfites*”) _andinum*, while Kennedy et al. (1987) ascribed *A. calvertense* to this genus. Similarly, if *Polyaspidoceras* is accepted as a synonym of *Kamerunoceras*, the species comprising the first group, such as *P. shimizui* Matsumoto, 1978, in my opinion, should be referred to Reyment’s genus.

The morphologically closest group to *Kamerunoceras* is possibly *Pseudaspidoceras*. However, the lack of siphonal tubercles in the latter enables the clear separation between these genera. The members of Reyment’s group also bear a marked resemblance to those of *Collignoniceras*, but unlike these, they never develop a siphonal keel.
With regard to phylogenetic relationships, most authors including Kennedy & Wright (1979) and Cooper (1997), although with subtle discrepancies, accepted that *Kamerunoceras* emerged from *Euomphaloceras* Spath, 1923, by increasing of the whorl height, flattening of the flanks and reduction in accessory ribs.

**Distribution:** Cited from the upper Cenomanian to middle Turonian of southern and western Europe, North and West Africa, Madagascar, the Middle East, Japan, North America, Mexico and South America.

*Kamerunoceras ganuzai* (Wiedmann, 1960)

**Plate 12, Figs. A–C**

1960 *Schindewolfites ganuzai* Wiedmann, p. 738, pl. 5, figs. 1–2; text-fig. 4.
1964 *Schindewolfites ganuzai* Wiedmann – Wiedmann, p. 125, figs. 8 a–b, 9.
1978 *Schindewolfites ganuzai* Wiedmann – Wiedmann & Kauffmann, pl. 9, fig. 5.
1979 *Schindewolfites ganuzai* Wiedmann – Wiedmann, pl. 9, fig. 5.
1979 *Kamerunoceras ganuzai* (Wiedmann) – Kennedy & Wright, p. 1169.
non 1982 *Kamerunoceras* ("Schindewolfites") ganuzai (Wiedmann) – Renz, p. 98, pl. 29, figs. 19 a–b; text-fig. 74 a.
1989 *Kamerunoceras ganuzai* (Wiedmann) – Lamolda et al., text-fig. 3, fig. 6.
1991 *Kamerunoceras pueblense* (Cobban & Scott) – Santamaría-Zabala, p. 101, pl. 4, figs. 1 a–b.
aff. 1991 *Kamerunoceras aff. pueblense* (Cobban & Scott) – Santamaría-Zabala, p. 105, pl. 4, figs. 4 a–b.
1995 *Kamerunoceras pueblense* (Cobban & Scott) – Santamaría-Zabala, p. 24, pl. 1, fig. 2.
1997 *Schindewolfites ganuzai* Wiedmann – Wiese, pl. 4, figs. 5–6.
1998 *Kamerunoceras ganuzai* (Wiedmann) – Küchler, pl. 5, figs. 9 a–b, 10; pl. 6, fig. 3; pl. 9, figs. 1 a–b, 2 a–b, 3 a–b, 4 a–b, 6.
2004 *Kamerunoceras ganuzai* (Wiedmann) – Barroso-Barcenilla, p. 93.

**Type:** The holotype is specimen CE 1162/7 of the GPIT, collected from the *Spathites* (Ingridella) malladae Zone of Ganuza, Spain, and figured first by Wiedmann (1960, pl. 5, figs. 1–2; text-fig. 4).

**Material and dimensions:**

| PU-S-294 | ~ 423 | ~ 155 |

**Description:** This small sized specimen shows evolute coiling and subcircular whorl section. It has ribs that arch over the flanks and disappear as they reach the middle part of the ventral region, where constrictions may occur. It lacks intercalated ribs, and intercostal spaces are practically smooth. Umbilical tubercles are rounded, inner and outer ventrolateral tubercles are spiny and siphonal tubercles are elongated in the direction of coiling.

**Discussion:** Based on only two whorl fragments, Wiedmann (1960, 1964) proposed this peculiar species highlighting its unique ornamentation as the main differential characteristic. Subsequently, Renz (1982) assigned to *Kamerunoceras* ("Schindewolfites") ganuzai an ammonite obtained from the Lower Turonian of Venezuela. Lamolda et al. (1989) classified as *K. ganuzai* some specimens that were later referred to *Kamerunoceras pueblense* (Cobban & Scott, 1972) by Santamaría-Zabala (1991, 1995), and were newly attributed to Wiedmann's species by Küchler (1998).

