Revision of the family Hemiporitidae (Scleractinia, Late Cretaceous)

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ABSTRACT
The Late Cretaceous scleractinian family Hemiporitidae (suborder Faviina) is revised. The family is characterized by having large trabeculae, compact and strong septa with poor ornamentation at their lateral faces, short and non-confluent costae, a strong lamellar columella, a septothecal wall, and an endotheca made of thick tabulae. Together with the name-giving genus *Hemiporites* Alloiteau, 1952, the two coral genera *Cerionefocoenia* Reig Oriol, 1995 and *Pachynefocoenia* Reig Oriol, 1989 from the Late Cretaceous of Spain are assigned to the family. All genera are revised on the basis of the types of their respective type species. Further genera formerly or currently assigned to the Hemiporitidae family are discussed. The family occurs from the Turonian to Maastrichtian.

KEY WORDS
Scleractinia,
Hemiporitidae,
Late Cretaceous.

RÉSUMÉ
Révision de la famille Hemiporitidae (Scleractinia, Crétacé supérieur).
Une révision de la famille Hemiporitidae (sous-ordre Faviina, ordre Scleractinia) du Crétacé supérieur est proposée. La famille est caractérisée par de grands trabécules, des éléments radiaires forts et compacts, avec peu d'ornementation sur leurs faces latérales, des côtes courtes et non-confluentes, une columelle lamellaire, une muraille septothécale, et une endothèque de planchers forts. La famille contient le genre *Hemiporites* Alloiteau, 1952 et les genres *Cerionefocoenia* Reig Oriol, 1995 et *Pachynefocoenia* Reig Oriol, 1989 du Crétacé supérieur d'Espagne. Tous les genres sont révisés sur la base des types de leurs espèces types. D'autres genres, assignés à la famille dans le passé et récemment, sont discutés. La famille a une distribution stratigraphique allant du Turonien au Maastrichtien.

MOTS CLÉS
Scleractinia,
Hemiporitidae,
Crétacé supérieur.

INTRODUCTION

The post-paleozoic corals (order Scleractinia) are traditionally subdivided into suborders and families. While the number of suborders is fairly low (24) and includes many (generally accepted) synonyms, the number of families is very high (155) of which only a few are synonymous. About 1610 available genera of the order Scleractinia are known, on average a little bit more than ten per family (all numerical data from the authors database; Löser 2005). Families greatly assist in subdividing the suborders, since well-defined families have well-confined stratigraphic ranges that can help us better understand coral evolution. Unfortunately, many of these families bear the problem that their characteristics and constitution are poorly known because the characteristics of their type genera (and respective type species) are poorly investigated and/or poorly documented. Many are in need of revision.

The Muséum national d'Histoire naturelle in Paris keeps more than 1000 type specimens of Scleractinian coral species, among them about 300 types of type species, which are the key to the genera and numerous families. Since the coral collection is continuously recorded in a database (http://coldb.mnhn.fr/colweb/), knowledge about available material has increased over past years. In addition, access to the type material and thin sections has become easier and modern methods such as high resolution scanning allow samples and sections to be digitised. All this helps to greatly improve our knowledge of post-paleozoic corals. This contribution will be the first of several revisions of scleractinian coral families.

MATERIAL AND METHODS

The material described here comes from the following localities (locality codes refer to Löser *et al.* 2005):
– France, Aude, Tuilerie Saint-Michel, W Padern (F.2145). Turonian;
– Spain, Lérida, Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur, Puigmanyons (E.865). Olistostromes of Puigmanyons. Early Late Campanian;
– Spain, Lérida, Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur, Torallola (E.1331). Olistostromes of Puigmanyons. Early Late Campanian.

The present study is entirely based on type material and on thin sections obtained from it. The measurements in the descriptions are based on 20 measurements of the calicular diameter and 30 measurements of the distance between the calicular centres in each colony. The values given follow the pattern "lowest value-average-highest value" (Fig 1). The average was calculated based on all 20 (30) measurements. Measurements and calculations were carried out using the computer program PaleoTax/Measure (http://www.paleotax.de/measure).

