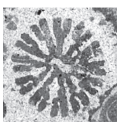
Middle Albian corals from the Espinazo del Diablo Formation (Lampazos area, Sonora, Mexico)

Alejandro Samaniego-Pesqueira, Hannes Löser & Josep Anton Moreno-Bedmar



In this study, we describe a coral fauna from limestones of the Middle Albian, in the Espinazo del Diablo Formation, at a distance of 10 km to the southeast of Tepache town, which is in the Lampazos area of Mexico. The corals did not form bioconstructions. A total of 46 species assigned to 22 genera that belong to the superfamilies Actinastraeoidea, Cladocoroidea, Cyclolitoidea, Eugyroidea, Heterocoenioidea, Misistelloidea, Stylinoidea, and Thamnasterioidea are reported. One genus and three species are described as new. The new genus *Pentacoeniopsis* belongs to the family Solenocoeniidae. The generic composition shows that the fauna is dominated by Early Cretaceous corals, and almost all species were indicated in the Early Aptian and Early Albian. Four genera have a range beyond the Santonian. Due to the relatively high number of endemic taxa, the coral fauna of the Lampazos area shows a low number of species that are shared with other studied areas, and coral fauna of the Bisbee Basin are the nearest with only 15 shared taxa. •
Key words: corals, Scleractinia, Albian, Sonora, Mexico, Cretaceous, taxonomy, new taxa.

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Early Cretaceous shallow marine coral faunas from northwestern Mexico have been reported at an increasing rate during the past 20 years (Baron-Szabo & González-León 1999, 2003; Löser 2011a, 2013a, 2015b, 2016b). Most of the shallow marine deposits of northern Mexico belong to the Lower Cretaceous, such as the Late Barremian to Early Aptian lower Cerro de Oro Formation (González-León & Lucas 1995), the Late Aptian to Early Albian Mural Limestone in Sonora (González-León *et al*. 2008), and the Early Albian Alisitos Formation from Baja California (Payne *et al*. 2004, Masse *et al*. 2007). Shallow marine rocks of a comparable age in the USA are known from Arizona (Stoyanow 1949; Scott 1979, 1981, 1987), New Mexico (Kues & Lucas 2001, Turnšek *et al*. 2003), and Texas (Löser & Minor 2007). It is noteworthy that the lower Mural Limestone is represented by siliclastic rock, while the upper Mural Limestone and the Alisitos Formation are carbonates.

The invertebrate fossils – including corals – from the Albian Espinazo del Diablo Formation in Sonora are until now poorly reported, in comparison with the above-mentioned areas. The preliminary report of the coral fauna (Baron-Szabo & González-León 1999) noted 13 species. Most of these species were not reported from the Upper Aptian to Lower Albian rocks of the nearby Mural Formation. Due to the close paleogeographic position of the coral fauna from the Bisbee Basin in the present study, a similar taxonomic composition could be expected, even if both faunas show a small difference in age. Further, the coral faunas from the Mural Formation range from the Late Aptian to Early Albian, but those from the Espinazo del Diablo Formation are of a Middle Albian age. Coral faunas, such as various Middle Albian formations (which are species-poor) of the Fredericksburg Group of the Texas platform (Wells 1933), are poorly known (Löser 2013a, 2016b). Middle Albian shallow marine corals are also known from Greece (Löser & Raeder 1995). Apart from this, all coral records of the Middle Albian are restricted to small solitary ahermatypic deep-water corals. A more detailed examination of the coral fauna of the Espinazo del Diablo Formation in Mexico does, therefore, fills a gap in the knowledge of Albian coral faunas at a global scale.

Geological setting

Outcrops of Lower Cretaceous rocks are restricted in the Sonora State because the Tertiary volcanic rocks cover great extensions (Scott & González-León 1991). The more important Cretaceous are, predominantly, the marine sequences of Sonora State, the Bisbee Group in north Sonora, and the Lampazos in east-central Sonora (Scott & González-León 1991). The present work is focused on the Albian coral record of the Sierra Espinazo del Diablo within the Lampazos area, where a Lower Cretaceous succession (Aptian–Albian) consists of an approximately 2,500 m thick sedimentary log that is exposed (González-León 1988). The Cretaceous strata has been affected by the Cretaceous–Paleogene Mexican orogen (Fitz-Díaz *et al*. 2018), consisting of at least two episodes of normal faulting, and also by Tertiary intrusive and effusive volcanic rocks (Scott & González-León 1991, Monreal & Longoria 2000). The more visible structures in the Sierra Espinazo del Diablo are tight folds trending northwest-southeast, with a vergence towards the southwest (Monreal & Longoria 2000).

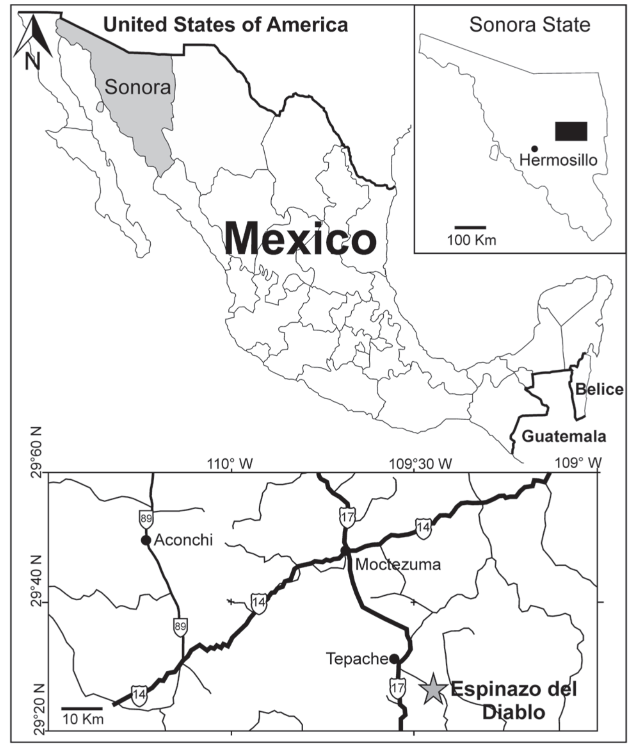


Figure 1. Location of Espinazo del Diablo Formation.

Study area

The Lampazos Group (González-León *et al*. 2008) is composed of several formations: El Aliso, Agua Salada, Espinazo del Diablo, and Nogal, which is lateral equivalent to the Los Picachos Formation (Herrera & Bartolini 1983, González-León 1988). In the present work, we take three sections of the Espinazo del Diablo Formation (29° 26′ 27.1″ N, 109° 27′ 27.6″ W; 29° 26′ 59.8″ N, 109° 28′ 20.9″ W; 29° 26′ 30.2″ N, 109° 27′ 28.3″ W), a calcareous formation in the middle-east of Sonora State, which is located 10 km to the southeast of Tepache town (Fig. 1). In this area there is an emergence of Early Cretaceous rocks (Scott & González-León 1991, Monreal & Longoria 2000), within which one can find a large number of fossils of different kinds: orbitolinids, bivalves, gastropods, foraminifera, rudists, and corals. Based on this, González-León (1988) assigned the Espinazo del Diablo Formation to the Early Albian.

The Agua Salada Formation, which was described by Herrera & Bartolini (1983) and later amended by González-León (1988), corresponds to a 250–350 m thick unit of basinal limestones and marls. The marls predominate in the upper part of the formation. The age of this formation is late Aptian to earliest Albian (Robert *et al*. 2018, Samaniego-Pesqueira *et al*. 2021). The Lampazos Formation overlies the Agua Salada Formation.

The Lampazos Formation was originally introduced in the literature by Solano Rico (1970) and Herrera & Bartolini (1983), and later redefined by González-León (1988). This formation is about 500 to 600 m thick, and mainly constituted by an alternation of limestones and thin marly intervals, sedimented in an open marine environment. In the Lampazos area, the age of this formation is Early to Middle Albian, according to González-León & Buitrón (1984). However, Monreal & Longoria (2000) extended its age range to the late Aptian–Middle Albian. In the Agua Salada area, between the uppermost Agua Salada Formation and the lowermost part of Lampazos Formation, ammonoids occur that indicate the Aptian-Albian boundary interval (Robert *et al*. 2018, Samaniego-Pesqueira *et al*. 2021). Therefore, the Lampazos Formation must be restricted to the Albian, as was also recently proposed by Saucedo-Samaniego *et al*. (2021). The studied fossils described in this paper come from the lower part of the Espinazo del Diablo Formation. This lithostratigraphic unit was originally introduced in the literature by Herrera & Bartolini (1983), and later redefined by González-León (1988). It can be subdivided into two parts: (1) the lower part, which is about 15 to 20 m thick, represents a thick-bedded to massive-bedded light gray limestone, that contains abundant rudists, corals, and orbitolinids; (2) the upper part, which is about 100 m thick, consists of an alternation of nodular thin-bedded to medium-bedded, locally fossiliferous limestone, and thin-bedded to thick-bedded shale and sandstone. The Espinazo del Diablo Formation ranges in thickness from 100 to 400 m and is mainly exposed in the Sierra Espinazo

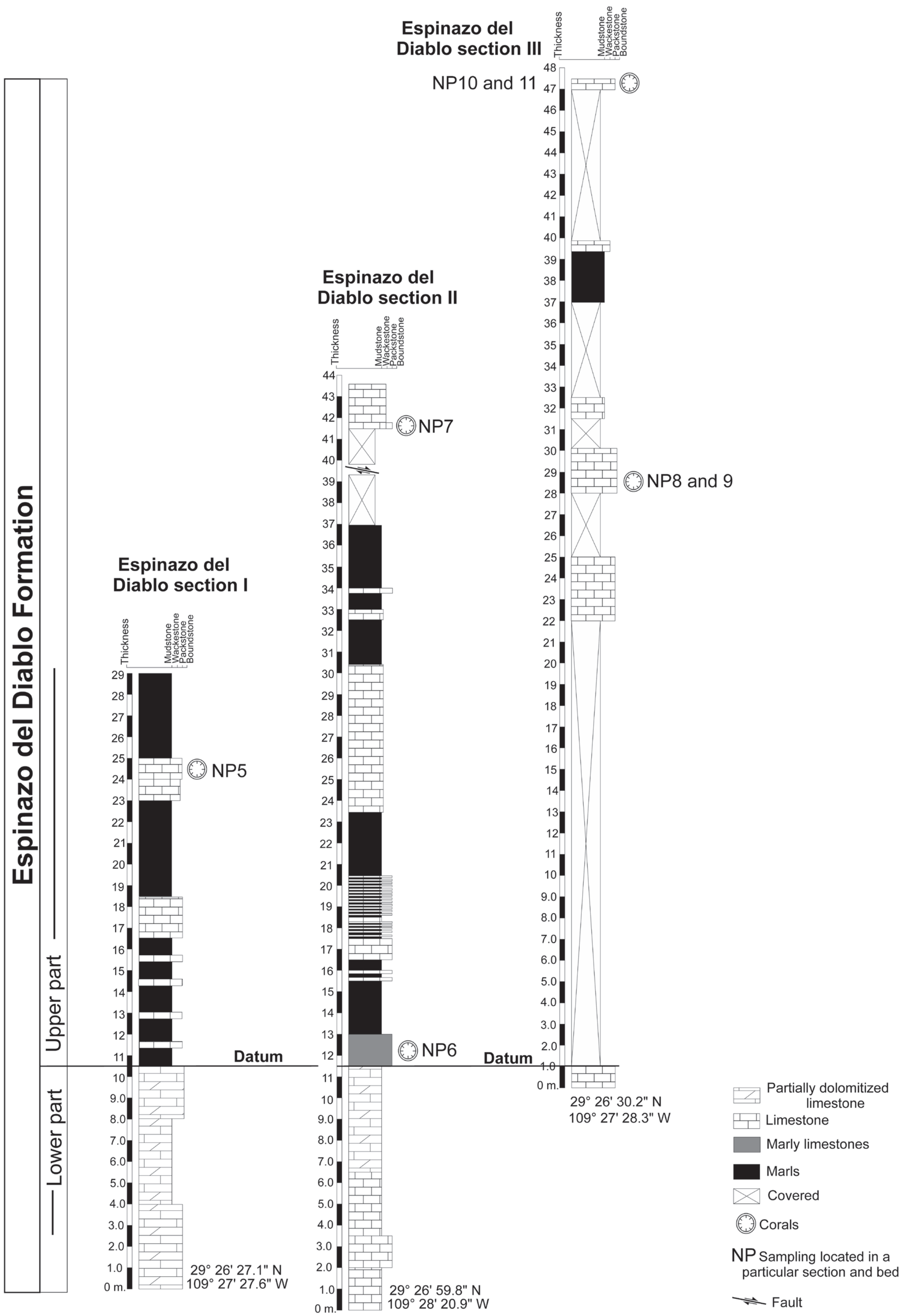


Figure 2. Stratigraphic sections I, II, and III of the Espinazo del Diablo Formation.

del Diablo and the Sierra de las Azules. In the landscape, this lithostratigraphic unit is easily recognizable because is more resistant to erosion than the underlying and overlying units. The Picachos and Nogal formations overlie the Espinazo del Diablo Formation.

The Picachos and the Nogal are the uppermost units of the Cretaceous sequence in the Lampazos area, and they are laterally equivalent. The Nogal Formation was described by González-León (1988), who subdivided it into three members: Member 1 is constituted by an alternation of shale and thin-bedded fine-grained sandstone, which is about 190 m in thickness. This member contains a rich record of gastropods and oysters. Member 2 was also sedimented in shoal marine environments, and is constituted by limestones with rudists, corals, algae, orbitolinids, and miliolids, exhibiting a thickness of 190 m. Member 3 is constituted by gray to reddish shales in the lower part of the member, and yellow shales in the upper part, where it alternates with thin-bedded sandstones and marly limestones. This member was deposited in an open marine environment and contains Upper Albian ammonites, that were recently studied by Robert *et al*. (2018). This member also contains other mollusks, such as bivalves and gastropods, and other fossils, such as echinoids. Its thickness is about 230 m. The Picachos Formation was proposed by Herrera & Bartolini (1983), and later amended by González-León (1988), as alternating limestones and shales. This formation, which was deposited in a shoal marine-restricted setting containing miliolids, bivalves, and gastropods, reaches a maximum thickness of 900 m.

Three stratigraphic sections were studied and named as Espinazo del Diablo I to III, because they were measured in the Sierra Espinazo del Diablo (Fig. 2). As previously noted, the Espinazo del Diablo Formation can be divided into two units: (1) the lower unit being a 15 to 30 m thick massive-bedded limestone, and (2) the upper unit being about 100 m thick and consisting of more heterogenous thin-bedded to medium-bedded limestones and nodular limestones, alternated with marly-limestones, marls, and sandstones. The boundary between the two units is very conspicuous, and we use this as a correlation marker in three studied sections (Fig. 2). The lower limestone-dominated unit contains, in some stratigraphic intervals, an abundant shoal marine fauna. The most abundant fossils are rudists, oysters, other bivalves, and corals. Despite the presence of corals, these intervals were not sampled because the corals are poorly preserved, due to the fact that the limestones were partially dolomitized (Fig. 2). All of the samples (NP5 to NP11) come from the upper unit (Fig. 2), which also contains a shoal marine fauna of oysters, other bivalves, corals, and orbitolinids. In this unit, the preservations of the corals are considerably better, and this has allowed their proper study, by means of thin sections.

Material

Most material studied was collected during fieldwork in 2013. Specimens described by Baron-Szabo & González-León (1999) were included, but could not be assigned to a specific bed within the above-shown sections (sample points BS and P4). The number of collected samples was about 300, of which 160 could be assigned to a genus. The material varies in its state of preservation, from poorly preserved specimens in most cases, to a good grade of preservation in some specimens. Notwithstanding, the relatively poor state of preservation of the corals considerably limits the taxonomic classification (especially with the new taxa). Only thin sections were used for the determination. The material described here is housed in the collection of the Universidad Nacional Autónoma de México, Instituto de Geología, Estación Regional del Noroeste (ERNO) in Hermosillo, Sonora State, Mexico.

Methods

Coral specimens were cut and polished. Thin sections in both transversal and longitudinal orientation were prepared where possible. Thin sections were scanned by passing light through them, using a flatbed scanner with an optical resolution of 6,400 dpi. Scanned images were then transferred to grayscale bit maps. Their quality was amended by histogram contrast manipulation (contrast stretching) where possible.

To gain more insight into the intraspecific variation of fossil corals, and to obtain a better strategy for comparing species, calicular dimensions of one or two thin sections of each species were systematically measured. To achieve statistical significance, the largest number of possible measurements was taken. This number was mainly determined by the size and quality of the thin section, and the size of the single corallites in relation to the size of the thin sections.

In colonial corals, for each type of measurement (calicular diameter and distance, width and distance of calicular row, septa per corallite) numerous values were recorded. The following statistical values were obtained from these measurements and counts: n – number of measurements; min–max – lowest and highest measured values; μ – arithmetic mean (average); s – standard deviation; v – Pearson's coefficient of variation; μ±s – first interval.

Thin sections were measured, and values were calculated using the Paleontological Database System PaleoTax, module PaleoTax/Measure (*https://www.paleotax.de/measure*; for details on the statistical background, refer to the work of Löser 2012). Characters that were visible on the fossils were compared against characters on specimens in worldwide fossil coral collections, and an associated image database [with 28,500 specimens, of which nearly 16,500 specimens are illustrated, all located in the Estación Regional de Noroeste (ERNO), Sonora State, Mexico]. Data storage and processing were carried out using the PaleoTax database programme (Löser 2004).

To compare the studied fauna with other coral faunas outside of the study area, a computer database of about 2,700 worldwide coral localities with coral indications was used (Löser 2002, 2005). To simplify the analysis, localities of the same age, within the same basin, on the same continental margin, or on the same interoceanic platform, were grouped together into one paleo-province (a type of large faunule, *sensu* Johnson 2007). Altogether, this produced 310 provinces. Only firmly dated localities were assigned to a province, to ensure that the following analysis is valid, and also to ensure that the studied locality was not included in any existing province. For the study area, an independent province was created, to allow a clear comparison between the existing provinces and the new material.

Interregional comparisons were carried out, between the new province and existing provinces which have at least three species in common with the fauna of the studied area. For details, see also Löser (2008a) and Löser & Minor (2007).

Systematic part

As already discussed in Löser *et al*. (2018) and Löser & Heinrich (2018), the preliminary classification system introduced by Löser (2016d) is used here. This system does not apply suborders, but instead it applies super-families that group families together. There are certain suborders that seem to be well-defined, adequately limited and easy to recognize; however, other suborders are poorly understood, without meaning, or they combine very heterogenous families. If we put the families of those suborders that seem to be well-defined to one side and focus on the remaining families that are in questionable suborders or even without suborder, it can be seen that there is a large number of families for which new suborders should be created. Since it does not make much sense to try to solve classification problems just by the introduction of new taxa, Löser (2016d) proposed for the moment not to apply suborders, but to apply superfamilies that group families together. Practically, suborders were replaced by superfamilies. In this way 27 superfamilies with 56 families (or informal groups) are distinguished. Families are much better-defined units than suborders, and they are covered by the Rules of Zoological Nomenclature (quite probably, being covered by the rules makes them better defined subunits). Moreover, contrary to the former classification system of suborders, the superfamilies may constitute monophyletic groups. A table that compares suborders and superfamilies was published in Löser (2016d: p. 63) and Löser *et al*. (2018: p. 34).

The basic characteristics for the definition of the superfamilies is the relative size of the trabeculae, in the ratio to the septa. Further distinction is based on the presence or absence of synapticulae and the septal perforation. Detailed discussion is given in the superfamilies and families description. In Mesozoic scleractinian corals the species within a genus are entirely distinguished on the basis of morphometric data (principally the dimensions of the corallite, the number and/or density of septa). Because the verbal description of the species would be the same for all species of the same genus, verbal descriptions are only given for the family and genus level. These descriptions are principally based on the type material (types of type species of genera).

The distribution data (as reflected in the synonymy lists) are almost entirely based on well-examined material; material that was not available for study and specimens insufficiently described and illustrated in the literature were not considered. To obtain better insight into the distribution patterns of the coral fauna of the Lampazos area, additional unpublished material was included. Therefore, distribution data indicated under 'Other occurrence' are also provided for species remaining in open nomenclature.

The abbreviations used in the synonymy lists follow Matthews (1973): * – earliest valid publication of the species name; p – the described material belongs only in part to the species concerned; v – the specimen was observed by the second author. A year in italics indicates that the quotation is provided with neither a description nor an illustration.

Institutional abbreviations: ERNO – Universidad Nacional Autónoma de México, Instituto de Geología, Estación Regional de Noroeste, Hermosillo, Mexico; PU – Museo di Geologia e Paleontologia dell' Università di Torino, Torino, Italy.

Abbreviations of measurements: c – calicular diameter (outer diameter); ccd – distance between calicular centres; cl – calicular diameter (lumen, calicular pit); clmax – large lumen; clmin – small lumen; cmax – larger outer calicular diameter; cmin – smaller outer calicular diameter; crd – distance of calicular series; crw – width of calicular series; s – number of septa in the adult corallite; sd – density of septa.

The following abbreviations are used in describing the dimensions of the corals: c – calicular diameter (outer diameter); ccd – distance between calicular centers; cdw – distance between calicular centers within calicular series; cl – calicular diameter (lumen, calicular pit); clmax – large lumen; clmin – small lumen; cmax – larger outer calicular diameter; cmin – smaller outer calicular diameter; crd – distance of calicular series; sd – density of septa; septa – number of septa in the adult corallite; sk – number of septa which reach the columella; sp – number of primary septa; td –density of trabeculae; w – wall thickness.

Superfamily Actinastreoidea Alloiteau, 1952

Description. – Cerioid, phaceloid, or plocoid colonies. Septa compact, mostly in a regular radial symmetry. Septa often connected to each other. Lateral faces with thorns, upper margin granulated. Microstructure of septa of medium-sized trabeculae. Lonsdaleoid septa present in one genus, main septa absent. Synapticulae absent. Pali in some genera present, columella in most genera. Endotheca varies, generally made of thin tabulae. Wall compact or subcompact, mainly septothecal. Marginarium in one genus. Coenosteum generally present, consists of isolated trabeculae or costae. Budding extracalicinal and intracalicinal.

Family Actinastreidae Alloiteau, 1952

Genus *Actinastraeopsis* Sikharulidze, 1977

Type species. – *Actinastraeopsis phaceloides* Sikharulidze, 1977.

Description. – *Actinastraeopsis* is a phaceloid coral with a corallite diameter of less than seven millimeters. The genus and its species were just recently revised in Löser (2013c).

***Actinastraeopsis birleyoe* (Gregory, 1899)**
Figure 4A

*v 1899 *Cladophyllia Birleyoe* Gregory; p. 457, text-fig. 1.
v 1944 *Cladophyllia stewartae* Wells, n.sp. – Wells, p. 442, pl. 74, figs 2, 3.
v 1997 *Pleurophyllia* sp. 2. – Baron-Szabo, p. 74, pl. 9, fig. 5.
2005 *Actinastraeopsis sikharulidzeae* Bugrova sp. nov. – Bugrova, p. 140, fig. 2, pl. 2.
v 2013c *Actinastraeopsis birleyoe.* – Löser, figs 1.1, 1.2.
v 2016 *Actinastraeopsis birleyoe.* – Löser & Zell, p. 6.

Material. – ERNO L-134002, L-134201; 1 thin section.

