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A Middle Cenomanian coral fauna from the Northern Calcareous Alps (Bavaria, Southern Germany) – new insights into the evolution of Mid-Cretaceous corals

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Abstract

In the Northern Calcareous Alps, relics of a formerly widely distributed shallow marine facies belonging to the Branderfleck Formation (Upper Albian to Early Turonian) crop out and contain locally abundant corals. The fauna described here derives from Middle Cenomanian sediments. It encompasses 39 species in 25 genera, belonging to seven scleractinian and one octocorallian order. One genus and two species are described as new. The fauna that was formerly located at the northern part of the Apulian plate (Austroalpine unit), south of the Penninic ocean, shows palaeobiogeographic relationships to Cenomanian faunas from the Pelagonium, the Aquitanian Basin, and the Bohemian Basin, indicating stronger connections to Tethyan than Boreal faunas. The fauna also shares species with Aptian and Albian, as well as Late Cretaceous faunas. Ten genera experienced a range extension; five genera have their last occurrence in the Middle Cenomanian fauna, and five genera their first occurrence. The fauna has an intermediate position between the Early Cretaceous and the post-Cenomanian corals showing that the faunal turnover at the Cenomanian/Turonian boundary was not marked by the sudden appearance of new faunal elements, but the disappearance of taxa. Many faunal elements that constitute post-Cenomanian faunas already existed in the Cenomanian but were very rare.

Key words: Cretaceous, Hexacorallia, Octocorallia, Branderfleck Formation, Taxonomy, New taxa

Zusammenfassung

In den Nördlichen Kalkalpen sind Relikte der ursprünglich weiter verbreiteten flachmarinen Branderfleck Formation (Oberalb-Unterturon) aufgeschlossen, die lokal häufig Korallen enthalten. Die hier beschriebene Fauna mittelcenomaner Sedimente erbrachte 39 Arten in 25 Gattungen, die zu sieben Unterordnungen der Scleractinia und einer Ordnung der Octocorallia gehören. Es werden eine neue Gattung und zwei neue Arten beschrieben. Die Fauna siedelte ursprünglich am nördlichen Rand der Apulischen Platte (Austroalpine Einheit), südlich des Penninischen Ozeans und zeigt paläobiogeographische Beziehungen zu cenomanen Korallenfaunen des Pelagonium, des Aquitanischen Beckens, und des Böhmischen Beckens mit ausgeprägteren Beziehungen zu tethyalen als borealen Faunen. Die beschriebene Vergesellschaftung hat auch Arten mit Faunen des Apts und Albs sowie der Oberkreide gemein. Zehn Gattungen erfuhren eine Erweiterung ihrer stratigraphischen Reichweite; fünf Gattungen hatten ihr letztes Auftreten im Mittelcenoman, und fünf Gattungen ihr erstes Auftreten. Die Korallenfauna nimmt eine Position zwischen Unterkreide- und post-cenomanen Faunen ein und zeigt, dass der Faunenwechsel an der Cenoman/Turon-Grenze nicht von einem plötzlichen Auftauchen neuer Faunenelemente gekennzeichnet war, sondern eher von einem Verlust der Diversität. Viele Elemente post-cenomaner Faunen existierten bereits im Cenoman, aber waren offenbar sehr selten.

Schlüsselwörter: Kreide, Scleractinia, Octocorallia, Branderfleck Formation, Taxonomie, Neue Taxa

1. Introduction

The diversity and abundance of coral faunas varied greatly throughout the Cretaceous period. Depending on the frequency of oceanic anoxic events (OAE; Erba 2004; Bodin et al. 2006; Jenkyns 2010) and the variation of the sea level (Hardenbol et al. 1998), conditions were more or less suitable for corals. With the Hauterivian, the Early Cretaceous presented an increasing amount of coral faunas (Löser 2013a; here, a fauna refers to an association of species found in the same lithostratigraphical unit of the same age, but not necessarily from the same outcrop or sample point), but their number gradually decreased in the central Tethys with the late Early Aptian, reaching a value as low as during the Berriasian during the Middle Albian (in the Western Tethys, Late Aptian to Albian faunas still persisted). During the Late Albian, the number of faunas increased dramatically, resulting in a very high number of faunas by the end of the Cenomanian. This large number is mainly due to increasing coral faunas at higher latitudes. At the Cenomanian/Turonian boundary, a sea level highstand followed by a sea level fall and OAE2 caused a remarkable drop of faunas and genera. Recovery started with the Late Turonian throughout the Santonian. Hauterivian to Early Albian coral associations are uniform on the generic level, but Late Cretaceous faunas from the Late Turonian on show a different inventory: on the one hand the suborders Amphiastraeina, Rhipidogyrina and Stylinina disappeared completely and various families became reduced in genera and species (Elasmocoeniidae, Microsolenidae, Montlivaltiidae). On the other hand, the suborder Meandrinina achieved a very high diversity and families of other suborders emerged or show an increase in diversity (Agatheliidae, Columastraeidae, Placosmiliidae). The patterns of this faunal turnover are poorly understood for several reasons. First, the number of Albian coral faunas is very low (Löser et al. in press) not allowing clear conclusions on coral evolution. Second, the Cenomanian coral faunas differ in their taxonomic composition depending on their palaeolatitude: because of increasing sea water temperature (Johnson et al. 1996), Late Albian to Cenomanian corals preferably colonized areas in Boreal regions. Cenomanian coral localities with more than three species (and more than 50% of hermatypic genera) total 58 localities (age assignments and species counts according to Löser et al. 2005) with higher latitude faunas clearly dominating (Tab. 1).

Table 1: Percentage of the geographic distribution of Cenomanian coral localities with more than three species (and more than 50% of hermatypic genera). Total number of localities 58.

Boreal (Belgium, Czech Republik, northern France, Germany)	55%
Aquitaine (central France)	14%
Northern Calcareous Alps (Southern Germany)	2%
Northern Africa and Levante (Algeria, Egypt, Tunisia)	7.5%
Western Atlantic (USA)	3.5%
Central Tethys (Italy, southern France)	3.5%
Eastern Tethys (Bulgaria, Greece, Serbia, Uzbekistan)	9%
Asia (India, Tibet)	5.5%

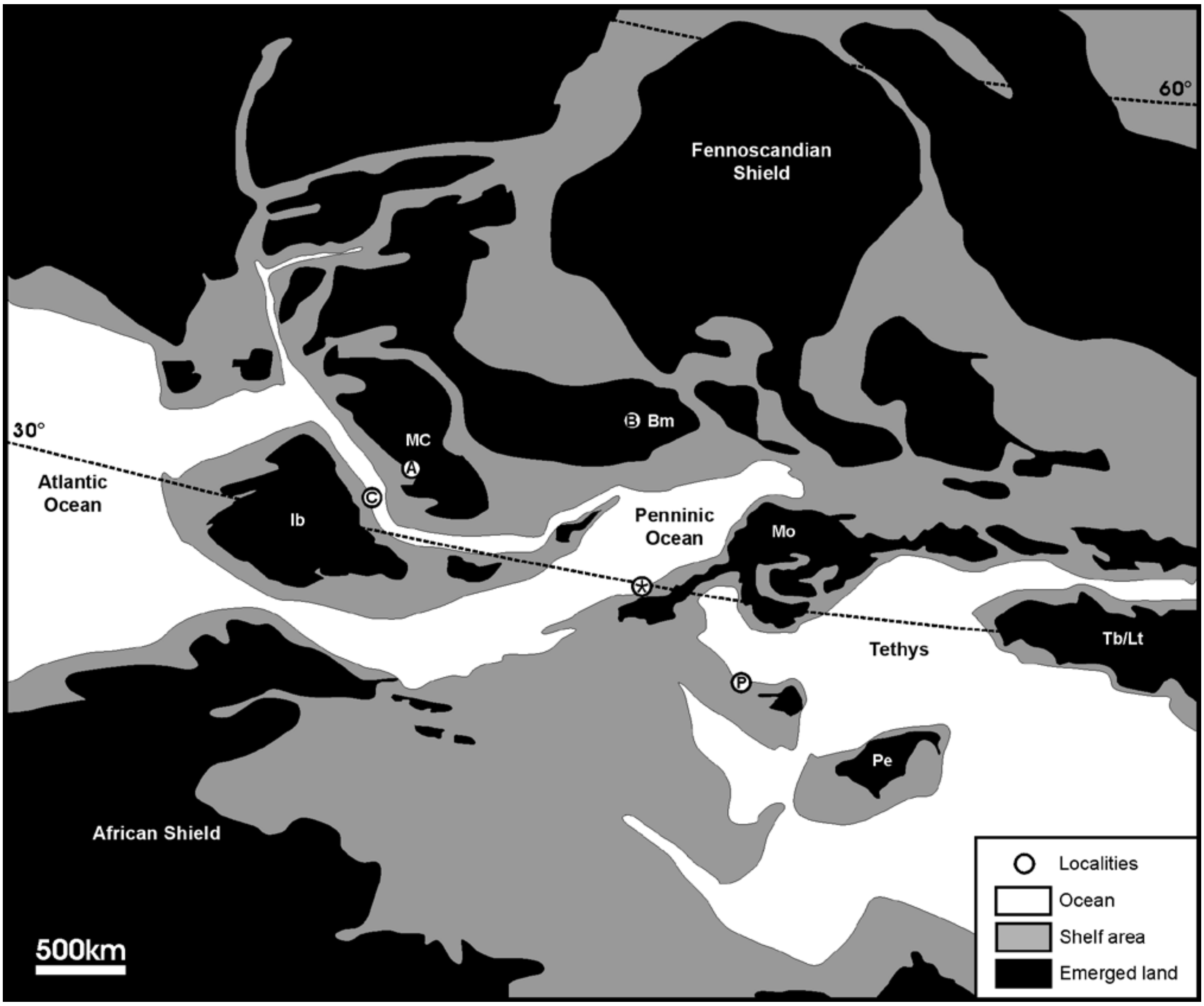
The Cenomanian was a rather short time period. Its coral distribution is characterised by two remarkable events: the Late Albian-Early Cenomanian sea level rise that led in various regions to transgression and the formation of highly diverse coral faunas. Species rich Late Albian to Early Cenomanian coral faunas are known from the Boreal areas (Saxon and Westphalia in Germany, Löser 1989, 1994, 1998; Devonshire in England, Jukes-Brown 1900), the Western Tethys (Cobreces in Northern Spain, Wilmsen 1996; Rochefort in France, Beltremieux 1866; Andalucia in Spain, Löser et al. in press), the Central Tethys (Kozani in Greece, Steuber & Löser 1997), the Eastern Tethys (Tamil-Nadu in India; Stoliczka 1873) and the Western Hemisphere (Texas, USA; Wells 1932).

The Middle Cenomanian was characterised by a global sea level fall and an accompanied regression in many areas. There are only few Middle Cenomanian coral faunas described. At the end of the Middle Cenomanian, the sea level increased again leading to a transgression in many areas, both Tethys and Boreal. Important Boreal faunas ranging from the late Middle Cenomanian to the Late Cenomanian are known from Belgium (Hainaut et al. 1975) the Czech Republic (Eliášová 1989, 1991, 1992, 1994, 1996, 1997a,b, 2004), France (Sarthe, Thomel 1965) and Germany (Löser 1989, 1998). From more southerly located areas, faunas are poorly reported, e.g. Southern France (Aude, Var; Fromentel 1862–87).

The Boreal faunas are for the most part taxonomically well studied. The taxonomy of the coral faunas from the Tethys is less well known, which makes comparison between Boreal and Tethyan faunas difficult, but several large coral faunas are under taxonomic revision by HL and were included in the taxonomic comparison with the present fauna. It is at least known that Boreal and Tethyal faunas differ in their general taxonomic composition (Löser 1998), but this difference is poorly quantified.

The present fauna comes from an area at the northern part of Apulia (Austroalpine unit) (Textfig. 1) that was separated from the Helvetic shelf by the ocean waters of the Penninic Ocean (Dercourt et al. 2000). At that time a landmass connected parts of Apulia with the more eastern situated Moesia microplate (Pfiffner 2010). The study area in the north of this landmass had a central position within the Western Tethys and its palaeogeographic position may therefore help to understand the relation between Tethyan and Boreal faunas on the one hand, and faunas far to the West (France, Spain) and East (Greece, India) on the other.

The fauna studied here derives from a locality of the lithostratigraphical unit of the Branderfleck Formation (see below for more explanation). There are few other coral faunas from other localities of the same unit described by Schlosser (1924) and Söhle (1897); Boden (1935) and Löser et al. (2002) mentioned material (Tab. 2). Some of these faunas encom-



Textfigure 1: Palaeogeographic map of the Western and Central Tethys (100ma, Late Albian, Base of the Dispar zone) with the study area and important Cenomanian faunas. Tectonic units: Bm, Bohemian Massif; Ib, Iberian Massif; MC, Massif Central; Mo, Moesia; Pe, Pelagonium; Tb/Lt, Tabas and Lut. Localities (circles): *, study area on the Austroalpine plate; A, Aquitanian Basin, SW margin of the Massif Central (coral faunas in Charente-Maritime, France); B, Bohemian Massif (not flooded before the late Middle Cenomanian; coral faunas in Bohemia, Czech Republic); C, Basque-Cantabrian Basin (coral faunas close to Santander, Cantabria, Spain); P, west Pelagonian zone (coral faunas in Kozani, Greece). Map © Ron Blakey, NAU Geology (http://cpgeosystems.com).

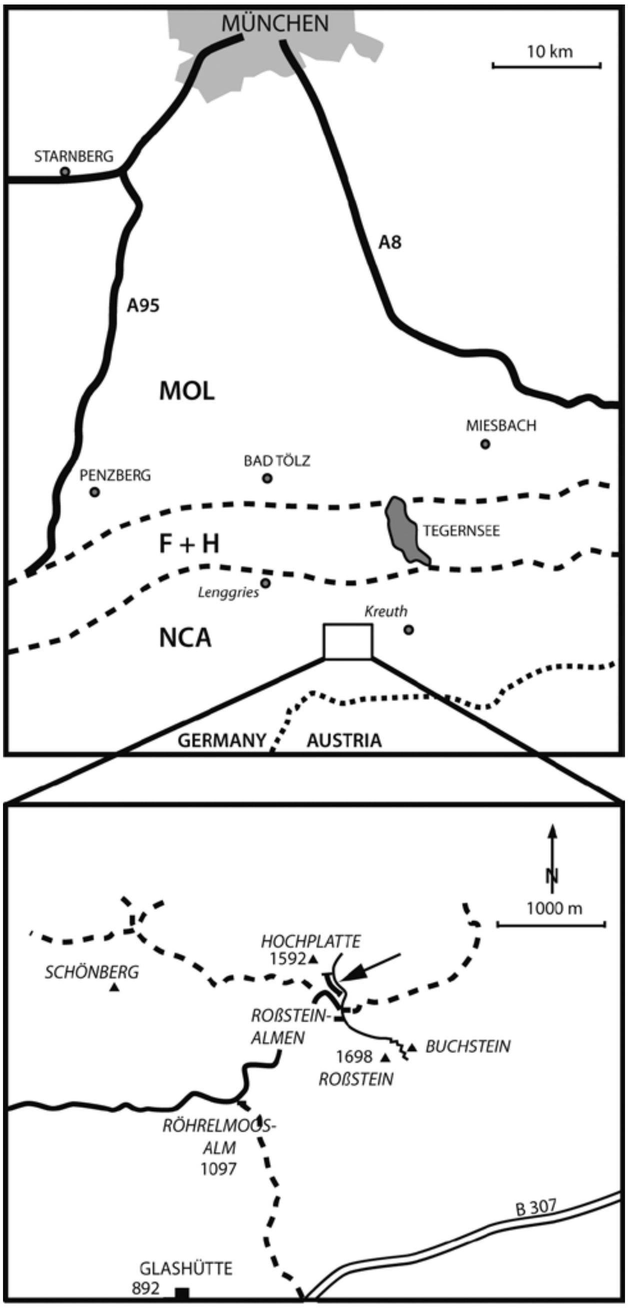
pass a considerable amount of ahermatypic solitary corals indicating a deeper marine environment. These faunas are taxonomically only revised so far as collection material is still available.

2. Study area

The locality Roßsteinalmen is situated in the Alpine Mountains about 50 km south of Munich, 9 km SE of the community Lenggries and 5 km W of the community Kreuth (Textfig. 2). The locality name refers to the Alpine pastures below the Roßstein peek, a famous walking tour destination in the Northern Calcareous Alps (NCA). At this locality, a small series of Cretaceous sediments crop out, which are attributed to a unit of fine and coarse, partly brecciated sediments, which were for a long time generally called „Cenoman Serie“ (e.g., Boden 1935). Outcrops of this lithostratigraphic unit are generally restricted to relatively small areas in the centre of synclinal structures along the northern border of the Northern Calcareous Alps („Randschuppe“), the western part of the Allgäu nappe and the northern part of the Lechtal nappe. They represent relics of a formerly more widely distributed facies, which have been protected from erosion by their tectonic position within the synclinal structures. In the upper tectonic units of the NCA (e.g., the nappes of the Tirolicum and, respectively, Juvavicum unit) this series is generally lacking for primary tectonic reasons (Doben & Risch 1996). The „Cenoman Serie“ is subdivided into two different formations on the basis of sedimentological and micropalaeontological data, (1) the Losenstein Formation with silty marls, turbitic sandstones and deep water conglomerates with exotic pebbles of

Table 2: Coral quotations from localities of the Branderfleckformation according to the literature.

Publication	Locality	Quotation
Söhle (1897)	Linderhof, Dreisäulergraben (Middle to Late Cenomanian)	*Astrocoenia turonensis* Fromentel, 1884
	Oberammergau, Labergebirge (Cenomanian)	*Trochosmilia complanata* Goldfuss, 1826 sensu Michelin, 1847
	Ruhpolding, Urschlau (Cenomanian)	*Aspidiscus cristatus* (Lamarck, 1801)
		Deltocyathus urschelaviensis Söhle, 1897
		Platycyathus cf. *orbignyi* Fromentel, 1862
	Ettal, Lichtenstättgraben (Early Cenomanian)	*Aspidiscus cristatus* (Lamarck, 1801)
Söhle (1899)	Linderhof, Dreisäulergraben (Middle to Late Cenomanian)	*Centrastrea insignis* Fromentel, 1887
Schlosser (1924)	Niederauer Berg, Riedleiten, S Wildbarren (Cenomanian)	*Platycyathus orbignyi* Fromentel, 1862
		Trochosmilia cf. *inconstans* Fromentel, 1862
	Ruhpolding, Urschlau (Cenomanian)	*Aspidiscus cristatus* (Lamarck, 1801)
		Cycloseris Cenomanensis (Milne Edwards & Haime, 1848)
		Leptophyllia cenomanensis Fromentel, 1863
		Leptophyllia patellata Lamarck, 1816 sensu Michelin, 1846
		Parasmilia Guillieri Fromentel, 1862
		Platycyathus orbignyi Fromentel, 1862
		Trochosmilia cenomanensis Fromentel, 1863
		Trochosmilia complanata Goldfuss, 1826
Boden (1935)	Roßstein-Almen (Middle Cenomanian)	*Astrocoenia* aff. *konincki* Milne Edwards & Haime, 1848
		Astrocoenia decaphylla Michelin, 1847
		Astrocoenia sp.
		Coelosmilia sp.
		Cycloseris cenomanensis (Milne Edwards & Haime, 1848)
		Heliastraea lepida (Reuss, 1854)
		Heliastraea sp.
		Heliopora n. sp.
		Trochosmilia cenomanensis Fromentel, 1863
		Trochosmilia cf. inconstans Fromentel, 1862
		Trochosmilia didymoides Fromentel, 1862
		Trochosmilia sp.
Löser el al. (2002)	Oberammergau, Labergebirge (Cenomanian)	*Dendrophyllia granosior* Söhle, 1897
	Ruhpolding (Cenomanian)	*Cycloseris* sp.
		Heterocoenia costata Felix, 1903
	Ruhpolding, Mühlenacker (Cenomanian)	*Astrocoenia* sp.
		Hydnophora sp.
		Litharaea sp.
		Mycetophyllia sp.
		Phyllosmilia cuneolus (Michelin, 1847)
		Thamnaraea sp.
		Thamnasteria sp.



Textfigure 2: Location of the section Roßsteinalmen and tectonic units. NCA, Northern Calcaerous Alps, F + H, Flysch and Helvetic unit, MOL, Molasse;

Middle Albian to Lower Cenomanian age and (2) the Branderfleck Formation consisting mainly of marls, calcareous sandstones and breccias (?Upper Albian to Turonian; Gaupp 1980, 1982; Weidich 1984a,b; Faupl & Wagreich 2000). At the northern border of the NCA the Branderfleck Formation follows conformably the rocks of the Losenstein Formation, whereas towards the south, e.g., on the Allgäu nappe and the Lechtal nappe, the Branderfleck formation overlies mostly rocks of Triassic or Jurassic age depending on the local tectonic situation. The Roßsteinalmen area belongs tectonically to the northern part of the Lechtal nappe and here the Branderfleck Formation overlies Upper Jurassic radiolarites and limestones (e.g., „Aptychenkalk“) with slight angular unconformity (Steinberg 1980; Weidich 1984b).

The section at the Roßsteinalmen is about 150 m thick and consists of sandy marls and sandstones alternating with thick carbonaceous fine breccias (Textfig. 3; Steinberg 1980; Weidich 1984b). The upper part is characterised by thick, coarse chaotic breccias that are interpreted by Weidich (1984b) as channel deposits cutting the marly series. The components of the breccias are mainly Triassic and Jurassic carbonates as well as „Cenomanian“ breccias and therefore, they reflect synorogenetic reworking of local material (e.g. Boden 1935; Kuhn 1991; Steinberg 1980). For the base, micropalaeontological data based on planctonic foraminifera (e.g., *Rotalipora cushmani*) indicate a Middle to lower Upper Cenomanian age, for the upper part (centre of the synclinal fold), the upper Cushmani zone and thus, an Upper Cenomanian age is confirmed (Weidich 1984b). The marls and sandstones of the section are partly rich in tests of the orbitolinid foraminifera (Steinberg 1980). This important index fossil family did not reach the Late Cenomanian (Schroeder & Neumann 1985). The only species known from the Middle Cenomanian is *Conicorbitolina conica* (d‘Archiac 1837), which was also indicated in the Branderfleck Fm by Schlagintweit & Wagreich (2005). The marls and sandstones are therefore of a Middle Cenomanian age.