The siphonal tubercles of the ammonite assigned to this species by Renz (1982) are too faint and its ribbing is too dense to include it into the variation range of *K. ganuzai*. This small ammonite could be a member of some densely ornamented taxon of the genus, such as *K. seitzi* (Riedel, 1932), or simply constitute the first whorls of a specimen of *K. andinum* Renz, 1982. On the contrary, as indicated by Santamaría-Zabala (1991, 1995), the *K. ganuzai* of Lamolda et al. (1989), although being a highly compressed specimen, have rounded whorl section, slightly oblique outer ventrolateral tubercles and conspicuous ribs that become slightly prorsiradiate on the outer third of the flanks. All these features fully apply to those of the specimens of *K. ganuzai* compacted in a direction perpendicular to the plane of symmetry.

Among the species of the genus that resemble *K. ganuzai* can be mentioned *K. inaequicostatus* (Wiedmann, 1960), whose tubercles are notably weaker than in the former and which therefore lacks spiny appearance. Furthermore, *K. ganuzai* coincides in the irregularity of its ornamentation with *K. schindewolfi* (Collignon, 1965a), as observed by Kennedy & Wright (1979), and bears a certain resemblance to *K. pueblense*. However, the characteristic arrangement of the ribs and tubercles, along with the rounded whorl section and the small size of Wiedmann's species, facilitate its differentiation.
Distribution: Only recorded in the Lower Turonian and, possibly, the lower part of the middle Turonian of Spain. In the Iberian Trough, *K. ganuzai* has been identified in the *Spathites (Ingridella) malladae* Subzone of the North-Ebro Area, although other authors have also obtained specimens from the Outer Navarro-Cantabrian Platform. Küchler (1998) used the term "ganuzai event" to describe a marked concentration of specimens of Wiedmann's species observed in a particular stratigraphic level of the Outer Navarro-Cantabrian Platform.

**Kamerunoceras turoniense** (d'Orbigny, 1850)

Plate 12, Figs. D–E; Plate 13, Figs. A–F

1850 Ammonites turoniensis d'Orbigny, p. 190.
1867 Ammonites salmuriensis Courtiller, p. 6, pl. 6, figs. 1–4.
1903 Ammonites salmuriensis Courtiller – Pervinquiére, figs. 6 a–c.
1907b Mortonoceras cf. salmuriensis (Courtiller) – Pervinquiére, figs. 6a–c.
1907c Mortonoceras cf. salmuriensis (Courtiller) – Pervinquiére, ps. 96–97.
1907 Mammites (Pseudaspidoceras) salmuriensis (Courtiller) – Pervinquiére, p. 314, pl. 19, figs. 1 a–b; text-fig. 120 [included the byzacena and zerhalmensis varieties].
1907 Mammites (Pseudaspidoceras) armatus Pervinquiére, p. 317, pl. 19, figs. 2–3; text-fig. 121, pl. 317, pl. 19, figs. 4 a–b [included the fraichichenis variety].
1931 Mammites (Pseudaspidoceras) armatus Pervinquiére – Basse, p. 37.
1937 cf. Mammites (Pseudaspidoceras) cf. salmuriensis (Courtiller) – Basse, p. 182.
1951 Pseudaspidoceras salmuriensis (Courtiller) – Wright & Wright, p. 27.
1959 Pseudaspidoceras salmuriensis (Courtiller) – Freund, p. 45.
1960 Pseudaspidoceras salmuriensis (Courtiller) – Wiedmann, p. 715 [included the fraichichenis subspecies].
1960 Pseudaspidoceras armatum (Pervinquiére) – Wiedmann, p. 715.
1961 Pseudaspidoceras salmuriensis (Courtiller) – Freund, p. 80, table 1.
1964 Pseudaspidoceras salmuriensis (Courtiller) – Wiedmann, p. 112 [included the fraichichenis subspecies].
1965 Pseudaspidoceras cf. armatum (Pervinquiére) – Wiedmann, p. 112.
1965a Kamerunoceras salmuriensis (Courtiller) – Collignon, p. 26, pl. 386, figs. 1659–1660.
1969 Proteanites salmuriensis (Courtiller) – Freund & Raaab, p. 69, pl. 5, figs. 4–6; text-figs. 14 c–j.
1977 Kamerunoceras salmuriensis (Courtiller) – Hancock et al., p. 156.
1978 Kamerunoceras salmuriense (Courtiller) – Kennedy & Hancock, pl. 18, figs. 1 a–c; pl. 19, figs. 1 a–b, 2 a–b.
1978 Pseudaspidoceras salmuriense (Courtiller) – Wiedmann & Kauffman, pl. 10, figs. 4 a–b.
1979 Pseudaspidoceras salmuriense (Courtiller) – Wiedmann, pl. 10, figs. 4 a–b.
1979 Pseudaspidoceras armatum (Pervinquiére) – Wiedmann, ps. 189, 193.
1979 Kamerunoceras turoniense (d'Orbigny) – Kennedy & Wright, p. 1170, pl. 2, figs. 1–11; pl. 3, figs. 1–2; pl. 4, figs. 1–3; text-figs. 2–3.
1981 Kamerunoceras turoniense (d'Orbigny) – Wright & Kennedy, p. 57, pl. 14, figs. 1–2, 10.
1982 Kamerunoceras turoniense (d'Orbigny) – Robaszyński et al., pl. 3, figs. 2 a–b.
1983 Kamerunoceras turoniense (d'Orbigny) – Cobban & Hook, p. 13, pl. 8, figs. 1–5, 9–11; text-fig. 8 a–b.
1985 Kamerunoceras turoniense (d'Orbigny) – Amédro & Hancock, figs. 9 c–d.
1990 Kamerunoceras turoniense (d'Orbigny) – Robaszyński et al., p. 262, pl. 15, figs. 1, 2 a–b.
1991 Kamerunoceras turoniense (d'Orbigny) – Santamaria-Zabalza, p. 106, pl. 5, fig. 3.
1995 Kamerunoceras turoniense (d'Orbigny) – Santamaria-Zabalza, p. 26, pl. 1, fig. 4; text-fig. 1 g.
1996 Kamerunoceras turoniense (d'Orbigny) – Wright, p. 167, text-figs. 126/2 c–e.
1997 Kamerunoceras turoniense (d'Orbigny) – Wiese, pl. 3, figs. 1–3; pl. 16, fig. 10.
1997 Kamerunoceras turoniense (d'Orbigny) – Cooper, fig. 4 d.
1998 Kamerunoceras turoniense (d'Orbigny) – Küchler, pl. 6, fig. 2; pl. 7, figs. 2 a–b, 3 a–b, 4–5; pl. 10, figs. 1 a–b.
2004 Kamerunoceras turoniense (d'Orbigny) – Barroso-Barcenilla, p. 94, pl. 3, figs. 3 a–b.