Dimensions. –
(ERNO L-134201)

	n	min–max	μ	s	cv	μ±s
cmin	9	3.27–4.93	4.20	0.60	14.5	3.59–4.81
cmax	9	4.58–5.63	4.98	0.32	6.4	4.66–5.31
ccd	9	2.65–8.17	5.32	2.08	39.1	3.24–7.40
s	31–37					

Remarks. – The species was revised in Löser (2013c); in its dimensions the studied material is very similar to the holotype of *Cladophyllia birleyoe*, but it differs in presenting the beginning of a fourth septal cycle.

Occurrence. – Sample point NP9. Other occurrence: Upper Barremian of the Eastern Tethys (Turkmenistan), Upper Barremian to Lower Aptian of the Central Tethys (Germany), Lower Aptian of the European Boreal (UK) and the Western Atlantic (Venezuela), Lower Albian of the Western Tethys (Spain), Upper Aptian of the Western Tethys (Spain).

***Actinastraeopsis organisans* (d'Orbigny, 1850)**
Figure 3A–C

*v 1873 *Stylosmilia organizans.* – de Fromentel, p. 422, pl. 84, fig. 1.
v 2013c *Actinastraeopsis organisans.* – Löser, figs 1.8–1.12 [= here older synonymy].

Material. – ERNO 2179, L-4311; 4 thin sections.

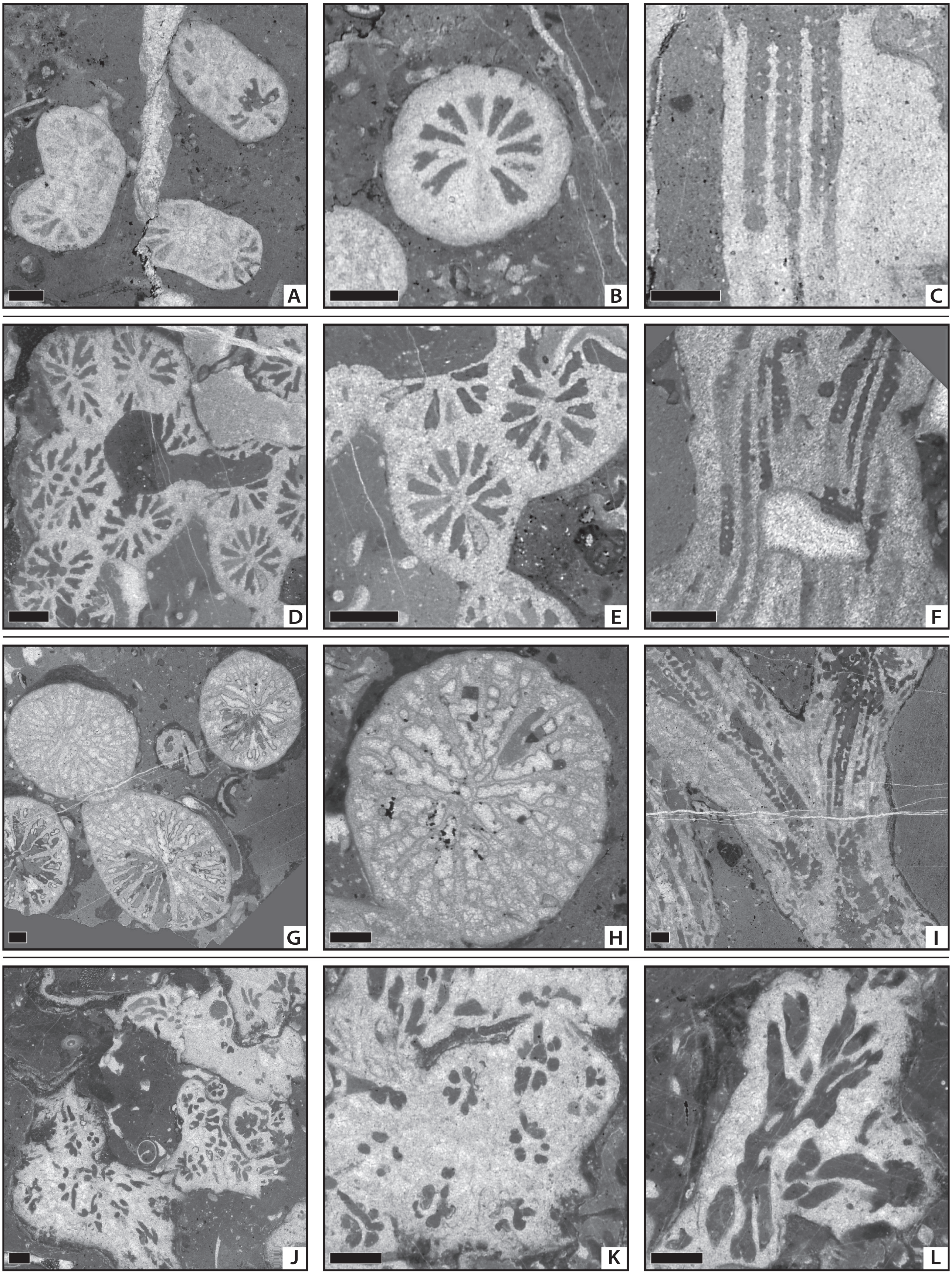
Dimensions. –
(ERNO L-4311)

	n	min–max	μ	s	cv	μ±s
clmin	15	1.30–1.94	1.58	0.20	12.6	1.38–1.79
clmax	15	1.68–2.39	1.96	0.22	11.4	1.74–2.19
cmin	30	1.84–2.51	2.11	0.19	9.2	1.92–2.31
cmax	25	2.34–3.23	2.66	0.25	9.6	2.40–2.92
s	24					

Remarks. – The species was revised in Löser (2013c); the material coincides well with the syntype of *Stylosmilia organizans* and the lectotype of *Cladophyllia miroi*.

Occurrence. – Sample points BS, P4. Other occurrence: Lower Hauterivian of the European Boreal (France), Hauterivian to Lower Albian of the Western Atlantic

Figure 3. A–C – *Actinastraeopsis organisans* (d'Orbigny, 1850), ERNO L-4311; A – transversal thin section; B – detail; C – longitudinal thin section. • D–F – *Actinastraeopsis phaceloides* Sikharulidze, 1977, ERNO L-130304; D – transversal thin section; E – transversal thin section, detail; F – longitudinal thin section. • G–I – *Actinastraeopsis* cf. *tuapensis* (Baron-Szabo & González-León, 2003), ERNO L-130301; G – transversal thin section; H – transversal thin section, detail; I – longitudinal thin section. • J–L – *Stelidioseris hourcqi* (Alloiteau, 1958), ERNO L-134512; J – transversal thin section; K – transversal thin section, detail; L – longitudinal thin section. Scale bar 1 mm.


A
B
C
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(Mexico, Colombia), Barremian of the Western Atlantic (Mexico), Upper Barremian to Lower Upper Aptian of the Western Tethys (France, Spain).

Actinastraeopsis phaceloides **Sikharulidze, 1977**
Figure 3D–F

*1977 *Actinastraeopsis phaceloides* Sikharulidze; p. 72, pl. 6, fig. 2, pl. 7, fig. 2, pl. 8, pl. 9, fig. 1, pl. 10, figs 1–6.
2013c *Actinastraeopsis phaceloides.* – Löser, fig. 2.1.

Material. – ERNO L-130304; 2 thin sections.

Dimensions. –
(ERNO L-130304)

	n	min–max	μ	s	cv	μ±s
clmin	21	1.01–1.37	1.16	0.10	8.8	1.05–1.26
clmax	20	1.39–1.92	1.65	0.17	10.4	1.47–1.82
cmin	11	1.40–1.80	1.54	0.12	7.7	1.42–1.66
cmax	11	1.83–2.37	2.03	0.16	7.9	1.87–2.20
ccd	20	1.61–2.31	1.85	0.17	9.2	1.68–2.03
s	10	17–23	20.1	1.66	8.2	18–22

Remarks. – The species was recently revised in Löser (2013c). The studied material has slightly smaller corallite dimensions than the material of Sikharulidze (1977).

Occurrence. – Sample point NP6. Other occurrence: Hauterivian of the Eastern Tethys (Georgia).

Actinastraeopsis **cf. *tuapensis*** **(Baron-Szabo & González-León, 2003)**
Figure 3G–I

v 1998 *Procladocora* cf. *simonyi* (Reuss 1854). – Schöllhorn, p. 90, pl. 22, figs 1, 2.
v 1999 *Pleurophyllia* aff. *trichotoma* Fromentel, 1856. – Baron-Szabo & González-León, p. 481, fig. 4f.
v 2013c *Actinastraeopsis* sp. – Löser, p. 7, fig. 3d.

Material. – ERNO 2197, L-130301, L-134204; 5 thin sections.

Dimensions. –
(ERNO L-130301)

	n	min–max	μ	s	cv	μ±s
clmin	13	3.56–4.89	4.17	0.37	9.1	3.79–4.55
clmax	11	4.34–5.80	4.97	0.39	8.0	4.57–5.36
cmin	25	4.79–6.92	5.78	0.56	9.8	5.21–6.35
cmax	21	5.37–7.42	6.38	0.56	8.8	5.81–6.94
ccd	20	5.65–7.92	6.80	0.76	11.2	6.03–7.56
s	48					

Remarks. – The studied material differs from the type material of *Actinastraeopsis tuapensis* in larger corallite dimensions. It represents probably a new species.

Occurrence. – Sample points NP6, NP9, BS. Other occurrence: Uppermost Aptian to Lower Albian of the Western Tethys (Spain, France).

Genus *Stelidioseris* Tomes, 1893

Type species. – Stelidioseris gibbosa Tomes, 1893.

Description. – Plocoid colony with a very narrow coenosteum that is made up of confluent costae. Corallites circular or polygonal. Septa in a regular radial symmetry. Septa of the first and second generations can be connected to the columella, younger septa can be connected to older septa. Septa of the second generation may be centrally swollen. Columella styliform and large. No pali. The genus was revised by Löser (2012).

Stelidioseris hourcqi **(Alloiteau, 1958)**
Figure 3J–L

*v 1958 *Actinastraea Hourcqi* n.sp.; Alloiteau, p. 108, pl. 6, fig. 8, pl. 7, fig. 3.
v 2013a *Stelidioseris hourcqi* (Alloiteau 1958). – Löser, Castro & Nieto, p. 12, pl. 1, figs 5, 6 [= here older synonymy].

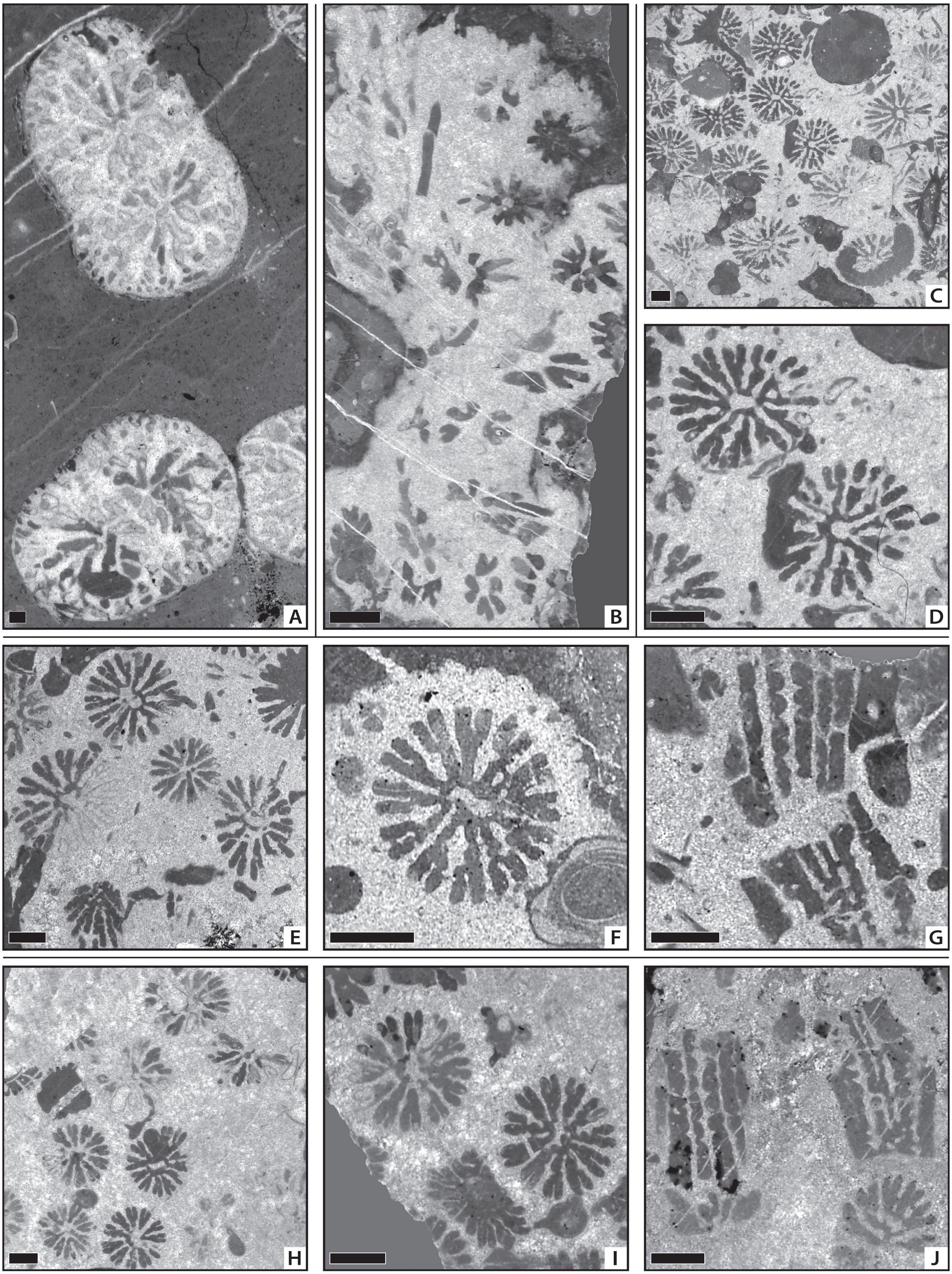
Material. – ERNO L-134512; 1 thin section.

Dimensions. –
(ERNO L-134512)

	n	min–max	μ	s	cv	μ±s
clmin	25	0.64–1.17	0.86	0.13	15.4	0.72–0.99
clmax	12	0.84–1.52	1.05	0.20	19.1	0.84–1.25
ccd	23	0.91–1.67	1.31	0.23	17.8	1.07–1.54
s	20	8–12	9.30	1.38	14.8	8–11

Remarks. – Astrocoenia scyphoidea has the priority over *Stelidioseris hourcqi*, but the type specimen of the first species is poorly preserved and has no polished section. So *Stelidioseris hourcqi* is given the preference.

Figure 4. A – *Actinastraeopsis birleyoe* (Gregory, 1899), ERNO L-134201, transversal thin section. • B – *Stelidioseris* sp., ERNO L-130108, transversal thin section. • C, D – *Eocolumastrea neuquensis* (Gerth, 1928), ERNO L-120519; C – transversal thin section; D – transversal thin section, detail. • E–G – *Eocolumastrea gortanii* (Prever, 1909), ERNO 2187; E – transversal thin section; F – transversal thin section – detail; G – longitudinal thin section. • H–J – *Eocolumastrea ramosa* (Stoliczka, 1873); H, I – ERNO L-130113, transversal thin section (H) and transversal thin section (I); J – ERNO L-130113, longitudinal thin section. Scale bar 1 mm.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Occurrence. – Sample point NP5. Other occurrence: Upper Barremian to Lower Aptian of the Western Atlantic (Mexico) and the Central Tethys (Germany), Upper Barremian to Upper Albian of the Western Tethys (France, Spain), Lower Aptian of the Central Tethys (Italy), Lower Albian of the Western Atlantic (Mexico, USA), Upper Albian of the Southern Tethys (Madagascar), Upper Cenomanian of the European Boreal (Czech Republic).

***Stelidioseris* sp.**
Figure 4B

Material. – ERNO L-130108; 1 thin section.

Dimensions. –
(ERNO L-130108)

	n	min–max	μ	s	cv	μ±s
clmin	25	0.72–1.19	0.93	0.12	12.9	0.81–1.05
clmax	20	0.98–1.38	1.17	0.11	9.7	1.05–1.28
ccd	25	1.13–2.13	1.54	0.29	18.8	1.25–1.83
s	12					

Remarks. – The material compares to *Stelidioseris hourcqi* but has clearly larger corallite dimensions. It compares also to *Stelidioseris ruvida* but has smaller dimensions than this species.

Occurrence. – Sample point NP5. Other occurrence: Valanginian to Aptian of the Western Atlantic (Mexico), Upper Barremian of the Western Tethys (France).

Superfamily Cladocoroidea d'Orbigny, 1851

Description. – Solitary and (cerioid, phaceloid, plocoid) colonial corals. Septa compact. Septal in regular thickness. Septal symmetry radial, regular or sub-regular. Septa often connected to each other. Septal lateral faces with thorns and/or granulae, septal upper margin with fine granulations. Lonsdaleoid septa and main septum absent. Microstructure of medium-sized trabeculae. Synapticulae absent. Pali present in some genera. Columella present in most genera, styliform, lamellar, parietal, or by septal fusion. Endotheca generally present. Marginarium absent. Wall present, septothecal; by septal thickening or by septa-like mural elements. Coenosteum present in plocoid genera. Budding extracalicinal (cerioid, plocoid) or intracalicinal (phaceloid).

Family Columastreidae Alloiteau, 1952

Description. – Plocoid colonies. Septal symmetry regular radial and mostly hexameral. Pali present in some genera. Columella varies: styliform, styliform and double, lamellar, or absent. Coenosteum with costae.

Genus *Eocolumastrea* Löser & Zell, 2015

Type species. – Columnocoenia bucovinensis Morycowa, 1971.

Description. – Plocoid coral with septa in a regular hexameral or decameral symmetry. Columella lamellar or small and styliform. Irregular pali at the first septal cycle, not very pronounced. Coenosteum narrow.

***Eocolumastrea gortanii* (Prever, 1909)**
Figure 4E–G

*v 1909 *Ulastraea Gortanii* Prever; p. 91, pl. 5, figs 6, 7.
v 2021 *Eocolumastrea gortanii* (Prever, 1909). – Garberoglio, Löser & Lazo, p. 6, fig. 5 [= here older synonymy].

Material. – ERNO 2187, 2188-I, 2189, L-120524, L-130101, L-130102, L-134001, L-134206, L-134301; 11 thin sections.

Dimensions. –
(ERNO 2187)

	n	min–max	μ	s	cv	μ±s
clmin	15	1.97–2.53	2.27	0.19	8.6	2.07–2.46
clmax	15	2.07–2.96	2.61	0.25	9.8	2.35–2.87
ccd	20	2.98–4.10	3.43	0.34	10.0	3.09–3.78
s	10	22–24	23.4	0.96	4.1	22–24

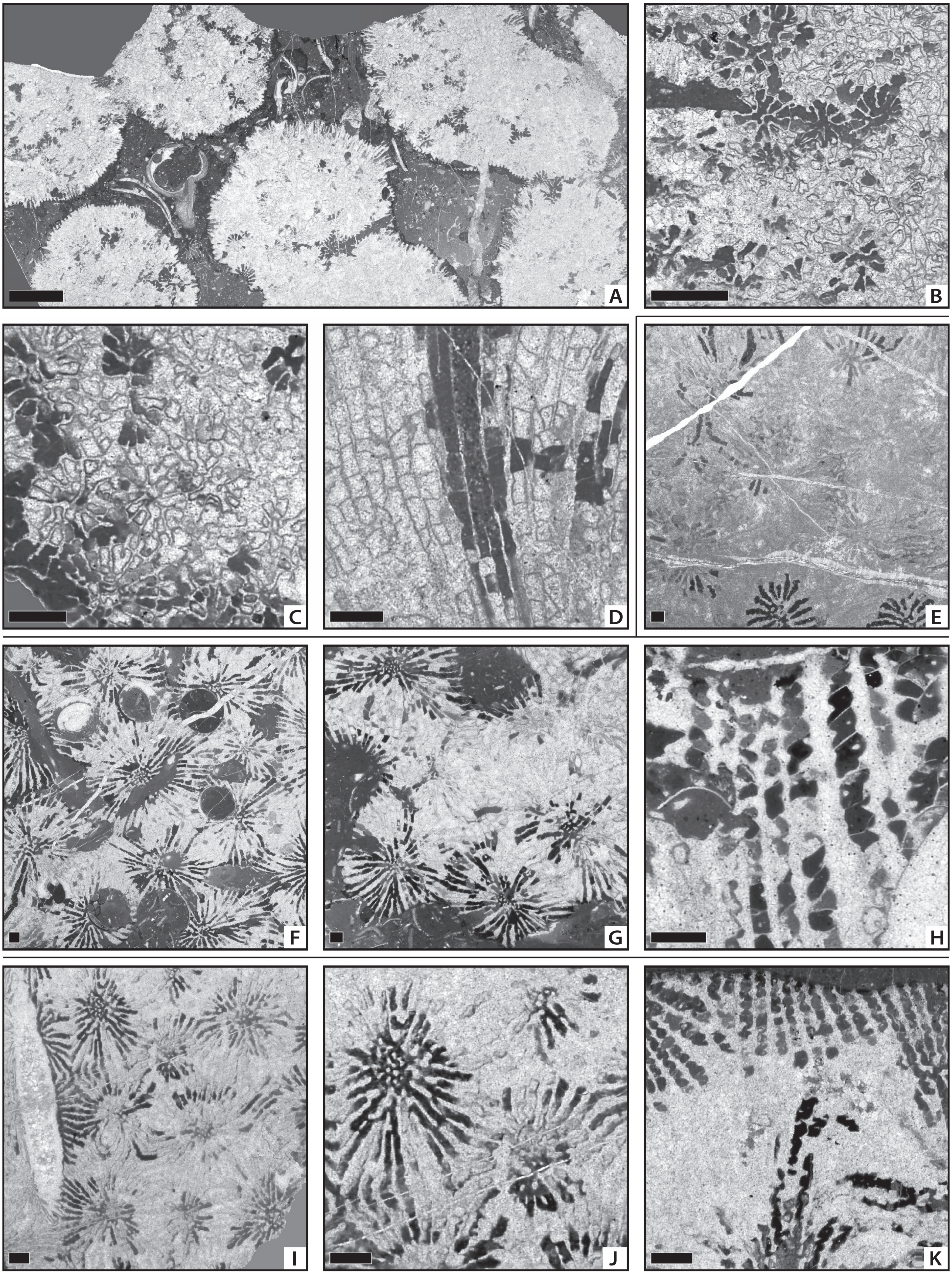
Remarks. – The material coincides well with the type material of the species and was just recently described in detail by Garberoglio *et al*. (2021).

Occurrence. – Sample points BS, NP5, BS. Other occurrence: The species has a worldwide distribution between the Upper Hauterivian and the Middle Cenomanian.

***Eocolumastrea neuquensis* (Gerth, 1928)**
Figure 4C, D

*v 1928 *Placocoenia neuquensis* Gerth; p. 6, pl. 1, fig. 5.
v 2021 *Eocolumastrea neuquensis* (Gerth, 1928). – Garberoglio, Löser & Lazo, p. 8, fig. 7 [= here older synonymy].