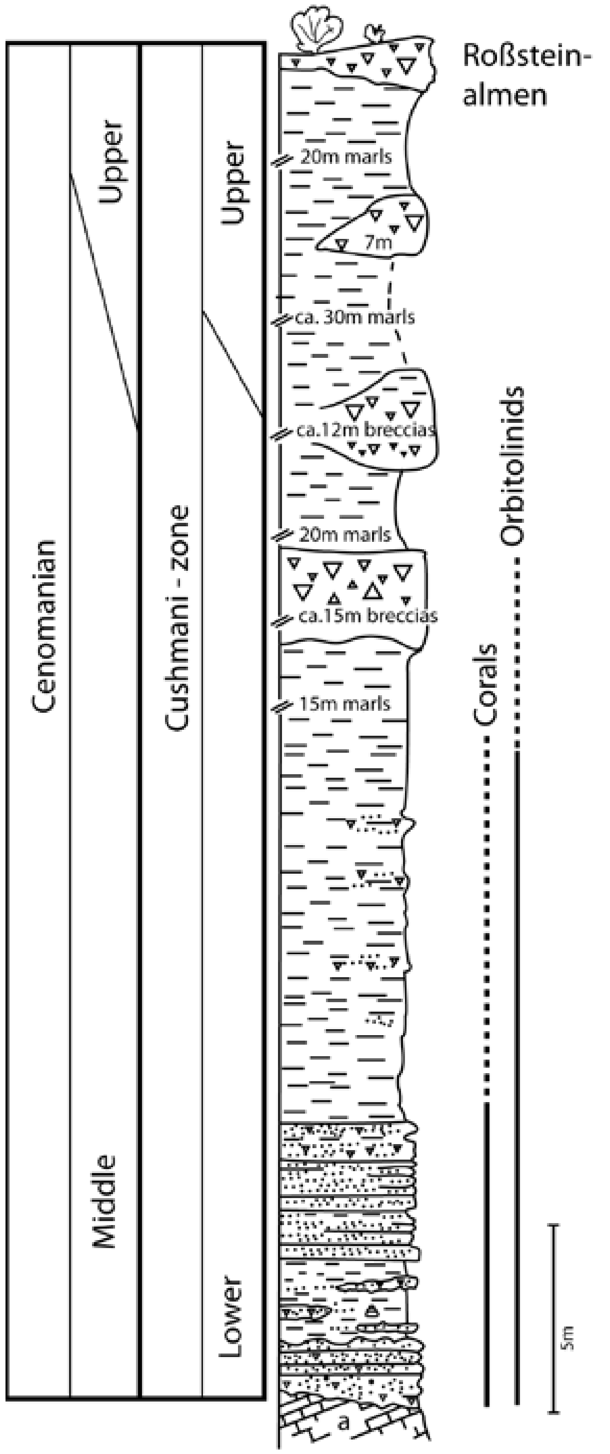
The corals described in this paper (except 2012 X 1) come from the lower part of the section (Textfig 2). Specimen 2012 X 1 comes from a higher level and probably has a lower Upper Cenomanian age. Macrofaunal elements are represented mainly by some gastropod and bivalve species, and a moderately diverse coral fauna. Boden (1935: 42) already emphasised the special, possibly endemic character of the corals at the Roßsteinalmen.

Palaeogeographically the Branderfleck Formation represents sediments deposited at the northern margin of the Austroalpine unit and thus, at the southern border of the Penninic Ocean (see Dercourt et al. 2000; Faupl & Wagreich 2000; Pfiffner 2010). For the clastics of the lower Branderfleck Formation, palaeocurrent data gives evidence of a source area located toward the south (Gaupp 1980). The uplift of the northern border of the Austroalpine unit may be linked to the formation of an accretionary wedge in the context of the beginning subduction of the Penninic Ocean (Pfiffner 2010). According to Weidich (1984b), the sediments at the Roßsteinalmen were deposited in water ranging from about 50 m deep on the inner shelf (base of the section) to about 100 m on a middle shelf area (upper part of the section).

3. Material and methods

3.1 Material

This study is mainly based on material from two



Textfigure 3: Section at the Roßsteinalmen (modified from Weidich 1984b); planktic foraminifera stratigraphy after Weidich (1984a, b), occurrence of corals and orbitolinid foraminifers after Steinberg (1980), Weidich (1984b), and personal observations. Scale only valid for the lower part of section.

large private collections of Alpine fossils that are now housed in the Bavarian State Collection for Palaeontology and Geology. One of the private collectors was Otto Hölzl, who visited the locality Roßsteinalmen repeatedly between 1941 and 1948. The other private collector, Alfred Holinka, collected fossils there between 1951 and 1961. Further material was sampled in the context of a diploma thesis (Steinberg 1980). Steinberg focussed her work on the geological mapping, but also identified and figured some of the corals. Additionally, some coral specimens were collected during fieldwork in 2012. Coral specimens and thin sections of this study are kept in the collection of the Bayerische Staatssammlung under accession numbers 1947 XVI, 1948 III, 1955 XIX, 1963 VI, 1980 XIII, 1991 X, 2010 VI, 2012 X. In total, 143 specimens are included in the present study.

The collection consists of hundreds of different specimens. Corals are available as isolated specimens with partially well-preserved surfaces and septal ornamentation. Small solitary corals (less than 30 mm high) dominate. Colonial corals are also small; the largest colonies may reach up to 60 mm in diameter. Only one exceptionally large coral colony could be found (*Pachygyra* sp.) reaching 40 cm in its largest dimension. Corals are mainly strongly recrystallized and fine skeletal structures (micro structures) are barely preserved.

3.2 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 and using a flat bed scanner with an optical resolution of 6,400 dpi. Scanned images were then transferred to grey scale 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 calices in relation to the size of the thin sections.

For each type of measurement (calicular diameter and distance, width and distance of calicular row) in one thin section the following values were obtained:

n	number of measurements
min–max	lowest and highest measured value
μ	arithmetic mean (average)
σ	standard deviation
v	coefficient of variation according to K.Pearson
$\mu \pm \sigma$	first interval

Thin sections were measured and values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (http://www.paleotax.de/measure), for details on the mathematical background see Löser (2012b). Characters visible on the fossils were compared against those on specimens in worldwide fossil coral collections and an associated image database (ca. 19,500 specimens, ca. 8,200 illustrated, located in the Estación Regional de Noroeste (ERNO), Sonora, Mexico). Data storage and processing were carried out using the PaleoTax database program (Löser 2004).

To compare the studied fauna with other coral faunas outside the study area, a computer database of about 2,700 world-wide coral localities with coral indications was used (Löser et al. 2002, 2005). To simplify the analysis, localities of the same age that are located in the same basin, on the same continental margin or the same interoceanic platform were grouped together into one palaeo-province (a type of a 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 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 having at least three species in common with the fauna of the studied area. For details see also Löser (2008) and Löser & Minor (2007).

4. Systematic description

Abbreviations

Collection abbreviations are as follows:

SNSB-BSPG: Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany;
CC: C. Colleté, private collection, Saint-Savine, France;
CGS: Ceská geologická sluzba, Praha, Czech Republic;
ERNO: Instituto de Geología, Estación Regional de Noroeste, Universidad Nacional Autónoma de México, Hermosillo, Mexico;
GZG: Geowissenschaftliches Zentrum Göttingen, Germany;
IGM: Instituto de Geología, Mexico City, Mexico;
IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
MB: Museum für Naturkunde der Humboldt-Universität, Berlin, Germany;
MHE: M. Heinrich, private collection, Eckental, Germany;
MHNG: Muséum d'histoire naturelle de la Ville de Genève, Switzerland;
MNHN: Muséum National d'Histoire Naturelle, Paris, France;
NHM: The Natural History Museum, London, UK;
PIW: Institut für Paläontologie der Universität Würzburg, Germany (now: SNSB-BSPG-PIW: München, Germany);
UP: Université de Provence, Coll. J.-P. Masse;
USNM: United States National Museum, Washington, D.C., USA.

The following abbreviations are used describing the dimensions of the corals:

c: calicular diameter;
c max: larger outer calicular diameter;
c min: smaller outer calicular diameter;
ccd: distance between calicular centres;
cl: calicular diameter (calicular pit);
cl max: large lumen;
cl min: small lumen;
crd: distance of calicular series;
crw: width of calicular series;
md: distance between monticule in a hydnophoroid colony;
ml: length of monticules in hydnophoroid colony;
s: number of radial elements in adult calices;
sd: density of radial elements;
si: number of septa in the isolated calice;
smo: number of radial elements in hydnophoroid colony.

The abbreviations used in the synonymy lists follow Matthews (1973): *, earliest valid publication of the species name; ?, the assignation of this description to the species is doubtful (so marked quotations are not reflected in the stratigraphic and palaeobiogeographic distribution); non: the described material does not belong to the species concerned; p, the described material belongs only in part to the species concerned; v, the specimen was observed by the author.

The distribution data (as reflected in the synonymy lists) are almost entirely based on well-examined material. Material only mentioned in the literature and material not available or insufficiently described and illustrated in the literature has not been taken into account. To obtain better insight into the distribution patterns of the present coral fauna, additional unpublished material – indicated by a collection acronym and sample number in parenthesis – has been included. Therefore distribution data indicated under 'Occurrence' are also provided for species remaining in open nomenclature.

Suborder Archeocaeniina Alloiteau, 1952

Family Actinastraeidae Alloiteau, 1952

Actinastrea d'Orbigny, 1849

Actinastrea regularis (de Fromentel, 1887)

Pl. 1, Figs 1–2

*v 1887 *Isastraea regularis* – Fromentel, part 16: pl. 191, fig. 4
v 1994 *Actinastrea subdecaphylla* (Oppenheim) – Liao & Xia: p. 87, pl. 10, figs 1–3, pl. 11, figs 1, 2, pl. 17, figs 5–8
v 2000 *Actinastrea elongata* Alloiteau, 1954 – Baron-Szabo: p. 96, pl. 1, fig. 6

Material: 1947 XVI 60; 1 thin section.

Dimensions:

(1947 XVI 60)

	n	min–max	μ	σ	cv	μ±σ
cl	25	1.66–2.29	1.9	0.17	8.8	1.73–2.06
ccd	35	1.77–2.69	2.22	0.26	11.8	1.95–2.48
s	10+10					

Description: Plocoid colony. Calicular outline polygonal. Septa compact, consist of few large trabeculae, in cross section externally thick, getting slightly thinner towards the centre. Symmetry of septa radial and regularly decameral. Cycles of septa subregular. Septal cycles differ in length. First septal cycle reaches to the centre of the calice, the second cycle is shorter. Septa of the second cycle occasionally attached to those of the first cycle. Septal distal margin unknown, lateral face with thorns, inner margin unknown. Pali or paliform lobes absent. All septa of the first cycle are attached to the columella. Costae hardly present, sub-confluent to non-confluent. Synapticulae absent. Columella styliform. Endotheca unknown. Wall compact, septothecal. Coenosteum very narrow, consists of large trabeculae. Budding extracalicinal.

Remarks: The specimen represents the first occurrence of the genus *Actinastrea* sensu stricto (not *Stelidioseris*; see discussion in Löser 2012a) at all.

Occurrence: Santonian of Austria (Oberösterreich) Russbach, Pass Gschütt area (MHE A0397); Austria (Salzburg) Rußbach, Randobach Mündung Stöcklwaldgraben. Upper Santonian of France (Aude) Les Corbières, Rennes-les-Bains. Campanian to Maastrichtian of China (Xizang) Gamba county, Mainde district, Zongshan Mt. Upper Campanian to Lower Maastrichtian of United Arab Emirates (Al Ain) Al Ain, Huwayyah Mt (NHM AZ571).

Stelidioseris Tomes, 1893

Stelidioseris minima (de Fromentel, 1857)
Pl. 1, Figs 3–4

*	1857	*Astrocoenia minima* – Fromentel: p. 47
	1886	*Astrocoenia colliculosa* – Trautschold: p. 10, pl. 5, figs 1 a–e
v	1897	*Astrocoenia minima* – Koby: p. 61, pl. 15, figs 1–3
v	1935	*Astrocoenia Cornueliana* d'Orb. – Cottreau: pl. 74, figs 6–7
v	1936	*Astrocoenia pseudominima* Koby 1896 – Hackemesser: p. 71, pl. 7, fig. 14
v	1964	*Actinastraea minima* (de Fromentel, 1857) – Morycowa: p. 14, pl. 1, fig. 1, pl. 2, fig. 1
v	1974	*Actinastrea crassoramosa* (Michelin) – Reyeros de Castillo: p. 12
v	1989	*Actinastraea minima minima* (de Fromentel, 1857) – Morycowa: p. 60, pl. 18, fig. 1
non	1990	*Actinastrea minima* (de Fromentel) – He & Xiao, pl. 18, fig. 10
v	2001	*Actinastrea* ? *minima* (de Fromentel 1857) – Löser: p. 42, pl. 1, fig. 2
non	2004	*Actinastraea minima* (de Fromentel, 1857) – Gameil & Aly: p. 268, pl. 1, figs 8, 9
v	2009	*Actinastrea minima* (de Fromentel, 1857) – Löser et al.: p. 337, fig. 2.9

Material: 1947 XVI 26, 1947 XVI 61; 2 thin sections.

Dimensions:
(1947 XVI 26)

	n	min–max	μ	σ	v	μ±σ
cl	17	1.12–1.64	1.35	0.16	11.9	1.18–1.51
ccd	25	1.31–2.16	1.68	0.26	15.2	1.42–1.93
s	10+10					

Description: Plocoid colony. Calicular outline polygonal. Septa compact, consist of few large trabeculae. Septa in cross section externally thick, getting slightly thinner towards the centre, septa of the first cycle with swellings (renflements). Cycles of septa subregular. Septal cycles differ in length and thickness. First septal cycle reaches to the centre of the calice, those of the second cycle are shorter. Septa of the second cycle often attached to those of the first cycle. Septal distal margin unknown, lateral face with fine thorns, inner margin unknown. Pali or paliform lobes absent. All septa of the first cycle are attached to the columella. Costae hardly present. They are confluent leaving regular small intercalicinal spaces (lacunes). Synapticulae absent. Columella styliform. Endotheca consists of thin tabulae. Wall compact, septothecal. Coenosteum very narrow, consists of costae. Budding unknown.

Other Occurrence: Cretaceous of Greece (Fokída) Kiona massif, Panourgias. Valanginian of France (Yonne) Bernouil (MHNG 4711). Hauterivian of Jamaica (Saint Catharine) Benbow Inlier, Copper. Lower Hauterivian (Radiatus zone) of France (Aube) Troyes, Vallières, France (Haute-Marne) Saint Dizier, France (Yonne) Fontenoy (SNSB-BSPG 2003 XX 5344), France (Yonne) Gy-l'Evêque. Lower Hauterivian of Ukraine (Krymskaya) Simferopolskij district, Alma river, Partizany. Barremian of France (Doubs) Morteau. Lower Aptian of Poland (Malopolskie, Wadowice) Lanckorona, Jastrzebia. Lower Albian (Tardefurcata zone) of Spain (Cataluña, Tarragona) Com. Baix Penedès, Mun. Masllorenç, Masarbones (SNSB-BSPG 2003 XX 6009). Lower to Middle Albian (Mammillatum - Lautus zone) of Greece (Viotía) Levadia, Agia Barbara (ERNO L-5386). Upper Albian of UK (Devonshire) Exeter, Haldon Hill (NHM R00807).

Suborder Faviina Vaughan & Wells, 1943

Family Columastraeidae Alloiteau, 1952

Neocoenia Hackemesser, 1936

Neocoenia cf. *casterasi* (Alloiteau, 1957)
Pl. 1, Figs 7–9

Material: 1947 XVI 33, 1991 X 48, 1991 X 73, 1991 X 74, 1991 X 75, 1991 X 76, 1991 X 77, 1991 X 78, 2012 X 4; 7 thin sections.

Dimensions:
(1991 X 48)

	n	min–max	μ	σ	v	μ±σ
cl	30	2.33–3.21	2.81	0.24	8.3	2.57–3.05
ccd	30	3.83–5.75	4.84	0.57	11.7	4.27–5.41
s	24					

(1947 XVI 33)

	n	min–max	μ	σ	cv	μ±σ
cl	25	2.22–2.97	2.58	0.23	8.9	2.35–2.81
ccd	30	3.05–4.67	3.78	0.45	11.9	3.33–4.23
s	24					

Description: Plocoid colony. Calicular outline circular, centres slightly depressed, margins slightly elevated. Septa compact. Microstructure of medium sized trabeculae. Septa (and costae) in cross section in the

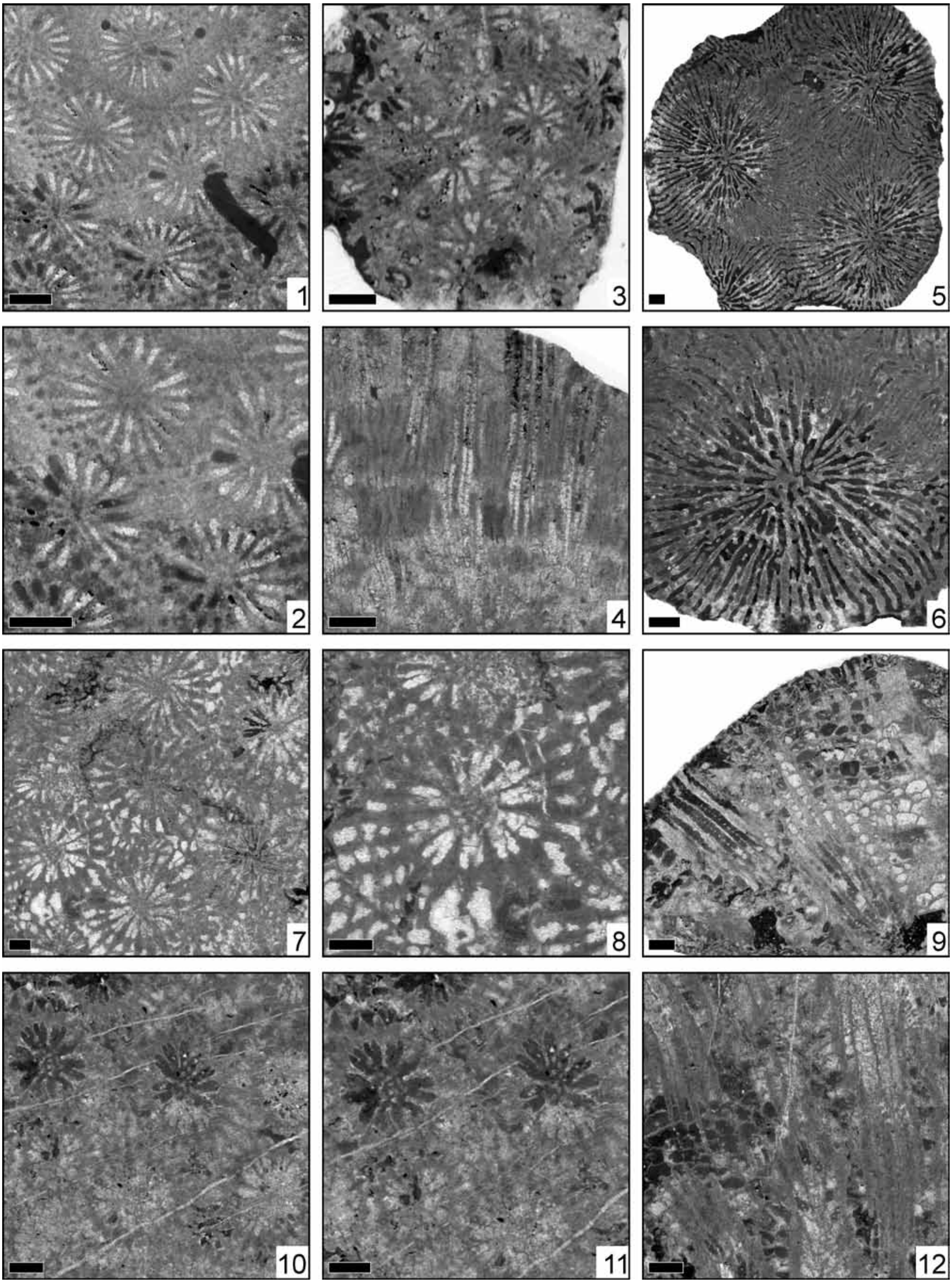


Plate 1: (1–2) *Actinastrea regularis* (de Fromentel, 1887), 1947 XVI 60. 1: transversal thin section. 2: transversal thin section, detail. **(3–4)** *Stelidioseris minima* (de Fromentel, 1857), 1947 XVI 26. 3: transversal thin section. 4: longitudinal thin section. **(5–6)** *Diploastrea* sp., 1991 X 97. 5: transversal thin section. 6: transversal thin section, detail. **(7–9)** *Neocoenia* cf. *casterasi* (Alloiteau, 1957), 1991 X 48. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. **(10–12)** *Neocoenia renzi* Hackemesser, 1936, 1947 XVI 8. 10: transversal thin section. 11: transversal thin section, detail. 12: longitudinal thin section. Scale bars = 1mm.

wall thick, thinner towards the centre. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length and thickness. First two septal cycles reach 40% of the calicular diameter, the third cycle is shorter. Septa of the third cycle occasionally attached to those of the second cycle. Septal distal margin unknown, lateral face with thorns, inner margin T-shaped in places and with thorns. Paliform lobes irregular on the first two cycles. Costae present but short, sub-confluent to non-confluent, surface unknown. Synapticulae absent. Columella small, substyliform. Endotheca consists of few thin tabulae. Wall compact, paraseptothecal. Coenosteum narrow, consists of costae and strong exothecal dissepiments. Budding extracalicinal.

Remarks: The present material has slightly smaller dimensions than *N. casterasi*.