Type: The lectotype designated by Kennedy & Wright (1979, p. 1173, pl. 3, figs. 1–2) is specimen 6785 of the d'Orbigny Collection of the MNHP, obtained from the middle Turonian of Tourtenay, France.

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Description: Large specimen with highly evolute coiling and suboval to subquadrat e whorl section with rounded margins. The flanks, slightly convex, and the wide venter are crossed by up to twenty-eight simple,
spaced and straight or very slightly curved ribs per whorl. Each one bears two umbilical, located at the lower part of the flanks, two inner ventrolateral, two outer ventrolateral and one siphonal tubercles. Costulation is usually more pronounced during ontogeny, in contrast to tuberculation. The umbilici are wide, shallow, with arched walls and rounded shoulders, and account for thirty-five to forty-five percent of the entire shell diameter. The suture lines are relatively simple, with narrow and deep ventral lobes and lateral lobes divided into three or four branches.

Discussion: D’ORBIGNY (1850) proposed his new species *Ammonites turoniensis*, but did not figure any of its types. A few years later, COURTILLER (1867) examined and illustrated several specimens, on which he based his description of *Ammonites salmuriensis*. PERVERNIQUE (1907) distinguished the varieties *byzacenica* and *zerhalmensis* in COURTILLER’s taxon and proposed the new species *Mammites (Pseudaspidoceras) armatus* with the variety *fraichichenhis*. WIEDMANN (1960, 1964) ascribed several Spanish specimens to the species of COURTILLER and PERVERNIQUE, and elevated the variety *fraichichenhis* to the specific status. KENNEDY & WRIGHT (1979) referred the species described by D’ORBIGNY to the genus *Kamerunoceras* REYMENT, 1954. Similarly, after examining the lectotype of *A. salmuriensis*, they considered this taxon as a synonym of *K. turoniense*. In their comprehensive revision of the genus, these authors also emphasized that *M. (P.) armatus* and its varieties were described on the basis of the small modifications they show with respect to the type of *A. salmuriensis*. Thus, they referred *Pseudaspidoceras salmuriensis*, *P. armatum* and *P. fraichichenhis* to *K. turoniense*. The view of KENNEDY & WRIGHT (1979) was accepted by almost all subsequent authors.