Figure 5. A–D – *Eocolumastrea* sp., ERNO L-130121; A – transversal thin section; B – transversal thin section, detail; C – transversal thin section, detail; D – longitudinal thin section. • E – *Astraeofungia decipiens* (Michelin, 1841), ERNO L-130303, transversal thin section. • F–H – *Ampakabastraea* sp. 1, ERNO L-134214; F – transversal thin section; G – transversal thin section – detail; H – longitudinal thin section. • I–K – *Ampakabastraea* sp. 2, ERNO L-134505; I – transversal thin section; J – transversal thin section – detail; K – oblique thin section. Scale bar 1 mm.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Material. – ERNO L-120518, L-120519; 1 thin section.

Dimensions. –
(ERNO L-120519)

	n	min–max	μ	s	cv	μ±s
clmin	35	1.88–3.06	2.52	0.33	13.4	2.18–2.86
clmax	30	2.40–4.34	3.22	0.51	15.8	2.71–3.74
ccd	35	2.38–5.32	3.67	0.82	22.3	2.85–4.49
s	24					

Remarks. – The material coincides in its corallite dimensions with the syntypes of the species (clmin = 2.5–2.9, ccd = 3.3–4.5, s = 24). The species was recently discussed in greater detail by Garberoglio *et al*. (2021).

Occurrence. – Sample point NP5. Other occurrence: The species has a world-wide distribution between the Upper Hauterivian and the Upper Cenomanian.

Eocolumastrea ramosa **(Stoliczka, 1873)**
Figure 4H–J

*v 1873 *Holocoenia ramosa* Stoliczka; p. 24, pl. 4, figs 4, 5.
v 2018 *Eocolumastrea gortanii* (Prever, 1909). – Löser, Steuber & Löser, p. 36, pl. 1, figs 7–9 [= here older synonymy].

Material. – ERNO L-130113, L-130122, L-134210, L-134302; 3 thin sections.

Dimensions. –
(ERNO L-130113)

	n	min–max	μ	s	cv	μ±s
clmin	15	1.88–2.42	2.10	0.15	7.5	1.94–2.26
clmax	15	2.15–2.96	2.55	0.24	9.6	2.30–2.80
ccd	15	2.81–3.86	3.30	0.32	9.7	2.98–3.62
s	24					

Remarks. – The species was revised in Löser & Zell (2015) as *Eocolumastrea bucovinensis*.

Occurrence. – Sample points NP5, NP9. Other occurrence: The species has a worldwide distribution between the Valanginian and the Cenomanian.

***Eocolumastrea*? sp.**
Figure 5A–D

Material. – ERNO L-130121, L-133901, L-133903, L-133906, L-134402, L-134403; 11 thin sections.

Dimensions. –
(ERNO L-130121)

	n	min–max	μ	s	cv	μ±s
clmin	20	1.02–1.64	1.33	0.17	13.3	1.15–1.51
clmax	20	1.44–2.19	1.75	0.22	12.9	1.53–1.98
ccd	25	1.65–3.02	2.26	0.36	16.0	1.90–2.63
s	25	14–24	18.8	3.29	17.5	16–22

Remarks. – The corals assigned to this species form plocoid colonies that occur in the form of thick branches. The material differs from *Eocolumastrea* by the wall that is made of septa-like mural elements, the absence of pali, and a less regular septal symmetry. The septal microstructure is not conserved. The assignation to *Eocolumastrea* is therefore preliminary.

Occurrence. – Sample points NP5, NP8, NP11.

Superfamily Cyclolitoidea Milne Edwards & Haime, 1849

Description. – Solitary and colonial corals. Septa with regular perforations, with perforations only in certain parts of the septa, or almost compact. Septa generally thick, without notable symmetry (except Negoporitidae). Septa often connected to each other. Septal lateral faces with pennulae and thorns. Septal distal margin with large granulae. Lonsdaleoid septa and main septum absent. Microstructure of large trabeculae. Synapticulae present. Pali in some genera probably present, but difficult to distinguish from the perforated inner margins of the septa. Columella poorly defined. Endotheca present or absent. When present, mostly thin tabulae. Marginarium absent. Wall poorly defined. Coenosteum varies depending on the organization type. Budding varies.

Family Latomeandridae de Fromentel, 1861

Description. – The family encompasses numerous solitary and colonial coral genera that show septa with perforations which are concentrated in the inner margin of the septa. The septa are thinner than in the Synastraeidae and less perforated than the Microsolenidae. The thickness of septa and the space between them is equilibrated.

Genus *Ampakabastraea* Alloiteau, 1958

Type species. – *Ampakabastraea ampakabensis* Alloiteau, 1958.

Description. – *Ampakabastraea* is closely related to *Astraeofungia* but has no confluent septa. The colonies are astreoid-cerioid with non- or subconfluent septa. The septa are almost compact with few perforations at the inner margins. The original stratigraphic range was indicated as Bathonian to Callovian. Comparable material from the Cretaceous reaches from the Valanginian of Puebla (Mexico) to the Early Cenomanian of Santander

(Spain). Except for *Brachyseris padernensis* Alloiteau, 1948 no Cretaceous species is formally established.

Remarks. – In the study area, the genus is represented by three species, but the state of conservation does not allow to establish new species.

***Ampakabastraea* sp. 1**
Figure 5F–H

Material. – ERNO 2193, L-120514, L-130127, L-134214, L-134303; 9 thin sections.

Dimensions. –
(ERNO L-134214)

	n	min–max	μ	s	cv	μ±s
cmin	6	6.08–8.20	7.30	0.77	10.5	6.53–8.07
cmax	6	9.02–11.1	9.90	0.87	8.8	9.03–10.8
ccd	18	5.80–11.0	8.00	1.38	17.2	6.62–9.39
s	8	37–48	40.4	3.73	9.2	37–44

Remarks. – The material represents the largest dimensions among the three species from the study area.

Occurrence. – Sample points NP5, NP9. Other occurrence: Lower Cenomanian of the Central Tethys (Greece).

***Ampakabastraea* sp. 2**
Figure 5I–K

Material. – ERNO L-120522, L-130117, L-130118, L-134505; 5 thin sections.

Dimensions. –
(ERNO L-134505)

	n	min–max	μ	s	cv	μ±s
cmin	20	3.37–4.51	4.02	0.33	8.4	3.68–4.36
cmax	20	4.04–5.67	4.78	0.47	9.9	4.31–5.26
ccd	25	3.56–4.80	4.10	0.36	8.7	3.74–4.46
s	15	34–46	38.7	3.59	9.3	35–42

Remarks. – The material presents the smallest dimensions compared to the other species from the study area.

Occurrence. – Sample point NP5.

***Ampakabastraea* sp. 3**
Figure 6A, B

v 2019a ?*Astraeofungia* sp. – Löser, Arias & Vilas, p. 265, figs 4.1–3.

Material. – ERNO L-120532; 1 thin section.

Dimensions. –
(ERNO L-120532)

	n	min–max	μ	s	cv	μ±s
clmin	5	4.64–9.58	6.70	1.90	28.4	4.79–8.61
clmax	5	6.38–8.59	7.60	1.01	13.3	6.58–8.61
ccd	6	5.29–8.13	6.97	1.16	16.6	5.81–8.14
s		32–60				

Occurrence. – Sample point NP5. Other occurrence: Upper Valanginian to Lower Albian of the Western Tethys (Spain).

Genus *Astraeofungia* Alloiteau, 1952

Type species. – *Astrea decipiens* Michelin, 1841.

Description. – Thamnasterioid colony, with mostly only at the inner margin perforated septa, that distinguish hardly in length and thickness. The corallites are regularly distributed, generally not. Costae run between all corallites.

***Astraeofungia decipiens* (Michelin, 1841)**
Figure 5E

*1841 *Astrea lamellistriata* Michelin; p. 18, pl. 4.8.
v 1891 *Thamnastraea Crespoi.* – Felix, p. 146, pl. 22, fig. 5.
v 1925 *Synastraea Tombeckiana* d'Orbigny. – Corroy, p. 309, pl. 8, fig. 2.
v 1935 *Synastrea Tombecki* d'Orb. – Cottreau, p. 39, pl. 75, fig. 4.
v 1957 *Astrea decipiens* Michelin. – Alloiteau, p. 213, figs 153–155, pl. 3, fig. 3, pl. 14, fig. 5, pl. 18, fig. 6.
v 1994 *Thamnasteria cotteaui* Fromentel. – Liao & Xia, p. 127, pl. 32, figs 6, 7.
v 1996 *Synastrea* cf. *dubia* Fromentel, 1861. – Baron-Szabo & Steuber, p. 25, pl. 14, figs 1, 7.
v 2013c *Astraeofungia tenochi* (Felix, 1891). – Löser, Werner & Darga, p. 58, pl. 7, figs 4–6.
v 2015 *Astraeofungia decipiens* (Michelin, 1841). – Löser, p. 281, fig. i.
v 2016a *Astrea decipiens* Michelin, 1841. – Löser, fig. a50a–c.

Material. – ERNO L-130303; 1 thin section.

Dimensions. –
(ERNO L-130303)

	n	min–max	μ	s	cv	μ±s
ccd	11	4.66–7.58	6.36	0.83	13.0	5.53–7.19
s	4	24–28	25.8	1.70	6.6	24–27

Remarks. – The specimen coincides in its corallite dimensions with the neotype of the species but has less septa.

Occurrence. – Sample point NP6. Other occurrence: Worldwide from the Kimmeridgian to the Middle Cenomanian.

***Astraeofungia hoffmeisteri* (Wells, 1933)**
Figure 6C–E

*v 1933 *Thamnasteria hoffmeisteri* Wells; p. 107, pl. 2, fig. 21, pl. 10, figs 18, 19.
v 2015a *Astraeofungia hoffmeisteri*. – Löser, appendix.

Material. – ERNO L-134218; 2 thin sections.

Dimensions. –
(ERNO L-134218)

	n	min-max	μ	s	cv	μ±s
ccd	20	3.08–5.39	4.13	0.80	19.4	3.33–4.94
s	6	21–25	22.8	1.72	7.5	21–25

Remarks. – The material compares well to the corallite dimensions of the holotype of the species.

Occurrence. – Sample point NP9. Other occurrence: Lower Hauterivian of the European Boreal (France), Upper Aptian of the Western Pacific (Japan), Albian to Lower Cenomanian of the Western Tethys (Spain, France) and the Western Atlantic (USA), Middle Cenomanian of the European Boreal (France).

***Astraeofungia nipponica* (Eguchi, 1951)**
Figure 7G–I

*v 1951 *Meandrarea nipponica* Eguchi, n. sp.; p. 51, pl. 16, figs 9, 10.
v 1999 *Microsolena kobyi* Prever, 1909. – Baron-Szabo & González-León, p. 487, fig. 6a.
v 2009 *Microsolena guttata* Koby, 1898. – Morycowa & Masse, p. 105, figs 4, 5a–c.
v 2019a *Microsolena nipponica* (Eguchi, 1951). – Löser, Arias & Vilas, p. 273, figs 7.7–9.

Material. – ERNO L-4866; 2 thin sections.

Dimensions. –
(ERNO L-4866)

	n	min–max	μ	s	cv	μ±s
ccd	12	4.12–6.72	5.52	0.88	16.0	4.64–6.41
s	4	52–83	62.8	14.38	22.9	48–77

sd = 7–8/2 mm

Remarks. – The material compares well to the holotype of the species which was just recently described (Löser *et al*. 2019a).

Occurrence. – Sample points P4. Other occurrence: Lower Hauterivian of the European Boreal (France), and the Western Pacific (Japan), Hauterivian to Lower Aptian of the Western Tethys (France, Spain), Lower Aptian of the Central Tethys (Greece), and the Western Tethys (France), Lower Albian of the Western Tethys (Spain), and the Western Atlantic (USA).

***Astraeofungia tenochi* (Felix, 1891)**
Figure 6F, G

v 1886 *Synastraea maeandra*. – de Fromentel, p. 598, pl. 173, fig. 2, pl. 175, fig. 2.
*v 1891 *Thamnastraea Tenochi* Felix; p. 145, pl. 22, figs 7, 7a.
v 1909 *Thamnastraea Vaughani*. – Prever, p. 71, pl. 2, figs 9, 9a.
v 1951 *Thamnasteria contorta* Eguchi, n.sp.; p. 30, pl. 5, figs 8, 9, pl. 6, figs 1, 3.
v 1951 *Thamnasteria jezoensis* Eguchi, n.sp.; p. 54, pl. 18, figs 5, 6.
v 1963 *Felixastraea mexicana* n.sp.; Reyeros Navarro, p. 13, pl. 5, figs 3, 4.
v 1983 *Thamnasteria crespoi* (Felix, 1891). – Reyeros de Castillo, p. 15, pl. 2, figs 1, 2.
v 2003 *Diploastrea harrisi* Wells, 1932. – Baron-Szabo & González-León, p. 212, fig. 8b, e.
v 2006 *Astraeofungia tenochi* (Felix, 1891). – Löser, p. 49, fig. 3k.
v 2013b *Astraeofungia tenochi* (Felix, 1891). – Löser, figs 3, 2.

Material. – ERNO L-120526; 1 thin section.

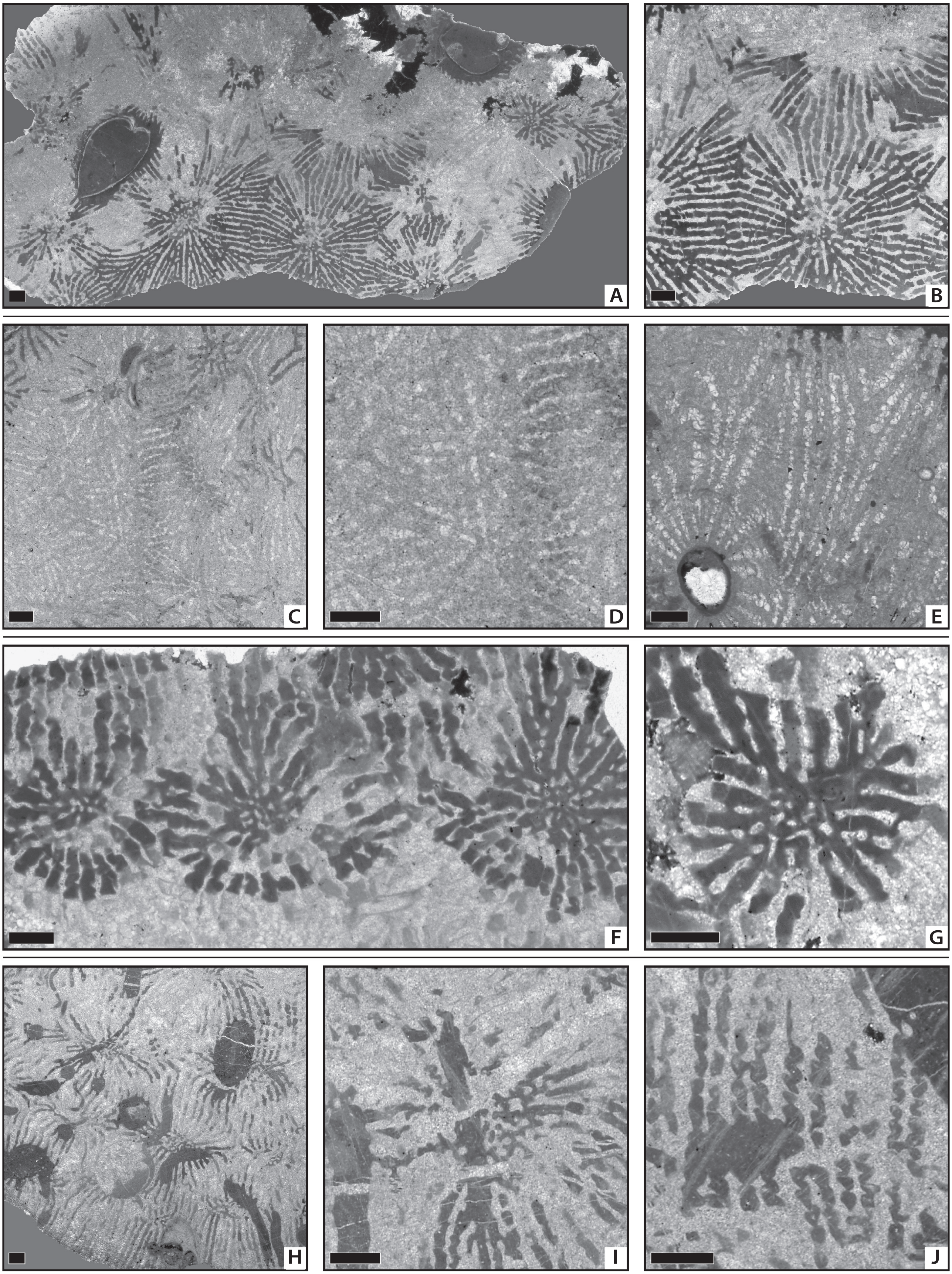
Dimensions. –
(ERNO L-120526)

	n	min–max	μ	s	cv	μ±s
ccd	16	4.00–5.85	4.93	0.59	11.9	4.34–5.52
s	8	23–30	25.3	2.54	10.0	23–28

Remarks. – The studied material compares, in its corallite dimensions, very well to the syntype reviewed by Löser (2006).

Occurrence. – Sample point NP5. Other occurrence: Worldwide from the Hauterivian to Uppermost Cenomanian.

Figure 6. A, B – *Ampakabastraea* sp. 3, ERNO L-120532; A – transversal thin section; B – transversal thin section, detail. • C–E – *Astraeofungia hoffmeisteri* (Wells, 1933), ERNO L-134218; C – transversal thin section; D – transversal thin section, detail; E – longitudinal thin section. • F, G – *Astraeofungia tenochi* (Felix, 1891), ERNO L-120526; F – transversal thin section; G – transversal thin section, detail. • H–J – *Dimorphastrea* sp., ERNO L-130138; H – transversal thin section; I – transversal thin section, detail; J – longitudinal thin section. Scale bar 1 mm.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Genus *Dimorphastrea* d'Orbigny, 1850

Type species. – *Dimorphastrea grandiflora* d'Orbigny, 1850.

Description. – Thamnasterioid colony with corallites arranged in concentric rows. The colony surface is plane, the corallite centers may be slightly depressed. Septa connect more between corallites of neighbored rows than with corallites of the same row. *Dimorphastrea* is similar to *Astraeofungia* and juvenile colonies of *Astraeofungia* and *Dimorphastrea* are difficult to distinguish.

***Dimorphastrea* sp.**
Figure 6H–J

v 2014 *Dimorphastrea* sp. 4. – Löser, p. 39, fig. 6e.

Material. – ERNO L-130138; 1 thin section.

Dimensions. –
(ERNO L-130138)

	n	min–max	μ	s	cv	μ±s
crd	5	3.74–6.27	4.81	1.01	21.0	3.80–5.82
cdw	10	3.95–6.68	5.42	0.88	16.2	4.54–6.30
s	5	34–43	39.8	3.70	9.2	36–44

Remarks. – This specimen is similar to *D. undulata* (d'Orbigny, 1850) but shows larger distances of the corallite rows.

Occurrence. – Sample point NP5. Other occurrence: Upper Aptian to Albian of the Eastern Tethys (Iran), Lower Albian of the Western Atlantic (Mexico), Lower Cenomanian of the Western Tethys (Spain), Upper Cenomanian of the European Boreal (Germany).

Genus *Latohelia* Löser, 1987

Type species. – *Synhelia reptans* Počta, 1887.

Description. – Phaceloid, rarely reptoid, coral with a small corallite diameter. The septa are little perforated and often connected to each other.

Remarks. – The material described here as *Latohelia* was formerly assigned to the genus *Calamophylliopsis*, which was established by Alloiteau (1952), and provided with more details in Alloiteau (1957). The illustration in Alloiteau (1957) does not show any diagnostic characteristics. Based on thin sections from the lectotype of *Calamophyllia flabellata* de Fromentel, 1861, type species of *Calamophylliopsis*, an updated description was provided by Löser (2016d), and the thin sections were illustrated. The type is a phaceloid coral with large corallites. The septa are almost compact and most of them form the columella by septal fusion. Synapticulae are absent, and the existence of pennulae is questionable. For unknown reasons, in the later literature, phaceloid corals with small corallite dimensions, perforated septa and pennulae were assigned to this genus (Morycowa & Lefeld 1966, Turnšek & Buser 1976, Turnšek *et al*. 1992). In *Latohelia*, the corallite arrangement is plocoid-phaceloid, the septa are perforated mainly at their inner margins, the septal lateral faces have pennulae, synapticulae are present, and the columella is composed of isolated trabeculae. Therefore, the Cretaceous material described as *Calamophylliopsis* is more closely related to *Latohelia*. *Calamophylliopsis* itself does not occur in the Cretaceous.

***Latohelia ruizi* (Bataller, 1947)**
Figure 7A–C

v 1944 *Calamophyllia sandbergeri* Felix 1891. – Wells, p. 438, pl. 71, figs 2, 3, pl. 74, figs 1, 5.
*v 1949 *Dendrosmilia Ruizi* Bataller; pp. 15, 20, text-fig.
v 2020 *Latohelia ruizi* (Bataller, 1947). – Löser, Mendicoa & Fernández Mendiola, p. 223, figs 3j–l.

Material. – ERNO L-134401, L-134503; 7 thin sections.

Dimensions. –
(ERNO L-134401)

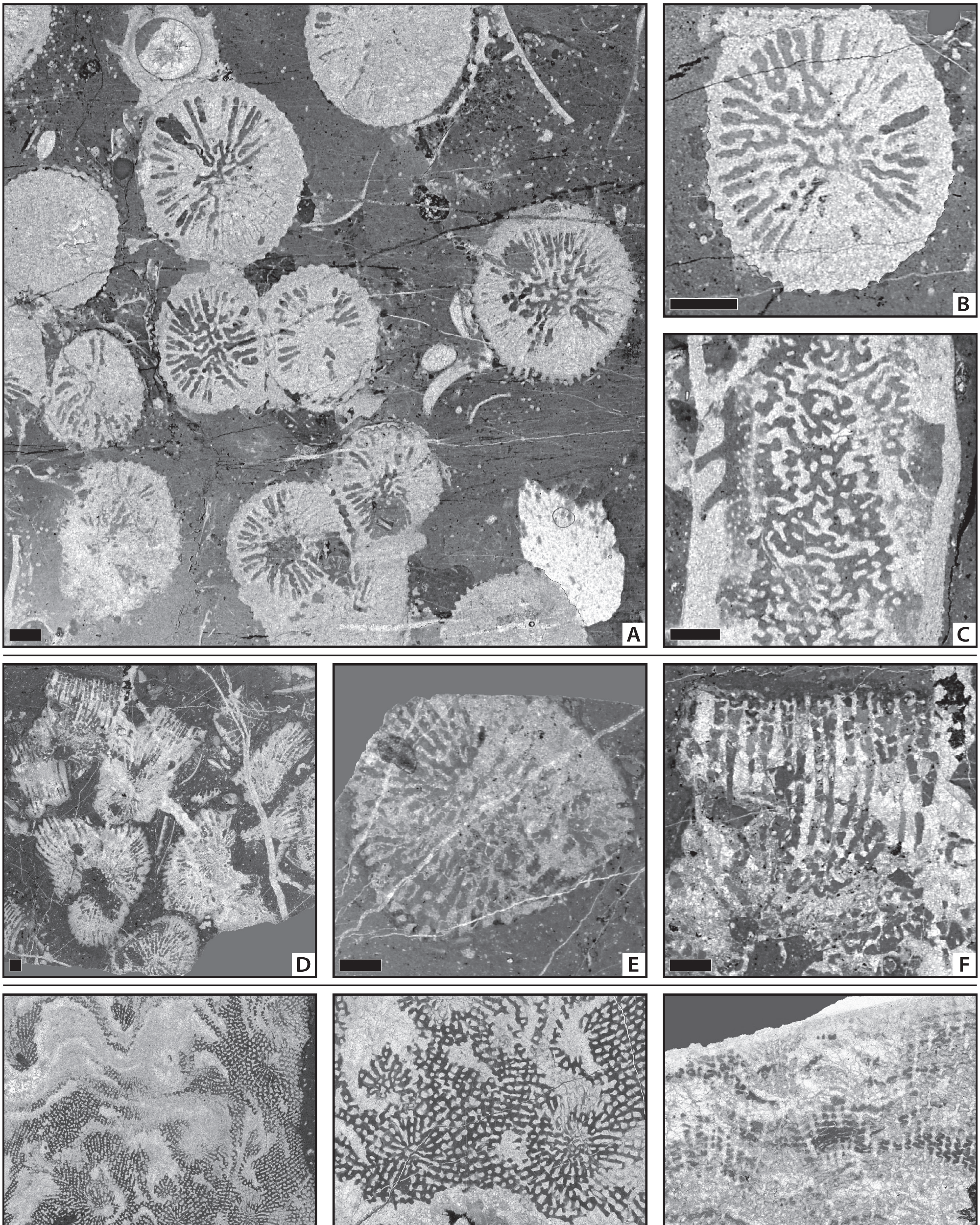
	n	min–max	μ	s	cv	μ±s
ccd	30	3.24–8.27	5.54	1.40	25.3	4.14–6.94
cmax	30	3.60–7.28	5.05	0.93	18.4	4.12–5.98
cmin	30	2.90–5.68	4.23	0.74	17.5	3.49–4.97
s	10	34–53	42.10	6.71	15.9	35–49

Occurrence. – Sample points NP11, NP5. Other occurrence: Lower Aptian of the Western Atlantic (Venezuela) and the Western Tethys (Spain).