Neocoenia renzi Hackemesser, 1936
Pl. 1, Figs 10–12

*v 1936 *Neocoenia renzi* n. g. n. sp. – Hackemesser: p. 24, pl. 3, figs 4–6
non 1991 *Neocoenia renzi* Hackemesser – Moosleitner: pl. 2, fig. 3, pl. 3, fig. 8
v 1992 *Stephanaxophyllia villaltai* n. sp. – Reig Oriol: p. 13, pl. 1, fig. 9, pl. 3, figs 3, 4
v 2011 *Neocoenia renzi* Hackemesser, 1936 – Löser: p. 8, pl. 1, figs 1–9

Material: 1947 XVI 10, 1947 XVI 46, 1947 XVI 8; 2 thin sections.

Dimensions:
(1947 XVI 8)

	n	min–max	μ	σ	v	μ±σ
cl	28	1.2–2.47	1.83	0.37	20.0	1.46–2.20
ccd	28	1.94–3.42	2.66	0.43	16.0	2.23–3.08
s	24					

Description: Plocoid colony. Calicular outline circular to slightly elliptical, centres slightly depressed, margins slightly elevated. Septa compact. Microstructure of medium sized trabeculae. Septa (and costae) in cross section in the wall thick, thinner towards the centre. Symmetry of septa radial and regularly hexameral. Cycles of septa subregular. Septal cycles differ in length and thickness. First two septal cycles reach 40% of the calicular diameter, the third cycle is shorter. Septa free. Septal distal margin unknown, lateral face with thorns, inner margin smooth. Paliform lobes irregular on the first two cycles. Costae present but short, sub-confluent to non-confluent. Synapticulae absent. Columella small, styliform to lamellar. Endotheca consists of numerous dissepiments. Wall compact, septothecal. Coenosteum narrow, consists of thin tabulae. Budding extracalicinal.

Occurrence: Cretaceous of Greece (Fokída) Kiona massif, Panourgias. Middle to Upper Turonian of Greece (Viotía) Akrefnio, Marmeko, iron ore mine (SNSB-BSPG 2003 XX 2189). Santonian of Austria (Oberösterreich) Russbach, Pass Gschütt area (MHE A0300). Lower Upper Campanian of Spain (Cataluña, Lérida) Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur, Torallola (MB K1111, K1175). Uppermost Campanian of Spain (Cataluña, Lérida) Com. Pallars Jussà, Mun. Isona i Conca Dellà, Isona, (Barranco de) La Posa.

Family Diploastraeidae Chevalier & Beauvais, 1987

?*Diploastrea* Matthai, 1914

The material is similar to the so-called *Diploastrea* from the Lower Cretaceous, but differs from *Diploastrea* by its slightly perforate septa, the presence of synapticulae and much larger trabeculae. It is related to material assigned to *Brachycaulia* - *B. felixi* Beauvais, 1982, and *B. glomerata* (Reuss, 1854). The present material cannot be assigend to *Brachycaulia* because the type species (*Brachycaulia jacobi*) belongs to the family Felixaraeidae.

?*Diploastrea tanohataensis* (Eguchi, 1951)
Pl. 2, Figs 7–9

vp 1932 *Siderastraea cuyleri* Wells, n.sp. – Wells: p. 243, pl. 37, fig. 9, pl. 39, fig. 1
v 1951 *Placocoenia tanohataensis* Eguchi, n.sp. – Eguchi: p. 26, pl. 3, figs 6–8

Material: 1947 XVI 47; 2 thin sections.

Dimensions:
(1947 XVI 47)

cmin	4.2–5.1
cmax	5.6–6.2
ccd	4.1–5.6
s	10+10+20
sd	8/2

Description: Astreoid colony. Calicular outline circular to polygonal. Septa with very few pores at the inner margin. Microstructure of septa of medium sized trabeculae. Septa in cross section externally thick, getting thinner towards the centre. Symmetry of septa radial and irregularly decameral. Cycles of septa subregular. Septal cycles differ in length and thickness. First two septal cycles reach to the centre of the calice, further cycles are shorter. Septa of the third cycle often attached to those of the second cycle. Septal distal margin unknown, lateral face occasionally with granulae, inner margin slightly swollen in places. Some septa may be attached to the columella. Costae present, very short, sub-confluent to non-confluent. Synapticulae rare, medium common, mainly in the wall region. Columella styliform. Endotheca absent. Wall absent. Coenosteum very narrow or absent. Budding extracalicinal.

Remarks: Holotype and paratype of *Siderastraea cuyleri* Wells, 1932 belong to the same genus related

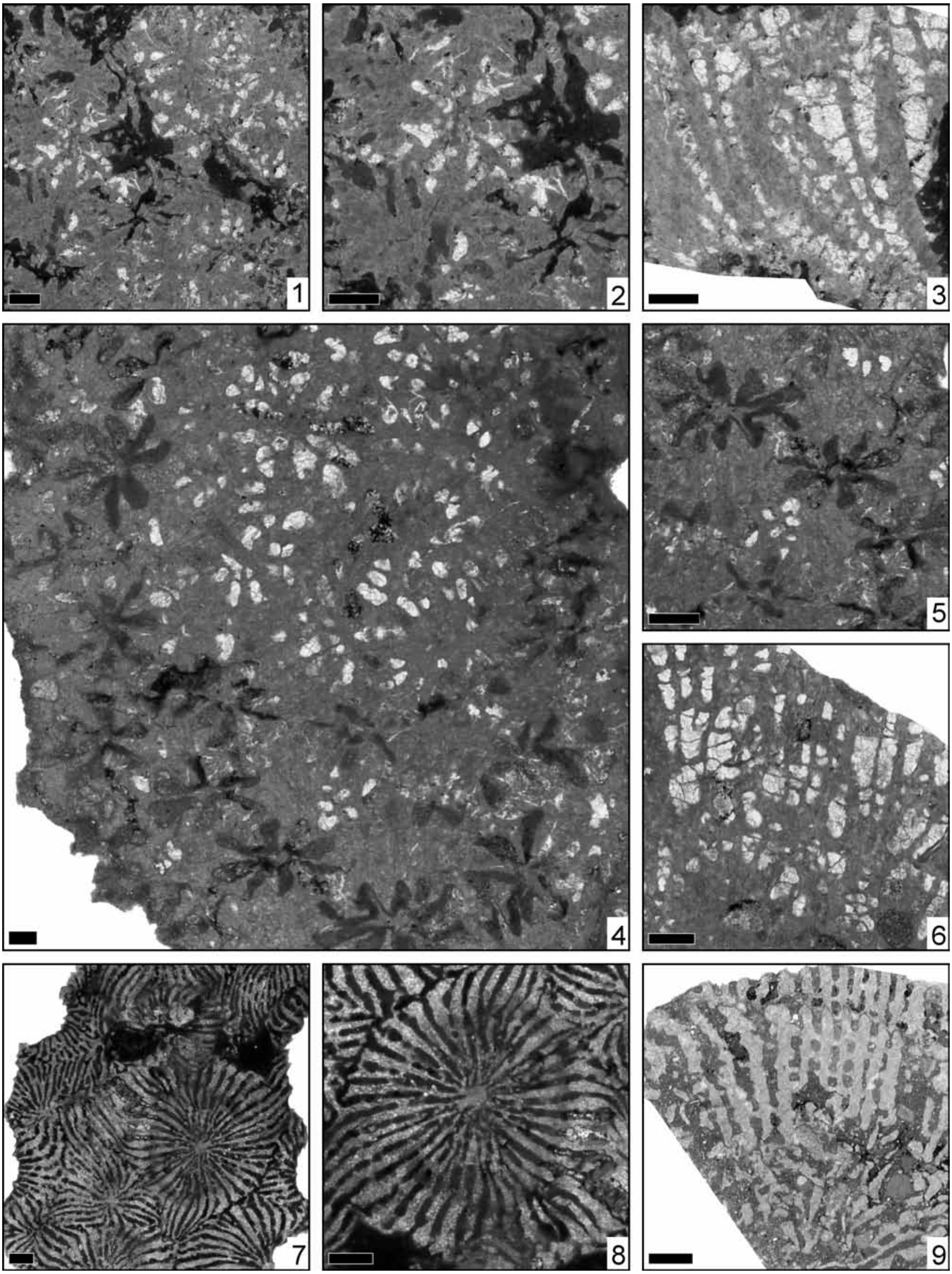


Plate 2: (1–3) *Columellophora* cf. *velimensis* Eliášová, 1989, 1947 XVI 54. 1: transversal thin section. 2: transversal thin section, detail. 3: longitudinal thin section. **(4–6)** *Columellophora* sp., 1947 XVI 51. 4: transversal thin section. 5: transversal thin section, detail. 6: longitudinal thin section. **(7–9)** ?*Diploastrea tanohataensis* (Eguchi, 1951), 1947 XVI 47. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. Scale bars = 1mm.

to *Diploastraea*, but to different species. Here, it is referred to the paratype.

Occurrence: Lower Aptian of Poland (Malopolskie, Wadowice) Lanckorona, Jastrzebia (ERNO L-5428). Lower Upper Aptian of USA (Texas) Travis County, Travis Peak, Cow Creek. Upper Aptian of Japan (Iwate-ken) Shimohei-gun, Tanohata-mura, Koikorobe. Lower Cenomanian of France (Charente-Maritime) Fouras (ERNO L-5614). Greece (Kozani) Kozani, Nea Nikopolis (ERNO L-6145). Lower Cenomanian (Dixoni zone) of Spain (Cantabria, Santander) Cobreces, Luaña playa (SNSB-BSPG 2007 V 61).

?*Diploastrea* sp.
Pl. 1, Figs 5–6

Material: 1991 X 97; 2 thin sections.

Dimensions:
(1991 X 97)

c min	7.5–7.6
c max	7.4–8.9
ccd	5.2–8.3
s	10+10+20+40+x (= 80–90)
sd	6/2

Description: Astreoid colony. Calicular outline circular. Septa with few pores at the inner margin. Microstructure of septa unknown. Septa in cross section externally thick, getting slightly thinner towards the centre. Symmetry of septa radial and irregularly decameral. Cycles of septa subregular. Septal cycles differ in length and thickness. First two septal cycles reach to the centre of the calice, further cycles are shorter. Septa of the third cycle often attached to those of the second cycle. Septal distal margin unknown, lateral face occasionally with granulae, inner margin slightly swollen in places. Some septa may be attached to the columella. Costae present, very short, sub-confluent to non-confluent. Synapticulae present, medium common, mainly in the wall region. Columella styliform, lamellar or by septal fusion in the centre of the calice. Endotheca unknown. Wall absent. Coenosteum very narrow or absent. Budding extracalicinal.

Occurrence: Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 5829).

Family Eugyridae Duncan, 1884

Columellophora Eliášová, 1989

Columellophora cf. *velimensis* Eliášová, 1989
Pl. 2, Figs 1–3

Material: 1947 XVI 54, 1991 X 105; 4 thin sections.

Dimensions:
(1947 XVI 54)

	n	min–max	μ	σ	cv	μ±σ
cl	10	2.00–2.45	2.21	0.16	7.5	2.04–2.37
ccd	10	1.93–4.12	2.86	0.71	25.0	2.14–3.58
s	8	9–14	10.87	1.72	15.8	9.1–12.6

Description: Hydnophoroid-cerioid colony with distinct calices. Calicular outline irregular, centres depressed. Septa compact, in cross section externally thick, getting thinner towards the centre. Symmetry of septa radial and irregularly hexameral. Cycles of septa subregular. Septal cycles differ in length. First septal cycle reaches to the centre of the calice, the second cycle is shorter. Septa occasionally connected to each other in the centre of the calice. Septal distal margin unknown, lateral face with thorns, inner margin swollen in places. Pali or paliform lobes absent. Costae absent. Synapticulae absent. Columella styliform or by septal fusion in the centre of the calice. Endotheca consists of regular tabulae and occasional dissepiments. Wall present, compact, septothecal. Coenosteum absent. Budding extracalicinal.

Remarks: The material differs from *C. velimensis* by its slightly smaller dimensions. In *C. velimensis* the calices are elliptical (or the thin section is oblique). Its smaller calicular dimensions are 2.4–2.7mm (first interval, four measurements). The present material differs from the type species also by its more hydnophoroid aspect.

Columellophora sp.
Pl. 2, Figs 4–6

Material: 1947 XVI 51; 2 thin sections.

Dimensions:
(1947 XVI 51)

	n	min–max	μ	σ	cv	μ±σ
cl	20	1.38–2.17	1.75	0.22	12.9	1.53–1.98
ccd	20	1.51–2.93	2.23	0.41	18.6	1.81–2.65
s	10	8–11	9.50	1.17	12.4	8.3–10.7

Description: Hydnophoroid–cerioid colony with distinct calices. Calicular outline irregular, centres depressed. Septa compact, in cross section externally very thick, getting thinner towards the centre. Symmetry of septa radial and irregularly hexameral. Cycles of septa subregular. Septal cycles differ in length. First septal cycle reaches to the centre of the calice, further cycle is subsequently shorter. Septa of the younger cycle often attached to those of the first cycle, and many septa of the first cycle fused in the centre of the calice. Septal distal margin unknown, lateral face occasionally with thorns, inner margin swollen in places. Pali or paliform lobes absent. Costae absent. Synapticulae absent. Columella styliform or by septal fusion in the centre of the calice. Endotheca consists of regular tabulae and occasional dissepiments. Wall present, compact, septothecal. Coenosteum absent. Budding extracalicinal.

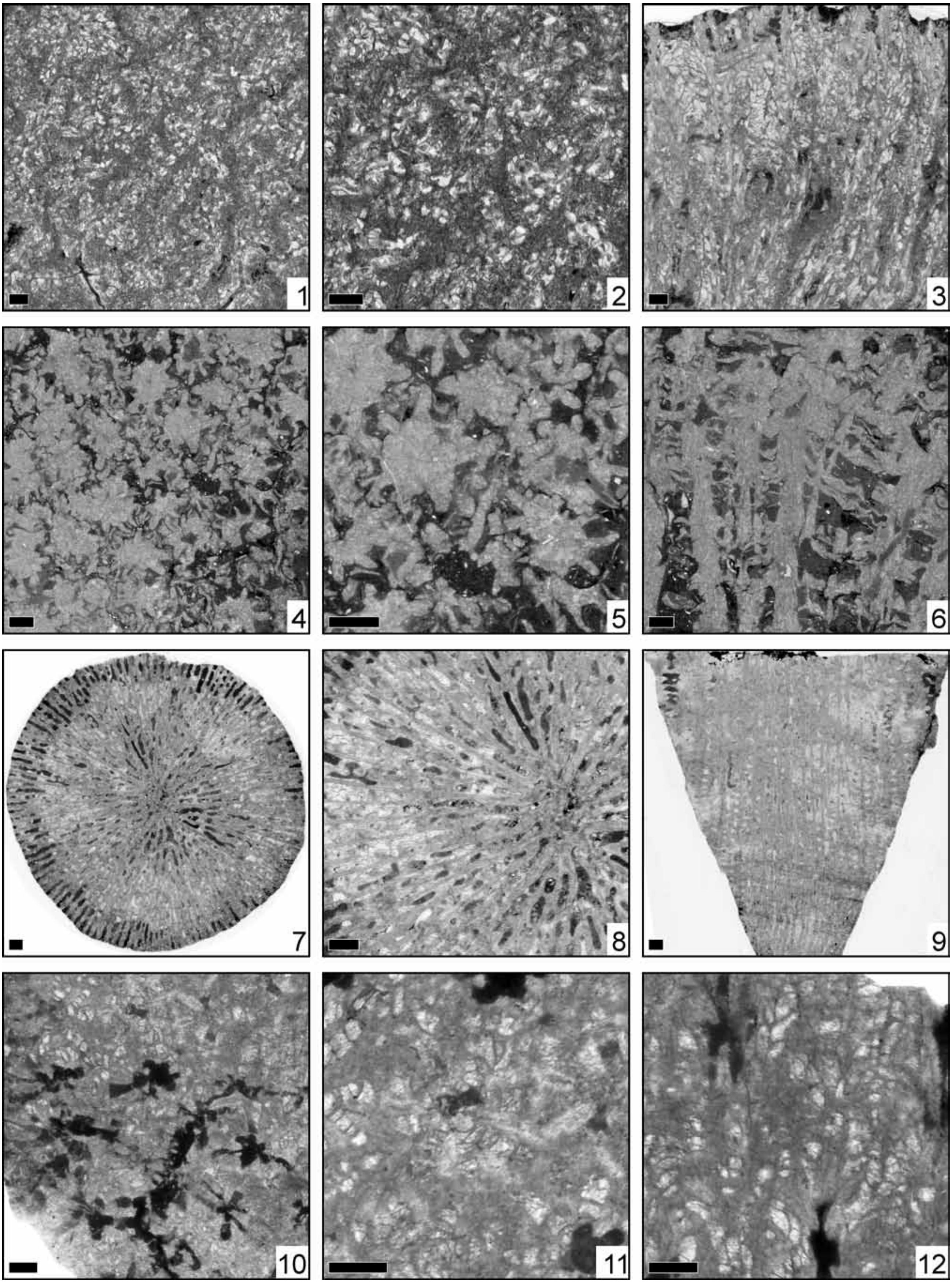


Plate 3: (1–3) *Felixigyra deangelisi* Prever, 1909, 1991 X 81. 1: transversal thin section. 2: transversal thin section, detail. 3: longitudinal thin section. **(4–6)** *Hydnophora* cf. *obliqua* Reig Oriol, 1992, 1947 XVI 21. 4: transversal thin section. 5: transversal thin section, detail. 6: longitudinal thin section. **(7–9)** *Trochoseropsis ettalensis* Söhle, 1897, 1947 XVI 15. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. **(10–12)** *Heterocoenia* sp., 1991 X 101. 10: transversal thin section. 11: transversal thin section, detail. 12: longitudinal thin section. Scale bars = 1mm.

Remarks: The material differs from the type species and the other species by much smaller dimensions and a lower number of septa.

Occurrence: Upper Cenomanian (Guerangeri zone) of Czech Republic (Central Bohemian region) Korycany (ERNO L-4750).

Family Merulinidae Verrill, 1866

Hydnophora Fischer de Waldheim, 1807

Hydnophora cf. *obliqua* Reig Oriol, 1992
Pl. 3, Figs 4–6

Material: 1947 XVI 21, 1947 XVI 22, 1963 VI 189, 1963 VI 190, 1991 X 59, 1991 X 60; 3 thin sections.

Dimensions:
(1947 XVI 21)

	n	min–max	μ	σ	v	μ±σ
md	25	1.53–2.37	1.86	0.24	12.7	1.61–2.09
ml	25	1.23–2.44	1.72	0.34	19.8	1.37–2.05
smo	15	9–17	12.5	2.7	21	9.8–15.1

(1963 VI 189)

	n	min–max	μ	σ	cv	μ±σ
md	30	1.16–2.04	1.61	0.23	14.2	1.38–1.84
ml	30	0.99–2.38	1.81	0.37	20.4	1.44–2.19
smo	20	6–14	10.0	2.53	25.3	7.5–12.5

Description: Hydnophoroid colony with conical monticules. Monticules densely packed. Calices indistinct. Septa compact, in cross section equal in thickness in the whole septum. Symmetry of septa irregular. Cycles of septa irregular, but size orders can be distinguished. Septal generations differ in length. Septa occasionally connected to each other. Septal lateral face with fine thorns, inner margin T-shaped or swollen in places. Pali or paliform lobes absent. Costae absent. Synapticulae absent. Columella lamellar, septa often connected to the columella. Endotheca consists of numerous thin tabulae. Wall absent. Coenosteum absent. Budding extracalicinal.

Remarks: The present material can only be compared on the basis of its dimensions, number of septa etc. because the type of *Hydnophora obliqua* is a small specimen without any polished surface or thin sections. In the present material the distance of the monticules is smaller.

Occurrence: Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 5899).

Hydnophora sp.
Pl. 4, Figs 8–9

v 1992 *Hydnophora* ?*oppenheimi* Angelis d'Ossat, 1905 – Eliášová: p. 407, pl. 6, fig. 2

Material: 1991 X 106; 1 thin section.

Dimensions:
(1991 X 106)

	n	min–max	μ	σ	cv	μ±σ
md	30	1.08–1.66	1.36	0.14	10.9	1.21–1.51
ml	30	0.68–1.87	1.18	0.29	25.0	0.89–1.48
smo	30	6–14	9.56	2.11	22.0	7.5–11.7
sd	3/mm					

Description: Hydnophoroid colony with conical or short polygonal monticules. Calices indistinct. Septa compact, in cross section externally thick, getting thinner towards the centre. Symmetry of septa irregularly radial, but two size orders can be distinguished. Septal size orders differ in length. Septa free. Septal distal margin unknown, lateral face occasionally with thorns, inner margin swollen in places. Pali or paliform lobes absent. Costae absent. Synapticulae absent. Columella absent. Endotheca unknown. Wall absent. Coenosteum absent. Budding intracalicinal.

Occurrence: Upper Cenomanian (Guerangeri zone) of Czech Republic (Central Bohemian region) Korycany.

Suborder Fungiina Verrill, 1868–70

Family Agariciidae Gray, 1847

Trochoseropsis Söhle, 1897

Trochoseropsis ettalensis Söhle, 1897
Pl. 3, Figs 7–9

*v 1897 *Trochoseropsis Ettalensis* – Söhle: p. 45, pl. 7, figs 2, 2 a–b
v 2013a *Trochoseropsis ettalensis* Söhle, 1897 – Löser, 6b–i

Material: 1947 XVI 15, 1947 XVI 16, 1947 XVI 24, 1947 XVI 28, 1947 XVI 29, 1991 X 63; 2 thin sections.

Dimensions:
(1947 XVI 15)

c	19–20
s	140
sd	8/4mm

Description: Solitary cylindric coral. Calicular outline circular. Septa with few pores, in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septa irregularly radial. Cycles of septa subregular. Septal cycles differ in length, almost not in thickness. Quarter of all septa reach to the calicular centre. Septa of younger cycles often attached to those of older generations, and some septa of the older cycles fused in the centre of the calice. Septal distal margin unknown, lateral face with numerous thorns, inner margin slightly swollen in places. Pali or paliform lobes absent. Synapticulae present, medium common. Columella formed by septal fusion in the centre of the calice. Endotheca absent. Wall absent (probably due to preservation).