Abbreviations

Institutional abbreviations

MB	Museum für Naturkunde der Humboldt-Universität, Berlin;
MGSB	Museo Geológico del Seminario de Barcelona;
MNHN	Muséum national d'Histoire naturelle, Paris.

Other abbreviations

c min	smaller outer calicular diameter;
c max	larger outer calicular diameter;
cl min	smaller calicular diameter (calicular pit);
cl max	larger calicular diameter (calicular pit);
ccd	distance between the calicular centres;
s	number of septa.

SYSTEMATICS

Order SCLERACTINIA Bourne, 1900
Suborder FAVIINA Vaughan & Wells, 1943

Family Hemiporitidae Alloiteau, 1952

Range. — Turonian to Maastrichtian.

Diagnosis. — Cerioid and plocoid colonies. Septa compact, made of large trabeculae. Lateral faces of septa poorly ornamented. Septa may be connected to each other in the centre of the calice. Septa inner margin swollen. Costae short and non-confluent. Synapticulae absent. Columella lamellar, strong. Wall septothecal, in places paraseptothecal, subcompact. Endotheca present. Budding extracalicinal and intracalicinal.

Systematic position

The scleractinian coral family Hemiporitidae was established by Alloiteau (1952) within the suborder Meandrinina (Meandrina *auct.*) Alloiteau, 1952. The problematic background of

the suborder Meandrinina has been discussed in Löser *et al.* (2010). It is one of the most problematic groups of the order Scleractinia because it groups together material differing in various aspects. The suborder was originally established as a group with small trabeculae and therefore poorly ornamented or smooth septal distal borders. This concept was weakened in Alloiteau (1957) with details on the micro architecture of *Hemiporites* Alloiteau, 1952, the name-giving genus of the Hemiporitidae family (which has been assigned to the Meandrinina suborder). Material presented by him and later by Beauvais (1982) show rather large trabeculae. That qualifies the family belonging to the Faviina suborder as a family presenting large trabeculae and sparse septal ornamentation. The material studied here show traces of preserved microstructure and confirms the existence of large trabeculae and sparse ornamentation of the septal lateral faces (Fig. 2E). The family is therefore transferred into the suborder Faviina.

Baron-Szabo (2008) included the family Hemiporitidae into the Agatheliidae Beauvais & Beauvais, 1975 family. Both families differ in many features (size of trabeculae, ornamentation of septal faces, constitution of the wall) and are not synonymous.

Comparison

The Hemiporitidae shares with the Placocoeniidae Duncan, 1884 the microstructure, septal formation, and the columella, but differ in the formation of the coenosteum and the short costae. They differ from the Placosmiliidae Duncan, 1884 by the formation of the inner margin of the septa and larger trabeculae.

Genera of the family

When established, the family Hemiporitidae encompassed four genera: *Ficariastraea* Alloiteau, 1952, *Hemiporites*, *Placocaeniopsis* Alloiteau, 1952 and *Nefocoenia* Oppenheim, 1930. Later, other genera were assigned to this family. Here, only the genera *Cerionefocoenia*, *Hemiporites* and *Pachynefocoenia* Reig Oriol, 1989 are included. For the systematic position of the other genera see below.

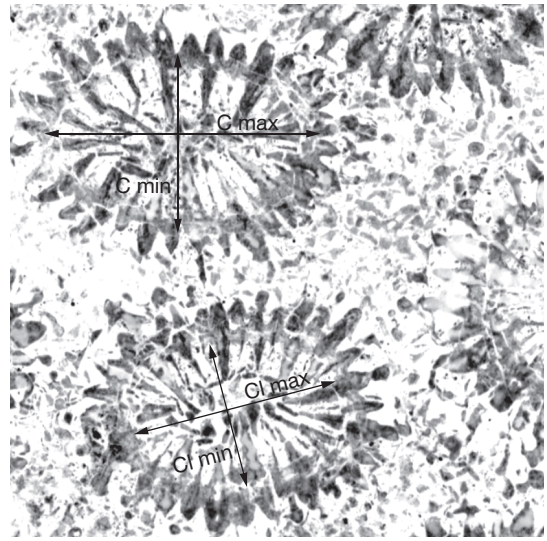

Fig. 1. — Schematic illustration showing how the calicular outer (**c min**, **c max**) and inner (**cl min**, **cl max**) diameter values were measured. Abbreviations: see Material and methods.