After examining the originals of COURTILLER and PERVERNIQUE in the MNHN, I have come to the conclusion that *A. salmuriensis*, *M. (P.) armatus* and their respective varieties may be included in the wide morphological variability of *K. turoniense*. In particular, the description of *A. salmuriensis* seems to be based on somewhat more compressed specimens, with lower siphonal ridge and less robust tubercles than the lectotype of D’ORBIGNY’s species. Compared to typical specimens of COURTILLER’S taxon, *A. salmuriensis byzacenica* has less ribs per whorl, while *A. salmuriensis zerhalmensis* shows slight modifications in the shape and position of some tubercles. It may be observed in the herein refigured types, that *M. (P.) armatus* (Plate 13, Figs. A–C) has somewhat narrower umbilici, more marked ribs and tubercles and discretely different sutures, while its variety *fraichichenhis* (Plate 13, Figs. D–F) has robust and concave ribs and weak tubercles, with respect to the lectotype of *K. turoniense*.

Distribution: Identified in the middle Turonian of France, Tunisia, Madagascar, the UK, Israel, Spain, the USA and, possibly, Syria. However, Corban (1984) and Kennedy (1984, 1994) pointed out that, besides appearing in the middle Turonian Collignoniceras woolgari Zone, the species may also occur in the Lower Turonian *Mammites nodosoides* Zone. These possible geographical differences in the vertical distribution of *K. turoniense*, as suggested by Robaszynski et al. (1990), are likely to be the consequence of faunal provincialism.
Conclusions

In the present work have been described new specimens from the Lower Turonian of the Iberian Trough assigned to the species Spathites (Jeanrogericeras) tavense, S. (J.) saenzi, S. (J.) postsaenzi, S. (J.) obliquus, S. (J.) reveliereanus, S. (Ingridella) malldae, S. (I.) depressus, S. (Spathites) laevis, S. (S.) sulcatus, Mammites nodosoides, Kamerunoceras ganuzai and K. turoniense. Among these species, S. (J.) tavense had never previously been mentioned from the palaeogeographical region. During the revision has been noticed the presence of Turonian of the Iberian Trough, where the species S. U.) combesi, S. (Ingridella) malladae, S. (Spathites) laevis, S. (S.) sulcatus, Mammites nodosoides, K. ganuzai, K. inaequicostatus and K. turoniense have been properly identified.

Furthermore, the range of the Acanthoceratidae presented here has been determined (Text-fig. 9). Definitively, the records of S. (Jeanrogericeras) extend from the Choffaticeras (Choffaticeras) quaasi to Mammites nodosoides zones. Among its species, S. (J.) tavense and S. (J.) saenzi have been obtained in the lower part of the Choffaticeras (Choffaticeras) quaasi Zone, and S. (J.) postsaenzi in the upper part of this biostratigraphic unit. S. (J.) obliquus has been identified in the Spathites (Ingridella) malldae and Wrightoceras munieri subzones. Many specimens of S. (J.) reveliereanus have been collected from the Spathites (Ingridella) malldae Subzone to the top of the Wrightoceras munieri Subzone. Finally, S. (J.) combesi, which is the youngest species of this subgenus registered in the Iberian Trough, has been identified in the Wrightoceras munieri Subzone. The occurrence of S. (Ingridella) comprises the Spathites (Ingridella) malldae and Mammites nodosoides zones. To be more precise, S. (I.) malldae has been identified in the eponymous subzone and the lower part of the Choffaticeras (Leoniceras) luciae Subzone, and S. (I.) depressus has been collected from the Wrightoceras munieri Subzone. S. (S.) laevis and S. (S.) sulcatus, the identified members of S. (Spathites), also come from the Wrightoceras munieri Subzone. The only species of Mammites obtained in this palaeogeographical region, M. nodosoides, has been collected in its eponymous zone. With regard to Kamerunoceras, records of K. ganuzai have been obtained in the Spathites (Ingridella) malldae Subzone, and of K. turoniense in middle Turonian levels.