Occurrence: Lower Albian, Mammillatum (Mammillatum zone) of France (Aude) Padern, SE Le Crès,

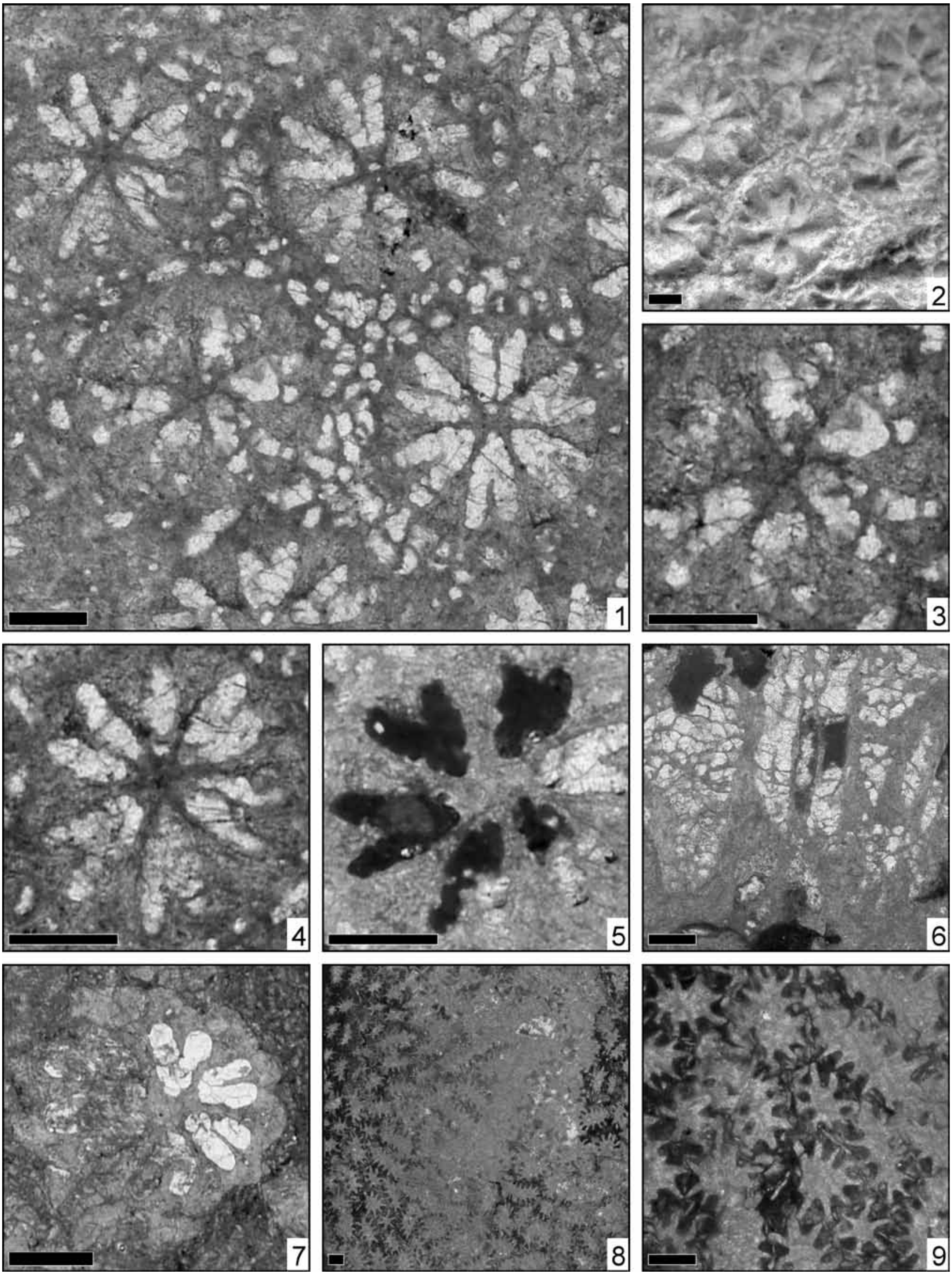


Plate 4: (1–6) *Eothelia hoelzli* n. gen. n. sp., Holotype, 1991 X 42. 1: transversal thin section. 2: colony surface. 3: transversal thin section, detail. 4: transversal thin section, detail. 5: transversal thin section, detail. 6: longitudinal thin section. **(7)** *Eothelia hoelzli* n. gen. n. sp., Paratype, 1991 X 103, transversal thin section, detail. **(8–9)** *Hydnophora* sp., 1991 X 106. 8: transversal thin section. 9: transversal thin section, detail. Scale bars = 1mm.

1.45 km WWS Padern. Lower Cenomanian (Mantelli zone) of Germany (Bayern) Ettal, Lichtenstättgraben.

Suborder Heterocoeniina Beauvais, 1974

Family Agatheliidae Beauvais & Beauvais, 1975

Eothelia n. gen.

Type species: *Eothelia hoelzli* n.sp.

Derivatio nominis: *Eo*- (greek) for early -*thelia* to shows its affinity to *Agathelia*.

Diagnosis: Plocoid coral colony with circular calices. Thick, compact septa in a regular septal symmetry, made of small trabeculae. Septal faces with thorns and apophysal septa. Septa in a regular hexameral symmetry. Septa of the first cycle attached to each other in the centre of the calice forming the columella, septa of the seond cycle shorter. Endotheca by few tabulae, coenosteum by dissepiments and rare trabeculae.

Description: Plocoid colony. Calicular outline circular. Calices slightly elevated. Septa compact. Microstructure of small sized trabeculae, septa with a median dark line. Septa in cross section thick close to the wall and with a triangular outline. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length and thickness. First septal cycle reaches to the centre of the calice, the second cycle is shorter. Septa of the second cycle rarely attached to those of the first cycle, all septa of the first cycle connected in the centre of the calice. Septal distal margin smooth (probably due to preservation), lateral face with fine thorns and some apophysal septa, inner margin rarely branching. Pali or paliform lobes absent. Costae hardly present, non-confluent. Synapticulae absent. Columella formed by septal fusion in the centre of the calice. Endotheca consists of few tabulae. Wall compact, parathecal. Coenosteum narrow (ca. 25% of the calicular diameter), consists of dissepiments and rare trabeculae. Budding extracalicinal.

Systematic position: The thickness of septa and their microstructure, the ornamentation of the septal surface and septal inner margin clearly identifies the new genus as a member of the family Agatheliidae. This family was for a long time considered to belong to the Stylinidae. Because of the strong ornamentation of the lateral septal faces, the absence of auriculae, the trabecular wall in most members, and the constitution of the coenosteum, the family is assigned to the suborder Heterocoeniina (see also Löser et al. in press).

Comparison: In comparison to *Agathelia*, *Caelumastrea* and *Canleria*, it lacks the trabecular wall and has a pronounced columella formed by septal fusion. In the other three genera, a columella sensu stricto does not exist, but it can be formed by trabecular extensions.

Species: *Eothelia hoelzli* n.sp., *Eothelia bavarica* n.sp.

Distribution: Currently the genus is only known from the Middle Cenomanian of the Roßsteinalmen area.

Eothelia bavarica n. gen., n. sp.
Pl. 5, Figs 1–4

Diagnosis: *Eothelia* with an inner calicular diameter of 1.5–1.9mm and 12 septa.

Derivatio nominis: After the state Bavaria.

Locus typicus: Germany, Bavaria, Roßsteinalmen (ca. 47°38’0”N 11°40’45”E, WGS84).

Stratum typicum: Branderfleck Fm, Middle Cenomanian.

Types: Holotype 1991 X 93 with three thin sections, paratype 1947 XVI 52 with one thin section.

Further material: 1947 XVI 13, 1947 XVI 57 1947 XVI 58, 1947 XVI 59.

Comparison: The species differs from the type species by smaller calicular dimensions.

Dimensions:

(1991 X 93)

	n	min–max	μ	σ	cv	μ±σ
cl	18	1.45–2.13	1.72	0.2	11.5	1.52–1.91
ccd	20	2.59–3.37	3.0	0.2	6.5	2.80–3.19
s	6+6					

(1947 XVI 52)

	n	min–max	μ	σ	cv	μ±σ
cl	8	1.67–2.14	1.92	0.16	8.5	1.75–2.08
ccd	8	2.48–3.88	2.95	0.44	14.8	2.50–3.38
s	6+6					

Description: As for the genus.

Eothelia hoelzli n. sp.
Pl. 4, Figs 1–7

Diagnosis: *Eothelia* with an inner calicular diameter of 2.4–2.7mm and 12 septa.

Derivatio nominis: After Otto Hölzl, who collected the majority of the studied material.

Locus typicus: Germany, Bavaria, Roßsteinalmen (ca. 47°38’0”N 11°40’45”E, WGS84).

Stratum typicum: Branderfleck Fm, Middle Cenomanian.

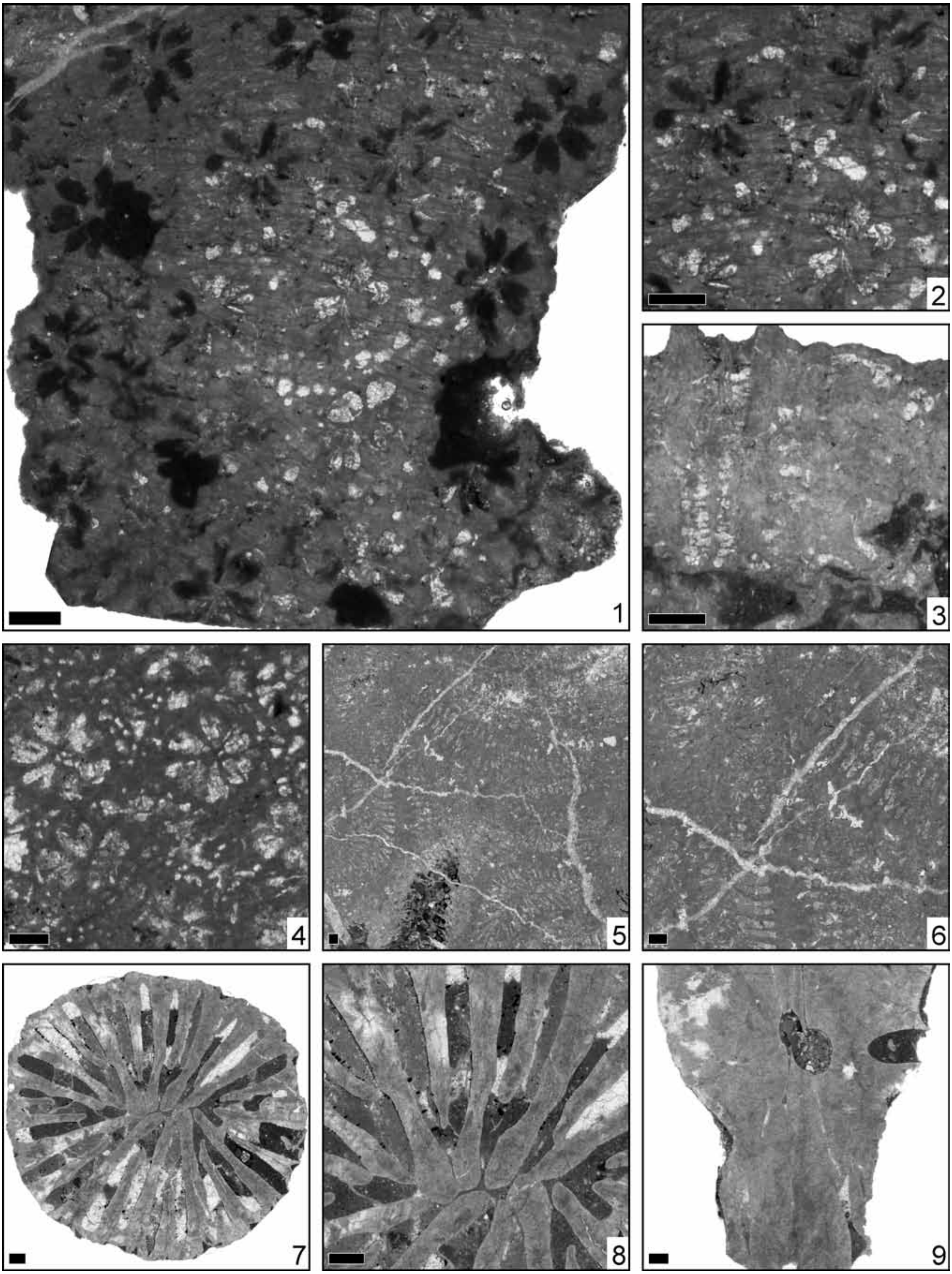


Plate 5: (1–3) *Eothelia bavarica* n. gen. n. sp., Holotype, 1991 X 93. 1: transversal thin section. 2: transversal thin section, detail. 3: longitudinal thin section. **(4)** *Eothelia bavarica* n. gen. n. sp., Paratype, 1947 XVI 52, transversal thin section. **(5–6)** *Pachygyra krameri* Oppenheim, 1930, 2012 X 1. 5: transversal thin section. 6: transversal thin section, detail. **(7–9)** *Ceratosmilia arnaudi* Alloiteau, 1957, 1991 X 47. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. Scale bars = 1mm.

Types: Holotype 1991 X 42 with three thin sections, paratype 1980 XIII 13 with one thin section, paratype 1991 X 103 with one thin section.

Further material: 1991 X 92.

Dimensions:

(1991 X 42)

	n	min–max	μ	σ	cv	μ±σ
cl	15	2.37–2.84	2.57	0.14	5.7	2.42–2.71
c	15	2.74–3.49	3.09	0.21	6.9	2.88–3.31
ccd	15	2.91–4.12	3.37	0.27	8.2	3.09–3.64

(1991 X 103)

cl	3	2.03–2.75	2.47	0.38	15.5	2.08–2.85
c	4	3.08–3.72	3.33	0.28	8.5	3.04–3.61

(1980 XIII 13)

cl	7	2.15–2.92	2.48	0.26	10.7	2.21–2.75
c	7	3.17–3.55	3.37	0.14	4.2	3.22–3.51

Description: As for the genus.

Family Heterocoeniidae Oppenheim, 1930

Heterocoenia Milne Edwards & Haime, 1848

Heterocoenia sp.
Pl. 3, Figs 10–12

Material: 1991 X 101; 3 thin sections.

Dimensions:

(1991 X 101)

	n	min–max	μ	σ	cv	μ±σ
cl	10	2.11–2.54	2.35	0.13	5.6	2.21–2.47
ccd	10	2.42–3.53	3.07	0.36	11.6	2.71–3.42
s	6+6					

Description: Plocoid colony. Calicular outline irregular. Septa compact, in cross section externally thick, getting thinner towards the centre. Symmetry of septa radial and regularly trimeral. Cycles of septa subregular. Septal cycles differ in length, almost not in thickness. First septal cycle reaches 25% of the calicular diameter, further cycles are shorter. Septa free. Septal distal margin unknown, lateral face with numerous fine thorns, inner margin with thorns. Pali or paliform lobes absent. Costae present, short, nonconfluent. Synapticulae absent. Columella absent. Endotheca consists of numerous dissepiments. Wall present, subcompact, septothecal. Coenosteum medium broad, consists of large trabeculae and dissepiments. Budding extracalicinal.

Occurrence: Cenomanian (Dixoni zone) of Spain (Cantabria, Santander) Cobreces, Luaña playa (PIW 1998 X 8).

Suborder Meandrinina Alloiteau, 1952
Family Felixigyra group (informal)

Remarks: This informal group of the family level encompasses the genera *Felixigyra*, *Rhipidomeandra* Morycowa & Masse, 1998, and *Wellsimeandra* Idakieva & Cheshmedzhieva, 2003. For details see Löser (2013, in press).

Felixigyra Prever, 1909

Felixigyra deangelisi Prever, 1909
Pl. 3, Figs 1–3

v 1909 *Felixigyra Deangelisi* – Prever: p. 118, pl. 12, figs 7, 8
v 2010b *Felixigyra deangelisi* Prever, 1909 – Löser: p. 192, figs 3, 4, pl. 1, figs 1–3

Material: 1947 XVI 62, 1991 X 81, 1991 X 98, 1991 X 99; 3 thin sections.

Dimensions:

(1991 X 81)

	n	min–max	μ	σ	v	μ±σ
crw	15	0.88–1.36	1.08	0.14	13.0	0.93–1.22
md	15	1.75–2.07	1.89	0.1	5.1	1.79–1.99
sd	5–6/2mm					

Description: Hydnophoroid colony. Monticules conical, thick, often connected to each other. Calices distinct. Septa compact. Microstructure of septa unknown. Septa in cross section externally slightly thicker, get slightly thinner towards the centre. No septal symmetry, but size orders can be distinguished. Septal generations differ in length and thickness. First septal generation reaches close to the centre of the calice, further generations are subsequently shorter. Septa occasionally connected, only by the means of dissepiments. Septal distal margin unknown, lateral face rarely with medium size thorns, inner margin swollen in places. Pali or paliform lobes absent. Costae unknown. Synapticulae absent. Columella absent. Endotheca consists of thin tabulae and dissepiments. Wall present, compact, septothecal. Coenosteum absent. Budding intracalicinal, polystomodeal.

Occurrence: Lower Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Cerasetti and margine N di Fossa Mezza Spada. Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis.

Family Phyllosmiliidae Felix, 1903

Aulosmilia Alloiteau, 1952

Remarks: Distinction of species in *Aulosmilia* is difficult because the septal number increases with the size of the coral (Baron-Szabo 2003). So it is unknown whether the present material all belongs to one species, representing different stages of ontogeny, or to different species that reached different adult sizes.

Aulosmilia ? *bipartita* (Reuss, 1854)
Pl. 6, Figs 1–2

Material: 1991 X 84; 1 thin section.

Dimensions:

	(1991 X 84)
c min	12
c max	25
s	140
sd	6/2

Description: Solitary turbinate coral. Calicular outline elliptical, pit depressed. Septa compact. Microstructure of small sized trabeculae, septa with a median zigzag dark line. Septa in cross section externally slightly thicker, get slightly thinner towards the centre. Septa of the three first cycles are unproportionally thicker. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length and thickness. Four septal cycles reach close to the centre of the calice, further cycles are shorter. Septa occasionally connected to each other in the centre of the calice. Septal upper margin smooth, lateral face with numerous thorns, inner margin T-shaped and swollen. Various septa are connected to the columella. Pali or paliform lobes absent. Costae present but short, smooth on their surface. Synapticulae absent. Columella lamellar, discontinuous, very deep in the calice. Endotheca not easily observable but dissepiments exist. Wall compact, septothecal.

Aulosmilia ? *consobrina* (Reuss, 1854)
Pl. 6, Figs 3–4

Material: 1947 XVI 17, 1947 XVI 18, 1947 XVI 19, 1991 X 82, 1991 X 83; 4 thin sections.

Dimensions:

	(1947 XVI 17)
c min	10
c max	15
s	96
sd	6/2mm

	(1991 X 83)
c min	12
c max	22
s	96
sd	7/2mm

Description: Solitary turbinate coral. Calicular outline elliptical, pit depressed. Septa compact. Microstructure of small sized trabeculae, septa with a median zigzag dark line. Septa in cross section externally slightly thicker, get slightly thinner towards the centre. Septa of the three first cycles are unproportionally thicker. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length and thickness. Three septal cycles reach close to the centre of the calice, further cycles are shorter. Septa of younger cycles rarely connected to septa of older ones. Septal upper margin smooth, lateral face with numerous thorns, inner margin T-shaped and swollen. Pali or paliform lobes absent. Costae present but short, smooth on their surface. Synapticulae absent. Columella lamellar, discontinuous, very deep in the calice. Endotheca not easily observable but dissepiments exist. Wall compact, paraseptothecal.

Aulosmilia ? *inconstans* (de Fromentel, 1862)
Pl. 6, Figs 7–9

Material: 1947 XVI 36, 1947 XVI 37, 1991 X 41, 1991 X 53, 1991 X 54, 1991 X 55, 1991 X 56, 1991 X 57, 1991 X 58, 1991 X 85, 1991 X 86, 1991 X 87; 3 thin sections.

Dimensions:

	(1947 XVI 36)
c min	30
c max	40
s	96
sd	6/2mm

	(1991 X 41)
c min	25
c max	39
s	96
sd	8/5mm

Description: Solitary turbinate coral. Calicular outline elliptical, pit depressed. Septa compact. Microstructure of small sized trabeculae, septa with a median zigzag dark line. Septa in cross section externally slightly thicker, get slightly thinner towards the centre. Septa of the three first cycles are unproportionally thicker. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length and thickness. Four septal cycles reach close to the centre of the calice, further cycles are shorter. Septa free. Septal upper margin smooth, lateral face with numerous thorns, inner margin T-shaped and swollen. Pali or paliform lobes absent. Costae present but short, smooth on their surface. Synapticulae absent. Columella lamellar, discontinuous, very deep in the calice. Endotheca not easily observable but numerous lateral dissepiments exist. Wall not preserved.

Pachygyra Milne Edwards & Haime, 1848

Pachygyra krameri Oppenheim, 1930
Pl. 5, Figs 5–6

* 1930 *Pachygyra krameri* n. sp. – Oppenheim: p. 448, pl. 13, fig. 1
1980 *Pachygyra krameri* Oppenheim 1930 – Vidal: p. 43, pl. 11, fig. 8

Material: 2012 X 1; 1 thin section.

Dimensions:

	(2012 X 1)
crw	3.2–4.3
crd	7.5–11.7
sd	9/5mm

Description: Meandroid colony. Calicular rows elevated over the colony surface. Calicular rows long and curved. Calices indistinct. Septa compact. Microstructure of small sized trabeculae, septa with a median dark line. Septa in cross section externally thick, getting thinner towards the centre, first generation unproportionally thicker than other generations. Symmetry of septa irregular, but size orders can be distinguished. Septal generations differ in length and thickness. First septal generation reaches to the centre of the calicular row, further generations are subsequently shorter. Septa of the first generation occasionally connected to each other, by the means of their swollen inner margins. Septal distal margin smooth (probably due to preservation), lateral face occasionally with thorns, inner margin T-shaped and swollen. Pali or paliform lobes absent. Costae short, non-confluent. Synapticulae absent. Columella lamellar, discontinuous. Endotheca unknown. Wall compact, paraseptothecal. Coenosteum medium broad, consists of costae and (?) exothecal dissepiments. Budding intracalicinal.