Genus *Hemiporites* Alloiteau, 1952

Type species. — *Hemiporites jacobi* Alloiteau, 1952 by original designation.

Range. — Turonian.

Diagnosis. — Plocoid colony. Calices circular to elliptical. Septa compact, made of large trabeculae. Septa free, not attached to each other in the calicular center. Septal lateral faces with few thorns, but generally poorly ornamented. Septal inner margin swollen. Septa with regular radial symmetry. Septal cycles differ in length and thickness. Paliform lobes or pali absent. Costae short, non-confluent, same in number as septa. Columella lamellar, thick. Wall septothecal or septoparathecal, not always compact. Endotheca made by thick tabulae. Coenosteum made by thick trabeculae and tabulae.

Hemiporites jacobi Alloiteau, 1952 (Fig. 2A-F)

Hemiporites Jacobi [sic] Alloiteau, 1952: 641; 1957: 233, figs 169-172, pl. 9, fig. 10, pl. 18, fig. 12.

non *Hemiporites jacobi* – Kuzmicheva 1982: 104, pl. 1, fig. 5; 2002: 180, pl. 27, fig. 5.

HOLOTYPE. — MNHN.F.R10937.

MATERIAL EXAMINED. — Holotype and four unnumbered thin sections (MNHN.F) of which one could clearly be identified as having been obtained from the holotype (illustrated here in Fig. 2A-E).

OCCURRENCE. — Turonian of Tuilerie Saint Michel, W Padern (Aude, France).

DIMENSIONS
cl min = 1.8-2.43-3.2 mm.
cl max = 2.9-3.42-4 mm.
ccd = 3.8-5.3-6.7 mm.
s = 32-40.

DESCRIPTION
Plocoid colony with elliptical or circular calices that are arranged in irregular rows. Septa compact, made of large trabeculae. Septa free, not attached to each other. Septa bicuneiform in outline, having the thickest part in the wall. Septal lateral faces with few thorns, generally poorly ornamented. Septal inner margin swollen, more pronounced in the first septal cycle. Septa have regular radial decameral symmetry. Septal cycles differ in length and thickness, but the last cycle is not complete. Costae short and non-confluent. Columella lamellar, thick, in places connected to the septa of the first cycle. Wall compact, septothecal by thickening of septa. Endotheca made by thick tabulae. Coenosteum made by thick isolated trabeculae and tabulae.

Genus *Cerionefocoenia* Reig Oriol, 1995

TYPE SPECIES. — *Cerionefocoenia iberica* (by original designation).

SPECIES INCLUDED. — Type species.

RANGE AND GEOGRAPHICAL DISTRIBUTION. — Early Late Campanian of northern Spain.

DIAGNOSIS. — Cerioid colony with polygonal or elongated calices. Septa compact, thick, in a radial symmetry. Septal faces smooth. Costae are confluent to non-confluent. Wall septothecal, but incomplete, leaving in places channel-like connections between calices. Columella lamellar. Endotheca consists of few dissepiments. Budding intracalicinal.

REMARKS
This genus was originally placed in the Faviidae family, which is probably only a *lapsus calami* – the derivation of the genus name from *Nefocoenia* refers to a genus of the Hemiporitidae family and it is probably that Reig Oriol was aware of this.

Cerionefocoenia iberica Reig Oriol, 1995 (Fig. 2G-I)

Cerionefocoenia iberica Reig Oriol, 1995: 24, pl. 3, figs 3, 4.

HOLOTYPE. — MGSB 55826.

MATERIAL EXAMINED. — Holotype with two thin sections.