***Latohelia* cf. *ruizi* (Bataller, 1947)**
Figure 7D–F

Material. – ERNO L-120507; 1 thin section.

Figure 7. A–C – *Latohelia ruizi* (Bataller, 1947), ERNO L-134401; A – transversal thin section; B – transversal thin section, detail; C – longitudinal thin section. • D–F – *Latohelia* cf. *ruizi* (Bataller, 1947), ERNO L-120507; D – transversal thin section; E – transversal thin section, detail; F – longitudinal thin section. • G–I – *Astraeofungia nipponica* (Eguchi, 1951), ERNO L-4866; G – transversal thin section; H – transversal thin section, detail; I – longitudinal thin section. Scale bar 1 mm.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Dimensions. – (ERNO L-120507): cmin = 5.2–6.5; cmax = 6.4–9.5; septa = 45–47.

Remarks. – The species has larger corallite dimensions than *L. ruizi.*

Occurrence. – Sample point NP5. Other occurrence: Berriasian of the Western Atlantic (Mexico).

Family Microsolenidae Koby, 1889

Description. – Solitary (not in the Cretaceous) and colonial (cerioid, hydnophoroid, meandroid, phaceloid, plocoid, thamnasterioid) colonies. Septa completely and regularly perforated. Interseptal space larger than or equal to septal thickness.

Genus *Microsolena* Lamouroux, 1821

Type species. – *Microsolena porosa* Lamouroux, 1821.

Description. – Thamnasterioid coral with corallites regularly distributed. Septa connect all corallites without forming rows. Colony surface plane.

***Microsolena* cf. *formosa* Morycowa & Decrouez, 2006**
Figure 8A–C

v 1999 *Microsolena kobyi* Prever, 1909. – Baron-Szabo & González-León, p. 487, fig. 6a.

Material. – ERNO 2195; 2 thin sections.

Dimensions. –
(ERNO 2195)

	n	min–max	μ	s	cv	μ±s
ccd	5	5.99–11.9	8.82	2.11	23.9	6.70–10.9
s	3	43–63	52.3	10.1	19.2	42–62

Remarks. – The material is similar to *M. formosa* but it has a lower number of septa (60–80 in the holotype of *M. formosa*). The type material of *M. formosa* was not available for study.

Occurrence. – Sample points BS. Other occurrence: Upper Barremian to Lower Aptian of the Western Atlantic (Mexico), Lower Aptian of the Central Tethys (Greece), Lower Coniacian of the Western Tethys (Spain).

***Microsolena* sp. 1**
Figure 8D, E

Material. – ERNO L-134520; 2 thin sections.

Dimensions. – (ERNO L-134510): ccd = 10–12 mm; s = 57–59.

Remarks. – The corallite distance of the specimen is even higher than in *M. formosa*, which is one of the species with the largest corallite dimensions in the Cretaceous and has less septa than *M. formosa*.

Occurrence. – Sample point NP5.

***Microsolena* sp. 2**
Figure 8F–H

v 1997 *Microsolena distefanoi* (Prever, 1909). – Baron-Szabo, p. 82, pl. 13, fig. 5.
v 1999 *Microsolena distefanoi* (Prever, 1909). – Baron-Szabo & González-León, p. 486, fig. 5f.
v 2013a *Microsolena* sp. 1. – Löser, Vilas & Arias *in* Löser *et al.*, p. 206, fig. 5g, h.

Material. – ERNO 2191; 4 thin sections.

Dimensions. –
(ERNO 2191)

	n	min–max	μ	s	cv	μ±s
ccd	10	4.05–7.20	5.89	1.04	17.7	4.85–6.94
s	5	32–42	37.4	3.84	10.2	34–41

sd = 7/2 mm

Remarks. – The material has a similar corallite distance to *M. nipponica* but has less septa.

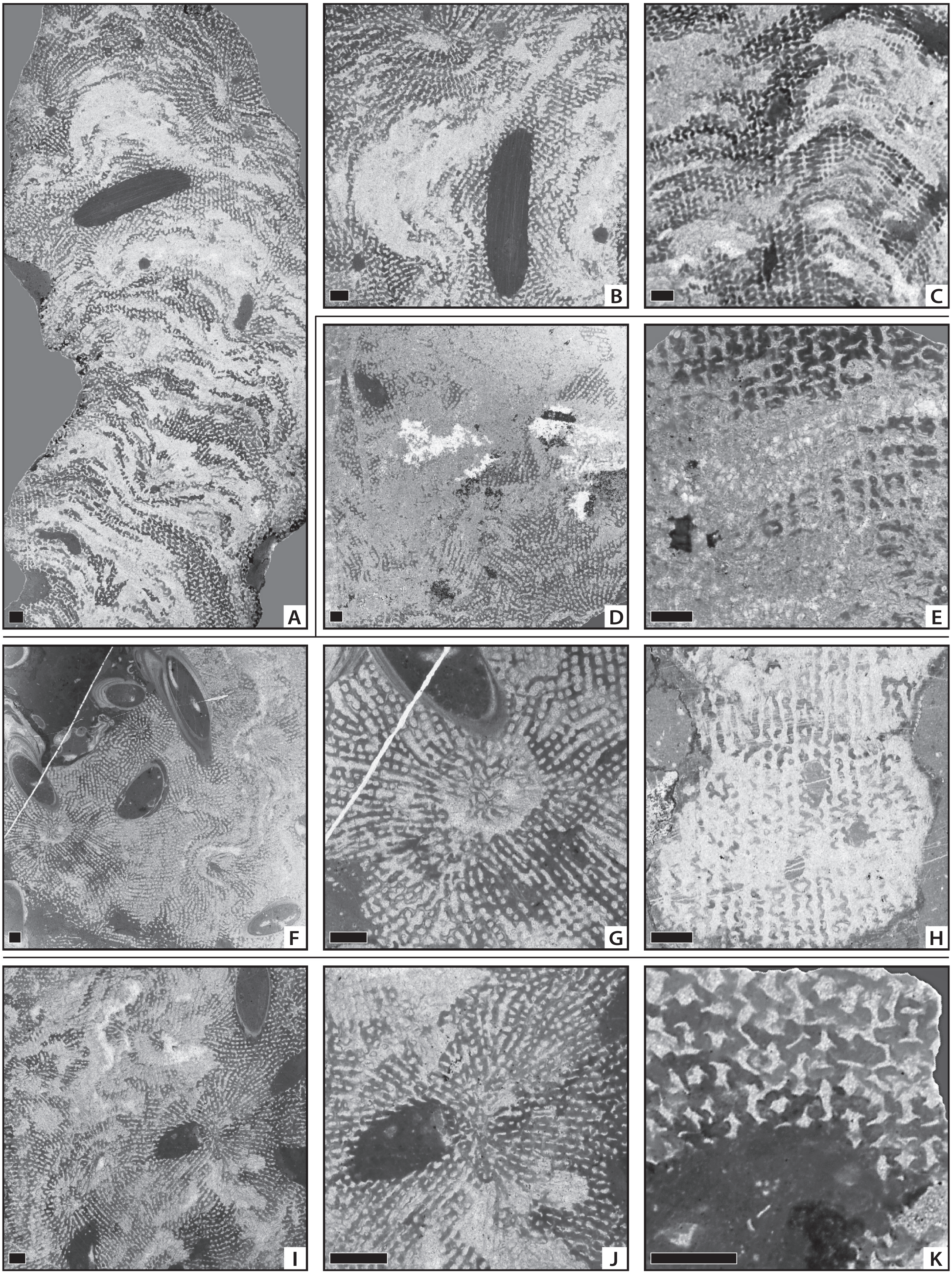
Occurrence. – Sample point BS. Other occurrence: Lower Hauterivian of the European Boreal (France), Lower Aptian of the Western Tethys (Spain), Lower Albian of the Western Atlantic (Mexico), Upper Turonian to Lower Coniacian of the Central Tethys (Austria).

Genus *Polyphylloseris* de Fromentel, 1857

Type species. – *Polyphyllastrea convexa* d'Orbigny, 1850.

Description. – Like *Microsolena*, but the corallites are

Figure 8. A–C – *Microsolena* cf. *formosa* Morycowa & Decrouez, 2006, ERNO 2195; A – transversal thin section; B – transversal thin section, detail; C – longitudinal thin section. • D, E – *Microsolena* sp. 1, ERNO L-134510; D – transversal thin section; E – longitudinal thin section. • F–H – *Microsolena* sp. 2, ERNO 2191; F – transversal thin section; G – transversal thin section, detail; H – longitudinal thin section. • I–K – *Polyphylloseris conophora* (Felix, 1891), ERNO L-130120; I – transversal thin section; J – transversal thin section, detail; K – longitudinal thin section. Scale bar 1 mm.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slightly erected and the coenosteum is more developed. Since the radial elements are running straight from the center of the corallites, they are subconfluent. The trabeculae close to the center of the corallites are inclined and, therefore, pennulae appear at the surface of the colony.

Polyphylloseris conophora **(Felix, 1891)**
Figure 8I–K

*v 1891 *Mastophyllia conophora* Felix; p. 146, pl. 23, figs 9, 9a.
v 2006 *Polyphylloseris conophora* (Felix, 1891). – Löser, p. 44, fig. 4h, i [= here older synonymy].
v 2011b *Polyphylloseris distefanoi* (Prever, 1909). – Löser, p. 348, pl. 1, figs 1–4.
v 2016d *Mastophyllia conophora* (Felix, 1891). – Löser, fig. m5.

Material. – ERNO L-130120; 1 thin section.

Dimensions. –
(ERNO L-130120)

	n	min–max	μ	s	cv	μ±s
ccd	6	5.99–7.50	6.84	0.57	8.4	6.26–7.42
s	4	62–68	65.3	2.75	4.2	62–68

Remarks. – The present material has slightly larger corallite dimensions and less septa than the lectotype of the species, but is still remaining in the range of the species.

Occurrence. – Sample point NP5. Other occurrence: Valanginian to Lower Albian of the Western Atlantic (Mexico, USA), Lower Hauterivian of the European Boreal (France), Barremian of the Western Atlantic (Mexico), Upper Barremian to Lower Aptian of the Southern Tethys (China), Lower Aptian of the Central Tethys (Italy, Serbia), Upper Aptian of the Western Pacific (Japan).

Polyphylloseris icaunensis **(d'Orbigny, 1850)**
Figure 9A–C

*v 1850 *Polyphyllastrea icaunensis* d'Orbigny; p. 94.
v 2001 *Polyphylloseris distefanoi* (Prever 1909). – Löser, p. 47, pl. 3, fig. 6.
v 2009 *Polyphylloseris distefanoi* (Prever, 1909). – Morycowa & Masse, p. 111, fig. 8d–f.
v 2009 *Polyphylloseris icaunensis* (d'Orbigny, 1849). – Morycowa & Masse, p. 108, fig. 8a–c.
v 2012 *Polyphylloseris* cf. *kobyi* (Prever, 1909). – Bover Arnal, Löser & Moreno Bedmar *in* Bover Arnal *et al*., p. 58, fig. 11d, h, l.
v 2013b *Polyphylloseris kobyi* (Prever, 1909). – Löser, figs 3, 7.
v 2013a *Polyphylloseris polymorpha* (Felix, 1891). – Löser, Castro & Nieto, p. 27, pl. 9, figs 3, 4.

Material. – ERNO L-120503, L-130107, L-130109; 4 thin sections.

Dimensions. –
(ERNO L-130107)

	n	min–max	μ	s	cv	μ±s
ccd	20	4.30–7.28	5.55	0.95	17.1	4.59–6.50
s	10	30–48	38.5	6.18	16.0	32–45

Remarks. – The specimen compares well to the type of the species. The type material of *Polyphyllastrea icaunensis* was found in the d'Orbigny collection in 2016. Therefore, comparable material was assigned to other species in the past.

Occurrence. – Sample point NP5. Other occurrence: Lower Hauterivian of the European Boreal (France), Barremian to Lower Aptian of the Central (Greece) and Western Tethys (France, Spain), Upper Albian of the Western Tethys (Spain).

Polyphylloseris **cf.** ***mammillata*** **Eguchi, 1951**
Figure 9D–F

Material. – ERNO L-120501, L-120533, L-120537, L-134508; 5 thin sections.

Dimensions. –
(ERNO L-120537)

	n	min–max	μ	s	cv	μ±s
ccd	15	6.38–9.44	7.53	1.10	14.6	6.42–8.63
s	8	43–58	47.9	4.67	9.7	43–53

Remarks. – The specimens are similar to *P. mammillata* but present a slightly larger distance of the corallites. *Polyphylloseris mammillata* itself is poorly defined because the type of the species is not available.

Occurrence. – Sample point NP5. Other occurrence: Valanginian to Aptian of the Western Atlantic (Mexico), Aptian to Lower Albian of the Western Atlantic (Mexico, USA), Upper Aptian of the Western Tethys (Spain).

Superfamily Eugyroidea Achiardi, 1875

Description. – Colonial (cerioid, flabelloid, hydnophoroid, meandroid, phaceloid, plocoid) corals. Septa compact. Septal symmetry generally regular, in various systems, or in size orders. Septa poorly ornamented. Microstructure poorly known, probably of small trabeculae. Lonsdaleoid septa only in the felixigyrids; main septa absent. Synapticulae and pali absent. Columella rare. Endotheca well-developed, generally as dense, thick and regular tabulae. Marginarium absent. Wall compact and mostly septothecal, by thickening or tabulotheca. Coenosteum and budding varies.

Family Cladophylliidae Morycowa & Roniewicz, 1990

Description. – Colonial phaceloid corals. Septal symmetry regular or subregular, hexameral. Columella formed by septal fusion.

Genus *Cladophyllia* Milne Edwards & Haime, 1851

Type species. – *Lithodendron dichotoma* Goldfuss, 1826.

Description. – Phaceloid colony with small corallites (less than 5 mm). The septal symmetry is regular. The septa are connected to each other and form the columella by septal fusion.

***Cladophyllia clemencia* de Fromentel, 1857**
Figure 9G, H

*v 1857 *Cladophyllia Clemencia* de Fromentel; p. 29, pl. 3, figs 2, 3.
v 1873 *Cladophyllia Clemencia.* – de Fromentel, p. 416, pl. 75, fig. 3.
v 1997 *Cladophyllia* cf. *rollieri* (Koby, 1888). – Baron-Szabo, p. 40, text-figs a–c, pl. 9, fig. 4.
v 2006 *Cladophyllia* cf. *clemencia* (de Fromentel, 1857). – Löser & Ferry, p. 475, fig. 3.9.
v 2008 *Cladophyllia clemencia* de Fromentel, 1857. – Roniewicz, p. 104, fig. 6b, c.
v 2014 *Pleurophyllia minuscula* Roniewicz, 1976. – Baron-Szabo, pl. 85, fig. 4.

Material. – ERNO L-120538, L-133902, L-133904, L-134101, L-134207, L-134208; 4 thin sections.

Dimensions. –
(ERNO L-134101)

	n	min–max	μ	s	cv	μ±s
clmin	13	0.75–1.04	0.85	0.07	8.7	0.77–0.92
clmax	10	1.07–1.40	1.22	0.11	9.4	1.10–1.33
cmin	12	1.29–1.73	1.52	0.14	9.4	1.38–1.67
cmax	10	1.63–2.21	1.88	0.20	10.6	1.68–2.08
s	12					

Remarks. – The material is similar to the syntype of the species, but it presents less septa. In the syntype exists the beginning of a third septal cycle.

Occurrence. – Sample points NP8, NP5, NP8, NP9. Other occurrence: Valanginian to Lower Aptian of the Central Tethys (Bulgaria, Germany), Lower Hauterivian of the European Boreal (France), Lower Barremian of the Western Tethys (France), Upper Barremian to Lower Aptian of the Central Tethys (Germany), Lower Aptian of the Western Atlantic (Mexico).

Family Solenocoeniidae Roniewicz, 2008

Description. – Cerioid and plocoid colonies. The septa are generally short. No columella.

Remarks. – This family is applied instead of the Cyathophoridae family. The latter should not be used because the material of the type species of the name-giving genus *Cyathophora* does not present the characteristics ascribed to it. There is no other family name available for the moment except the Solenocoeniidae.

Genus *Cryptocoenia* d'Orbigny, 1849

Type species. – *Astrea alveolata* Goldfuss, 1826.

Description. – Plocoid colony. Corallite outline circular. Symmetry of septa radial and regularly hexameral or decameral. Septa very short, free. Pali absent. Costae present, sub-confluent to non-confluent. Columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, tabulothecal. Coenosteum medium broad, consists of costae and tabulae.

Remarks. – *Cryptocoenia* (*Cyathophora* by other authors) is one of the most common genera in the Late Jurassic to Early Cretaceous. It was recently revised (Löser 2016d). The literature reports about 65 species from the Jurassic and Cretaceous. However, about half of them could be synonyms.

***Cryptocoenia ivanovskii* (Kuzmicheva, 2002)**
Figure 9I, J

1993 *Cyathophora steinmanni* Fritzsche 1924. – Baron-Szabo, p. 155, pl. 1, fig. 4.
*2002 *Hexapetalum ivanovskii* Kuzmicheva; p. 132, pl. 10, fig. 1.

Material. – ERNO 2181, L-120520, L-120525, L-130130, L-130134, L-134506; 7 thin sections.

Dimensions. –
(ERNO 2181)

	n	min–max	μ	s	cv	μ±s
clmin	15	1.99–2.59	2.34	0.18	8.0	2.16–2.53

clmax	15	2.10–3.30	2.77	0.35	12.7	2.42–3.13
ccd	15	2.79–4.02	3.36	0.42	12.7	2.93–3.79
s	12					

Remarks. – The material coincides well with the corallite dimensions given by Kuzmicheva (2002).

Occurrence. – Sample points BS, NP5. Other occurrence: Berriasian of the Central Tethys (Ukraine), Lower Hauterivian of the European Boreal (France), Upper Aptian of the Western Tethys (Spain).

***Cryptocoenia* cf. *kiliani* (Prever, 1909)**
Figure 10A–C

v 1964 *Cyathophora minima* Étallon 1862. – Morycowa, p. 22, pl. 3, fig. 1, pl. 5, fig. 4.
v 1981 *Cyathophora pygmaea* Volz 1903. – Turnšek & Mihajlovic, p. 18, pl. 13, figs 1, 2.
v 2003 *Confusaforma weyeri* Löser, 1987. – Baron-Szabo & González-León, p. 207, fig. 7b.
v 2010 *Cryptocoenia miyakoensis* (Eguchi, 1936). – Löser, p. 593, fig. 3.7.
v 2015b *Cryptocoenia* cf. *kiliani* (Prever, 1909). – Löser, p. 19, fig. 3a–c.

Material. – ERNO L-134211; 2 thin sections.

Dimensions. –
(ERNO L-134211)

	n	min–max	μ	s	cv	μ±s
clmin	25	0.78–1.11	0.96	0.09	10.2	0.86–1.06
clmax	25	1.04–1.50	1.27	0.13	10.8	1.13–1.41
ccd	20	1.10–1.47	1.26	0.13	10.4	1.13–1.40
s	6					

Remarks. – The specimen is similar to the figured syntype (PU 18114#1) of *Polytremacis kiliani* (Prever, 1909), but differs in a slightly larger corallite diameter.

Occurrence. – Sample point NP9. Other occurrence: Upper Barremian of the Western Tethys (France), Lower Aptian of the Central Tethys (Poland, Serbia), Lower Albian of the Western Atlantic (Mexico).

***Cryptocoenia regularis* (de Fromentel, 1884)**
Figure 9K, L

*v 1884 *Cyathophora* (*Cyathocoenia*) *regularis* de Fromentel; p. 540, pl. 149, fig. 2.
v 1897 *Cryptocoenia Picteti.* – Koby, p. 32, pl. 2, figs 11, 11a.

Material. – ERNO 2180, L-130103; 2 thin sections.

Dimensions. –
(ERNO 2180)

	n	min–max	μ	s	cv	μ±s
clmin	20	2.22–2.75	2.45	0.17	7.0	2.28–2.62
clmax	20	2.43–3.07	2.79	0.17	6.3	2.61–2.97
ccd	30	2.53–3.34	2.90	0.22	7.8	2.67–3.12
s	12					

Remarks. – The material coincides well with the only syntype of the species. The species was, in the past, often mentioned in the literature but almost always was not illustrated. The material illustrated by Koby (1897) is poorly preserved, and the material described and illustrated by Eliášová (1992) belongs to *Cryptocoenia bernensis* (Étallon, 1864).

Occurrence. – Sample points NP5, BS. Other occurrence: Lower Valanginian of the Western Tethys (Spain), Lower Hauterivian of the European Boreal (France), Barremian of the Central Tethys (France), Lower Albian of the Western Tethys (Spain).

Genus *Pentacoeniopsis* gen. nov.