Remarks: The only specimen of this species represents the largest sample found in the outcrop area; it measures about 30x20x15cm. The skeleton is completely recrystallized not giving a good thin section. The description in Oppenheim (1930: 448) is not very detailed, but at least the width of the calicular rows is reported (4mm).

Occurrence: Santonian of Austria (Salzburg) Rußbach, Zimmergraben; Spain (Cataluña, Lérida) Com. Pallars Jussà, Mun. Isona i Conca Dellà, Collades de Bastús.

Family Plesiosmilia group (informal)

Ceratosmilia Alloiteau, 1957

Ceratosmilia arnaudi Alloiteau, 1957
Pl. 5, Figs 7–9

*v 1957 *Ceratosmilia Arnaudi* nov. sp. – Alloiteau: p. 116, 421, fig. 74, pl. 3, fig. 7
? 1995 *Ceratosmilia arnaudi* Alloiteau, 1957 – Cheshmedzhieva: p. 41, pl. 6, figs 7, 8
? 1997a *Ceratosmilia* (?) *arnaudi* Alloiteau, 1957 – Eliášová: p. 68, pl. 8, figs 3 a, b, 4

Material: 1947 XVI 38, 1947 XVI 39, 1947 XVI 44, 1991 X 47, 1991 X 52, 1991 X 89, 1991 X 90, 1991 X 91, 1991 X 104, 2012 X 3; 5 thin sections.

Dimensions:

	(1991 X 47)
c	15–17 mm
s	30

	(1947 XVI 44)
c	12.5–19 mm
s	40

	(2012 X 3)
c	16.3–17.2 mm
s	48

Description: Solitary turbinate coral. Calicular outline circular. Septa compact, in cross section externally slightly thicker, get slightly thinner towards the centre. Microstructure of small trabeculae with a median dark line. Symmetry of septa radial and irregularly hexameral. Cycles of septa subregular. Septal cycles (generations) differ in length and thickness. First two septal cycles reach to the centre of the calice, further cycles are shorter. Septa rarely connected to each other. Septal upper margin smooth, lateral face smooth (probably due to preservation), inner margin slightly swollen in places. Pali or paliform lobes absent. Costae present, smooth on their surface. Synapticulae absent. Columella absent. Endotheca not well observable but marginal dissepiments exist. Wall septothecal by septal splitting.

Remarks: *Ceratosmilia* is a poorly known genus. The type species comes from the Lower Cenomanian of La Rochelle (Charente-Maritime, France) and its type is very poorly preserved. For this reason it cannot be assured that the present material belongs to *Ceratosmilia*. The wall formation is different; the wall seems to be parathecal in the type specimen, but in the present material it is made by external ends of the septa that split off and form the wall (as in the Lower Jurassic *Axosmiliopsis*). The septal symmetry in the present sample is less regular than in the type specimen. The systematic position is preliminary; it is possible that the genus belongs to the Caryophylliidae.

Occurrence: Lower Cenomanian of France (Charente-Maritime) Fouras; France (Charente-Maritime) Ile d'Aix; France (Charente-Maritime) Piédemont; France (Charente-Maritime) Rochefort.

Paramontlivaltia Alloiteau, 1952

Paramontlivaltia ruvida (Prever, 1909)
Pl. 6, Figs 10–12

*v 1909 *Epismilia ruvida* – Prever: p. 113, text-fig. 19
v 1909 *Trochosmilia polymorpha* – Prever: p. 108, text-figs 12, 13, pl. 10, figs 5–23

Material: 1947 XVI 30, 1947 XVI 31, 1947 XVI 32; 2 thin sections.

Dimensions:

	(1947 XVI 30)
c	12–14
s	48

Description: Solitary turbinate coral. Calicular outline circular. Calicular pit depressed. Septa com-

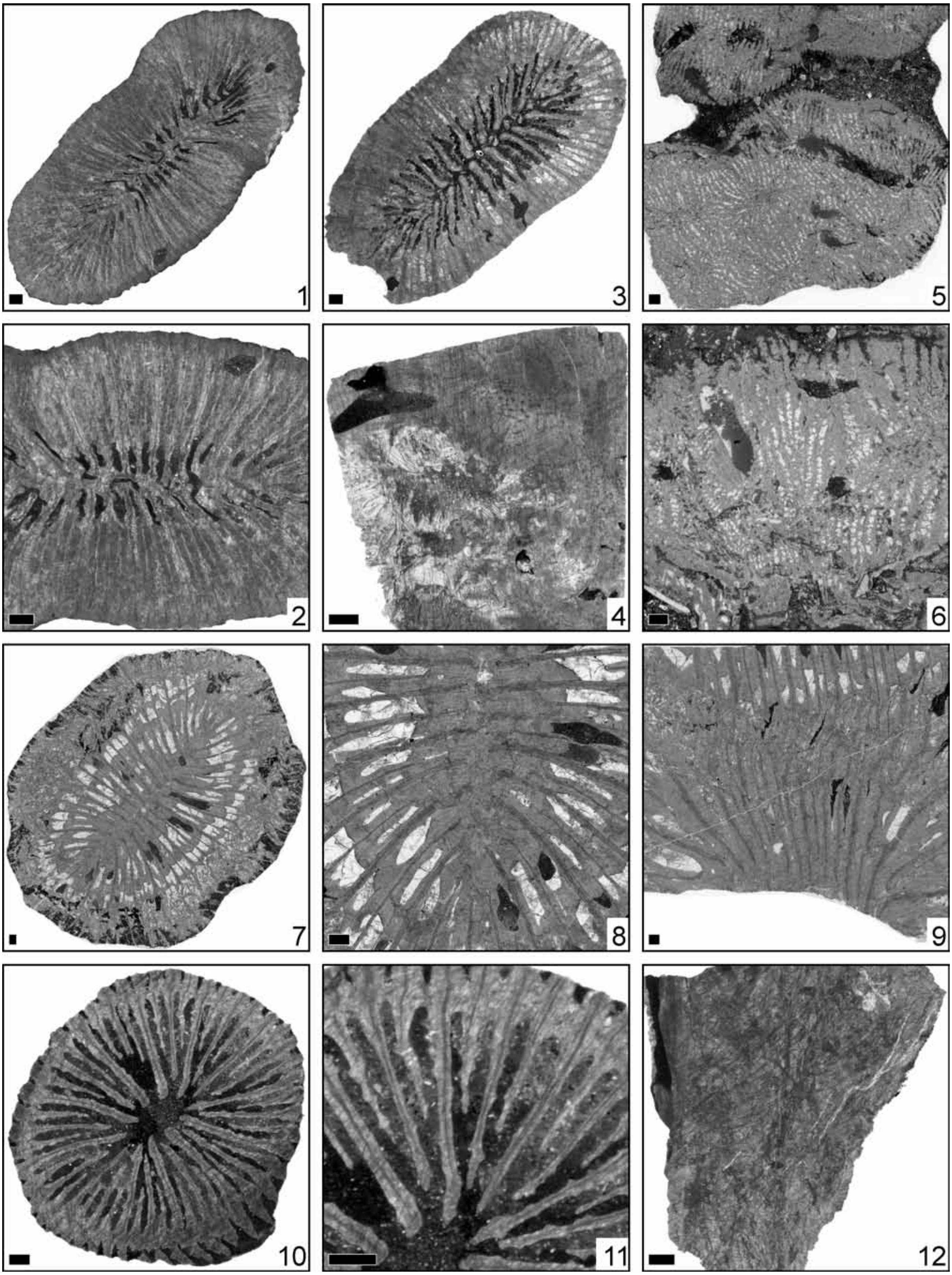


Plate 6: (1–2) *Aulosmilia* ? *bipartita* (Reuss, 1854), 1991 X 84. 1: transversal thin section. 2: transversal thin section, detail. **(3–4)** *Aulosmilia* ? *consobrina* (Reuss, 1854), 1991 X 83. 3: transversal thin section. 4: longitudinal thin section. **(5–6)** *Dimorphastrea regularis* (de Fromentel, 1857), 1947 XVI 9. 5: transversal thin section. 6: longitudinal thin section. **(7–9)** *Aulosmilia* ? *inconstans* (de Fromentel, 1862), 1947 XVI 36. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. **(10–12)** *Paramontlivaltia ruvida* (Prever, 1909), 1947 XVI 30. 10: transversal thin section. 11: transversal thin section, detail. 12: longitudinal thin section. Scale bar = 1mm.

pact. Microstructure of small sized trabeculae, septa with a median line. Septa in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septa radial and regularly hexameral. Cycles of septa regular. Septal cycles differ in length and thickness. First two septal cycles reach 40% of the calicular diameter, further cycles are shorter. Septa free. Septal upper margin smooth, lateral face with granules, inner margin smooth. Pali or paliform lobes absent. Costae present, smooth on their surface. Synapticulae absent. Columella absent. Endotheca not well observable but marginal dissepiments exist. Wall not compact, septothecal.

Remarks: *Paramontlivaltia* is a poorly defined genus. It is applied according to the concept presented by its author. The genus is comparable to *Montlivaltia* but has smaller trabeculae and therefore has a different ornamentation of the septa (upper margin, costae, lateral faces). The genus is comparable to *Plesiosmilia* but lacks a columella.

Occurrence: Lower Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre; Fossa Agnese; Fossa Mezza Spada; Margine N di Fossa Mezza Spada. Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 7446).

Suborder Microsolenina
Morycowa & Roniewicz, 1995

Family Leptophylliidae Vaughan, 1905

Acrosmilia d'Orbigny, 1849

Acrosmilia sp.
Pl. 7, Figs 1–3

v 1897 *Leptophyllia patellata* – Söhle: p. 44, pl. 6, fig. 5
v 1989 *Acrosmilia patellata* (Michelin 1845) – Löser: p. 131, text-fig. 34, pl. 26, fig. 1

Material: 1947 XVI 4, 1947 XVI 5, 1991 X 64, 1991 X 65, 1991 X 66, 1991 X 68, 1991 X 69; 1 thin section.

Dimensions:

(1947 X 4)

c	21–28mm
s	240
sd	9/5mm

Description: Solitary cylindric coral. Calicular outline elliptical, centre slightly depressed. Septa irregularly perforated, more common at their inner margin. Microstructure of large trabeculae. Septa in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septa irregular. Cycles of septa irregular, but size orders can be distinguished. Septal generations differ in length and thickness. First septal generation reaches close to the centre of the calice, further generations are subsequently shorter. Septa of younger generations occasionally connected to septa of older ones. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae present, with thick granules on their surface. Synapticulae present, medium common. Columella absent or as some small elements, presumably trabecular extensions of septal inner margins. Endotheca consists of numerous dissepiments. Wall absent (probably due to preservation).

Occurrence: Hauterivian of France (Haute-Marne) Saint Dizier (MNHN nn). Aptian of Mexico (Puebla) San Juan Raya (IGM 9244). Lower Cenomanian (Mantelli zone) of Germany (Bayern) Ettal, Lichtenstättgraben. Lower Cenomanian (Dixoni zone) of Spain (Cantabria, Santander) Cobreces, Luaña playa (SNSB-BSPG 2007 V 13-1-41). Upper Cenomanian (Plenus zone) of Germany (Sachsen) Dresden-Plauen, Ratssteinbruch, southern quarry. Cenomanian (Juddi zone) of France (Aude) Les Corbières, Sougraigne, Source Salée (MNHN nn).

Astraeofungia Alloiteau, 1952

Astraeofungia tenochi (Felix, 1891)
Pl. 7, Figs 4–6

vp 1886 *Synastraea maeandra* – Fromentel: p. 598, pl. 173, fig. 2, pl. 175, fig. 2
*v 1891 *Thamnastraea Tenochi* – Felix: p. 145, pl. 22, figs 7, 7 a
v 1909 *Thamnastraea Vaughani* – Prever: p. 71, pl. 2, figs 9, 9 a
v 1951 *Thamnasteria contorta* Eguchi, n.sp. – Eguchi: p. 30, pl. 5, figs 8, 9, pl. 6, figs 1, 3
v 1951 *Thamnasteria jezoensis* Eguchi, n.sp. – Eguchi: p. 54, pl. 18, figs 5, 6
v 1983 *Thamnasteria crespoi* (Felix, 1891) – Reyeros de Castillo: p. 15, pl. 2, figs 1, 2
v 1989 *Thamnastraea tenochi* Felix – Carreño et al.: p. 100, fig. 35h
v 2003 *Diploastrea harrisi* Wells, 1932 – Baron-Szabo & González León: p. 212, figs 8B, E
v 2006 *Astraeofungia tenochi* (Felix, 1891) – Löser: p. 49, fig. 3K

Material: 1947 XVI 27, 1991 X 79; 3 thin sections.

Dimensions:

(1947 XVI 27)

	n	min–max	μ	σ	v	μ±σ
ccd	10	5.28–6.6	6.0	0.45	7.4	5.54–6.44
s	24–30					
sd	12/5mm					

(1991 X 79)

	n	min–max	μ	σ	cv	μ±σ
ccd	15	4.89–6.41	5.71	0.48	8.3	5.23–6.18
s	30–40					
sd	10/5					

Description: Thamnasterioid colony. Calicular centres slightly depressed. Septa perforated at their

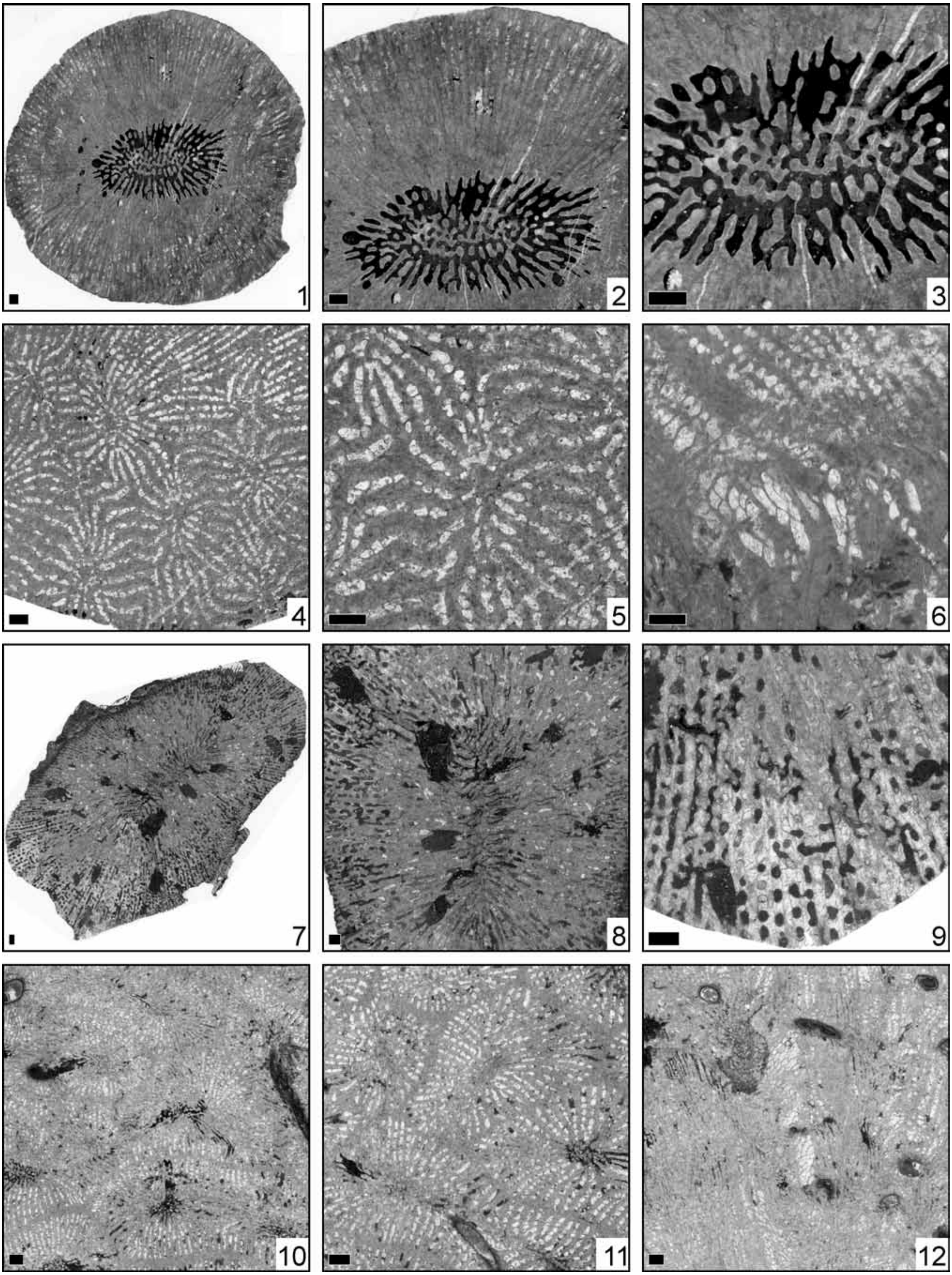


Plate 7: (1–3) *Acrosmilia* sp., 1947 XVI 4. 1: transversal thin section. 2: transversal thin section, detail. 3: transversal thin section, detail. **(4–6)** *Astraeofungia tenochi* (Felix, 1891), 1947 XVI 27. 4: transversal thin section. 5: transversal thin section, detail. 6: longitudinal thin section. **(7–9)** *Leptophyllaraea* cf. *granulata* (de Fromentel, 1863), 1991 X 67. 7: transversal thin section. 8: transversal thin section, detail. 9: transversal thin section, detail. **(10–12)** *Microphyllia* cf. *oldhamiana* (Stoliczka, 1873), 1991 X 49. 10: transversal thin section. 11: transversal thin section, detail. 12: longitudinal thin section. Scale bar = 1mm.

inner margin. Microstructure of large trabeculae. Septa in cross section externally thick, getting thinner towards the centre. Symmetry of septa irregular. No septal generations. Most septa reach close to the calicular centre. Septa occasionally connected to each other close to the centre of the calice, or in the space between the calices. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent or sub-confluent. Synapticulae present, occasional, mainly in the space between calices. Columella consists of a more solid element. Endotheca consists of numerous dissepiments. Wall absent. Budding extracalicinal.

Occurrence: Lower Hauterivian (Radiatus zone) of France (Yonne) Fontenoy (SNSB-BSPG 2003 XX 5200); Gy-l'Evêque (MHNG 4560). Barremian of Mexico (Puebla) Tehuacán, San Antonio Texcala. Upper Barremian to Lower Aptian (Lenticularis zone) of Mexico (Sonora) Municipio Ures, Cerro de Oro. Lower Aptian of Italy (Abruzzi, L'Aquila) Monti d'Ocre, Fossa Cerasetti. Lower Upper Aptian of Algeria (Tebessa) Commune Ouenza, Ouenza Mt (UPM 5139). Spain (Cataluña, Lérida) Com. La Noguera, Mun. Vilanova de Meià, Montsec de Rubies, section NW La Cabrua quarry/4 (SNSB-BSPG 2003 XX 6326). Upper Aptian of Japan (Hokkai-do) Asibetsu-shi, Shimonoshita tunnel. Uppermost Aptian of Japan (Iwate-ken) Shimohei-gun, Tanohata-mura, Haipe, northern cliff. Lower Albian (Tardefurcata zone) of Spain (Cataluña, Barcelona) Com. Alt Penedès, Castellvi de la Marca, Can Pascual (SNSB-BSPG 2003 XX 6285); Spain (Cataluña, Tarragona) Com. Baix Penedès, Mun. Masllorenç, Masarbones (ERNO L-6034). Lower Albian of Mexico (Oaxaca) Tepelmeme, El Rodeo Ranch; Mexico (Sonora) Municipio Ures, Cerro de Oro (ERNO L-4352). Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 5823). Middle to Upper Cenomanian (Rhotomagense - Geslinianum zone) of France (Sarthe) Le Mans (MHNG 4542). Upper Cenomanian of Czech Republic (Central Bohemian region) Kolín, Planany (OKSB n/a). Upper Cenomanian (Plenus zone) of Germany (Sachsen) Dresden-Plauen, Ratssteinbruch, southern quarry (SNSB-BSPG 2009 XVII 76).

Dimorphastrea d'Orbigny, 1850

Dimorphastrea regularis (de Fromentel, 1857)
Pl. 6, Figs 5–6

*	1857	*Oroseris regularis* – Fromentel: p. 34
	1861	*Oroseris regularis* – Fromentel: p. 171
v	1877	*Oroseris regularis* – Fromentel: p. 478, pl. 117, fig. 2
v	1997	*Thamnoseris arborescens* Felix, 1891 – Baron-Szabo: p. 88, pl. 16, figs 2, 4
v	2013	*Dimorphastrea regularis* (de Fromentel, 1857) – Löser et al., pl. 8, fig. 10

Material: 1947 XVI 11, 1947 XVI 9; 2 thin sections.

Dimensions:
(1947 XVI 9)

	n	min–max	μ	s	v	μ±s
ccd	5	5.38–7.0	6.13	0.66	10.7	5.46–6.78
crd	4.9–5.7					
s	30–36					
sd	8/3mm					

Description: Thamnasterioid colony with calices arranged in rows. Septa perforated at their inner margin. Microstructure of large trabeculae. Septa in cross section externally thick, getting thinner towards the centre. Symmetry of septa irregular. No septal cycles. Most septa reach close to the calicular centre. Septa occasionally connected to each other close to the centre of the calice. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent. Synapticulae present, occasional, mainly in the space between calices. Columella consists of isolated trabeculae or one more solid element. Endotheca consists of thin tabulae. Wall absent. Budding intracalicinal.

Occurrence: Lower Hauterivian (Radiatus zone) of France (Yonne) Gy-l'Evêque. Lower Albian of Mexico (Sonora) Municipio Ures, Cerro de Oro (ERNO L-4943). Lower Upper Albian (Inflatum zone) of Spain (Valencia, Alicante) Sierra de Llorençá. Lower Cenomanian (Dixoni zone) of Spain (Cantabria, Santander) Cobreces, Luaña playa (SNSB-BSPG 2007 V 143). Upper Turonian to Lower Coniacian of Austria (Tirol) Brandenberg, Haidach. Lower Upper Campanian of Spain (Cataluña, Lérida) Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur, Torallola, south of (MB K1174#1).