OCCURRENCE. — Early Late Campanian of Puigmanyons (Lérida, Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur).

DIMENSIONS
cl min = 0.9-1.1-1.4 mm.
cl max = 1.2-1.9-2.7 mm.
ccd = 1.5-1.9-2.2 mm.
s = 20-30.
sd = 10-11/2 mm.

DESCRIPTION
Cerioid colony with polygonal and often elongated calices that give the colony a meandrinoid appearance, even though each calicular pit normally has only one centre. Two centres may be present when one calice is about the divide into two calices. Septa thick and compact, generally free, but often connected to the columella. Their symmetry is radial, but irregular. Generations differ in length. Normally a first cycle reaches to the columella, and a second is only preserved as very short ridges. Septal faces smooth. The costae are confluent to non-confluent. The septothecal wall is incomplete, so that calices communicate through gaps in the wall. The columella is thick, lamellar and very often connected to septa. The columella can have small thorns that look like septa of the second generation proposing septal budding but this is not the case. The endotheca is poorly preserved and consists of few dissepiments.

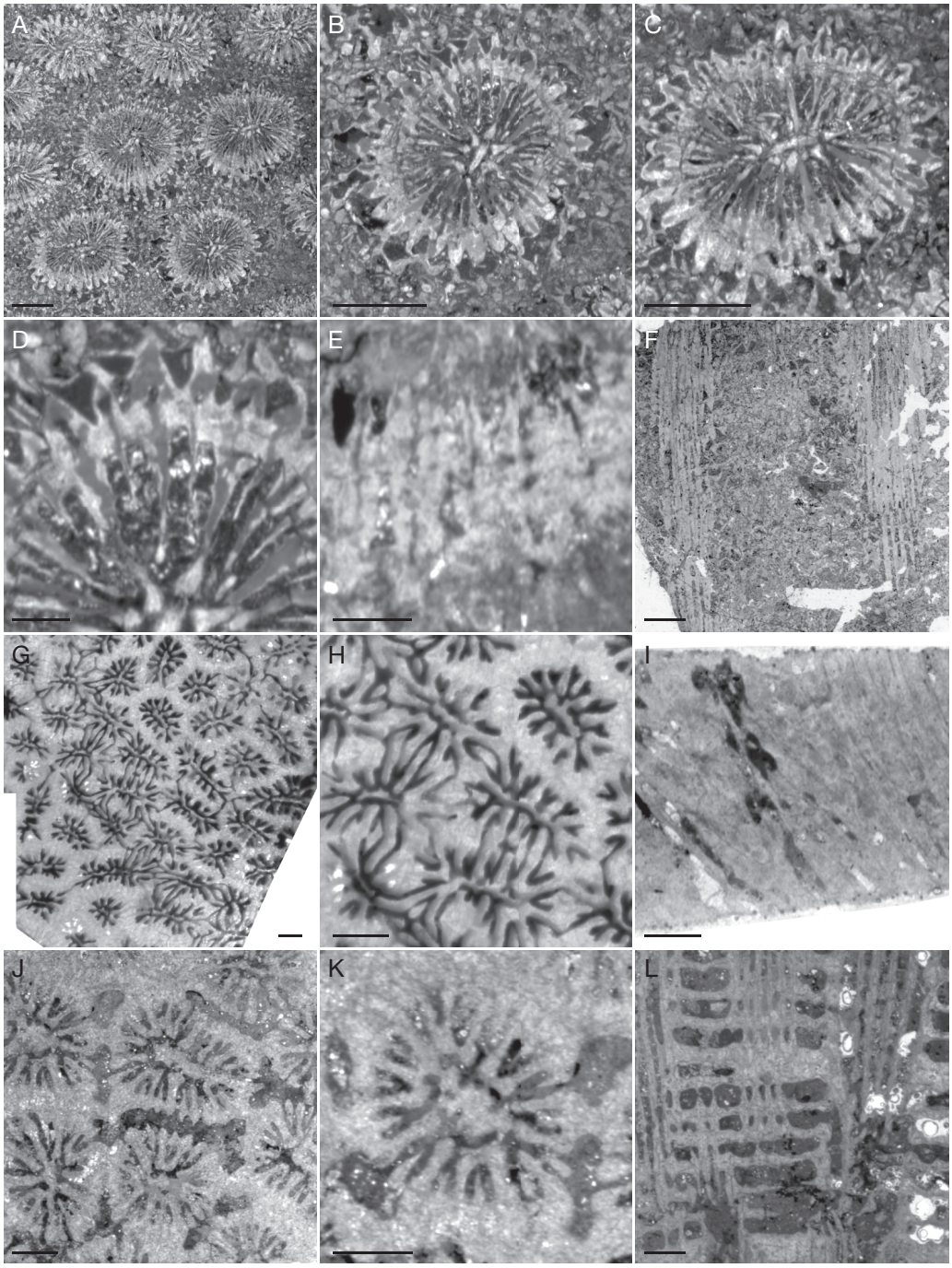

Fig. 2. — **A**-**F**, *Hemiporites jacobi* Alloiteau, 1952: **A**-**E**, holotype MNHN.F.R10937 (transverse thin section); **F**, unnumbered thin section that may belong to the holotype (longitudinal thin section); **G**-**I**, *Cerionefocoenia iberica* Reig Oriol, 1995, holotype MGSB 55826; **G**, **H**, transverse thin sections; **I**, longitudinal thin section; **J**-**L**, *Pachynefocoenia danieli* Reig Oriol, 1989, holotype MGSB 47205. Scale bars: A-C, F-L, 2 mm; D, E, 500 µm.

Genus *Pachynefocoenia* Reig Oriol, 1989

TYPE SPECIES. — *Pachynefocoenia danieli* (by original designation).

SPECIES INCLUDED. — Type species.

RANGE AND GEOGRAPHICAL DISTRIBUTION. — Campanian to Early Maastrichtian of northern Spain and United Arab Emirates-Oman border area.

DIAGNOSIS. — Plocoid colony. Septa compact, thick, in a radial symmetry. Septal faces smooth. Costae are non-confluent. Wall incomplete, septoparathecal. Columella lamellar. Endotheca consists of thin subtabular dissepiments. The coenosteum is made of thick tabulae. Budding intracalicinal.