In terms of the phylogeny of the group, three possible evolutionary lineages have been identified within the subgenus S. (Jeanrogericeras), two of them joining S. (J.) subconciliatus with S. (J.) saenzi and S. (J.) postsaenzi, and with S. (J.) obliquus, respectively, and the other one joining S. (J.) tavense, S. (J.) reveliereanus and S. (J.) combesi (Text-fig. 9). All of them progressively becoming more depressed forms. Within S. (Ingridella), a subgenus that derived from S. (Jeanrogericeras), another lineage joining S. (I.) malldae and S. (I.) depressus

Text-fig. 10. Observed phases in the evolution of the family Acanthoceratidae from the Lower Turonian of the Iberian Trough.
has been identified. \textit{S. (Spathites)} and \textit{Mammites} seem to be phylogenetically very close to \textit{S. (Jeanrogericeras)}, from which they could be derived.

After observing the distribution of the family, five evolutionary main phases can be distinguished in the Lower Turonian of the Iberian Trough. These are characterized by the successive predominances of \textit{Spathites (Jeanrogericeras)} 1, of \textit{Spathites (Ingridella)}, of \textit{Spathites (Jeanrogericeras)} 2, of \textit{Mammites} and of \textit{Spathites and Mammites} (Text-fig. 10). The first one has been identified in the \textit{Choffaticeras (Choffaticeras) quaasi} Zone, and during this phase Acanthoceratidae are represented by the subgenus \textit{S. (Jeanrogericeras)}, exactly by the latest specimens of \textit{S. (J.) subconciliatus}, by the second generation of taxa directly or indirectly derived from this species, such as \textit{S. (J.) saenzi} and \textit{S. (J.) postsaenzi}, and by \textit{S. (J.) tavense}. Some of these ammonites, like \textit{S. (J.) subconciliatus} and \textit{S. (J.) tavense}, maintain certain morphological similarities with the upper Cenomanian genus \textit{Metoicoceras}. The second phase, that of \textit{Spathites (Ingridella)}, has been registered in the \textit{Spathites (Ingridella) malladae Subzone}. In it, members of \textit{Spathites (Ingridella)}, specifically of \textit{S. (I.) malladae}, dominate the family, which is also represented by \textit{S. (J.) obliquus}, \textit{S. (J.) reveliereanus} and \textit{K. ganuzai}. The third phase, named of \textit{Spathites (Jeanrogericeras)} 2, has been identified in the \textit{Choffaticeras (Leoniceras) luciae} Subzone, and is exclusively characterized by \textit{S. (J.) reveliereanus}. The fourth phase, called of \textit{Mammites}, has been registered in the \textit{Mammites nodosoides} Zone. In it the members of the family mainly belong to \textit{Mammites}, specifically to \textit{M. nodosoides}, but there are also some specimens of \textit{S. (J.) reveliereanus}. Finally, the phase of \textit{Spathites} and \textit{Mammites}, the fifth and last one, has been identified in the \textit{Wrightoceras munieri} Subzone. In this phase, Acanthoceratidae are abundant and diverse, being represented by the three subgenera of \textit{Spathites}, \textit{S. (Jeanrogericeras)}, \textit{S. (Ingridella)} and \textit{S. (Spathites)}, and by \textit{Mammites}. It includes the species \textit{S. (J.) obliquus}, \textit{S. (J.) reveliereanus}, \textit{S. (J.) combesi}, \textit{S. (I.) depressus}, \textit{S. (S.) laevis}, \textit{S. (S.) sulcatus} and \textit{M. nodosoides}.

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References


Explanation of the Plates

Plate 1

_Spathites (Jeanrogericeras) tavense_ (Faraud, 1940) – A, B, lateral and apertural views of CB-R-546, from the Choffaticeras (Choffaticeras) quassi Zone of Condernios, ×1.

_Spathites (Jeanrogericeras) saenzi_ (Wiedmann, 1960) – C, D, E, F, lateral, ventral, lateral and apertural views of CA-S-504, from the Choffaticeras (Choffaticeras) quassi Zone of Condernios, ×1. G, H, lateral and ventral views of TA-S-118, from the Choffaticeras (Choffaticeras) quassi Zone of Tamajon, ×1.

Plate 2

_Spathites (Jeanrogericeras) saenzi_ (Wiedmann, 1960) – A, B, C, D, E, lateral, apertural, ventral, lateral and apertural views of FT-S-841, from the Choffaticeras (Choffaticeras) quassi Zone of Fuentetoba, ×5/6.
Plate 3

*Spathites (Jeanrogericeras) postsaenzii* (Wiedmann, 1960) – A, B, C, D, lateral, ventral, lateral and apertural views of FT-S-725, from the *Choffaticeras (Choffaticeras) quaasi* Zone of Fuentetoba, × 5/6. E, F, lateral and ventral views of FV-R-846, from the *Choffaticeras (Choffaticeras) quaasi* Zone of Fuentetoba, × 5/6.