Leptophyllaraea Alloiteau, 1952

Leptophyllaraea cf. *granulata* (de Fromentel, 1863)
Pl. 7, Figs 7–9

Material: 1991 X 67, 1991 X 88; 1 thin section.

Dimensions:
(1991 X 67)

c	55x65mm
sd	9/5mm
s	ca. 500

Description: Solitary cylindric coral. Calicular outline elliptical, centre slightly depressed. Septa irregularly perforated, more common in the middle of the septal blade. Microstructure of large trabeculae. Septa in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septa irregular. Cycles of septa irregular, but size orders can be distinguished. Septal generations differ in length and thickness. First septal generation

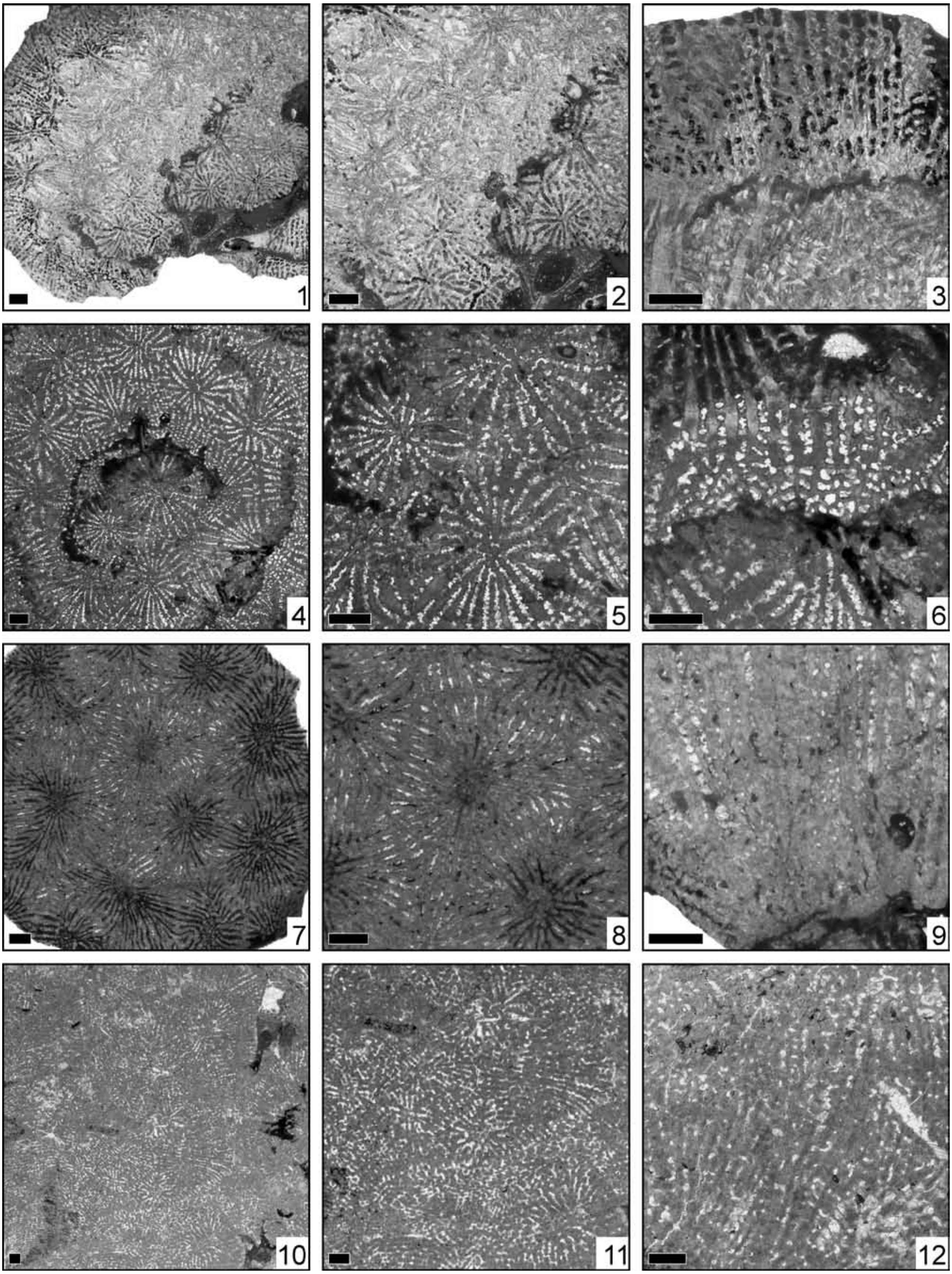


Plate 8: (1–3) *Negoporites* cf. *quartus* Eliášová, 1995, 1947 XVI 45. 1: transversal thin section, detail. 2: transversal thin section, detail. 3: longitudinal thin section. **(4–6)** *Negoporites* sp., 1947 XVI 53. 4: transversal thin section. 5: transversal thin section, detail. 6: longitudinal thin section. **(7–9)** *Thalamocaeniopsis* sp., 1947 XVI 56. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. **(10–12)** *Dimorpharaea japonica* Eguchi, 1951, 1991 X 80. 10: transversal thin section. 11: transversal thin section, detail. 12: longitudinal thin section. Scale bar = 1mm.

reaches close to the centre of the calice, further generations are subsequently shorter. Septa of younger generations occasionally connected to septa of older ones. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae present, with thick granules on their surface. Synapticulae present, very abundant. Columella absent or as some small elements, presumably trabecular extensions of septal inner margins. Endotheca unknown. Wall absent (probably due to preservation).

Remarks: The material is represented by very large individuals representing a high number of septa. As in *Aulosmilia*, septal number correlates with the diameter of the coral. *Leptophyllaraea* is distinguished from *Acrosmilia* by its more centrally perforate septa and much more abundant synapticulae. The present material is closely related to the type species but has slightly larger dimensions and a much higher number of septa.

Microphyllia d'Orbigny, 1849

Microphyllia cf. *oldhamiana* (Stoliczka, 1873)
Pl. 7, Figs 10–12

Material: 1991 X 49, 1991 X 50, 1991 X 51; 3 thin sections.

Dimensions:
(1991 X 49)

	n	min–max	μ	σ	v	μ±σ
crd	15	4.76–7.47	5.8	0.83	14.3	4.96–6.62
ccd	5	3.58–8.7	6.16	2.06	33.4	4.09–8.22
s	40					
si	80					
sd	6/2mm					

Description: Meandroid colony. Calicular pit depressed, rows short and straight. Calices distinct. No neighbouring calices in one row. Valley septa present. Septa perforated at their inner margin. Microstructure of large trabeculae. Septa in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septa irregular. Cycles of septa irregular, but size orders can be distinguished. Most septa reach close to the calicular centre. Septa occasionally connected to each other close to the centre of the calice. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae absent. Synapticulae present, almost only in the wall. Columella consists of isolated trabeculae. Endotheca consists of numerous dissepiments. Wall present, compact, synapticulothecal. Collines tectiform. Coenosteum absent. Budding intracalicinal, polystomodeal and complete.

Remarks: Differs from *M*. *oldhamiana* by a higher number of septa (18–20 in the type).

Negoporites Eliášová, 1989

Remarks: The genus was originally (Eliášová 1989) assigned to the family Poritidae, later to the newly erected family Negoporitidae Eliášová, 1995 within the suborder Microsolenina. Here, this family is not accepted. The genus *Negoporites* is not well defined; the type of its type species *Porites michelini* Reuss, 1846 is lost. The neotype designated by Eliášová (1989: 117) is invalid, because it does not fulfil IRZN Art. 75; particularly acticle 75.3 was not taken into account. Moreover, the family Leptophylliidae unifies more than 50 genera (Löser 2009) and needs a profound revision. It does not seem useful to just separate one genus into a new family without knowing its relationships to other genera.

Negoporites cf. *quartus* Eliášová, 1995
Pl. 8, Figs 1–3

Material: 1947 XVI 45; 1 thin section.

Dimensions:
(1947 XVI 45)

	n	min–max	μ	σ	v	μ±σ
cl	10	1.89–2.48	2.12	0.22	10.5	1.89–2.34
ccd	20	1.85–2.68	2.33	0.28	11.9	2.04–2.60
s	20–24					
sd	4/1mm					

Description: Plocoid colony. Calicular outline circular. Colony surface plan. Septa with few pores, in cross section externally thick, getting thinner towards the centre. Symmetry of septa bilateral. Cycles of septa subregular. Septal cycles differ in length, almost not in thickness. Half of all septa reach to the calicular centre. Septa of younger cycles often connected to septa of older ones. Septal distal margin unknown, lateral face with pennulae, inner margin smooth. Pali or paliform lobes absent. Some septa may be attached to the columella. Costae present, sub-confluent to non-confluent. Synapticulae present, abundant, mainly in the coenosteum and wall. Columella small, substyliform. Endotheca absent. Wall subcompact, synapticulothecate. Coenosteum narrow, consists of trabeculae and synapticulae. Budding extracalicinal.

Remarks: The material differs from *N. quartus* by smaller calicular dimensions and a lower number of septa.

Negoporites sp.
Pl. 8, Figs 4–6

Material: 1947 XVI 53; 1 thin section.

Dimensions:
(1947 XVI 53)

	n	min–max	μ	σ	cv	μ±σ
cl	13	2.57–3.52	3.09	0.27	8.8	2.81–3.36
ccd	15	3.02–4.3	3.55	0.39	10.9	3.16–3.93
s	28–30					
sd	4/1mm					

Description: Plocoid colony. Calicular outline circular. Colony surface plan. Septa with few pores, in cross section externally thick, getting thinner towards the centre. Symmetry of septa bilateral. Cycles of septa subregular. Septal cycles differ in length, almost not in thickness. Half of all septa reach to the calicular centre. Septa of younger cycles often connected to septa of older ones. Septal distal margin unknown, lateral face with pennulae and thorns, inner margin smooth. Pali and paliform lobes absent. Some septa may be attached to the columella. Costae present, sub-confluent to non-confluent. Synapticulae present, abundant, mainly in the coenosteum and wall. Columella small, substyliform. Endotheca absent. Wall subcompact, synapticulothecate. Coenosteum narrow, consists of trabeculae and synapticulae. Budding extracalicinal.

Remarks: The specimen differs from all known species by its large dimensions.

Thalamocaeniopsis Alloiteau, 1954

Thalamocaeniopsis sp.
Pl. 8, Figs 7–9

Material: 1947 XVI 56, 1948 III 2; 4 thin sections.

Dimensions:
(1947 XVI 56)

	n	min–max	μ	σ	cv	μ±σ
cl min	10	2.61–4.35	3.45	0.51	15.0	2.93–3.97
cl max	10	3.77–5.36	4.44	0.52	11.7	3.92–4.96
ccd	15	3.15–4.68	3.92	0.45	11.5	3.46–4.37
s	5	43–64	54.0	8.15	15.1	45.84–62.15
sd	4/1mm					

Description: Cerioid colony. Calicular outline polygonal. Calicular centres slightly depressed. Septa perforated at their inner margin. Microstructure of large trabeculae. Septa in cross section externally thick, getting thinner towards the centre. Symmetry of septa irregular. No septal cycles or septal symmetry. Half of all septa reach close to the calicular centre. Septa occasionally connected to each other close to the centre of the calice. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent or sub-confluent. Synapticulae present, occasional, mainly in the space between calices. Columella consists of isolated trabeculae or one more solid element. Endotheca consists of few thin tabulae. Wall subcompact, made of synapticulae. Budding extracalicinal.

Family Microsolenidae Duncan, 1884

Dimorpharaea de Fromentel, 1861

Dimorpharaea japonica Eguchi, 1951
Pl. 8, Figs 10–12

* 1951 *Dimorpharaea* ? *japonica* Eguchi, n. sp. – Eguchi: p. 37, pl. 11, fig. 6

Material: 1991 X 80; 2 thin sections.

Dimensions:
(1991 X 80)

	n	min–max	μ	σ	v	μ±σ
crd	5	3.02–4.45	3.44	0.61	17.8	2.82–4.04
s	20–24					
sd	4/1					

Description: Thamnasterioid colony with calices arranged in irregular rows. Calicular centres slightly depressed. Septa regularly perforated. Microstructure of large trabeculae. Septa in cross section equal in thickness in the whole septum. No septal symmetry. Half of all septa reach to the calicular centre. Septa occasionally connected to each other. Septal distal margin with large regular granules, lateral face with pennulae, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent, with thick granules on their surface. Synapticulae present, abundant, mainly in the space between calices. Columella poorly defined, probably substyliform. Endotheca consists of numerous large and thin tabulae. Wall absent. Budding intracalicinal, polystomodeal and complete.

Occurrence: Lower Hauterivian (Radiatus zone) of France (Aube) Troyes, Vallières (CC 131). Lower Upper Aptian of Spain (Cataluña, Lérida) Com. La Noguera, Mun. Vilanova de Meià, Montsec de Rubies, section NW La Cabrua quarry/4 (SNSB-BSPG 2003 XX 6317). Upper Aptian of Japan (Iwate-ken) Shimohei-gun, Tanohata-mura, Koikorobe. Lower Albian of Mexico (Sonora) Municipio Ures, Cerro de Oro (ERNO L-4906). Lower Cenomanian (Mantelli zone) of Germany (Nordrhein/Westfalen) Mülheim/Ruhr, Kassenberg (SNSB-BSPG 2003 XX 1089). Lower Cenomanian (Saxbii - Dixoni zone) of Germany (Sachsen) Meißen-Zscheila, Trinitatis church (ERNO L-6165).

Family Synastraeidae Alloiteau, 1952

Synastrea Milne Edwards & Haime, 1848
Synastrea sp.
Pl. 9, Fig. 1
Material: 1991 X 95, 1991 X 96; 1 thin section.

Dimensions:
(1991 X 95)

ccd	2.6–4.8
s	ca. 80
sd	6/2

Description: Thamnasterioid colony. Calicular centres slightly depressed. Septa perforated at their inner margin. Microstructure of large trabeculae. Septa in cross section externally thick, getting thinner towards the centre. Symmetry of septa irregular. Cycles of septa irregular, size orders can hardly be distinguished. Half of all septa reach to the calicular centre. Septa occasionally connected to each other close to the centre of the calice. Septal distal margin coarsely granulated, lateral face with pennulae and thorns, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent or sub-confluent. Synapticulae present, occasional, mainly in the space between calices. Columella consists of isolated trabeculae or one more solid element. Endotheca unknown. Wall absent. Budding extracalicinal.

Remarks: Only small juvenile colonies were available that did not allow much preparation.

Suborder Stylinina Alloiteau, 1952

Family Cyathophoridae Duncan, 1884

Cryptocoenia d'Orbigny, 1849

Cryptocoenia aguilerai (Reyeros Navarro, 1963)
Pl. 9, Figs 4–6

v	1963	*Cyathophora atempa* Felix 1891 – Reyeros Navarro: p. 8, pl. 4, figs 7, 8
*v	1963	*Procyathophora aguilerai* n.sp. – Reyeros Navarro: p. 8, pl. 3, figs 3, 5
v	1989	*Procyathophora aguilerai* Reyeros – Carreño et al.: p. 97, fig. 33k
v	1996	*Cyathophora steinmanni* Fritzsche, 1924 – Baron-Szabo & Steuber: p. 8, pl. 1, figs 5, 6
v	1997	*Cyathophora haysensis* Wells, 1932 – Baron-Szabo: p. 39, pl. 3, fig. 5
v	2010	*Cryptocoenia aguilerai* (Reyeros Navarro, 1963) – Löser et al.: p. 322, fig. 3.11
v	2013a	*Cryptocoenia aguilerai* (Reyeros Navarro, 1963) – Löser: p. 31, fig. 11a–c
v	2013	*Cryptocoenia aguilerai* (Reyeros Navarro, 1963) – Löser et al.: pl. 9, figs 8–9

Material: 1991 X 70; 2 thin sections.

Dimensions:

(1991 X 70)

	n	min–max	μ	σ	v	μ±σ
cl	10	1.83–3.17	2.76	0.36	13.0	2.40–3.12
ccd	15	3.47–4.58	3.89	0.32	8.2	3.56–4.21
s	24					

Description: Plocoid colony. Calicular outline circular. Septa compact. Symmetry of septa radial and regularly hexameral. Cycles of septa subregular. Septal cycles differ in length. Septa very short, free. Septal lateral face smooth, inner margin smooth. Pali or paliform lobes absent. Costae present, sub-confluent to non-confluent. Synapticulae absent. Columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, probably septothecal. Coenosteum medium broad, consists of costae and tabulae. Budding extracalicinal.

Occurrence: Upper Barremian to Lower Aptian (Sartousi-Weissi zone) of Germany (Bayern) Allgäuer Helvetikum, Brandalpe. Aptian of Spain (Cantabria, Santander) Punta des Calderon N Santillana del Mar (SNSB-BSPG 1967 I 109); Mexico (Puebla) San Juan Raya. Lower Aptian of Greece (Viotía) Arachova; Mexico (Puebla) San Juan Raya, Barranco Grande (ERNO L-R11723). Lower Albian (Tardefurcata zone) of Spain (Cataluña, Tarragona) Com. Baix Penedès, Mun. Masllorenç, Masarbones (SNSB-BSPG 2003 XX 6026). Spain (Cataluña, Tarragona) Com. Baix Penedés, Mun. Montmell, Marmellà, Can Xuec (SNSB-BSPG 2003 XX 6222). Lower to Middle Albian of Spain (Valencia, Alicante) Sierra de Seguili. Lower Albian, Mammillatum (Mammillatum zone) of France (Aude) Padern, SE Le Crès, 1.45 km WWS Padern. Lower Upper Albian (Inflatum zone) of Spain (Valencia, Alicante) Sierra de Llorençá. Upper Albian of UK (Devonshire) Exeter, Haldon Hill (NHM R05391). Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 5860).

Cryptocoenia bulgarica (Toula, 1884)
Pl. 9, Figs 2–3

*v	1884	*Astrocoenia bulgarica* nov. sp. – Toula: p. 1317, pl. 6, fig. 4
v	1889	*Cryptocoenia ramosa* nov. spec. – Toula: p. 83, pl. 5, figs 10, 11
v	1891	*Cyathophora atempa* – Felix: p. 155, pl. 25, figs 7, 8
v	1964	*Adelocoenia biedai* n.sp. – Morycowa: p. 26, text-fig. 2, pl. 4, fig. 2, pl. 5, fig. 5
	1993	*Pseudocoenia beskidena* Eliasova 1981 – Baron-Szabo: p. 155, text-fig. 3, pl. 2, fig. 1
v	1995	*Procyathophora biedai* (Morycowa 1964) – Löser & Raeder: p. 43
v	1996	*Pentacoenia elegantula* d'Orbigny, 1850 – Baron-Szabo & Steuber: p. 8, pl. 3, fig. 3
v	2004	*Adelocoenia desori* (Koby, 1897) – Löser & Mohanti: p. 580, figs 2ab
v	2010a	*Cryptocoenia bulgarica* (Toula, 1884) – Löser: p. 592, fig. 3.5
v	2010a	*Cryptocoenia ramosa* Toula, 1889 – Löser: p. 595, fig. 3.9
v	2013a	*Cryptocoenia bulgarica* (Toula, 1884) – Löser: p. 33, figs 11d–e

Material: 1947 XVI 48, 1955 XIX 28, 1991 X 71; 2 thin sections.

Dimensions:

(1947 XVI 48)

	n	min–max	μ	σ	cv	μ±σ
cl	15	1.38–1.86	1.63	0.15	9.0	1.48–1.77
ccd	15	1.9–2.84	2.25	0.3	13.4	1.94–2.55
s	24					

Description: Plocoid colony. Calicular outline circular. Septa compact. Symmetry of septa radial and regularly hexameral. Cycles of septa subregular. Septal cycles differ slightly in length. Septa very short, reduced to ridges, free. Septal lateral face unknown, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent or sub-confluent, surface unknown. Synapticulae absent. Columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, probably para-thecal. Coenosteum narrow, consists of costae and tabulae. Budding extracalicinal.