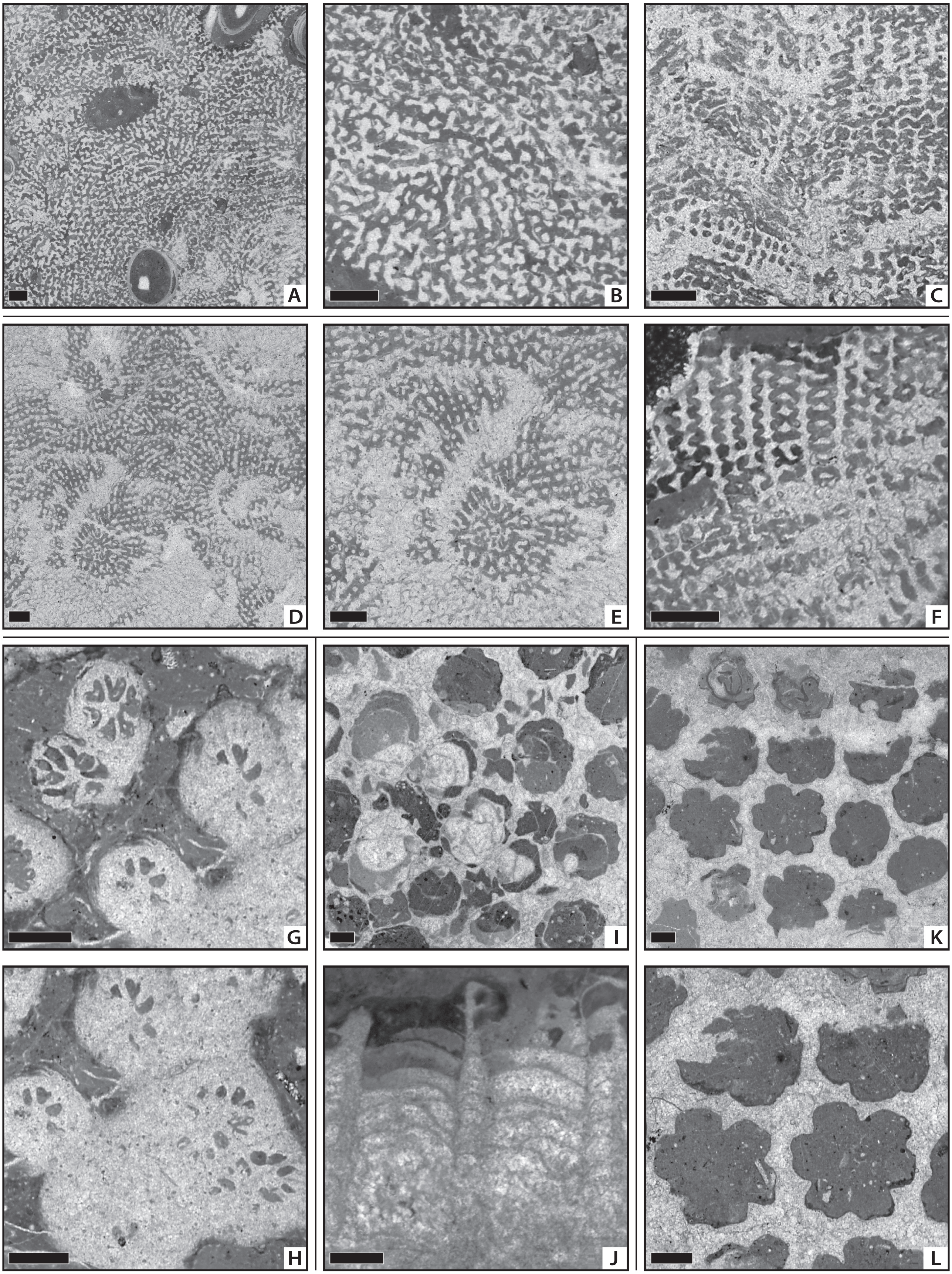
Type species. – Pentacoeniopsis sonorensis sp. nov.

Etymology. – In relation to the genus *Pentacoenia*.

Diagnosis. – Plocoid colonial coral colony with circular to slightly elliptical corallites. The septal symmetry is pentameral. The septa are compact. No columella, pali or synapticulae. The wall is compact and septothecal. The endotheca consists of tabulae and dissepiments.

Description. – Plocoid colony. The corallite outline is circular. The corallite diameter is below three millimetres in all known species. The septa are compact. The microstructure of the septa is unknown. The symmetry of the septa is radial and pentameral. The septal cycles are subregular. Two cycles resulting in ten septa. The

Figure 9. A–C – *Polyphylloseris icaunensis* (d'Orbigny, 1850), ERNO L-130107; A – transversal thin section; B – transversal thin section, detail; C – longitudinal thin section. • D–F – *Polyphylloseris* cf. *mammillata* Eguchi, 1951, ERNO L-120537; D – transversal thin section; E – transversal thin section, detail; F – longitudinal thin section. • G, H – *Cladophyllia clemencia* de Fromentel, 1857, ERNO L-134101; G – transversal thin section; H – transversal thin section. • I, J – *Cryptocoenia ivanovskii* (Kuzmicheva, 2002), ERNO 2181; I – transversal thin section; J – longitudinal thin section. • K–L – *Cryptocoenia regularis* (de Fromentel, 1884), ERNO 2180; K – transversal thin section; L – transversal thin section, detail. Scale bar 1 mm.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septal cycles can almost not be differentiated. The septa are short and are not connected to each other. Septal distal margin unknown, lateral face smooth, inner margin smooth. Pali, synapticulae and a columella are absent. The endotheca consists of tabulae. The wall is compact and paraseptothecal. The coenosteum is broad and consists of dissepiments, costae and large isolated trabeculae. The budding is extracalicinal.

Discussion. – The very short septa compare well to all other members of the family. The most striking difference is the isolated trabeculae in the coenosteum. This characteristic is so far only known from the genus *Pseudocoeniopsis* Roniewicz, 1976. But here, the trabeculae are not isolated elements (for instance, as in members of the family Agatheliidae; Löser *et al*. 2019b), but are coastal pali as described by Löser (2016d: p. 33). In the new genus, the pali are isolated and not related to septa. This configuration proposes a mixed microstructure consisting of large trabeculae in the coenosteum and, very probably, small trabeculae in the septa. The assignation to the family Solenocoeniidae is, therefore, preliminary.

Remarks. – The new genus compares to *Pentacoenia* due to the pentameral septal symmetry, but possesses a coenosteum that consists of – besides dissepiments and costae – isolated trabeculae (probably external pali).

Species included. – The type species and material in open nomenclature.

***Pentacoeniopsis sonorensis* sp. nov.**
Figure 10D–G

v 1999 *Cyathophora miyakoensis* (Eguchi, 1936). – Baron-Szabo & González-León, p. 478, fig. 4b.

Types. – Holotype: ERNO L-120531. Paratype: ERNO L-130110.

Type horizon and locality. – Espinazo del Diablo Fm., Cretaceous, Middle Albian. Mexico, Sonora, Municipio San Pedro de la Cueva, Tepache, Lampazos area, Espinazo de Diablo, NP5 1-1 (29° 26′ 26.1″ N, 109° 27′ 27″ W).

Material. – ERNO 2178, 2190, L-120527, L-120531, L-130115; 8 thin sections.

Etymology. – After the Mexican state Sonora.

Diagnosis. – *Pentacoeniopsis* with a small corallite diameter of 1–1.3 mm (first interval), a larger corallite diameter of 1.1–1.4 mm (first interval) and 8–10 septa.

Description. – As for the genus.

Remarks. – This species has the smallest corallite dimensions compared to the other unnamed species.

Dimensions. –
(Holotype ERNO L-120531)

	n	min–max	µ	s	cv	µ±s
clmin	20	0.98–1.41	1.19	0.10	9.1	1.08–1.30
clmax	20	1.01-1.54	1.27	0.16	12.9	1.10–1.44
ccd	20	2.09–3.29	2.66	0.37	13.9	2.29–3.03
s	7	8–10	8.71	0.95	10.9	8–10

(Paratype ERNO L-130110)

	n	min–max	µ	s	cv	µ±s
clmin	25	0.85–1.18	1.06	0.10	9.7	0.95–1.16
clmax	25	1.03–1.44	1.19	0.10	9.0	1.08–1.30
ccd	25	1.73–2.46	2.10	0.23	11.0	1.86–2.33
s	26	8–11	9.42	0.80	8.5	9–10

Occurrence. – Sample points NP5, BS.

***Pentacoeniopsis* sp. 1**
Figure 11A–C

Material. – ERNO 2278, L-120516; 3 thin sections.

Dimensions. –
(ERNO 2278)

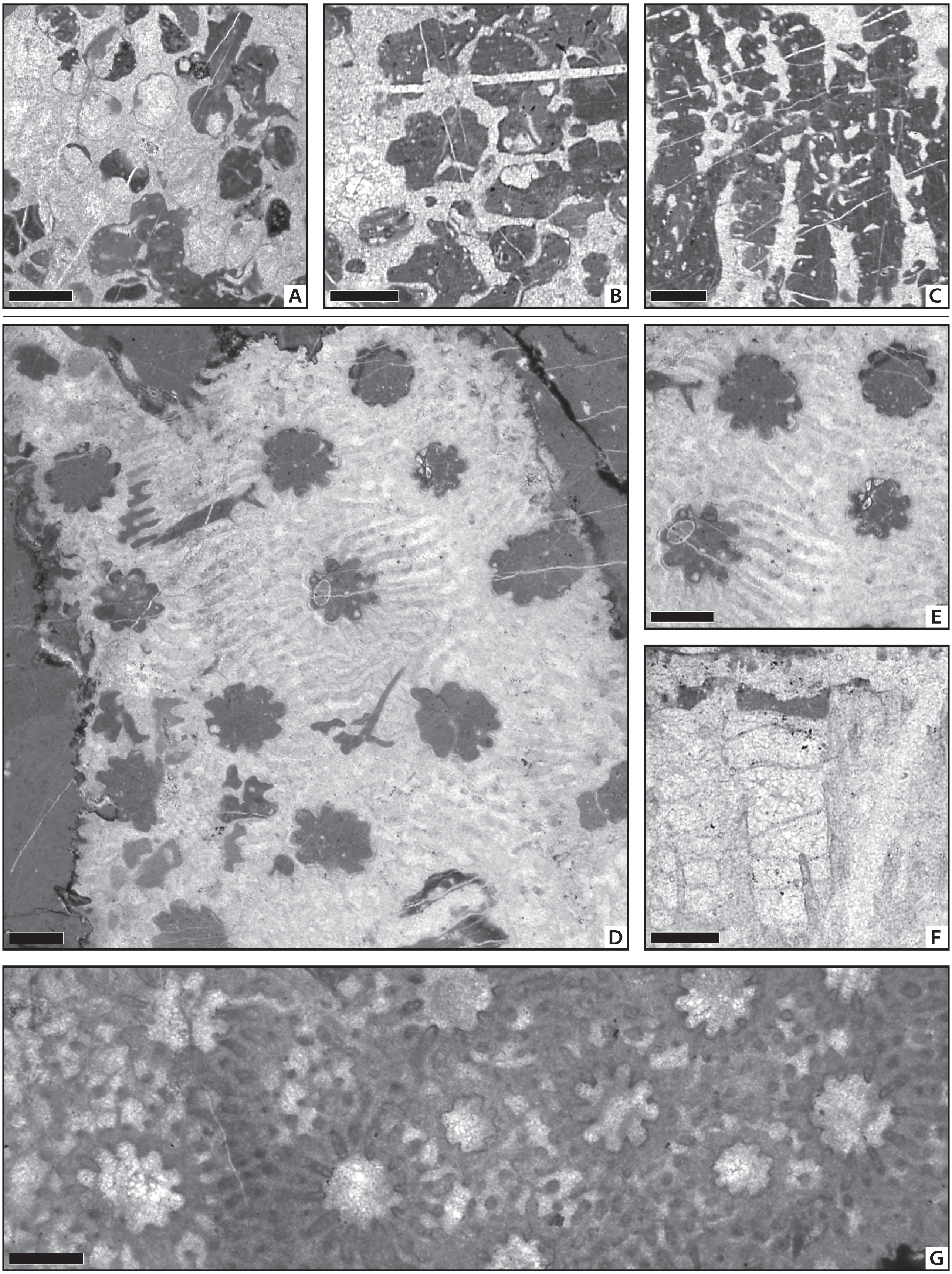
	n	min–max	µ	s	cv	µ±s
clmin	10	1.10–1.49	1.33	0.14	10.2	1.19–1.46
clmax	10	1.36–1.92	1.65	0.19	11.7	1.46–1.84
s	10					

(ERNO L-120516)

	n	min–max	µ	s	cv	µ±s
clmin	17	1.04–1.45	1.24	0.11	9.4	1.13–1.36
clmax	17	1.23–1.97	1.58	0.21	13.2	1.37–1.79
ccd	12	1.83–3.72	2.59	0.64	24.8	1.94–3.23
s	14	7–10	9.28	0.99	10.7	8–10

Remarks. – The material has slightly larger dimensions than *P. sonorensis*. It could present a new species, but both specimens are poorly preserved.

Figure 10. A–C – *Cryptocoenia* cf. *kiliani* (Prever, 1909), ERNO L-134211; A – transversal thin section; B – transversal thin section, detail; C – longitudinal thin section. • D–G – *Pentacoeniopsis sonorensis* gen. et sp. nov.; D–F – holotype ERNO L-120531, transversal thin section (D), transversal thin section detail (E) and longitudinal thin section (F); G – paratype ERNO L-130110, transversal thin section. Scale bar 1 mm.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Occurrence. – Sample point NP5.

***Pentacoeniopsis* sp. 2**
Figure 11D, E

Material. – ERNO L-130114; 2 thin sections.

Dimensions. –
(ERNO L-130114)

	n	min–max	μ	s	cv	μ±s
clmin	20	1.41–1.91	1.67	0.16	10.0	1.51–1.84
clmax	20	1.68–2.30	2.01	0.18	9.3	1.82–2.20
ccd	20	2.65–3.59	3.05	0.26	8.8	2.78–3.32
s	20	7–10	9.30	0.86	9.2	9–10

Remarks. – The material presents larger corallite dimensions than *P. sonorensis* and *P*. sp. 1.

Occurrence. – Sample point NP5.

***Pentacoeniopsis* sp. 3**
Figure 11F, G

Material. – ERNO L-130106; 1 thin section.

Dimensions. –
(ERNO L-130106)

	n	min–max	μ	s	cv	μ±s
clmin	7	1.92–2.33	2.06	0.15	7.4	1.90–2.21
clmax	7	2.37–2.71	2.54	0.12	4.9	2.41–2.66
s	3	9–10	9.66	0.57	5.9	9–10

Remarks. – The specimen presents the largest corallite dimensions of the genus. The material is not well enough preserved to allow the description of a new species.

Occurrence. – Sample point NP5.

Superfamily Heterocoenioidea Oppenheim, 1930

Description. – Solitary and colonial (cerioid, phaceloid, and plocoid) corals. Septa compact, thick, with ornamented lateral faces. Symmetry radial and bilateral. Lonsdaleoid septa may occur. Septal microstructure with small trabeculae, visible as a medium-width dark line. Synapticulae absent, pali absent. Columella rarely developed. Endotheca well-developed. Marginarium present in some genera. Wall trabecular or septothecal. Budding extracalicinal.

Family Carolastraeidae Eliášová, 1976a

Description. – Colonial (cerioid, phaceloid, plocoid) corals with septa in a bilateral septal symmetry. One or various larger septa can be present in one face of the corallite. A main septum can be present. Lonsdaleoid septa and a marginarium are absent.

Remarks. – This family was originally assigned to the suborder Amphiastreina, but rather strongly ornamented septa are not typical of this suborder.

Genus *Carolastraea* Eliášová, 1976a

Type species. – *Carolastraea fraji* Eliášová, 1976a.

Description. – Phaceloid coral with a thick wall and a bilateral septal symmetry. One septum is clearly larger than all others.

***Carolastraea fraji* Eliášová, 1976a**
Figure 12A–E

*v 1976a *Carolastraea fraji* Eliášová; p. 178, pl. 1, figs 1, 2, pl. 2, figs 1, 2.
v 2016b *Carolastraea fraji* Eliášová, 1976. – Löser, fig. c11a–c.

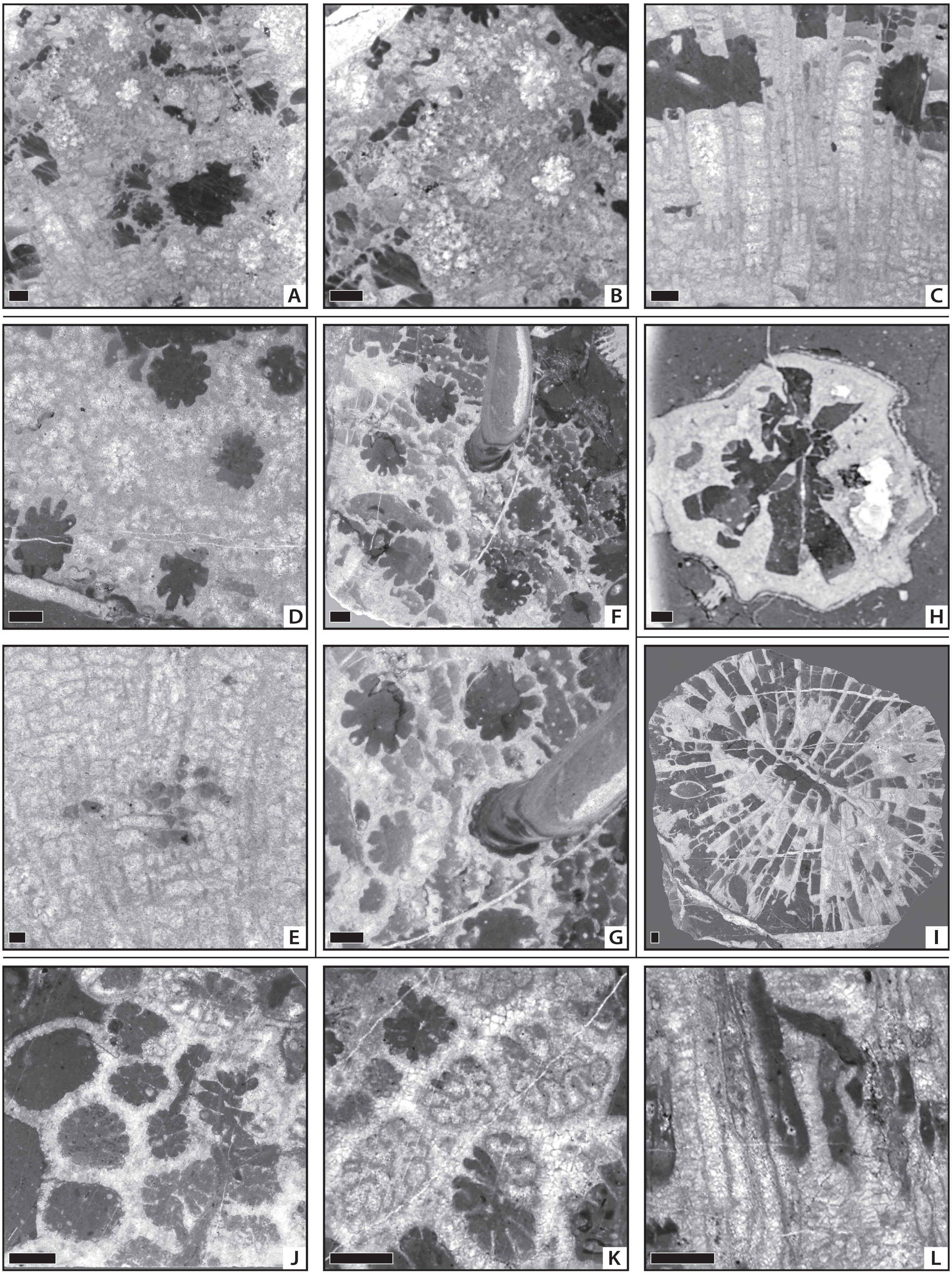
Material. – ERNO L-130401, L-130402, L-130403, L-134202, L-134203, L-134205, L-134209, L-134212, L-134504; 10 thin sections.

Dimensions. –
(L-134202)

	n	min–max	μ	s	cv	μ±s
clmin	26	0.75–1.20	0.99	0.13	13.5	0.86–1.13
clmax	26	0.99–1.45	1.23	0.13	11.3	1.09–1.36
cmin	26	1.50–2.49	2.02	0.25	12.4	1.77–2.27
cmax	26	2.02–3.11	2.50	0.34	13.5	2.16–2.84
s	16	9–14	12.12	1.58	13.0	11–14

Remarks. – The present material has the same corallite dimensions as the holotype of *Carolastraea fraji*. The large stratigraphic gap between both occurrences alone does

Figure 11. A–C – *Pentacoeniopsis* sp. 1, ERNO 2278; A – transversal thin section; B – transversal thin section, detail; C – longitudinal thin section. • D, E – *Pentacoeniopsis* sp. 2, ERNO L-130114; D – transversal thin section; E – longitudinal thin section. • F, G – *Pentacoeniopsis* sp. 3, ERNO L-130106; F – transversal thin section; G – transversal thin section, detail. • H – *Heterosmilia spinosa* Kolodziej *et al*. 2012, ERNO 2194-2, transversal thin section. • I – *Plesiosmilia coquandi* (d'Angelis d'Ossat, 1905), ERNO L-134216, transversal thin section. • J–L – *Latusastrea* sp., ERNO L-130302; J – transversal thin section; K – transversal thin section, detail; L – longitudinal thin section. Scale bar 1 mm.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not allow to establish a new species. *Carolastraea graeca* Baron-Szabo & Steuber, 1996 has the same corallite dimensions but belongs to *Palaeohelia*.

Occurrence. – Sample points NP7, NP9. Other occurrence: Tithonian to Lower Berriasian of the Central Tethys (Czech Republic).

Genus *Latusastrea* d'Orbigny, 1849

Type species. – *Explanaria alveolaris* Goldfuss, 1829.

Description. – Plocoid colony. Corallites with a rhomboid outline, not facing above but facing to one side of the colony. A clear bilateral symmetry with septa in two groups of the corallite. On one face of the corallite, one group with one septum longer and thicker than all others, and other, four to six, stronger septa. On the other face the septa are thinner and shorter.

Remarks. – The genus *Latusastreopsis* Morycowa & Marcopoulou-Diakantoni, 1997 is considered a junior synonym but illustrates much better the morphology of *Latusastrea* than the silicified and poorly preserved type material of the type species of *Latusastrea*. This genus is similar to *Pleurocoenia* d'Orbigny, 1849. *Pleurocoenia* has a cerioid corallite arrangement, whereas *Latusastrea* is plocoid with large distances between the individuals. *Latusastrea* has well developed septa, whereas in *Pleurocoenia* only one septum is well developed. The present material lies in between both genera because it shows well developed septa and a cerioid corallite arrangement. Similar is *Latusastrea rubrolineata* Löser *et al*. 2009 and material of this species shown in Löser (2016d). Both – *L. rubrolineata* and the present material – probably present a new genus. The present material differs from *L. rubrolineata* by having larger corallite dimensions.

***Latusastrea*? sp.**
Figure 11J–L

Material. – ERNO L-130302; 3 thin sections.

Dimensions. –
(ERNO L-130302)

	n	min–max	μ	s	cv	μ±s
clmin	22	0.98–1.72	1.27	0.20	16.0	1.07–1.48
clmax	22	1.41–2.20	1.77	0.24	13.7	1.53–2.02
s	22	12–15	13.6	1.09	8.0	12–15

Occurrence. – Sample point NP6.

Family Heterocoeniidae Oppenheim, 1930

Description. – Only phaceloid and plocoid colonies. Symmetry radial, cycles subregular. A larger septum is often present. Lonsdaleoid septa and a marginarium can be present.

Genus *Heterosmilia* Kolodziej *et al*., 2012

Type species. – *Heterosmilia spinosa* Kolodziej *et al*. 2012.

Description. – Phaceloid colony. Septal symmetry radial but with one larger septum that has lateral apophyses.