Plate 4

*Spathites (Jeanrogericeras) obliquus* (Karrenberg, 1935) – A, B, C, D, lateral, ventral, lateral and apertural views of CB-R-23, from the *Spathites (Ingridella) malladae* Subzone of Condemios, × 1. E, F, lateral and ventral views of PU-S-310, from the *Mammites nodosoides* Zone of Puenedey, × 1.

*Spathites (Jeanrogericeras) reveliereanus* (Courtiller, 1860) – G, ventral view of TA-S-116, from the *Spathites (Ingridella) malladae* Subzone of Tamajón, × 1.

Plate 5

*Spathites (Jeanrogericeras) reveliereanus* (Courtiller, 1860) – A, B, apertural and lateral views of TA-S-116, from the *Spathites (Ingridella) malladae* Subzone of Tamajón, × 1. C, D, lateral and ventral views of TA-R-144, from the *Choffaticeras (Leoniceras) luciae* Subzone of Tamajón, × 1.

*Spathites (Jeanrogericeras) combesi* (Sornay, 1951) – E, F, lateral and apertural views of FT-S-809, from the *Wrightoceras munieri* Subzone of Fuentetoba, × 1.

Plate 6

*Spathites (Jeanrogericeras) combesi* (Sornay, 1951) – A, B, ventral and lateral views of FT-S-809, from the *Wrightoceras munieri* Subzone of Fuentetoba, × 1.

*Spathites (Ingridella) malladae* (Fallot, 1931) – C, D, E, apertural, lateral and ventral views of FT-S-851, from the *Spathites (Ingridella) malladae* Subzone of Fuentetoba, × 1.

Plate 7

*Spathites (Ingridella) malladae* (Fallot, 1931) – A, B, C, D, E, F, G, ventral, lateral and apertural (complete), and apertural, lateral, ventral and lateral (without a fragment of body chamber) views of CA-S-511, from the *Spathites (Ingridella) malladae* Subzone of Fuentetoba, × 5/6.

Plate 8

*Spathites (Ingridella) malladae* (Fallot, 1931) – A, B, apertural and lateral views of CA-R-605, from the *Spathites (Ingridella) malladae* Subzone of Condemios, × 1.

*Spathites (Ingridella) depressus* (Wiedmann, 1960) – C, D, apertural and lateral views of FS-R-802, from the *Wrightoceras munieri* Subzone of Fuentetoba, × 1.

Plate 9

*Spathites (Ingridella) depressus* (Wiedmann, 1960) – A, B, C, D, E, F, G, ventral, lateral and apertural (complete), and ventral, lateral, apertural and lateral (without a fragment of body chamber) views of FT-S-762, from the *Wrightoceras munieri* Subzone of Fuentetoba, × 4/5.

Plate 10

*Spathites (Spathites) laevis* (Karrenberg, 1935) – A, B, lateral and apertural views of CA-R-516, from the *Wrightoceras munieri* Subzone of Condemios, × 1.

*Spathites (Spathites) sulcatus* (Wiedmann, 1960) – C, D, E, F, G, H, ventral, lateral, apertural and lateral (with preserved phragmocone), and apertural and lateral (without a fragment of preserved phragmocone) views of CA-R-672, from the *Wrightoceras munieri* Subzone of Condemios, × 1.
Plate 11

*Mammites nodosoides* (Schlüter, 1871) – A, B, C, D, apertural, lateral, lateral and ventral views of MS-6, from an unknown Spanish locality, × 5/6.

Plate 12


*Kamerunoceras turoniense* (d’Orbigny, 1850) – D, E, lateral and apertural views of PU-S-308, from the middle Turonian of Puentedey, × 1.

Plate 13

*Kamerunoceras turoniense* (d’Orbigny, 1850) – A, B, C, ventral, lateral and apertural views of the holotype of *Mammites (Pseudaspидoceras) armatus* Pervinquière, 1907, specimen J04258 of the MNHN, × 5/6. D, E, F, lateral, ventral and lateral views of the syntype of *Mammites (Pseudaspидoceras) armatus var. fraichichensis* Pervinquière, 1907, specimen J04307 of the MNHN, × 5/6.
F. Barroso-Barcenilla: Revision and New Data of the Ammonite Family Acanthoceratidae de Grossouvre, 1894.
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