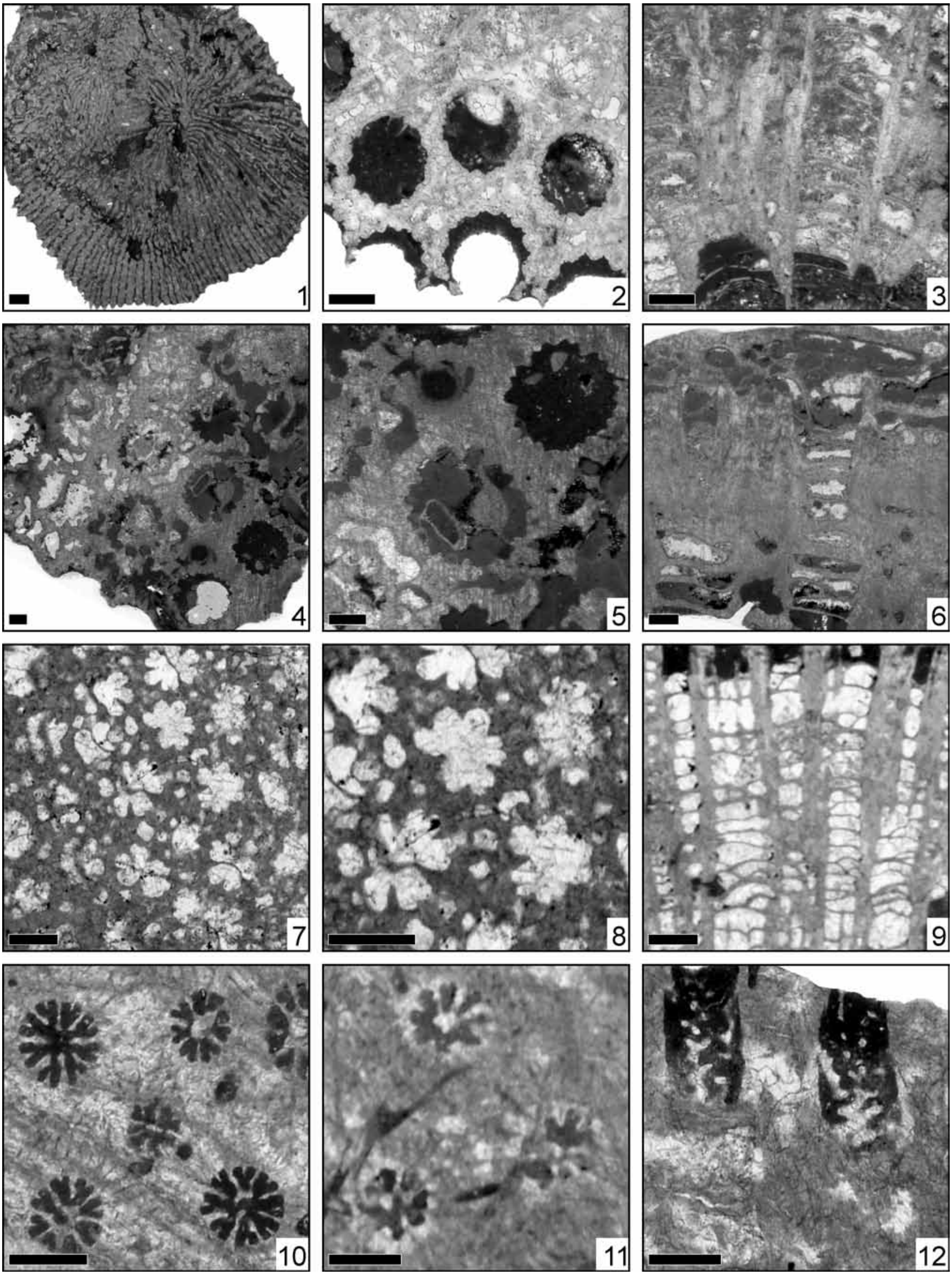


Plate 9: (1) *Synastrea* sp., 1991 X 95, transversal thin section. **(2–3)** *Cryptocoenia bulgarica* (Toula, 1884), 1947 XVI 48. 2: transversal thin section. 3: longitudinal thin section. **(4–6)** *Cryptocoenia aguilerai* (Reyeros Navarro, 1963), 1991 X 70. 4: transversal thin section. 5: transversal thin section, detail. 6: longitudinal thin section. **(7–9)** *Cryptocoenia fontserei* (Bataller, 1947), 1991 X 43. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. **(10)** *Stylina inwaldensis* (Ogilvie, 1897), 1947 XVI 42, transversal thin section. **(11–12)** *Stylina inwaldensis* (Ogilvie, 1897), 1947 XVI 35. 11: transversal thin section. 12: longitudinal thin section. Scale bar = 1mm.

Occurrence: Barremian of Mexico (Puebla) Tehuacán, San Antonio Texcala. Barremian (Moutoniceras - Giraudi zone) of France (Drôme) Serre de Bleyton. Upper Barremian of Poland (Malopolskie, Tarnów) Tarnów, Trzemesna. Lower Aptian of Greece (Viotía) Arachova; Mexico (Michoacán) Turitzio, Loma de San Juan (ERNO L-4879); Serbia (East Serbia) Pirot. Upper Aptian to Middle Albian of USA (Texas) Comal County, North side Canyon Lake. Uppermost Aptian to Lower Albian of Spain (Vascongadas, Vizcaya) Gamecho, Playa de Laga. Lower Albian of Mexico (Sonora) Municipio Arizpe, Arizpe, Cerro La Ceja (ERNO L-4267); Municipio Cucurpe, Cucurpe, La Mesa (ERNO L-4829); Municipio Opodepe, Tuape, Cerro de la Espina (ERNO 2201). Lower Albian (Mammillatum zone) of France (Aude) Padern, SE Le Crès, 1.45 km WWS Padern. Middle Albian of Greece (Viotía) Aliartos, Korónia. Upper Albian of UK (Devonshire) Exeter, Haldon Hill (NHM R23570). Cenomanian of Greece (Fokída) Kiona massif, Panourgias (ERNO L-5904); India (Tamil Nadu [= Madras]) Kunnam. Lower Cenomanian of Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 5855). Upper Cenomanian (Guerangeri zone) of Czech Republic (Central Bohemian region) Korycany, Netreba (CGS HF 1481).

Cryptocoenia fontserei (Bataller, 1947)
Pl. 9, Figs 7–9

*v 1947	*Cyathophora Fontserei* Bataller 1944 – Bataller: p. 48, text-fig.
1949	*Cyathophora Fontserei* Bataller 1944 – Bataller: p. 15, 25, text-fig.
v 1974	*Cyathophora pygmaea* Volz – Turnšek & Buser: p. 12, 33, pl. 4, fig. 1
v 1994	*Adelocoenia pygmaea* (Volz 1903) – Löser: p. 10, text-figs 4, 5, pl. 12, figs 1, 2

Material: 1947 XVI 12, 1947 XVI 20, 1947 XVI 23, 1947 XVI 49, 1947 XVI 6, 1955 XIX 27, 1955 XIX 29, 1991 X 43; 2 thin sections.

Dimensions:
(1991 X 43)

	n	min–max	μ	σ	v	μ±σ
cl	30	0.81–1.23	1.03	0.13	12.9	0.89–1.16
ccd	30	0.91–1.57	1.24	0.17	14.1	1.06–1.41
s	6–12					

Description: Plocoid colony. Calicular outline irregular circular. Septa compact. Symmetry of septa radial and regularly hexameral. Cycles of septa subregular; the second cycle is in places not developed. Septal cycles differ in length and thickness. Septa short, free. Septal lateral face smooth, inner margin smooth. Pali or paliform lobes absent. Costae present, confluent or sub-confluent. Synapticulae absent. Columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall present, compact, paraseptothecal. Coenosteum narrow, consists of costae and thick tabulae. Budding extracalicinal.

Occurrence: Lower Aptian of Spain (Vascongadas, Vizcaya) Bilbao, Mina Abandonada; Slovenia (West Slovenia) Banskja Planota, Osojnica. Lower Cenomanian (Mantelli zone) of Germany (Nordrhein/Westfalen) Mülheim/Ruhr, Kassenberg. Lower Cenomanian of France (Charente-Maritime) Fouras (ERNO L-5593). Middle Cenomanian (Mantelli-Rhotomagense zone) of Belgium (Hainaut) Tournai (IRScNB I. G. 6852).

Family Stylinidae d'Orbigny, 1851

Stylina de Lamarck, 1816

Stylina inwaldensis (Ogilvie, 1897)
Pl. 9, Figs 10–12

*v 1897	*Diplocoenia inwaldensis* – Ogilvie: p. 165, pl. 18, figs 7–8
v 1897	*Heliocoenia dendroidea* Etallon, 1859 – Ogilvie: pl. 17, fig. 10
v 1897	*Stylina foliosa* – Ogilvie: p. 170, pl. 16, fig. 15
v 1897	*Stylina milleporacea* – Ogilvie: p. 173, pl. 17, fig. 8
v 1944	*Stylina sucrensis* Wells, n.sp. – Wells: p. 435, pl. 70, fig. 1
v non 1955	*Diplocoenia inwaldensis* Ogilvie – Geyer: p. 195
v 1971	*Stylina parvistella* Volz, 1903 – Morycowa: p. 45, pl. 7, fig. 1
1981	*Stylina parvistella* Volz 1903 – Turnšek & Mihajlovic: p. 14, pl. 8, figs 1–3
2002	*Stylina elegans* Eichwald, 1865 – Kuzmicheva: p. 173, pl. 25, fig. 5
v 2005	*Stylina parvistella* Volz, 1903 – Götz et al.: p. 874, fig. 8A
v 2013b	*Stylina inwaldensis* (Ogilvie, 1897) – Löser: p. 22, fig. 3.11
v 2013	*Stylina inwaldensis* (Ogilvie, 1897) – Löser et al.: figs 4g–i

Material: 1947 XVI 35, 1947 XVI 42, 1991 X 44, 1991 X 45, 1991 X 46, 2010 VI 1; 8 thin sections.

Dimensions:
(1947 XVI 35)

	n	min–max	μ	σ	v	μ±σ
cl	15	0.73–1.08	0.88	0.11	12.1	0.77–0.98
ccd	20	1.6–2.72	2.19	0.37	17.0	1.81–2.56
s	8–16					

(1947 XVI 42)

	n	min–max	μ	σ	cv	μ±σ
cl	10	0.77–1.02	0.93	0.08	8.4	0.85–1.01
ccd	15	1.23–1.97	1.66	0.22	13.3	1.43–1.88
s	16					

Description: Plocoid colony. Calicular outline circular to elliptical. Septa in cross section externally thick, then equal in thickness, first cycle unproportionally thicker than the second cycle. Symmetry of septa radial and regularly octameral. Cycles of septa regular. Septal cycles differ in length and thickness. First septal cycle reaches 35% of the calicular diameter, second cycle is shorter. Septa free, but can be connected to the columella. Septal distal margin unknown, lateral face occasionally with granulae, inner margin with auriculae. Pali or paliform lobes absent. Costae present, non-confluent. Synapticulae absent. Columella styliform. Endotheca consists of thin tabulae. Wall present, compact, probably parathecal. Coenosteum broad. Constitution of the coenosteum unknown. Budding extracalicinal.

Remarks: The material represents the latest indication of the genus *Stylina* and of the family Stylinidae presently known.

Occurrence: Tithonian of Czech Republic (?) Stramberg, Koniakau; Stramberk. Hauterivian of Spain (Valencia, Castellón) La Avellà, Catí. Lower Hauterivian (Radiatus zone) of France (Yonne) Fontenoy; Gy-l'Evêque; Leugny. Lower Hauterivian of Ukraine (Krymskaya) Bakhchisarajskij district, Bodrak river, Trudolyubovka. Lower Aptian of Mexico (Puebla) Tehuacán, Atecoxco, La Compañía; Serbia (East Serbia) Zljebine; Venezuela (Sucre) Cumaná, Las Cinco Ceibas. Lower Aptian (Lenticularis zone) of Romania (Suceava) Pojorîta area, Cîmpulung-Moldovenesc, Valea Seaca. Lower Cenomanian (Dixoni zone) of Spain (Cantabria, Santander) Cobreces, Luaña playa (SNSB-BSPG 2007 V 185).

Suborder Coenothecalia Bourne, 1895

Family Helioporidae Moseley, 1876

Polytremacis d'Orbigny, 1849

Polytremacis bofilli (Bataller, 1936)
Pl. 10, Figs 1–3

*v 1936 *Polytremacis Bofilli* Bataller – Bataller: p. 46, pl. 3, fig. 48

Material: 1947 XVI 14, 1947 XVI 25, 1947 XVI 50, 1991 X 40, 1991 X 61; 2 thin sections.

Dimensions:
(1947 XVI 14)

	n	min–max	μ	σ	v	μ±σ
cl	17	1.25–1.71	1.46	0.13	9.0	1.32–1.59
ccd	30	1.78–3.86	2.9	0.45	15.3	2.45–3.34
s	30–32					

Description: Plocoid colony. Calicular outline circular, calicular pit depressed. Septal spines in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septal spines irregular, size orders cannot be distinguished. The septal spines are short and reaches maximum 10% of the calicular diameter, most being shorter. Endotheca consists of numerous thin tabulae. Wall compact. Coenosteum broad, consists of tubes. Budding extracalicinal.

Remarks: The present material has a slightly higher number of septa than the type of *Polytremacis bofilli*.

Occurrence: Lower Santonian of France (Var) Le Beausset (MNHN nn). Lower Upper Campanian of Spain (Cataluña, Lérida) Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur, Torallola.

Polytremacis ramosa (d'Orbigny, 1850)
Pl. 10, Figs 4–6

*v 1850 *Dactylacis ramosa* – Orbigny, (2): p. 183
v 1898 *Polytremacis urgonensis* – Koby: p. 87, pl. 21, fig. 5
v 1932 *Epiphaxum labyrinthicum* Wells, n.sp. – Wells: p. 254, pl. 37, fig. 8

Material: 1947 XVI 40, 1947 XVI 41, 1947 XVI 7, 1991 X 62; 2 thin sections.

Dimensions:
(1947 XVI 7)

	n	min–max	μ	s	v	μ±s
cl	25	0.5–0.82	0.66	0.08	12.2	0.57–0.74
ccd	25	0.99–1.55	1.21	0.16	13.2	1.05–1.37
s	16–18					

Description: Plocoid colony. Calicular outline circular, calicular pit depressed. Septal spines in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septal spines irregular, but two size orders can be distinguished. Septal spine generations differ in length and thickness. First septal generation reaches 10% of the calicular diameter, those of the other generation are slightly shorter. Endotheca consists of numerous thin tabulae. Wall compact. Coenosteum broad, consists of tubes. Budding extracalicinal.

Remarks: The type material of *Polytremacis ramosa* encompasses small ramose growing specimens. The present material consists of small massive colonies, but growth form is given less importance.

Occurrence: Cretaceous of France (Yonne) Foix (MHNG 4450). Barremian of France (Doubs) Morteau. Aptian of Mexico (Puebla) San Juan Raya (IGM 9209). Lower Albian (Tardefurcata zone) of USA (Texas) Hays County, Blanco River, Pleasant Valley Crossing. Lower Albian of Mexico (Sonora) Municipio Opodepe, Tuape, Cerro de la Espina (ERNO L-4256); Municipio Ures, Cerro de Oro (ERNO L-4393). Cenomanian of France, Sicards (MNHN nn). Lower Cenomanian of France (Charente-Maritime) Ile d'Aix. Turonian to Santonian of France (Vaucluse) Orange, Piolenc (FSL 390797). Lower Coniacian of Spain (Cataluña, Lérida) Pallars Jussa, Congost d'Erinya/IF (SNSB-BSPG 2007 IV CEIF39).

Polytremacis vermiculata (Felix, 1903)
Pl. 10, Figs 7–9

*v 1903 *Aulopsammia vermiculata* nov. sp. – Felix: p. 358, pl. 22, fig. 9, text-fig. 67
non 1930 *Epiphaxum vermiculatum* Felix sp. – Oppenheim: p. 24, pl. 41, fig. 1, pl. 42, fig. 7

1982 *Epiphaxum vermiculata* (Felix) 1903 – Beauvais, (3): p. 27, pl. 61, figs 3, 4

v 2000 *Polytremacis blainvilleana* (Michelin, 1841) – Baron-Szabo: p. 128, pl. 13, figs 3, 4

Material: 1947 XVI 43, 1947 XVI 55; 2 thin sections.

Dimensions:

(1947 XVI 43)

	n	min–max	µ	σ	cv	µ±σ
cl	15	0.97–1.24	1.09	0.08	7.2	1.01–1.17
ccd	15	1.39–2.36	1.88	0.32	17.1	1.55–2.19
s	22–24					

Description: Plocoid colony. Calicular outline circular, calicular pit depressed. Septal spines in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septal spines irregular, but two size orders can be distinguished. Septal spine generations differ in length and thickness. First septal generation reaches 10% of the calicular diameter, those of the other generation are slightly shorter. Endotheca consists of numerous thin tabulae. Wall compact. Coenosteum broad, consists of tubes. Budding extracalicinal.

Remarks: The type of the species was available for study. It cannot be assigned to *Aulopsammia* (= *Epiphaxum*) because it is a massive, not reptoid coral with a well-developed coenosteum as in *Polytremacis*.

Occurrence: Lower Cenomanian of France (Charente-Maritime) Fouras (SNSB-BSPG 2003 XX 1708); France (Charente-Maritime) Rochefort (MNHN nn); Greece (Kozani) Kozani, Nea Nikopolis (SNSB-BSPG 2003 XX 5821). Upper Turonian of France (Vaucluse) Orange, Uchaux (GZG nn). Upper Santonian of Austria (Salzburg) Rußbach, Neffgraben. Lower Upper Campanian of Spain (Cataluña, Lérida) Com. Pallars Jussà, Mun. Pallars Jussà, Pobla de Segur, Torallola (MB K1196). Maastrichtian of Jamaica, probably Cambridge area (USNM #585f); United Arab Emirates (Al Ain) Al Madam, Buhays Mt.

Polytremacis sp.
Pl. 10, Figs 10–12

Material: 1947 XVI 63; 1 thin section.

Dimensions:

(1947 XVI 63)

	n	min–max	µ	σ	cv	µ±σ
ccd	20	0.67–1.09	0.85	0.12	14.9	0.72–0.98
cl min	20	0.29–0.47	0.38	0.05	14.0	0.33–0.44
s	7	10–17	13.71	2.56	18.6	11.2–16.3

Description: Plocoid colony. Calicular outline circular, calicular pit depressed. Septal spines in cross section externally slightly thicker, getting slightly thinner towards the centre. Symmetry of septal spines irregular. There are no size orders. Septal spines are very short. Endotheca consists of numerous thin tabulae. Wall compact. Coenosteum broad, consists of tubes. Budding extracalicinal.

Remarks: This specimen is similar to *Polytremacis ramosa* but differs by smaller calicular dimensions and fewer septal spines.

Table 3: List of coral species found in the study area.

Acrosmilia sp.
Actinastrea regularis (Fromentel, 1887)
Astraeofungia tenochi (Felix, 1891)
Aulosmilia ? *bipartita* (Reuss, 1854)
Aulosmilia ? *consobrina* (Reuss, 1854)
Aulosmilia ? *inconstans* (de Fromentel, 1862)
Ceratosmilia arnaudi Alloiteau, 1957
Columellophora cf. velimensis Eliášová, 1989
Columellophora sp.
Cryptocoenia aguilerai (Reyeros Navarro, 1963)
Cryptocoenia bulgarica (Toula, 1884)
Cryptocoenia fontserei (Bataller, 1947)
Dimorpharaea japonica Eguchi, 1951
Dimorphastrea regularis (de Fromentel, 1857)
"*Diploastrea*" *tanohataensis* (Eguchi, 1951)
"*Diploastrea*" sp.
Eothelia bavarica n.gen. n. sp.
Eothelia hoelzli n. gen. n. sp.
Felixigyra deangelisi Prever, 1909
Heterocoenia sp.
Hydnophora cf. *obliqua* Reig Oriol, 1992
Hydnophora sp.
Leptophyllaraea cf. *granulata* (Fromentel, 1863)
Microphyllia cf. *oldhamiana* (Stoliczka, 1873)
Negoporites cf. *quartus* Eliášová, 1995
Negoporites sp.
Neocoenia cf. *casterasi* (Alloiteau, 1957)
Neocoenia renzi (Hackemesser, 1936)
Pachygyra krameri Oppenheim, 1930
Paramontlivaltia ruvida (Prever, 1909)
Polytremacis bofilli (Bataller, 1936)
Polytremacis ramosa (Orbigny, 1850)
Polytremacis vermiculata (Felix, 1903)
Polytremacis sp.
Stelidioseris minima (de Fromentel, 1857)
Stylina inwaldiensis (Ogilvie, 1897)
Synastrea sp.
*Thalamocaeniopsis*sp.
Trochoseropsis ettalensis Söhle, 1897

5. Results

5.1 Species richness and faunal composition

The studied fauna of the Roßsteinalmen section does not show any indication of reworking of older sediments and can be regarded as autochthonous. However, it comes from different horizons that may represent slightly different ecological conditions and may explain the relatively high number of species (Tab. 3). Autochthonous Cretaceous coral faunas have on average between 20 and 30 species (see discussion in Löser & Minor 2007; Bover-Arnal et al. 2012). Although the species inventory is dominated by colonial forms (20 genera of colonial corals, five of solitary ones), the collection is dominated by solitary forms representing a total of about 80%. A sample bias can be excluded because recent collec-