***Heterosmilia spinosa* Kolodziej *et al*., 2012**
Figure 11H

v 2008c *Hexasmilia* sp. – Löser, p. 51, figs 5.8, 5.9.
*v 2012 *Heterosmilia spinosa* Kolodziej, Ivanov & Idakieva, p. 319, fig. 22.

Material. – ERNO 2194-2.

Dimensions. – (ERNO 2194): c = 11 mm; cl = 9.4 mm; s = 12.

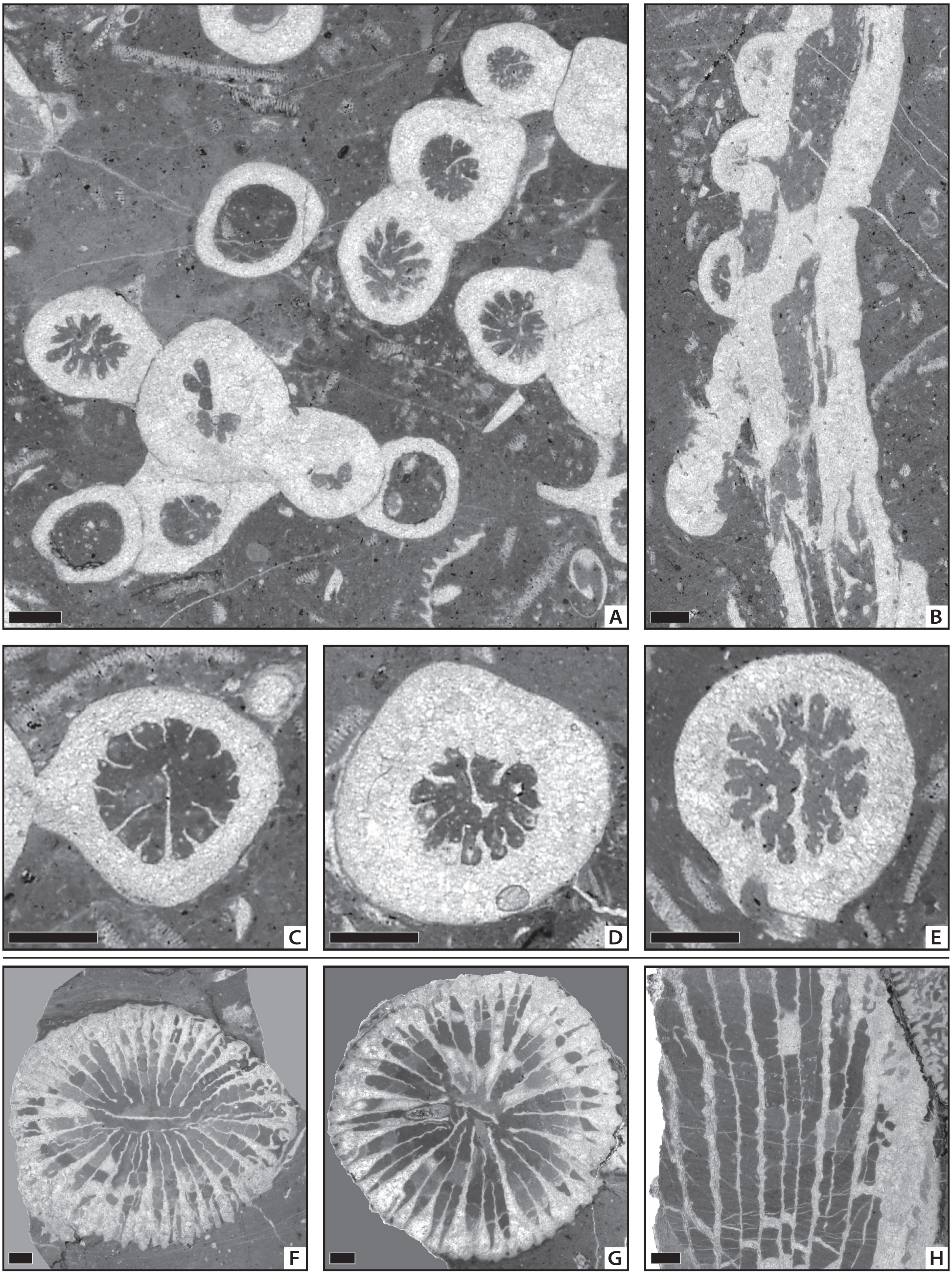
Remarks. – In its corallite dimensions, the material coincides well with the holotype of the species. Kolodziej *et al.* (2012) comments that a third septal cycle can be observed if the material is well preserved, which is not the case in our specimen.

Occurrence. – Sample point BS. Other occurrence: Upper Barremian of the Central Tethys (Bulgaria), Uppermost Aptian of the Western Tethys (Spain).

Superfamily Misistelloidea Eliášová, 1976b

Description. – Solitary and colonial (phaceloid, plocoid) corals. Septa compact, in varying thickness, in a subregular radial symmetry. Septa not connected to each other (*Plesiosmilia* Group) or only in the center of the corallite (Misistellidae). Lateral faces with fine granulae

Figure 12. A–E – *Carolastraea fraji* Eliášová, 1976a; A–D – ERNO L-134202, transversal thin section (A), longitudinal thin section (B), transversal thin section – detail (C) and transversal thin section – detail (D); E – ERNO L-130401, transversal thin section, detail. • F–H – *Montlivaltoides tolmachoffana* (Wells, 1932); F – ERNO L-120511, transversal thin section; G – ERNO L-120529, transversal thin section; H – ERNO L-130129, longitudinal thin section. Scale bar 1 mm.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or smooth, upper margin smooth. Lonsdaleoid and main septa absent. Microstructure of septa of small trabeculae. Synapticulae absent. Pali absent, columella present in most genera, lamellar or by septal fusion. Endotheca present. Marginarium absent. Wall absent, but an epitheca is often present (when preserved). Coenosteum varies. Budding intracalicinal.

***Plesiosmilia* Group**

Description. – Solitary and phaceloid corals. The septa are always free. A lamellar columella is present in some genera. One or two septa may be connected to the columella.

***Plesiosmilia* Milaschewitsch, 1876**

Type species. – *Plesiosmilia turbinata* Milaschewitsch, 1876.

Description. – Solitary turbinate coral. Septa compact, not connected to each other, in a regular radial symmetry. Septa can be connected to the columella. Wall absent. Epitheca present but rarely preserved. Endotheca well developed. Columella lamellar.

Remarks. – The type of the type species of *Plesiosmilia*, *Plesiosmilia turbinata* Milaschewitsch, 1876, is a silicified specimen from the Late Jurassic of Southern Germany. *Axosmilia* could be a senior synonym of latter genus but the type of its type species is so poorly preserved that a detailed comparison is not possible.

***Plesiosmilia coquandi* (d'Angelis d'Ossat, 1905)**
Figure 11I

*v 1905 *Peplosmilia Coquandi* d'Angelis d'Ossat; p. 239, pl. 17, figs 2a, b.
v 1905 *Peplosmilia Casañasi.* – d'Angelis d'Ossat, p. 241, pl. 17, fig. 5a–d.
v 1905 *Pleurosmilia Vaughani.* – d'Angelis d'Ossat, p. 234, pl. 16, fig. 3.
v 1933 *Pleurosmilia whitneyi* n.sp. – Wells, p. 62, pl. 2, fig. 20, pl. 5, fig. 5.
v 2018 *Plesiosmilia vaughani* (Angelis d'Ossat, 1905). – Löser, Steuber & Löser, p. 57, pl. 13, figs 1–3.

Material. – ERNO L-120515, L-134216, L-134217; 1 thin section.

Dimensions. – (ERNO L-134216): c = 34 × 39; s = 96.

Remarks. – D'Angelis d'Ossat (1905) established several new taxa from the Lower Albian of the Montmell Formation (NE Spain) that all belong to the same species. *Peplosmilia coquandi* is preferred because it is established based on the best-preserved specimen among the other types and it is available for study. Our specimens present slightly smaller corallite dimensions than the available syntype of the species.

Occurrence. – Sample points NP5, NP9. Other occurrence: Lower Hauterivian of the European Boreal (France), Uppermost Aptian to Lower Albian of the Western Tethys (Spain), Lower Albian of the Western Atlantic (Mexico), Lower Cenomanian of the Western Atlantic (USA) and the Central Tethys (Greece).

***Plesiosmilia quaylei* (Wells, 1933)**
Figure 13A, B

vp 1926 *Pleurosmilia hennigi* n.sp. – Dietrich, p. 87, pl. 7, fig. 6a–c.
*v 1933 *Pleurosmilia quaylei* n.sp.; Wells p. 63, pl. 2, fig. 16, pl. 5, figs 3, 4.
v 2008b *Plesiosmilia bofilli* (d'Angelis d'Ossat, 1905). – Löser, p. 54, pl. 4, fig. 1.

Material. – ERNO L-120517, L-4361; 2 thin sections.

Dimensions. – (ERNO L-4361): c = 23–35 mm; s = 65.

Remarks. – The material presents similar corallite dimensions and septal counts compared to the holotype of the species. *P. hennigi* has not the priority because only one paralectotype of this species belongs to *Plesiosmilia quaylei*.

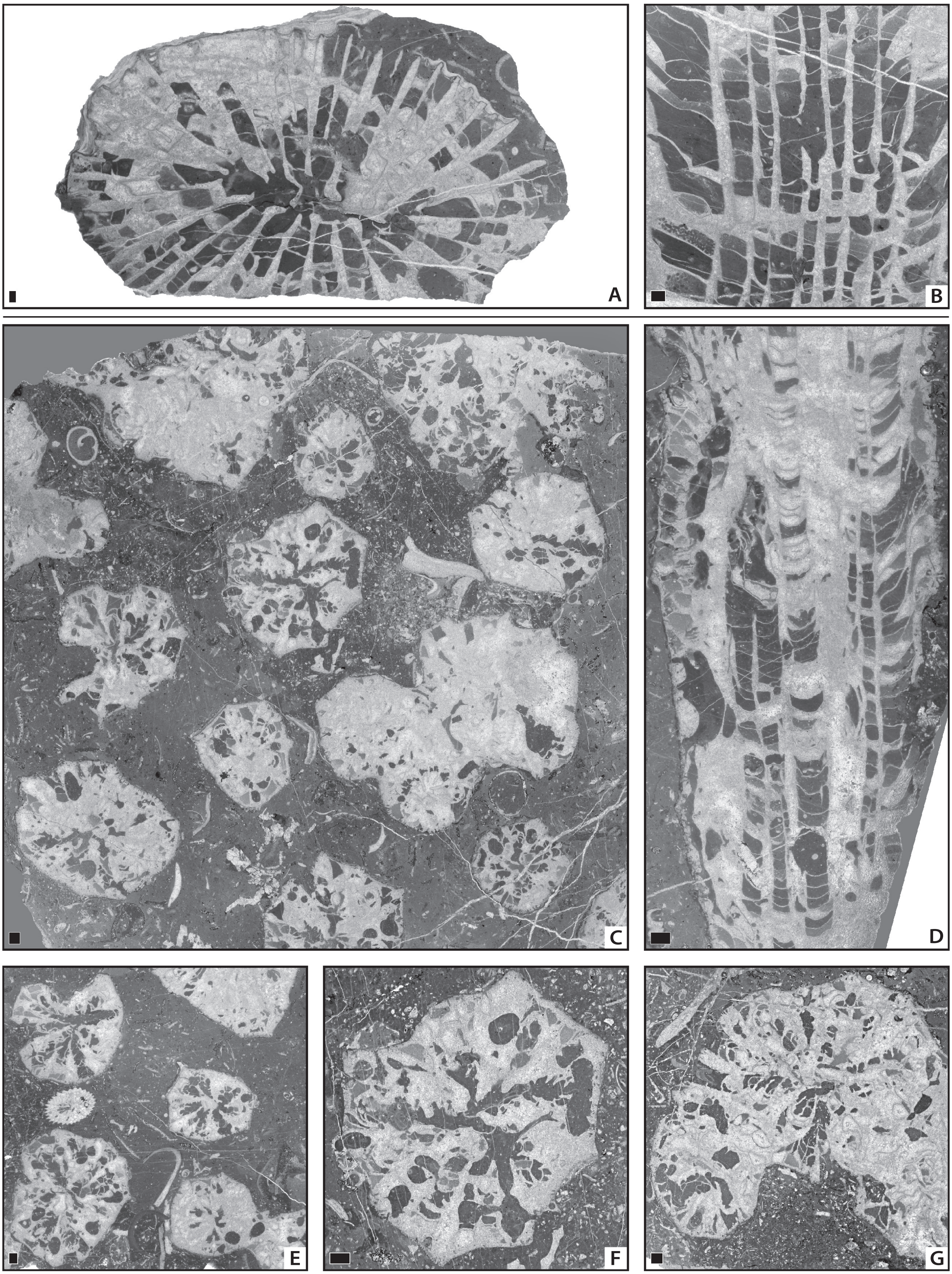
Occurrence. – Sample point P4. Other occurrence: Upper Valanginian to Lower Aptian of the Southern Tethys (Tanzania), Lower Cenomanian of the Western Atlantic (USA).

Genus *Montlivaltoides* He & Xiao, 1990

Type species. – *Montlivaltoides typicus* He & Xiao, 1990.

Description. – Phaceloid coral. Septa not connected to each other, in a regular radial symmetry. Wall absent.

Figure 13. A, B – *Plesiosmilia quaylei* (Wells, 1933), ERNO L-4361; A – transversal thin section; B – longitudinal thin section. • C–G – *Apoplacophyllia polygonata* sp. nov., holotype ERNO L-134213; C – transversal thin section; D – longitudinal thin section; E – transversal thin section, detail; F – transversal thin section, detail; G – transversal thin section, detail. Scale bar 1 mm.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Epitheca present. Endotheca well developed. Columella unknown.

Remarks. – The genus is based on highly recrystallized material without preserved microstructure. Apart from the publication, additional photographs of thin sections of the type species were available for study but they could not confirm the taxonomic position of the genus. The existence of a columella cannot not be confirmed, but according to a written personal communication from Xinyi He, this characteristic may vary. The present material shows clearly a columella. In the future, it may be necessary to establish a new genus for those species that have a columella.

Montlivaltoides tolmachoffana **(Wells, 1932)**
Figure 12F–H

*v 1932 *Aplosmilia* (?) *tolmachoffana* Wells; p. 234, pl. 30, fig. 2, pl. 31, fig. 2.
v 1999 *Placophyllia bandeli* Baron-Szabo, 1998. – Baron-Szabo & González-León, p. 475, fig. 3e, f.

Material. – ERNO 2192, 2194, 2196, L-120511, L-120523, L-120529, L-120530, L-120535, L-130104, L-130105, L-130111, L-130112, L-130116, L-130119, L-130128, L-130129, L-134502, L-134507, L-134509; 14 thin sections.

Dimensions. – (ERNO L-120529): c = 11 mm; s = 44.

Remarks. – The material has slightly larger corallite dimensions than the holotype of the species.

Occurrence. – Sample points NP5, BS. Other occurrence: Upper Barremian to Lower Albian of the Western Atlantic (Mexico, USA), Lower Aptian of the Central Tethys (Greece), Upper Aptian of the Western Pacific (Japan).

Superfamily Rhizangioidea d'Orbigny, 1851

Description. – Solitary and colonial (astreoid, cerioid, plocoid, reptoid, and thamnasterioid) corals. Septa almost not perforated. Normal septal thickness, septal symmetry regular radial or irregular, septa often and regularly connected to each other. Upper septal border and lateral faces with granulations. No lonsdaleoid septa, no main septum. Microstructure of medium-sized trabeculae. Synapticulae present. Pali absent. Columella present, styliform or by septal fusion. Endotheca present. Marginarium absent. Wall absent or present. Coenosteum depending on the colony type. Budding extracalicinal.

Family Rhizangiidae d'Orbigny, 1851

Description. – Astreoid, cerioid, plocoid, reptoid, and thamnasterioid colonies. The symmetry is regular or subregular radial in varying systems, or irregular. The columella is formed by septal fusion.

Genus *Eosiderastrea* Löser, 2016c

Type species. – *Siderastrea cuyleri* Wells, 1932.

Description. – Astreoid colony with large corallites. Septal symmetry irregularly radial, in various systems. Septa are quite regularly connected to each other. In the corallite center, septa of the first cycles fuse to form the columella.

Eosiderastrea **cf. *stefani*** **Löser, 2016c**
Figure 14H, I

v 2016c *Eosiderastrea* sp. 4. – Löser, p. 396, pl. 6, figs 10–12.
v 2017 *Eosiderastrea* sp. – Löser & Bilotte, p. 6, fig. 6a–c.
v 2018 *Eosiderastrea* sp. 2. – Löser, Steuber & Löser, p. 68, pl. 20, figs 4–6.

Material. – ERNO L-130135, L-130306, L-133907; 4 thin sections.

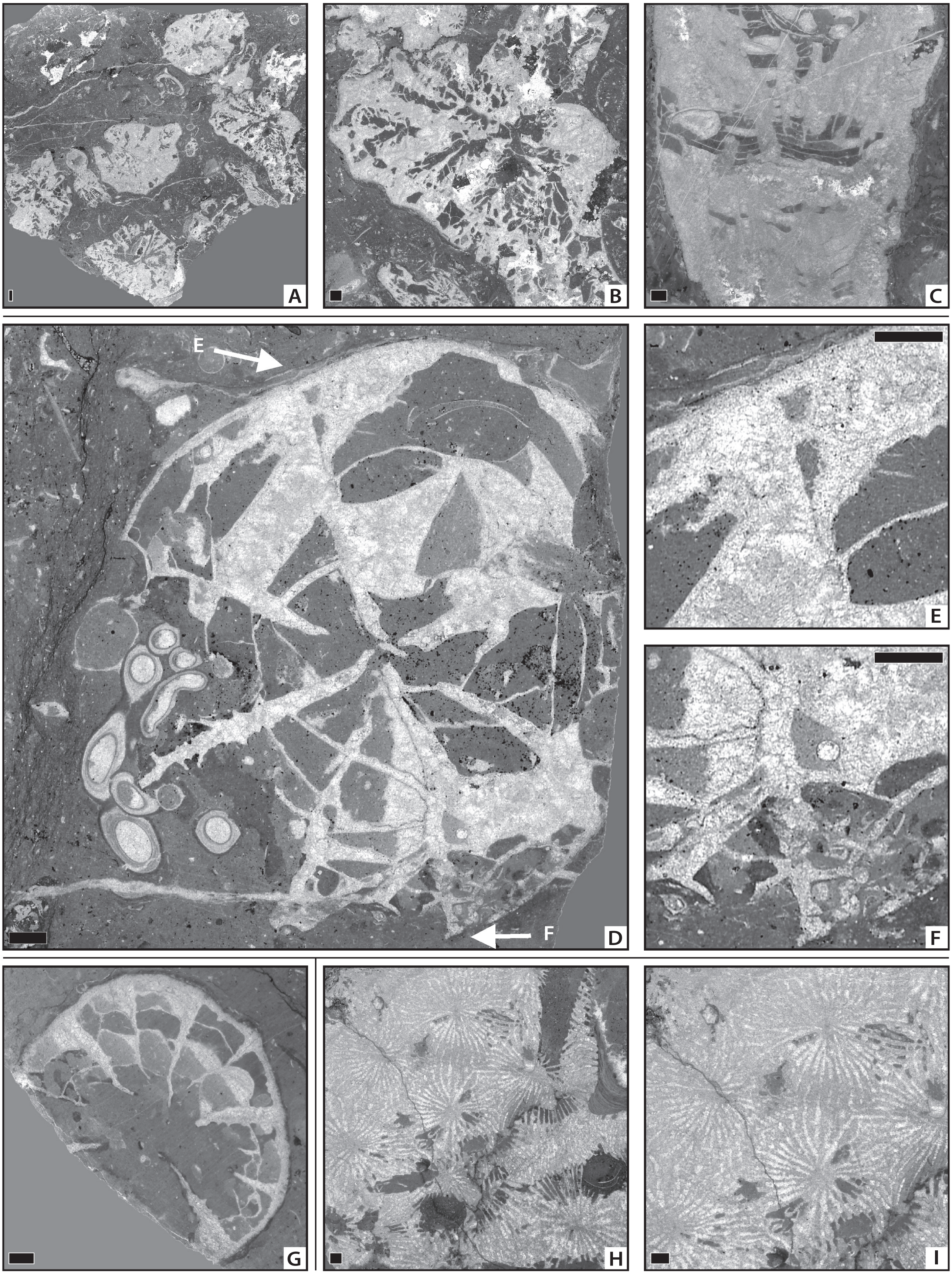
Dimensions. –
(ERNO L-130135)

	n	min–max	μ	s	cv	μ±s
ccd	8	4.95–7.53	6.54	1.03	15.8	5.51–7.58
cmin	7	5.46–7.79	6.92	0.79	11.4	6.13–7.72
s	6	36–49	41.3	5.39	13.0	36–47

Remarks. – The material is similar to *Eosiderastrea stefani*, but it has slightly larger corallite dimensions.

Occurrence. – Sample points NP8, NP6, NP5. Other occurrence: Uppermost Aptian to Cenomanian of the Western Tethys (France, Spain), Lower Cenomanian of the Central Tethys (Greece), Uppermost of the Western Tethys (France).

Figure 14. A–C – *Apoplacophyllia hackemesseri* (Morycowa & Marcopoulou-Diacantoni, 2002), ERNO L-4310; A – transversal thin section; B – transversal thin section, detail; C – longitudinal thin section. • D–F – *Aulastraeopora aguedae* sp. nov. holotype ERNO L-134511; D – transversal thin section; E – transversal thin section, detail; F – transversal thin section, detail. • G – *Aulastraeopora deangelisi* Prever, 1909, ERNO L-120502, transversal thin section. • H, I – *Eosiderastrea* cf. *stefani* Löser, 2016c, ERNO L-130135; H – transversal thin section; I – transversal thin section, detail. Scale bar 1 mm.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Family Thamnasteriidae Reuss, 1864

Description. – Thamnasterioid colonies. Corallites small. The septa are in an irregular radial symmetry. The columella is styliform.

Genus *Ahrdorffia* Trauth, 1911

Type species. – *Porites stellulata* Reuss, 1854.

Description. – Thamnasterioid colony with small corallites. The costae are confluent to sub-confluent. Corallites often difficult to recognize, when small or arranged with large distances. Septa without symmetry, in a low number, and often connected to each other. Columella small and styliform.

Remarks. – The genus is usually considered to be a junior synonym of *Mesomorpha* Pratz, 1882, but because *Mesomorpha* is preoccupied by an earlier described taxon, it is replaced by a junior synonym. The distinction of the species within the genus is complicated because the corallite distance, as well as the number of septa per corallite, vary considerably within one colony. For more details on the genus see Löser *et al.* (2019b).

Ahrdorffia urgonensis **(Koby, 1898)**
Figure 15A, B

*v 1898 *Thamnastraea urgonensis* Koby; p. 82, pl. 19, figs 4–8, pl. 20, figs 1, 2.
v 2010 *Mesomorpha urgonensis* (Koby, 1898). – Löser, p. 587, fig. 3.1 [= here older synonymy].
v 2019b *Ahrdorffia urgonensis* Koby, 1898. – Löser, Heinrich & Schuster, p. 312, fig. 508a, b, c.

Material. – ERNO L-120539; 1 thin section.