Pachynefocoenia danieli Reig Oriol, 1989 (Fig. 2J, K)

Pachynefocoenia danieli Reig Oriol, 1989: 9, pl. 1, figs 1, 2, pl. 4, figs 3, 4.

Barysmilia iberica Baron-Szabo, 1998: 144, pl. 6, figs 1-3; 2000: 114, pl. 8, figs 1, 3.

HOLOTYPE. — MGSB 47205.

MATERIAL EXAMINED. — Holotype with two thin sections. Holotype of *Barysmilia iberica* (MB K1155) with two thin sections.

OCCURRENCE. — Early Late Campanian of Torallola (Spain, Lérida, Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur), Late Campanian to Maastrichtian of Al Ain, Huwayyah Mt, SW corner and Al Madam, Faijyah Mt, southern tip (United Arab Emirates, Al Ain).

DIMENSIONS
c min = 2.3-2.5-3.1 mm.
c max = 2.4-3.0-3.9 mm.
cl min = 1.8-2.4-3.1 mm.
cl max = 1.7-1.9-2.4 mm.
ccd = 2.2-2.7-3.3 mm.
s = 20-30.
sd = 8/2 mm.

DESCRIPTION
Plocoid colony with rectangular, elliptical or circular calices. The rectangular or elliptical calices are the result of the beginning of intracalicinal budding. Septa compact and straight, often connected in the calicular centre forming a kind of incomplete crown. Septal faces smooth in the type material (Baron-Szabo 1998 reports fine thorns and granules). Septal symmetry generally regular in six systems and three cycles resulting in 24 septa, but this number can be lower in younger calices and higher in larger calices. Septal insertion as described by Baron-Szabo (1998: 144-145) could not be found in the type material. The septa of the various cycles are distinguished by thickness and length. Septa bicuneiform in outline, with short costae. The costae are non-confluent, but in places calices are connected to each other by a kind of apophyses. The wall is incomplete and septothecal, in places supported by thin dissepiments. The columella is strong and lamellar, often connected to septa of the first cycle. The endotheca is poorly developed and consists of thin subtabular dissepiments. The coenosteum is made of very thick tabulae. Microstructure not preserved in the type material.