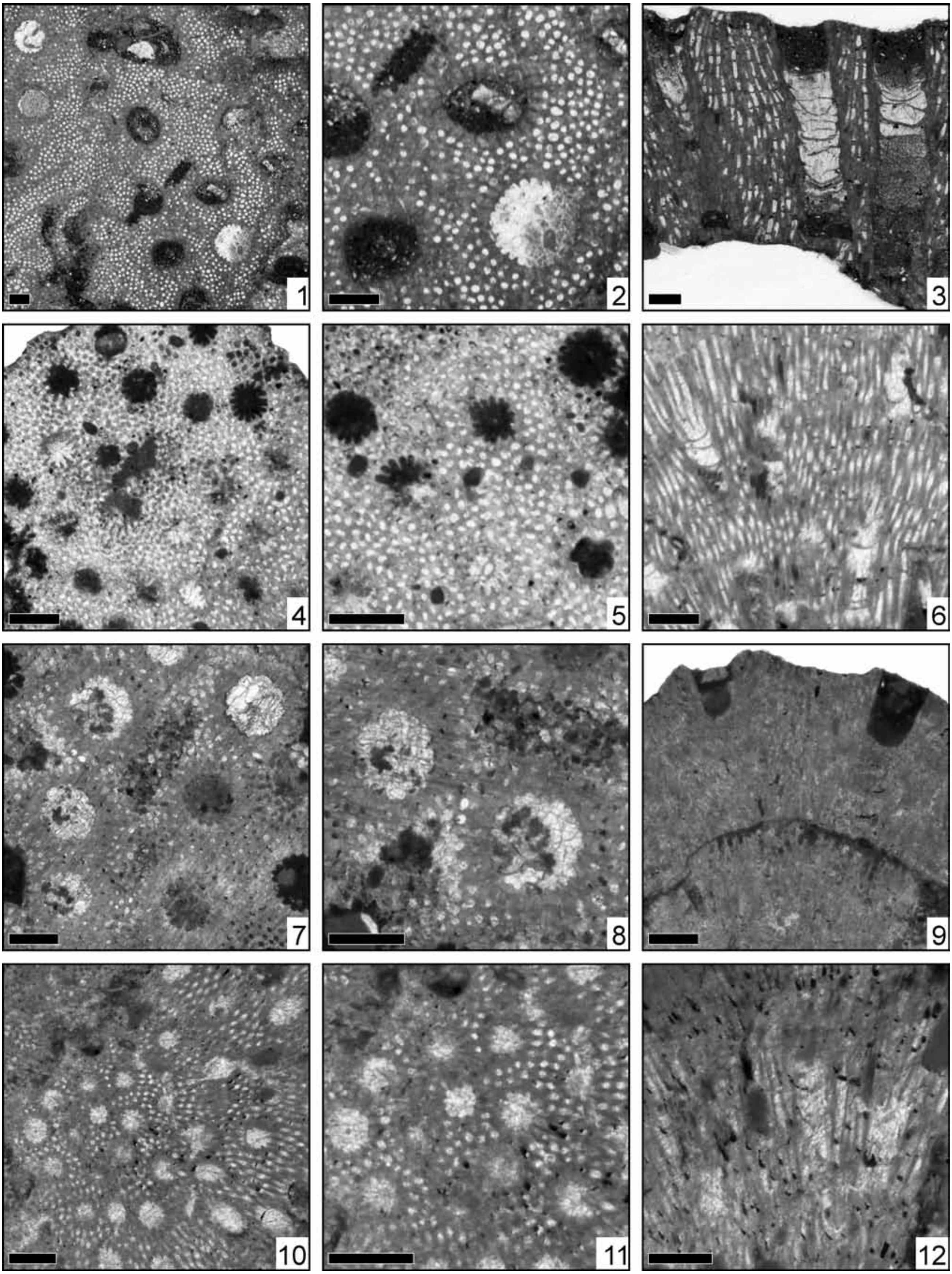
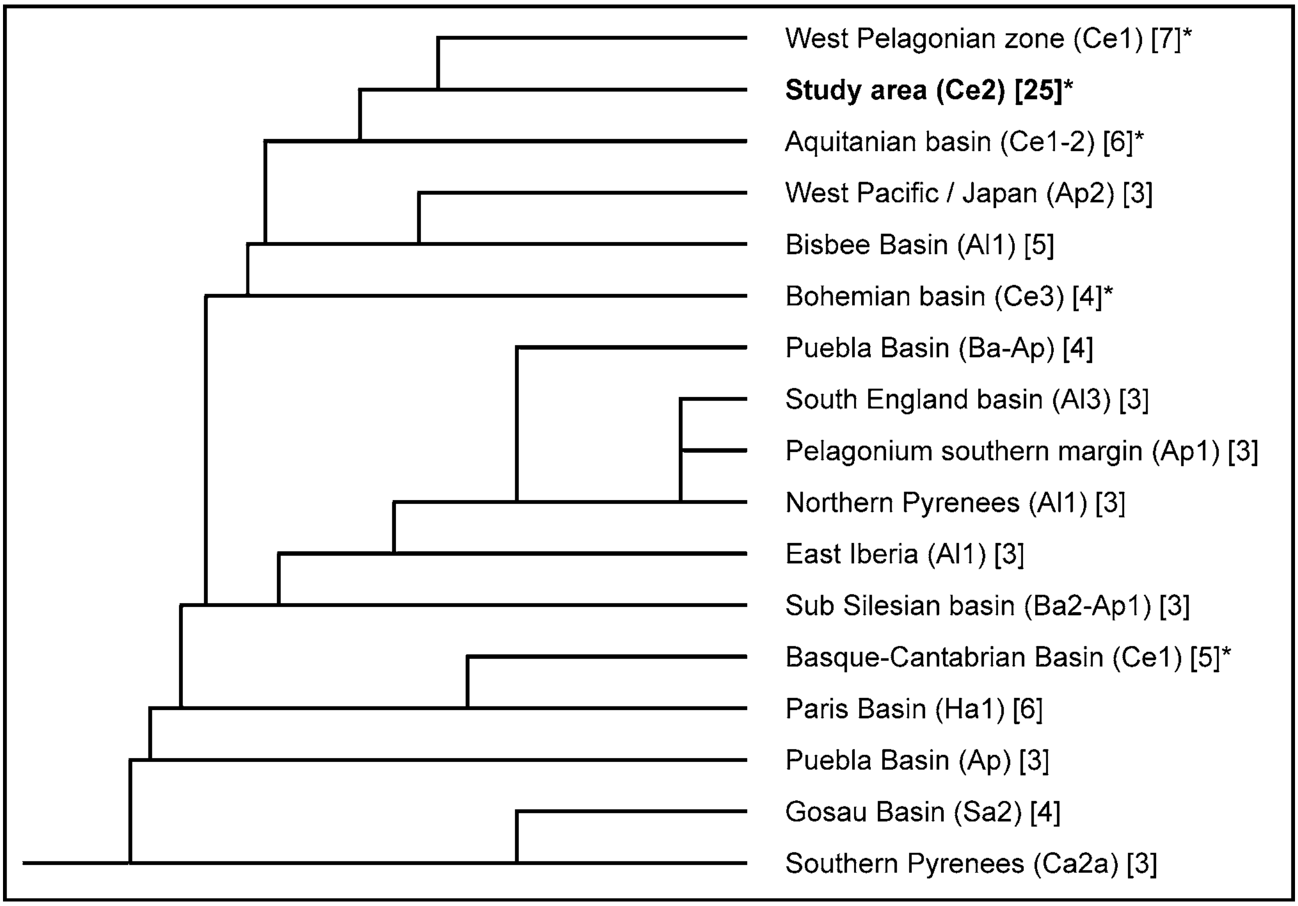


Plate 10: (1–3) *Polytremacis bofilli* (Bataller, 1936), 1947 XVI 14. 1: transversal thin section. 2: transversal thin section, detail. 3: longitudinal thin section. **(4–6)** *Polytremacis ramosa* (d'Orbigny, 1850), 1947 XVI 7. 4: transversal thin section. 5: transversal thin section, detail. 6: longitudinal thin section. **(7–9)** *Polytremacis vermiculata* (Felix, 1903), 1947 XVI 43. 7: transversal thin section. 8: transversal thin section, detail. 9: longitudinal thin section. **(10–12)** *Polytremacis* sp., 1947 XVI 63. 10: transversal thin section. 11: transversal thin section, detail. 12: longitudinal thin section. Scale bar = 1mm.

tion yielded almost only solitary corals and very few colonial corals. Although it is unknown whether the solitary corals lived in symbiosis with zooxantellate algae, it is assumed for the colonial corals (Löser et al. 2013). The small size of the coral colonies suggests unfavorable conditions with limited light being a possible explanation. There is also a certain indication for an influx of sediment; most colonial corals have very small calicular dimensions, which is taken as an indicator for sediment stress (Sanders & Baron-Szabo 2005). The type of sediment may also indicate a soft substrate that may have also inhibited coral growth (Thayer 1975). All those limiting factors had no influence on the diversity, as also shown in Löser (2010a) for Upper Barremian fauna.

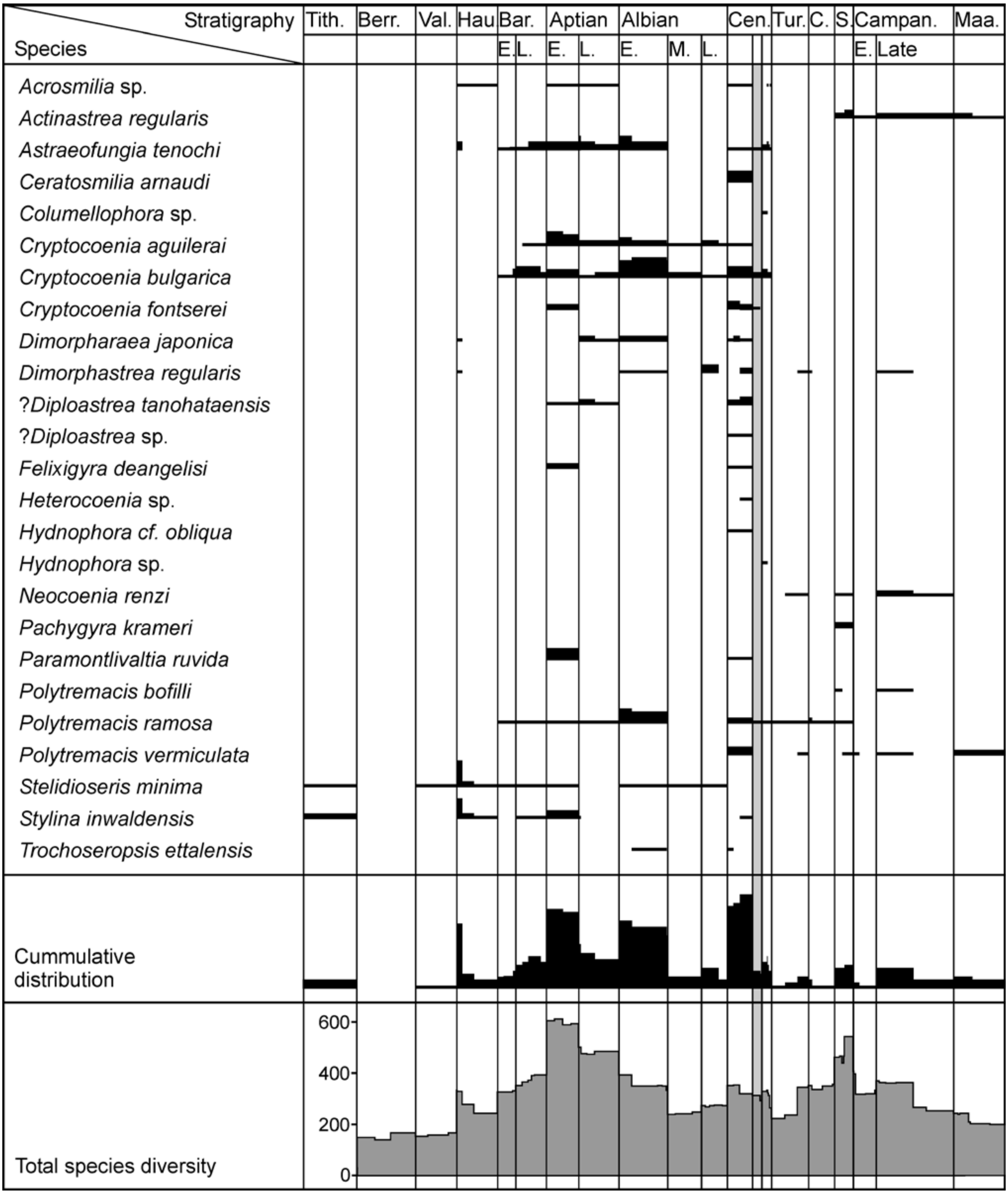
5.2 Species distribution

The studied fauna shows, at the species level, strong relationships to other Cenomanian faunas (Textfig. 4) in the Tethys as well as intermediate faunas between the Tethys and the Boreal (e.g. the Bohemian Basin). Relationships to Boreal faunas (in the sense of faunas north of the Rhenish/Bohemian massif) exist only with the South England Basin, but not with faunas from Northern France (e.g. Le Mans) or Germany (Westphalia, Saxony). This distribution pattern can only be explained by varying sea water temperatures. Boreal faunas have a different faunal inventory; many genera that are not rare in Tethyan faunas are absent in Cenomanian Boreal faunas (for the study area: *Actinastrea*, *Ceratosmilia*, *Columellophora*, "*Diploastrea*", *Felixigyra*, *Heterocoenia*, *Hydnophora*, *Leptophyllaraea*, *Neocoenia*, *Pachygyra*, *Stylina*, *Synastrea*). The Bohemian Basin is considered an area that is more related to Tethyan faunas, with genera such as *Columellophora*, or *Hydnophora*. The Bohemian and the Saxonian Basin also share genera that are endemic to both areas (*Colonicyathus*, *Glenarea*, *Latohelia*), and also share genera that are cosmopolitian (*Canleria*, *Confusaforma*, *Cryptocoenia*, *Eocomoseris*, *Negoporites*, *Placophora*, *Stelidioseris*, among others, mainly of the Leptophylliidae family). And of course there are also Cenomanian coral genera that are restricted to more equatorial areas, such as *Apocladophyllia*, *Aulastraeopora*, *Aspidiscus*, *Columastrea*, "*Diploastrea*", *Heterocoenia*, *Parnassomeandra*, *Rhipidomeandra*, *Stylina*, *Tiarasmilia* that were never found in Boreal or intermediate areas. Aulastraeoporids (suborder Rhipidogyrina), Heterocoeniids, and Stylinids are the most obvious groups that preferred lower latitudes. This type of temperature-dependent distribution pattern is not unknown from the Jurassic (for instance Carpentier et al. 2006) but poorly quantified for the Cretaceous.

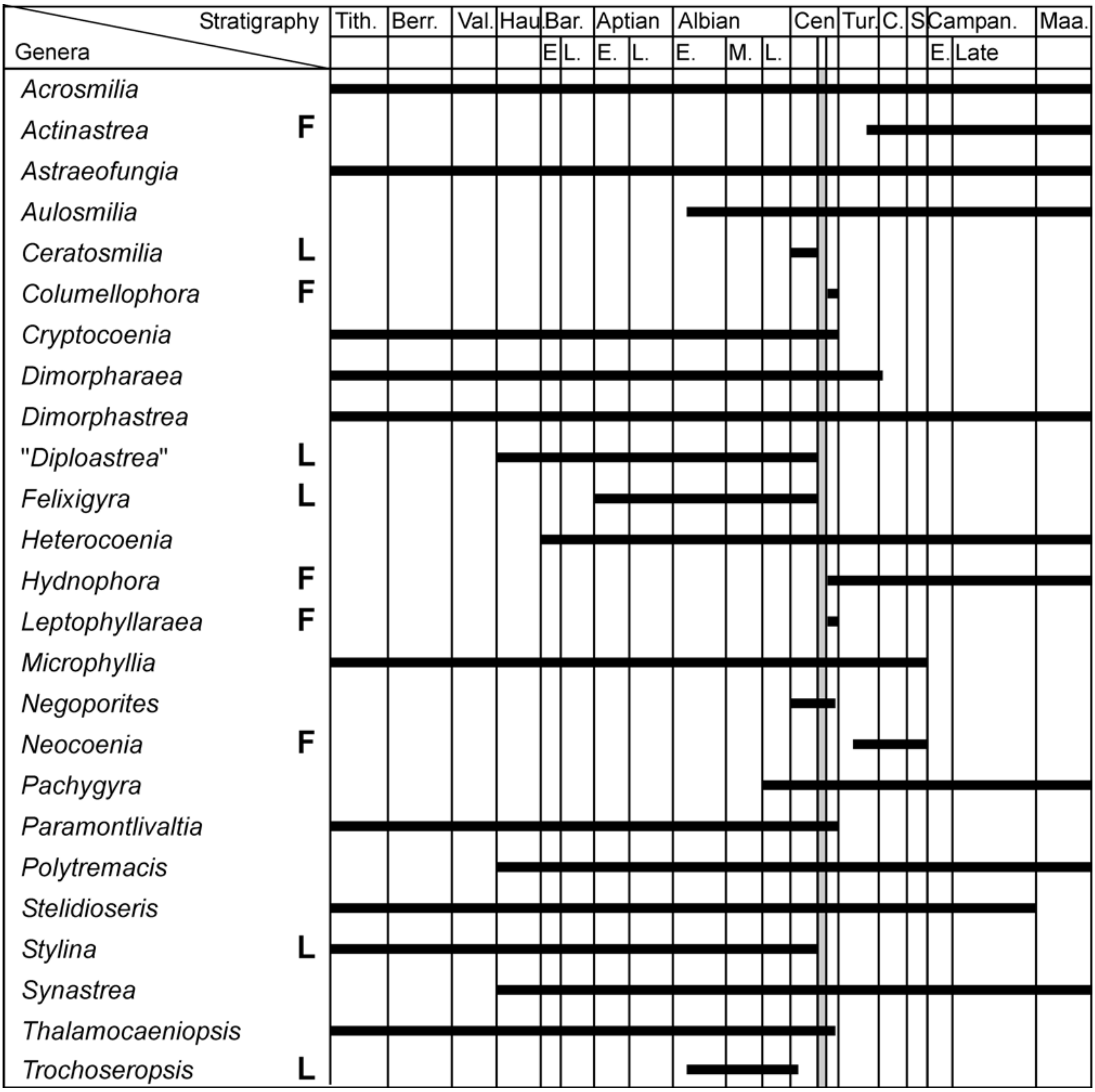


Textfigure 4: Correlation of provinces with joint species of the study area. Provinces with less than three joint species are omitted. The Correlation Ratio coefficient was applied. For details of calculation see Löser & Minor (2007). Provinces shown in Figures 1 are marked with an asterisk.

The ranges of the species of the present fauna (Textfig. 5) indicate stronger relationships to Early Cretaceous faunas than to faunas younger than Cenomanian. The species indicated in the study area have their most frequent occurrence in the Early Hauterivian, Early Aptian, Early Albian and Early Cenomanian. This pattern only partially coincides with global Cretaceous species diversity (Textfig. 5, bottom); the Early Albian and the Early Cenomanian show no diversity peaks. This indicates disproportionally higher relationship to Early Albian and Early Cenomanian faunas. Relationships to Late Cretaceous species coincide with the general diversity.



Textfigure 5: Stratigraphic distribution and commonness of species of the studied fauna. The thickness of the bars indicates the number of localities in which the species concerned was found until present. Grey bar indicates age level of the study area. Below, the distributions are summarized. In the bottom the total species diversity based on species ranges is given. Ranges based on Löser et al. (2002, 2005); localities with a range longer than 13.3ma are omitted from calculations, as well as localities with an uncertain stratigraphy.



Textfigure 6: Former stratigraphic distribution of genera of the studied fauna and new first (F) and last (L) occurrences from the present study (grey bar). Ranges according to Löser (2005) and unpublished data. Jurassic and Cenozoic not shown because of uncertainties about the ranges.

5.3 Generic distribution

Seven suborders out of ten (or eleven if the suborder Poritina is accepted) occurring in the Cretaceous (Löser 2009) are indicated in the study area, which is a normal value for Aptian to Cenomanian faunas (see Löser 2013a for comparison). Only the suborders Caryophylliina, Amphiastraeina, and Rhipidogyrina are absent. The suborder Amphiastraeina was very probably already extinct in the Middle Cenomanian; its latest indication presently known is from the Late Albian (Löser et al. in press). The suborder Rhipidogyrina was almost extinct; *Aulastraeopora* and *Apoplacophyllia* have their last occurrence during the Early Cenomanian, and only *Preverastraea* persisted (as its junior synonym *Saxuligyra*) into the Late Cenomanian. *Actinacis*, the only Poritid genus that occurs before the Turonian, is known from the Late Albian on, but is absent in the study area. Caryophylliid corals are probably absent due to ecological conditions; they are mostly found in much deeper environments.

The generic inventory (Textfig. 6) is a combination of Early and Late Cretaceous coral genera. Three abundant and important genera have their first occurrence in the studied fauna: *Actinastrea*, *Hydnophora* and *Neocoenia*. *Actinastrea* is restricted to the Late Cretaceous (Löser 2012a) and reached at least into the Maastrichtian. *Hydnophora* is an extant coral genus. Similiar material from the Early Cretaceous (e.g. *Eohydnophora*, see Löser 2010b) differs by a tabular endotheca and the strict absence of a columella. *Neocoenia* is a poorly documented genus that was just recently revised (Löser 2011). Three genera have their last occurrence in the fauna: *Felixigyra*, *Stylina* and the so-called "*Diploastrea*". *Felixigyra* (see Löser 2010b) is a rather rare genus that until now was only known from the Early Aptian, Early Albian and Early Cenomanian. *Stylina* probably occurs from the Middle Jurassic on and had its highest diversity during the Late Jurassic. Cretaceous material so far assigned to the extant coral genus *Diploastrea* cannot remain in this genus because it differs mainly by its septal microstructure. These Cretaceous "*Diploastrea*" species have been documented from the Hauterivian to the Early Albian.

There are more genera that have their first occurrence or last occurrence in the study area, but they are rare and therefore their distribution patterns are not well known. The last occurrence is also indicated for *Ceratosmilia* and *Trochoseropsis*; the first occurrence for *Columellophora* and *Leptophyllaraea*.

6. Discussion

Geologic stages are traditionally defined primarily using observations of changes in the lithology of marine sediments. The very long Albian stage (13.3 ma; Hardenbol et al. 1998) with its uniform mainly fine clastic sediments is followed by the short Cenomanian stage (5.4 ma). Coral evolution during the Albian is poorly known due the rareness of faunas (Löser 2013a; Löser et al. in press), but initial studies mainly indicate a loss in generic diversity in hermatypic corals in the Middle Albian, but an increase in ahermatypic taxa (Löser et al. in press: fig. 1). Already during the Late Albian diversity of genera increased and this increase continued during the Early Cenomanian. On a global scale, the Middle Cenomanian was marked by a decrease of diversity, followed by a small increase during the Late Cenomanian and a strong decrease from the Juddi zone on. The diversity decrease during the Middle Cenomanian is very probably due to a global sea level fall and loss of colonization area, and therefore also an absence of data.

The details of coral evolution during the Albian and Cenomanian, and the relationships between Cenomanian and Turonian fauna are difficult to decipher for several reasons. First, hermatypic Albian coral faunas are rare (with the exception of Early Albian faunas that are present in the Western Atlantic). Second, only Boreal Cenomanian coral faunas are well studied, Tethyan faunas are poorly known or are in need of revision. Third, initial studies on Early Cenomanian coral faunas (Cobreces in Northern Spain, Wilmsen 1996; Kozani in Greece, Steuber & Löser 1997) show that Boreal and Tethyal faunas differ up to the family level as explained above. During the Cenomanian, a higher marine temperature shifted coral growth to the north compared to today. Corals were absent in equatorial areas and occurred in the Central Tethys from 10°N (Tunisia, Egypt) up to 40°N (Belgium, Germany). Almost no firmly dated localities with hermatypic corals are known from the Early and Middle Turonian, and Late Turonian coral faunas show a different composition than Cenomanian faunas, not only regarding the percentage of families and suborders constituting the faunas, but also their generic inventory. This mainly concerns families such as Actinacididae, Actinastraeidae, Agatheliidae, Columastraeidae, Phyllosmiliidae, Placocoeniidae, and Placosmiliidae.

The present fauna may contribute to the question of when these new genera, that seem to appear suddenly in the Late Turonian, really evolved. The present fauna has an intermediate position between the Early Cretaceous and the post-Cenomanian corals showing that the faunal turnover after the Cenomanian/Turonian boundary was not marked by the sudden appearance of new faunal elements. The disappearance of taxa (Aulastraeoporidae, Cyathophoridae, Eugyridae, Felixigyra group, Stylinidae) or their strong reduction in diversity (Microsolenidae, Montlivaltiidae, Plesiosmilia group) had already partly happened during the Middle Cenomanian. The present fauna exemplifies that the post-Cenomanian faunal change was not as abrupt as it appears and that many elements already existed but played a subordinated role in Cenomanian faunas.

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