Dimensions. –
(ERNO L-120539)

	n	min–max	µ	s	cv	µ±s
ccd	20	0.78–1.79	1.27	0.27	21.9	0.99–1.55
s	5	17–21	18.6	1.51	8.1	17–20
sk	12	7–9	8.41	0.79	9.4	8–9

Remarks. – The present material has similar corallite dimensions and septal counts as the type material of the species.

Occurrence. – Sample point NP5. Other occurrence: Worldwide from the Hauterivian and Coniacian.

Superfamily Stylinoidea d'Orbigny, 1851

Description. – Solitary and colonial corals. Septa compact. Septal symmetry mainly regular, radial, or bilateral. First septal cycle (or cycles) generally thicker than later cycles. Septal lateral faces ornamented. Septal inner margins with auriculae. Lonsdaleoid septa present in two families. No main septa. Microstructure of small trabeculae. Synapticulae and pali absent. Columella present in two families. Endotheca well-developed. Marginarium absent. Wall compact, septothecal. Coenosteum present in some genera. Budding varies depending on the colony type.

Family Aulastraeoporidae Alloiteau, 1957

Description. – Solitary and colonial (astreoid, cerioid, phaceloid, plocoid) corals. Septal symmetry regularly radial. Lonsdaleoid septa common. Columella absent. Budding extracalicinal or intracalicinal (septal budding).

Genus *Apoplacophyllia* Morycowa & Marcopoulou-Diacantoni, 2002

Type species. – *Apoplacophyllia hackemesseri* Morycowa & Marcopoulou-Diacantoni, 2002.

Description. – Phaceloid colony that shares all characteristics of the family.

Remarks. – The thin sections of the type of the type species are small and poorly preserved. They do not give much information about the endotheca and the mode of budding. Material from other localities shows a well-developed endotheca made by numerous thin dissepiments (as in other members of the family) and a marginal intracalicinal budding. Formally, only the type species is described. The Aptian *Mitrodendron major* He & Xiao, 1990 and *Budia qiekanensis* He & Xiao, 1990 may belong to this genus.

Apoplacophyllia hackemesseri **Morycowa & Marcopoulou-Diacantoni, 2002**
Figure 14A–C

Material. – ERNO L-133905, L-4310; 3 thin sections.

*v 2002 *Apoplacophyllia hackemesseri* Morycowa & Marcopoulou-Diacantoni; p. 28, fig. 18a–f.
v 2016b *Apoplacophyllia hackemesseri* Morycowa & Marcopoulou-Diacantoni, 2002. – Löser, fig. a40a, b.

Dimensions. –
(ERNO L-4310)

	n	min–max	µ	s	cv	µ±s
cmin	6	13.9–17.7	15.6	1.57	10.1	14.0–17.1
cmax	6	15.5–21.0	18.7	1.91	10.1	16.8–20.6
s	18–24					

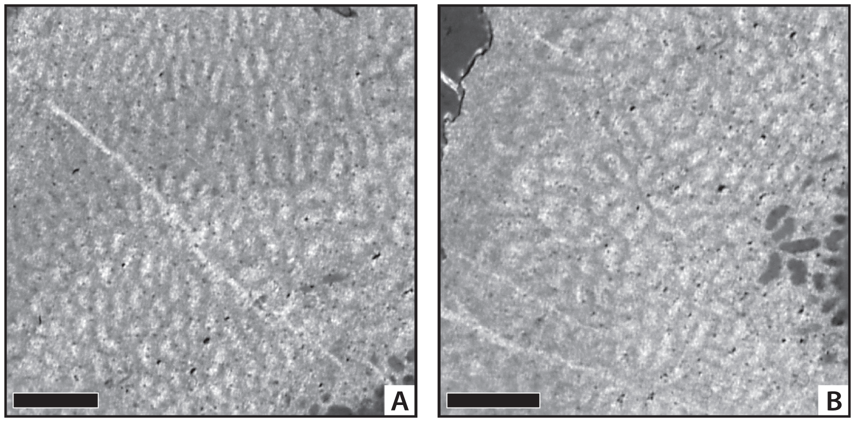

Figure 15. *Ahrdorffia urgonensis* (Koby, 1898), ERNO L-120539; A – transversal thin section; B – transversal thin section, detail. Scale bar 1 mm.

Remarks. – The corallite dimensions are similar to *Apoplacophyllia hackemesseri*.

Occurrence. – Sample points P4, NP8. Other occurrence: Lower Albian of the Western Tethys (Spain), Aptian to Cenomanian of the Central Tethys (Greece).

***Apoplacophyllia polygonata* sp. nov.**
Figure 13C–G

Holotype. – ERNO L-134213; 6 thin sections.

Type horizon and locality. – Cretaceous, Middle Albian, Espinazo del Diablo Formation. Mexico, Sonora, Municipio San Pedro de la Cueva, Tepache, Lampazos area, Espinazo de Diablo, sample point NP9 (29° 26′ 30.2″ N, 109° 27′ 28.3″ W).

Etymology. – In relation to the corallite outline of the coral.

Material. – Holotype and an additional specimen (L-4294); 11 thin sections.

Diagnosis. – An *Apoplacophyllia* with a corallite diameter between 9 and 15 mm and a maximal septal number of 24.

Description. – Phaceloid colony. The corallite outline goes from polygonal to irregular. The septa are compact. The microstructure of the septa is unknown due to the preservation (probably, it is composed by small-sized trabeculae). The septa in cross section are externally slightly thicker, tapering towards the center. The symmetry of the septa is radial and hexameral. Three septal cycles result in 24 septa. The septal cycles differ in length and thickness. The first septal cycle extends to the calicular center and the later cycles are subsequently shorter. Pali, costae, and synapticulae are absent. The endotheca is composed by tabulae. No wall. No coenosteum. The budding is intracalicinal.

Discussion. – The principal difference between this species and the type species are the much smaller corallite dimensions. *Mitrodendron major* He & Xiao, 1990 has much larger dimensions and *Budia qiekanensis* He & Xiao, 1990 has only two septal cycles.

Remarks. – The additional specimen of the new species (ERNO L-4294) comes from the Early Albian of Sonora but does not constitute a type specimen.

Dimensions. –
(ERNO L-134213)

	n	min–max	μ	s	cv	μ±s
cmin	9	8.09–11.5	9.87	1.36	13.7	8.51–11.2
cmax	9	9.85–17.0	13.2	1.93	14.6	11.3–15.1
ccd	11	7.98–17.7	13.0	2.95	22.6	10.1–16.0
s	18–24					

Occurrence. – Sample point NP9. Other occurrence: Lower Albian of the Western Atlantic (Mexico).

Genus *Aulastraeopora* Prever, 1909

Type species. – *Aulastraeopora deangelisi* Prever, 1909.

Description. – Cylindric solitary coral reaching large dimensions in some species. The septal symmetry has a basic number of six or (less common) four.

Remarks. – *Aulastreopora* is a solitary coral that may reach enormous dimensions (such as, for instance, the type of *Blothrocyathus harrisi* has a length of 36 cm). This genus was considered in Löser (2008a) and Morycowa & Kolodziej (2001).

***Aulastraeopora aguedae* sp. nov.**
Figure 14D–F

Types. – Holotype: ERNO L-134511. Paratype: ERNO L-134513.

Type horizon and locality. – Espinazo del Diablo Fm (Cretaceous, Middle Albian). Mexico, Sonora, Municipio San Pedro de la Cueva, Tepache, Lampazos area, Espinazo de Diablo, sample point NP5 (29° 26′ 26.1″ N, 109° 27′ 27″ W).

Material. – Type material; 2 thin sections.

Etymology. – This species is dedicated to Agueda Pesqueira, the mother of the first author (ASP), in appreciation of the great support delivered by her, and received by him during his university studies.

Diagnosis. – *Aulastraeopora* with a tetrameral symmetry and a corallite diameter between 12 and 15 mm.

Description. – Solitary cylindric coral with a diameter of 12–15 mm. The calicular outline is circular. The septa are compact. The microstructure is unknown due to the poor preservation. The septa in cross section are externally slightly thicker, tapering towards the center. The symmetry of the septa is radial and tetrameral. The cycles of the septa are regular. Two cycles resulting in eight septa. The septal cycles differ in length and thickness. The septa are not connected to each other. The septal distal margin is unknown. Synapticulae and a columella are absent. The endotheca is unknown, but rich endothecal elements are visible in the transverse thin sections. The wall has the same structure as the septa and is therefore septothecal.

Remarks. – The principal difference among all existing species is the tetrameral symmetry and the existence of only two septal cycles. Within the genus, only *A. schnauzeae* Löser, 1998 represents a tetrameral symmetry but three septal cycles. Moreover, in this species, the septa are very strong and a very high number of apophysal septa can be found. It is questionable whether *A. schnauzeae* belongs to the genus *Aulastraeopora* or rather represents a yet undescribed genus.

Dimensions. – (ERNO L-134511): c = 15.3–15.4 mm; s = 8. (ERNO L-134513): c = 12.1–13 mm; s = 8.

Occurrence. – Sample point NP5.

***Aulastraeopora deangelisi* Prever, 1909**
Figure 14G

*v 1909 *Aulastraeopora Deangelisi* Prever, p. 138, text-figs 32–37.
v 2008a *Aulastraeopora deangelisi* Prever, 1909. – Löser, p. 21, pl. 1, figs 1–7 [= here older synonymy].
v 2016b *Aulastraeopora deangelisi* Prever, 1909. – Löser, fig. a59a, b.
2016b *Budiopsis typicus* He & Xiao, 1990. – Löser, fig. b26.

Material. – ERNO L-120502, L-120504, L-120528, L-130137; 3 thin sections.

Dimensions. – (ERNO L-120502): c = 11.4; s = 12. (ERNO L-120504): c = 12.9; s = 12.

Remarks. – The material presents similar corallite dimensions and equal septal counts compared to the lectotype of *A. deangelisi*.

Occurrence. – Sample point NP5. Other occurrence: Worldwide from the Aptian to the Albian.

Discussion

Coral distribution in the sections

Coral frequency and species composition vary among the sections of the studied area, although few differences in the sedimentological data and associated invertebrate fossils (principally mollusks) could be found. Most beds yielded a low number of specimens and species, except for NP5. The correlation of the sample points (that partly corresponds to beds; Fig. 2) based on co-occurring species (Fig. 16) shows four major groups. Each group is composed by at least two sample points within the same stratigraphic column, except for NP5, which is the only bed in column I (Fig. 2). Sample point NP5 shows a positive correlation with the material described by Baron-Szabo & González-León (1999), collected in the study area but without an exact position in the section (BS in Fig. 16). Sample point NP5 is easily accessible and rich in coral material so that it is very probable that Baron-Szabo & González-León (1999) collected their material at the same place. Samples points NP9 and NP10 from section III show a strong correlation because the NP9 possesses a relatively high number of taxa that coincide with the three species of NP10. Sample points NP6 and NP7 from section II show a low correlation with other points. Finally, sample points NP11 and NP8 (both from section III), and P4 (without section) are relatively poor in species but form a distinctive group. The correlation

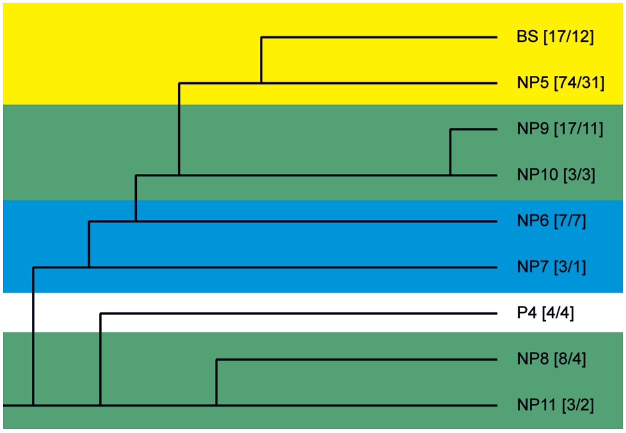

Figure 16. Correlation of the various beds and sample points based on the coral species. The Correlation Ratio coefficient was applied. Different clusters indicate different sections. Numbers of specimens and species in brackets. Abbreviations: NP – sample location shown in Fig. 2; BS – material published by Baron-Szabo & González-León (1999). This, and material from P4, are without sections.

shows that the taxonomical correlation of the coral assemblages is controlled by the geographic position of the sample points, rather than by slightly different ages. The geographic position may be related to specific regional paleoecological conditions that have changed little during the sedimentation of the succession.

Paleoecology

Corals represent two aspects of their growth. The first aspect is the way in which polyps are arranged in a colonial coral, and this is mainly controlled by the presence or absence of a wall, the confluence of septa, and a coenosteum (organization types; Löser 2016d: fig. 3.2.1). The second aspect is the growth form of the coral

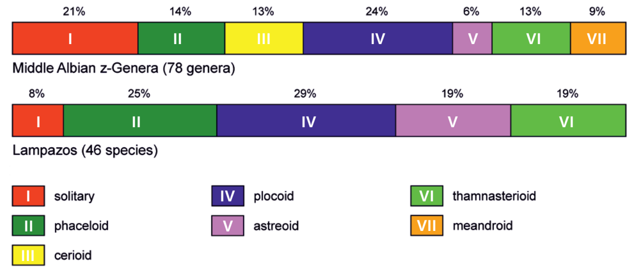

Figure 17. Organisation types of hermatypic (z-) coral genera worldwide (Middle Albian) compared to the coral fauna from the Lampazos area. Organisation data from Löser (2016d).

colony. It can be platy or it can be more or less erected above the ground. The dominating organization types in the coral fauna from the Lampazos area are phaceloid and plocoid. Cerioid and meandroid corals are absent (Fig. 17). When comparing the distribution of the organization type of the coral genera of the present fauna with the distribution worldwide during the Middle Albian (only hermatypic corals), it can be observed that phaceloid and astreoid corals are more common. When talking about the growth form, various plocoid taxa (e.g., *Cryptocoenia* cf. *kiliani*, *Eocolumastrea*? sp., *Latusastrea*? sp., *Stelidioseris hourcqi*, *Stelidioseris* sp.), and also thamnasterioid taxa, tend to form thick ramose colonies (Fig. 18). Both the organization type and growth form of the coral have a direct influence on the absolute growth rate. The growth rate of extant Scleractinian corals has been investigated for a long time; starting in the late 19th century with Agassiz (1890), Duncan (1878a, b), and LeConte (1875). Vaughan & Wells (1943) give a summary on the subject. The growth rate has two aspects, the annual increment in weight and the annual increase in height. Here, we consider only the increment in the height. Taking into account the organization type and the growth form of the coral colony, the phaceloid

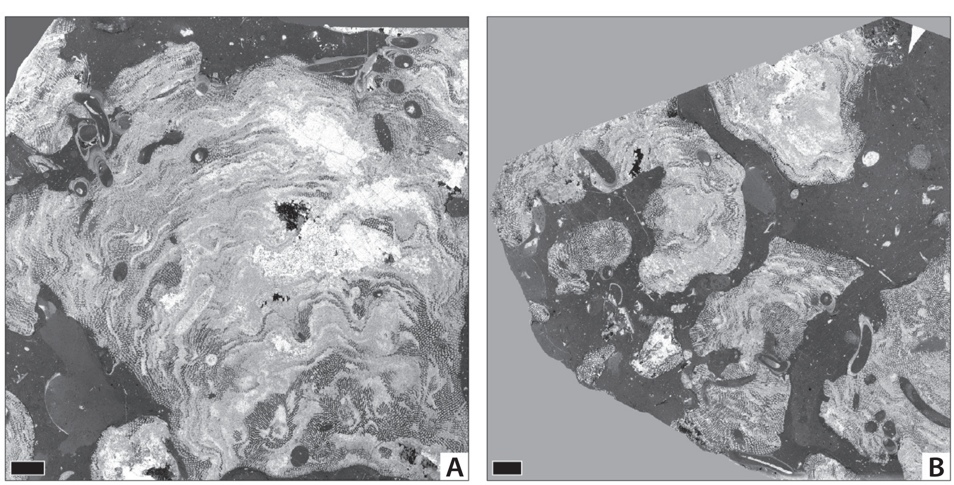

Figure 18. *Microsolena nipponica* (Eguchi, 1951), ERNO L-4866, Lampazos area, sample point P4; A – lower part of the colony in massive growth form; B – upper part of the same specimen with a thick ramose growth form. Scale bar 5 mm.

corals and thick branching corals show the highest growth rates, whereas the solitary, meandroid, and cerioid corals show the lowest rate. The growth rate of astreoid, plocoid, and thamnasterioid corals is intermediate. Apart from the organization type and growth form, the growth rate is also controlled by the fine structure of the skeleton. Corals with porous septal blades grow faster than corals with compact septa. In the studied material, all corals of the superfamily Cyclolitoidea have septa that are more or less perforated, being members of the family Microsolenidae more than of the family Latomeandridae. The corals of both families are principally astreoid and thamnasterioid, one genus (*Latohelia*) is phaceloid. Hence, they are better adapted to a higher sedimentation rate because they are able to grow as fast as the sediment supply.

Growth rate for one and the same species depends on many environmental factors, such as the season (sea water temperature and light intensity; Shinn 1966, Loya 1985, Houck *et al*. 1977), turbidity that results in lower light conditions (Shinn 1966), water depth (water energy, seawater temperature and light intensity; Miller 1995), and heterotrophy (Miller 1995). The influence of seasonal changes on growth rate can be the light intensity, as well as the temperature. Seawater temperatures that are too high do not create favorable conditions, because temperatures higher than the optimum of the coral lead to the expulsion of symbiotic algae (also called coral bleaching; Hughes *et al*. 2018 and the literature cited therein). Water depth is therefore crucial: corals in temperate environments will grow faster when they are close to the water surface because of the higher light concentration, whereas corals in tropical environments have higher growth rates in deeper zones (variation in coral growth, Baker & Weber 1975). Miller (1995) links the growth rate to the chlorophyll a concentration in the coral tissue, which is controlled by the light availability, and is an additional food source (heterotrophy). Modern corals in reefs have – thanks to their symbiotic algae – a preferred autotrophic mode of nutrition. This enables them to live in environments that are poor in organic nutrients, because they are either far from a source of nutrients (as in the Great Barrier Reef, east of Australia), or because there is no food supply due to arid climate conditions (as per the fringing reefs in the Red Sea). A high input of nutrients is life-threatening for corals because, on the one hand, they can be colonized by algae (for instance, as described in Burkepile *et al*. 2013), and on the other hand, there is the destruction rate of the reef by borers (Rice *et al*. 2020 and references cited therein). Most corals were infested by macro-borers during the most part of their lifetime. These borers are mainly bivalves and serpulids. Abundance of both micro- and macro-borings increased in relation to increasing input of nutrients, which coincides with the high sedimentation rates (see Fonseca *et al*. 2006).

Faunal composition and frequency

In order to compare the faunal composition of the studied fauna to other faunas, we set the global richness in genera per superfamily relative to the local richness of the studied fauna. The distribution patterns of the species per superfamily in the studied fauna correspond surprisingly well to the global distribution of genera among the superfamilies during the Middle Albian (Fig. 19). The only exception is the superfamily Actinastreoidea, which is more diverse in the Lampazos Fm. than elsewhere. This could be due to the regional sedimentary conditions to which dendroid and phaceloid corals were better adapted. The genus *Actinastraeopsis* forms phaceloid colonies and both present *Stelidioseris* species that have a plocoid corallite arrangement, but their growth form is thick branching.

The superfamilies Cyclolitoidea, Eugyroidea, and Actinastreoidea are rich in species and constitute more than half of the coral species of the study area. The most rich in species is the superfamily Cyclolitoidea, representing nearly 35% of all present species. These three superfamilies range throughout the Cretaceous, but the Eugyroidea have far more genera in the Lower Cretaceous. The next species-rich superfamilies are the Cladocoroidea and Stylinoidea, each with nearly 9% of all species; both superfamilies have their first occurrence in the Middle Jurassic. The three-remaining superfamilies Heterocoenioidea, Misistelloidea, and Thamnasterioidea encompass the remaining 17% of the present coral species in the study area. According to Löser (2016d) twenty superfamilies occur in the Middle Albian and eight of these occur in the study area.

The global frequency of Cretaceous corals genera was divided by Löser (2016d) into five frequency classes, ranging from very rare to very common, and calculated for four-time intervals (Berriasian to Valanginian, Hauterivian to Albian, Cenomanian to Santonian, and Campanian to Maastrichtian). The time interval Hauterivian to Albian encompasses four very common, nine common, thirteen occasional, 32 rare, and 185 very rare coral genera, which

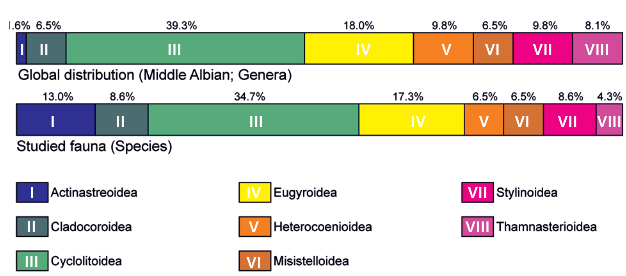

Figure 19. Comparison of the distribution of coral genera richness in the Middle Albian among superfamilies globally and in the study area (global data according to ranges in Löser 2016d).

Table 1. Global frequency of the coral genera of the study area according to Löser (2016d: fig. 6.3.3.4).

Frequency	Genus
Very common	*Cryptocoenia*
(13.6%)	*Eugyra*
	Stelidioseris
Common	*Astraeofungia*
(22.8%)	*Dimorphastrea*
	Eocolumastrea
	Plesiosmilia
	Polyphylloseris
Occasional	*Actinastraeopsis*
(18.2%)	*Ahrdorffia*
	Eosiderastrea
	Microsolena
Rare	*Aulastraeopora*
(13.6%)	*Cladophyllia*
	Latohelia
Very rare	*Ampakabastraea*
(31.8%)	*Apoplacophyllia*
	Carolastraea
	Heterosmilia
	Latusastrea
	Montlivaltoides
	Pentacoeniopsis

corresponds to a distribution of 1.7, 3.7, 5.3, 13.2, and 76.1%. In table 1, the genera found in the study area are assigned to their frequency classes, in accordance with Löser (2016d: fig. 6.3.3.4).

In the Lampazos area, the coral fauna consists of 13.6% very common, 22.8% common, 18.2% occasional, 13.6% rare, and 31.8% very rare coral genera. This differs from the worldwide genera composition pattern during the Hauterivian-Albian interval, which is especially noticeable in the case of the very rare genera category.

Endemism

Endemism of genera is not an exception in the Cretaceous coral faunas; a low number of abundant genera, distributed worldwide, face a high number of genera that are restricted to small areas (Löser 2016d: fig. 6.3.3.1). The present fauna encompasses 22 genera, of which *Pentacoeniopsis* is known only from here and *Carolastraea* shows a very long gap, with its last preceding known occurrence in the Berriasian. The material described here as *Latusastrea*? sp. probably represents a new genus that is restricted to the Western Atlantic. The same applies to *Eocolumastrea*? sp., that is only known from the study area. The two new species established here are, to date, only known from the study area. The high rate of endemism is not easily explained. The coral fauna from the Lampazos Fm. is only slightly younger than the coral faunas from the upper Mural Fm., and both faunas are very closely located, geographically. The coral fauna of the Lampazos Fm. shares many species with faunas of the Mural Fm., but all shared taxa belong to common genera. Albian corals are also known from the Texas platform (Löser & Minor 2007), where coral diversity is low and the number of shared taxa with the fauna studied is, with eleven taxa, rather low.