QUESTIONABLE GENERA

The genera listed below have been formerly or are presently assigned to the Hemiporitidae family, but it cannot be proven that they belong to this family. Further genera are listed whose current position is doubted and which may belong to the Hemiporitidae.

Genus *Neocoeniopsis* Alloiteau, 1957

TYPE SPECIES. — *Phyllocoenia excelsa* de Fromentel, 1884 by original designation.

REMARKS
The genus was originally assigned to the Phyllocaeninae Duncan, 1884 subfamily, which is probably a synonym of the Montastraeinae within the suborder Faviina. There exist four syntypes (MNHN A29626, M03760, M03769, M03773). Since only one sample has a polished surface and a thin section was prepared from a different sample, it cannot be determined whether all four samples belong to the same species (genus). The sectioned

specimen (M03760) and the sample with a thin section (A29626) show large trabecules and can therefore not belong to the Pachyphylliidae family (as proposed by Baron-Szabo 2003; the material illustrated there may belong to the genus *Paraplacocoenia* Beauvais, 1982). The material compares well to *Hemiporites*, but probably differs by a smaller columella and longer costae. A diagnosis cannot be given; this requires the selection of a lectotype and preparation of more thin sections from it.

Genus *Phyllastraea* de Fromentel, 1879

TYPE SPECIES. — *Phyllastraea hippuritorum* de Fromentel, 1879 (by monotypy).

REMARKS

The type of the type species is available (MNHN.F.M03765) but without thin sections. Thin sections found in the MNHN labelled as *Phyllastraea hippuritorum*, but without number, are poorly preserved and do not correspond to the type of the species. *Phyllastraea* is a plocoid colony with elliptical calices and compact and poorly ornamented septa with T-shaped inner margins. The costae are non-confluent. The wall is septothecal. The columella is lamellar. *Ficariastraea* Alloiteau, 1952 is an objective synonym. Baron-Szabo (2003) included *Phyllastraea hippuritorum* in the synonymy of *Agathelia asperella* Reuss, 1854. Both species differ in many features (ornamentation of septa, presence of a columella, thickness and formation of the wall) and are not identical.

Genus *Placogyriopsis* Alloiteau, 1957

TYPE SPECIES. — *Placogyriopsis corbariensis* Alloiteau, 1957 (by original designation).

REMARKS

The genus was originally assigned to the Dendrogyrinae subfamily (Dendrogyridae family, Meandrinina suborder). The only type specimen (MNHN.F.R10978) is a coral colony without a polished section and without cutting marks that would show that thin sections have been obtained from it. It is plocoid, the calices have an elliptical outline. The septa are compact, free, and show swollen inner margins. The columella is lamellar and thick. The type species is the only species, and its type is the only known sample. For the moment it is not possible to decide whether the genus belong to the Hemiporitidae family, but it is possible.

Genus *Placohelia* Pocta, 1887

TYPE SPECIES. — *Placohelia rimosa* Pota, 1887 (by monotypy).

REMARKS

The genus was revised by Eliášová (1991) and based on microstructural features was assigned to the Rhipidogyridae family. Thin sections obtained from the type specimen of the type species are poorly preserved and do not show any trace of microstructure. In its general structure – plocoid, free compact septa, lamellar columella – the material resembles members of the Hemiporitidae family.

Genus *Nefocoenia* Oppenheim, 1930.

TYPE SPECIES. — *Araeacis lobata* Reuss, 1854 (by subsequent designation by Wells [1936]).