Paleogeographic distribution

A comparison of the paleobiogeographic units for the time span from the Barremian to the Santonian (Fig. 20) is based on 37 species from the study area, that were also indicated in other areas. Although the overall number of shared species is high, the number of species shared with other faunules is relatively low. The present fauna shares the highest number species (15) with the Upper Aptian to Lower Albian coral fauna from the Bisbee Basin in Sonora (Mexico) and Arizona (USA). The next most closely related faunules are those from the Upper Aptian of the southern Pyrenees (Schöllhorn 1998), and the Upper Valanginian to Barremian of the Puebla Basin (Mexico). These faunules are grouped the cluster A (Fig. 20).

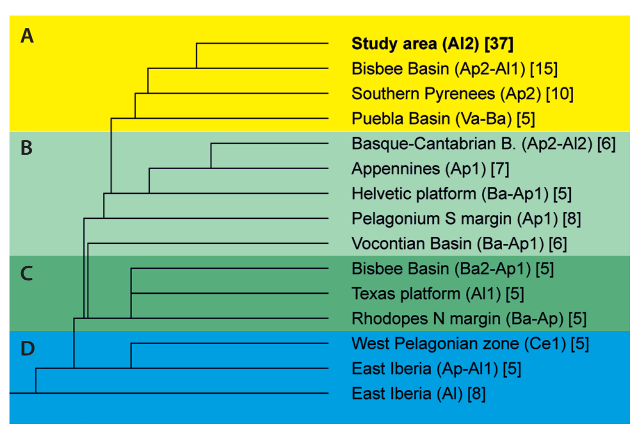

Figure 20. Correlation of provinces with joint species of the study area. Provinces with less than four joint species are suppressed, and only provinces between Barremian and Santonian age are shown. The Correlation Ratio coefficient was applied; the graph is logarithmic. The letters A to D indicate different clusters. Abbreviations: Va – Valanginian; Ba – Barremian; Ba2 – Upper Barremian; Ap – Aptian; Ap2 – Upper Aptian; Al – Albian; Al2 – Middle Albian; Ce1 – Lower Cenomanian.

The cluster B cluster encompasses various Tethyan faunas of a Barremian to Albian age. The cluster C contains two geographically more closely-related faunules from the Bisbee Basin and the Texas Platform. Finally, the cluster D gathers faunas from the West Pelagonian Zone (Greece; Löser *et al*. 2018), and the Aptian to Albian of East Iberia, including mainly coral faunas of the Montmell Fm., Lower Albian in age (Moreno Bedmar *et al*. 2017).

Nine decribed species are unknown outside of the studied area. Most of these species are probably new. Only three of them (*Pentacoeniopsis sonorensis*, *Apoplacophyllia polygonata*, and *Aulastraeopora aguedae*) are formally established here. The other part of the species remains in open nomenclature, because specimens studied are either too poorly preserved or too small in size to allow the formal description of new species (*Ampakabastraea* sp. 2, *Pentacoeniopsis* sp. 1, *Pentacoeniopsis* sp. 2, *Pentacoeniopsis* sp. 3), or the generic assignment is questionable (*Eocolumastrea*? sp., *Latusastrea*? sp.). For this material and several species that are only compared to other species (such as *Polyphylloseris* cf. *japonica* or *Eosiderastrea* cf. *crassicostata*), it would be possible to establish new taxa in the future.

Stratigraphic distribution

The stratigraphic range of the species from the Lampazos area shows a strong similarity with global ranges of Lower Cretaceous corals, mainly in the Upper Aptian to Lower Albian interval (Fig. 21). Only three species of the studied fauna were found elsewhere, before the Valanginian and only four after the Cenomanian–Turonian boundary. The summarized range of the species of the study area shows diversity peaks in the Early Hauterivian, Early Aptian, and Early Albian (Fig. 22), a diversity pattern that corresponds to the global coral richness pattern in the Cretaceous (Löser 2016d: fig. 6.1.1), but it starts to get harder to corroborate after the Cenomanian.

The generic composition of the Lampazos fauna (Fig. 23) shows that the fauna is dominated by Early Cretaceous genera. Twelve genera out of twenty became extinct globally before the Turonian. There are several genera that have their last occurrence at the end of the Middle Albian (*Actinastraeopsis*, *Carolastraea*, *Cladophyllia*, *Heterosmilia*, and *Latusastrea*), while other genera disappeared at the end of the Early Cenomanian (*Ampakabastraea*, *Apoplacophyllia*, and *Aulastraeopora*), and finally some other genera became extinct during the Late Cenomanian (*Cryptocoenia*, *Eocolumastrea*, *Latohelia*, and *Polyphylloseris*). Eight genera present in the study area passed the Cenomanian–Turonian boundary. Two genera have their last known occurrence in the studied fauna: *Carolastraea* and *Heterosmilia*. *Heterosmilia* is generally rare and was until now indicated up to the Aptian. The gap between the former last occurrence and the new occurrence of *Carolastraea* is a very long-time span. Because the Early Cretaceous coral faunas, particularly that of the Aptian and Albian, are well studied on a global scale, the Middle Albian *Carolastraea* represents rather heterochron homeomorphy: material from the Tithonian and Albian look very similar, but they have no direct phylogenetic relationship.

Age of the Espinazo del Diablo Formation

The coral fossil record described in this paper comes from the lower part of the Espinazo del Diablo Formation. There is no general consensus on the age of the formation, as published papers indicate uppermost Aptian–Lower Albian (Monreal & Longoria 2000), Lower Albian (González-León 1988), or Middle Albian age (Scott & González-León 1991, Baron-Szabo & González-León 1999, Robert *et al*. 2018, Samaniego-Pesqueira 2018). In the present contribution, we assign a Middle Albian age of the formation, following the latter authors (Fig. 25). The assignation of the Espinazo del Diablo Formation to the Middle Albian was first proposed by Scott & González-León (1991), based on foraminifers, rudists, other bivalves, and corals. In the recent works such as Robert *et al*. (2018), and the Master's thesis of Samaniego-Pesqueira (2018) the ammonoid record of the Agua Salada Formation was assigned to the Upper Aptian-lowermost Albian. Unfortunately, the Lampazos Formation, which underlies the Espinazo del Diablo Formation, yielded no ammonites. But this is not the case for the overlying Nogal Formation, which yielded ammonoids of, at the latest, Middle–early late Albian age (Scott & González-León 1991). On the other hand, Robert *et al*. (2018) correlated the ammonoid record with Early–late Albian. Accordingly, the ammonite record indirectly indicates the Lower Albian to the uppermost Middle Albian age of the Espinazo del Diablo Formation. A correlation between the Espinazo del Diablo Formation and other Albian shallow-water carbonate platforms of Mexico and the United States of America further refines its age (Fig. 25). In the Cerro Chino area of the Chihuahua State, the Aptian–Albian strata is quite similar to the Lampazos area. The Aptian–lowermost Albian rocks are basinal materials (La Peña Formation in Chihuahua), successively followed by a transgressive unit of Lower Albian age (Coyame Formation in Chihuahua); refer to Fig. 25. The Coyame Formation resembles the Lampazos Formation, with the difference being, that the Coyame yielded ammonites of Lower Albian age (Ovando-Figueroa *et al*. 2018), and thus probably embraced the complete Lower Albian interval. The Coyame Formation

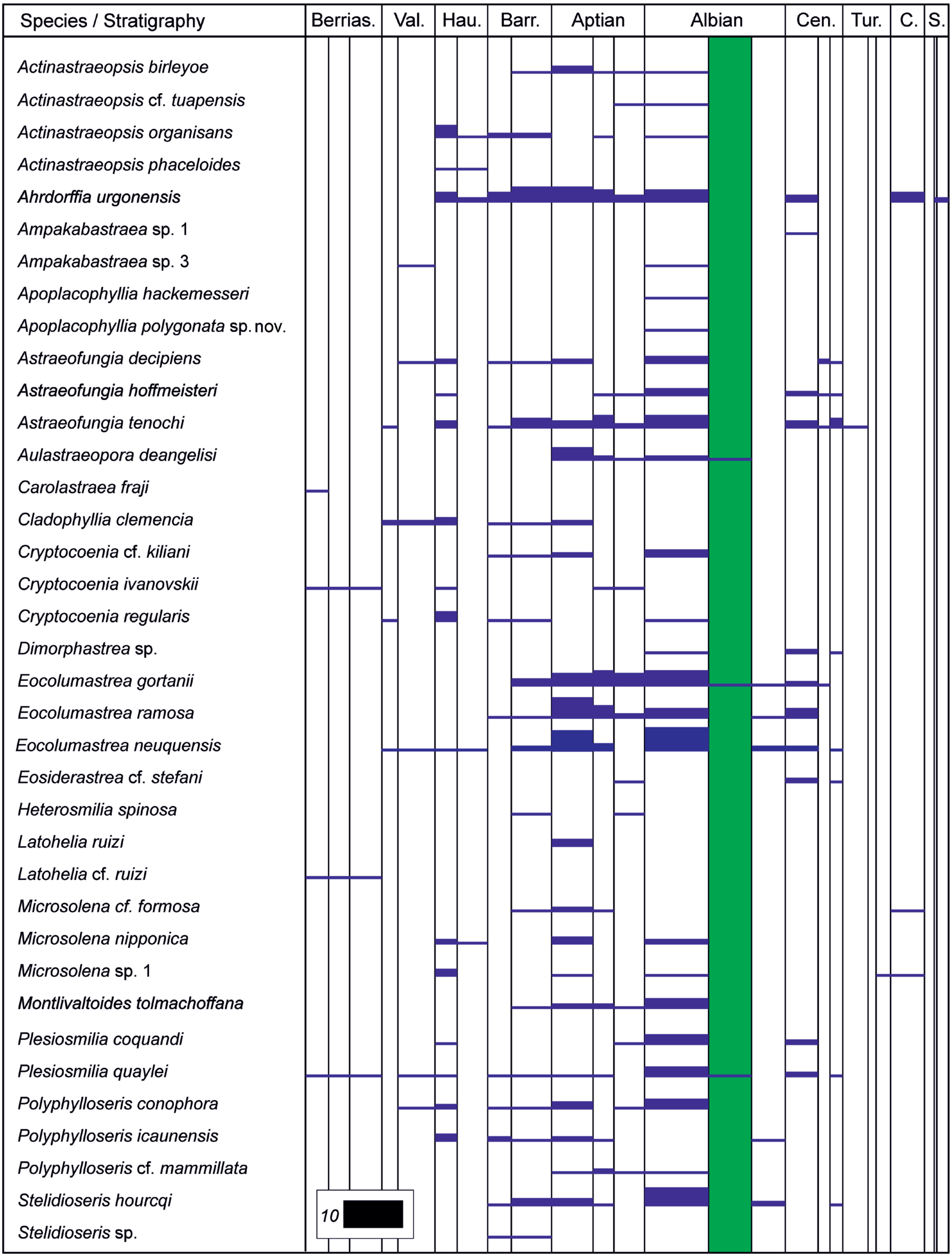

Figure 21. Stratigraphic distribution and commonness of species. The thickness of the bars indicates the number of localities in which the concerned species was found. The bar indicates the Albian age of the study area. Abbreviations: Berrias. – Berriasian; Val. – Valanginian; Hau. – Hauterivian; Barr. – Barremian; Cen. – Cenomanian; Tur. – Turonian; C. – Coniacian; S. – Santonian.

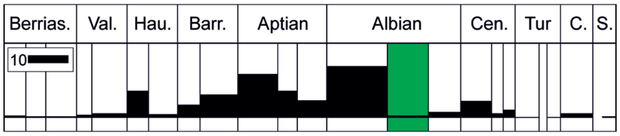

Figure 22. Summarized distribution and commonness of species. The bar indicates the Albian age of the study area. Abbreviations: Berrias. – Berriasian; Val. – Valanginian; Hau. – Hauterivian; Barr. – Barremian; Cen. – Cenomanian; Tur. – Turonian; C. – Coniacian; S. – Santonian.

is overlain by the shallow-water carbonate platform limestones of the Glen Rose Formation. The lowermost Glen Rose Formation is Middle Albian in age. The coeval stratigraphy of the Coahuila and Durango states is also correlatable with the stratigraphy of the Lampazos area (Fig. 25). In these states, the La Peña Formation, contrary to the Chihuahua's Peña Formation, contains no ammonoids in its upper part. However, this upper La Peña Formation was dated by way of microfossils, and its age range is the same (Aptian to lowermost lower Albian) as the Agua Salada or La Peña Formation in Cerro Chino area (Chihuahua) (Núñez-Useche *et al*. 2015). The transgressive unit that overlies the La Peña Formation is the Upper Tamaulipas Formation, but it yielded no ammonites. This formation laterally passes into the Aurora Formation, which is a shallow-water carbonate platform that is lower–upper Albian in age. The development of all of the aforementioned Albian shallow-water carbonate platforms was probably by a Middle Albian sea-level fall (Eguiluz de Antuñano *et al*. 2019 and further references therein). This sea-level fall can also be seen in the United States of America (New Mexico State, Fig. 25), where the U-Bar Formation includes Middle Albian and the lowermost upper Albian deposits of a shallow-water carbonate platform with abundant rudists (Reef limestone Member and Supra-reef limestone Member), that was developed during the Middle Albian and the lowermost upper Albian. The reef units are underlain by uppermost lower Albian marine deposits with an ammonite record (Fig. 25, Limestone-shale Member), and they are overlain by the Mojado Formation, which yielded lower upper Albian ammonoids (Lucas & Steps 1998). During the Early–late Albian, a global marine transgression took place (*e.g.*, Lucas & Estep 1998, Eguiluz de Antuñano *et al*. 2019). This sea-level rise flooded the shallow-water carbonate platforms locally, whereas in other areas the carbonate platforms caught up with the sea level. Fig. 25 shows carbonate platforms flooding into the Lampazos

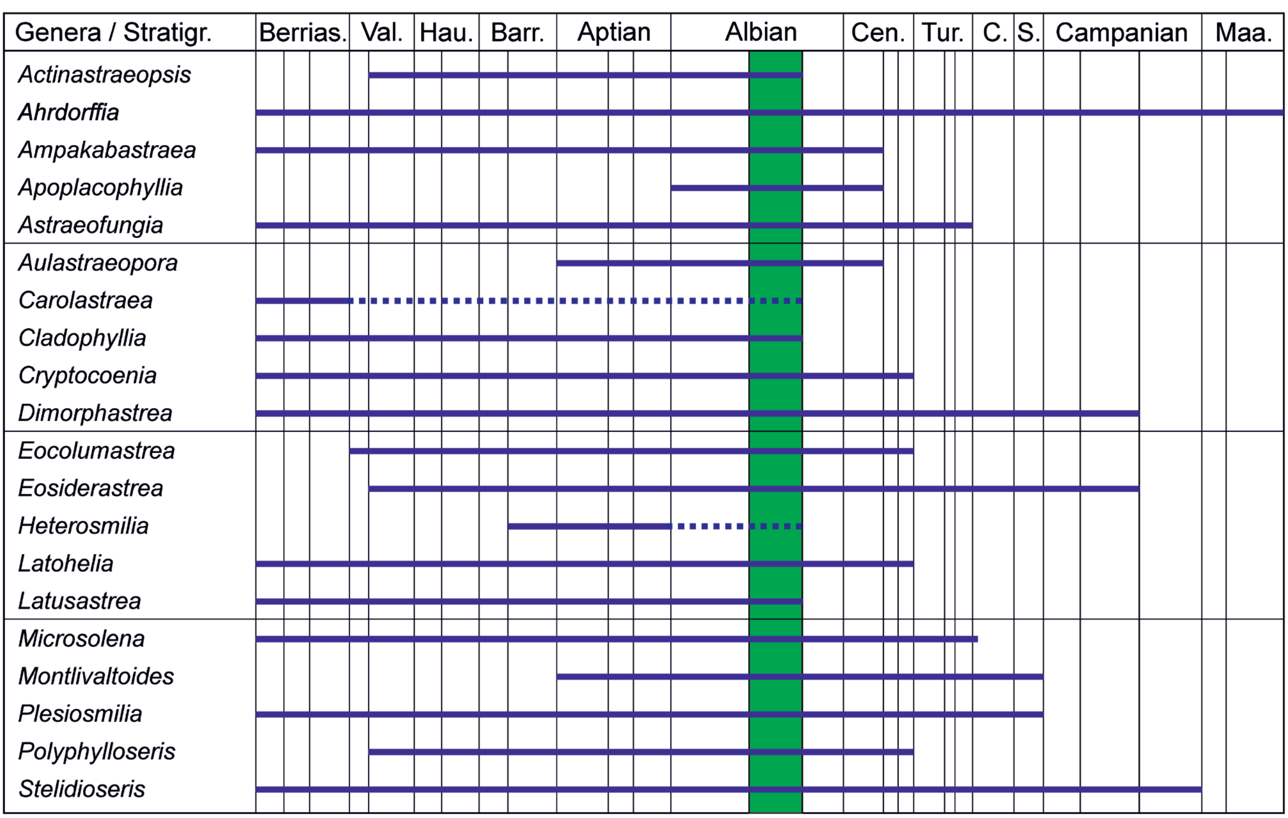

Figure 23. Stratigraphical ranges of the genera of the study area. The bar indicates the Albian age of the study area. The dotted lines indicate possible range extensions. Abbreviations: Berrias. – Berriasian; Val. – Valanginian; Hau. – Hauterivian; Barr. – Barremian; Cen. – Cenomanian; Tur. – Turonian; C. – Coniacian; S. – Santonian; Maa. – Maastrichtian.

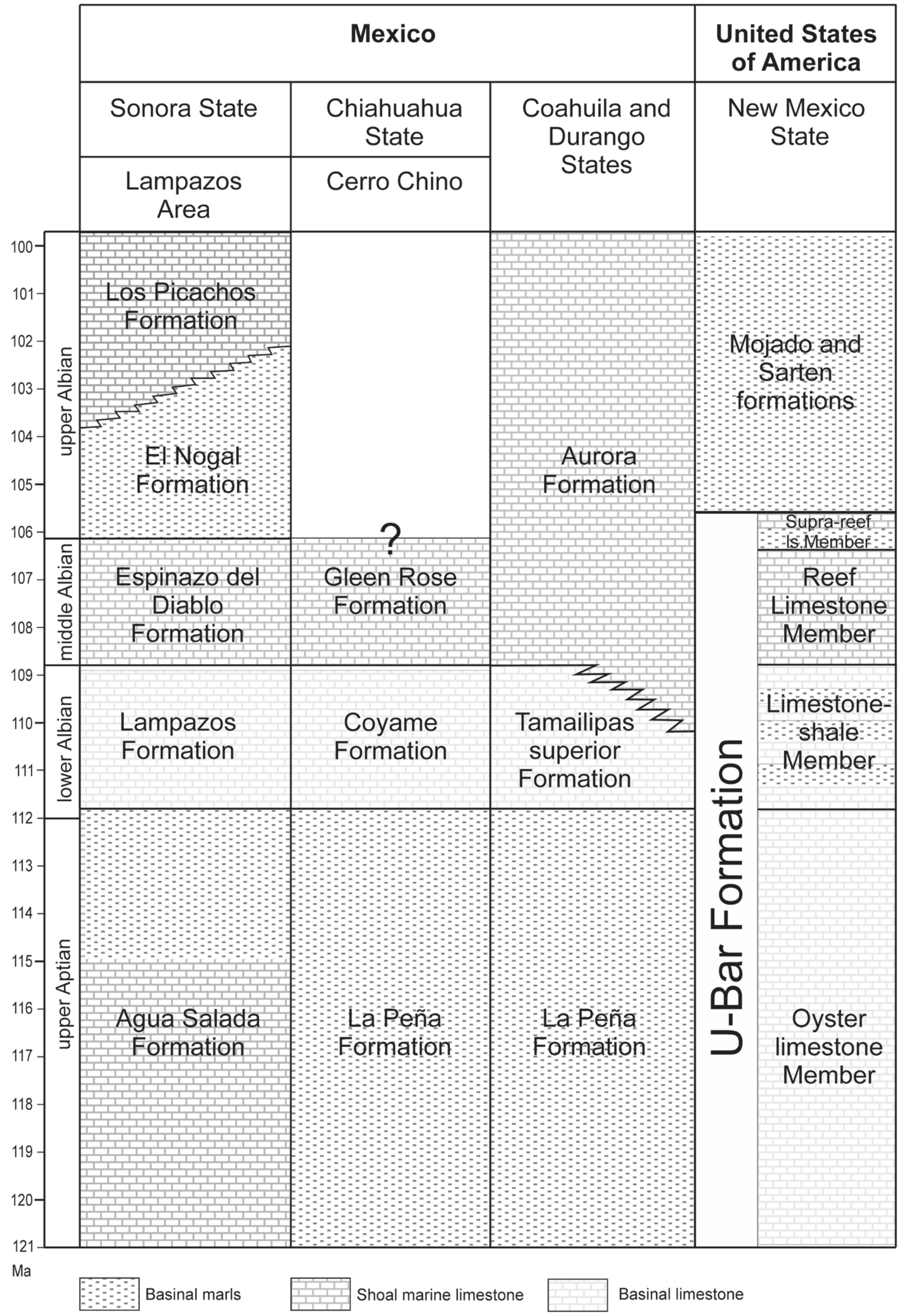

Figure 24. Correlation chart of the Aptian–Albian times of the Lampazos area and other selected areas. After Scott & González-León (1991), Robert *et al*. (2018), Samaniego-Pesqueira (2018), Ovando-Figueroa *et al*. (2018), Núñez-Useche *et al*. (2015), and Lucas & Estep (1998).

area and New Mexico, and the onset of transgressive tract deposits containing lower upper Albian ammonoids of the family Engonoceratidae. In summary, the Espinazo del Diablo Formation was deposited during the Middle Albian, as its development was related to an important North American sea-level fall. The Espinazo del Diablo carbonate platform was flooded by a prominent sea-level rise that started during the Early–late Albian.

Conclusion

The coral fauna from the Lampazos area consists of 46 species distributed among 22 genera. The genus *Pentacoeniopsis* and three species (*Apoplacophyllia polygonata*, *Pentacoeniopsis sonorensis* and *Aulastraeopora aguedae*) are new to science and, therefore, they are endemic to the area. Several specimens could not be assigned to a formally established species such as *Actinastraeopsis* cf. *tuapensis*, *Ampakabastraea* sp. 1, *A*. sp. 2 and *A*. sp. 3, *Pentacoeniopsis* sp. 1, *P*. sp. 2 and *P*. sp. 3. They may represent new taxa, but due to their scarcity and poor state of preservation of the fossil material they could not be erected. Therefore, there is a need for further studies in the area.

The endemism of genera in the study area is fairly similar to other Cretaceous coral faunas: a low number of common genera compares to a high number of very rare genera. The distribution patterns of the genera per superfamily in the Lampazos fauna compare well to the global distribution of genera among the superfamilies during the Middle Albian, with the only difference being that a greater diversity in the superfamily Actinastreoidea was found. The coral association from the Lampazos area shows a close relationship to other Lower Cretaceous coral faunas, mainly in the Lower Albian. Taking into consideration the number of shared species with other faunules in the world, the present fauna is most similar to those of the Upper Aptian to Lower Albian from the Bisbee Basin in Sonora and Arizona. The Espinazo del Diablo Formation is reported in the present study as deposited during the Middle Albian and associated to an important sea-level fall in North America. Subsequently, the deposited sediments were flooded by an outstanding sea-level rise during the Early–late Albian.

Acknowledgments

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