REMARKS

The genus was assigned by several authors (Alloiteau 1952; Baron-Szabo 1997) to the Hemiporitidae family. Oppenheim (1930: 417) did not base the new genus on the type material of its type species but material from his own collection that he believed identical to the species established by Reuss (1854). The type material of *Araeacis lobata* is not available and lost according to Beauvais (1982). The material depicted by Oppenheim (1930: pl. 19, fig. 6) shows long costae with a pronounced ornamentation. This sample appears much more like a genus of the Placocoeniidae family. Beauvais (1982) assigned the material described by Oppenheim (1930) to the genus *Neocoeniopsis* Alloiteau, 1957 (see above). Topotypical material assigned by Felix

(1903) to *Araeacis lobata* shows a structure different from that described by Oppenheim (1930): thick septa, in a regular hexameral symmetry with the first cycle disproportionately thicker than those of the other cycles (as in certain stylinids, rhipidogyrids and genera formerly or currently assigned to the Meandrinidae family such as *Meandroria*). The septa show a dark median line with small branches resulting in spines at the lateral septal faces. The septa are made of very small trabeculae. *Nefocoenia* does not belong to the Hemiporitidae family.

Genus *Placocaeniopsis* Alloiteau, 1952

TYPE SPECIES. — *Placocaeniopsis arnaudi* Alloiteau, 1952 (by original designation).

REMARKS

The genus, originally assigned to the Hemiporitidae, is according to Alloiteau (1952: 641) closely related to *Hemiporites* and *Phyllastraea*. The type of the type species is kept at the MNHN (MNHN.F.R10951) and was available for study, however it does not allow a diagnosis. Thin sections obtained from the type specimen in the past could not be found in the MNHN.F collection.

Genus *Placocolumastrea* Reig Oriol, 1989

TYPE SPECIES. — *Placocolumastrea torallolensis* Reig Oriol, 1989 (by original designation).

REMARKS

The genus was originally assigned to the Hemiporitidae family. Because of its septal faces ornamented with thorns and the equal thickness of septa it belongs to the Columastraeidae family.

DISCUSSION

The suborder Faviina is very rich in families and genera (*c.* 300). It appeared in the Middle Jurassic and persists into the present. The most important families are the Middle Jurassic to Early Cretaceous Montlivaltiidae, Middle Jurassic to Cretaceous Columastraeidae, Middle Jurassic to Extant Faviidae, Late Jurassic to Cretaceous Eugyridae, Late Cretaceous Placosmiliidae, Placocoeniidae and Brachyphylliidae. They can be grouped as follows: 1) the Montlivaltiidae and Placosmiliidae-forms with large calices, septa in two, rarely in three generations, without symmetry, septal lateral faces with vertical carinae, rare wall, and well developed endotheca; 2) Columastraeidae, Brachyphylliidae and Placocoeniidae-cerioid and plocoid forms with circular or polygonal calices, a regular hexameral septal symmetry, septal lateral faces with thorns, present wall and endotheca; 3) Eugyridae-meandrinoid and hydnophoroid members, almost smooth septal lateral faces, present wall and endotheca; 4) Cladocoridae-mainly phaceloid forms; and 5) Hemiporitidae-plocoid and cerioid forms without regular septal symmetry and septal faces with occasional thorns. Apart from these large groups exist some families with few genera (Diplocteniopsidae, Merulinidae, Mussidae, Oculinidae) and the very large family Faviidae, which consists of all genera that do not fit into one of the other families.

Hemiporitids are rather isolated within the suborder. They are most closely related to the Placocoenids, differing in a less regular septal symmetry, a more pronounced columella and much shorter costae. The family probably evolved together with the Placocoeniidae and Brachyphylliidae after OAE2 (Erba 2004) and has roots – together with the other two families – in the Columastraeidae.

The family Hemiporitidae shows a particular distribution pattern: it is only found in tropical regions. It is absent from the extremely species rich fauna of the Gosau Group (Austria; Turonian-Campanian), and is so far only found in the Late Cretaceous of southern France, Spain, and the Arabic Peninsula.

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