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Biostratigraphy and sedimentary sequences of the Toarcian Hainberg section (Northwestern Harz foreland, Northern Germany)

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Abstract

A temporary outcrop in southern Lower Saxony permitted the sedimentological, geochemical and palaeontological investigation of a 40.8 m thick Toarcian section, from the top of the Amaltheenton Formation, through the Posidonienschiefer and Jurensismergel Formations, to lower parts of the Opalinuston Formation. Bed by bed collected ammonites and belemnites, bivalve associations, as well as data from neighbouring sections indicate a largely complete sequence of ammonite zones and subzones for the Lower Toarcian. A prominent stratigraphic gap at the Posidonienschiefer/Jurensismergel Formation boundary probably comprises the Semipolitum Subzone as well as the Variabilis and Thouarsense Zones. Above a condensed Dispansum Zone follows the higher Upper Toarcian with a presumably largely complete sequence of zones and subzones, although direct evidence for this is only sporadic. However, a thin condensed bed with stromatolite crusts is recognisable at the boundary Pseudoradiosa to Mactra/Aalensis Subzone. The Toarcian/Aalenian boundary can only be drawn on basis of belemnite finds at another thin condensed bed. Only a few metres above, the Opalinum Zone is evident by ammonite findings.

Based on discontinuities, lithofacies, biofacies and correlations with neighbouring sections, a subdivision into alloformations, which largely correspond to formations, is applied. Based on that, a sequence stratigraphic interpretation with respect to third order transgression-regression cycles (T-R sequences) can be inferred: Above the regressive upper parts alloformation 1 (Amaltheenton Formation) with a maximum regression surface (mrs) near its top, the T-R sequence of the alloformation 2 (Posidonienschiefer Formation) is developed, with a maximum flooding surface (mfs) at the transition Falciferum/Commune Subzone and the regressive phase within the later Bifrons Zone. For the Commune Subzone, belemnite alignment indicates a seawater bottom current from SSE. The following maximum regression surface (mrs) lies near the Bifrons/Variabilis Zone boundary. The next sequence is not preserved at the studied location, but is preserved further East as well as further West, represented by the transgressive Dörnten Member (Variabilis and Thouarsense Zone). However, the regressive phase (Fallaciosum Subzone) is also missing there, indicated by a prominent sequence boundary with erosional relief at the base of the Dispansum Zone. The following alloformation 3 (Jurensismergel Formation and lowermost parts Opalinuston Formation) represents another T-R sequence with a maximum transgressive surface (base Mactra/Aalensis subzone) and a slightly thicker regressive Aalensis Subzone. The following maximum regression surface represents the boundary to alloformation 4 (major parts of Opalinuston Formation), followed again by a short transgressive phase (Pseudolotharingicum Subzone), condensation horizon and a longer regressive phase (Opalinum Zone).

These sequence stratigraphic interpretations are largely consistent with previous investigations in Northern and Southern Germany. Minor deviations in the timely position of maximum flooding and regression surfaces likely reflect effects of a higher subsidence at variable sedimentation rate in the North German Basin. With respect to the, at the site of investigation, incompletely exposed Opalinuston Formation, further studies on complete drill core sections are required.

Kurzfassung

Ein temporärer Aufschluss im südlichen Niedersachsen ermöglichte die sedimentologische, geochemische und paläontologische Untersuchung eines 40.8 m mächtigen Toarcium-Profils, vom Top der Amaltheenton-, über die Posidonienschiefer- und Jurensismergel-, bis zum tieferen Teil der Opalinuston-Formation. Horizontierte Ammoniten- und Belemnitenfunde, Bivalvenassoziationen, sowie Daten aus benachbarten Profilen lassen für das Untere Toarcium eine weitgehend vollständige Abfolge von Ammoniten-Zonen und -Subzonen erkennen. Eine markante Schichtlücke an der Posidonienschiefer/Jurensismergel-Formationsgrenze umfasst wahrscheinlich die Semipolitum-Subzone sowie die Variabilis- und Thouarsense-Zone. Über einer kondensierten Dispansum-Zone folgt das höhere Ober-Toarcium mit einer vermutlich weitgehend vollständigen, allerdings nur punktuell direkt belegbaren, Zonen- und Subzonen-Abfolge. Eine dünne, stromatolithführende Kondensationslage ist nur für den Grenzbereich Pseudoradiosa- zu Mactra/Aalensis-Subzone erkennbar. Die Grenze Toarcium/Aalenium kann nur mittels Belemnitenfunden an einer weiteren dünnen Kondensationlage festgelegt werden. Erst wenige Meter darüber kann die Opalinum-Zone mittels schlecht erhaltener Ammoniten wahrscheinlich gemacht werden.

Auf Grundlage von Diskontinuitäten, Lithofazies, Biofazies und Korrelationen mit Nachbarprofilen wird eine Unterteilung in Alloformationen, welche weitgehend den Formationen entsprechen, durchgeführt. Darauf aufbauend kann eine sequenzstratigraphische Interpretation bezüglich Transgressions-Regressions-Zyklen (T-R-Sequenzen) dritter Ordnung abgeleitet werden: Über dem regressiven höheren Teil der Alloformation 1 (Amaltheenton-Formation) mit einer maximalen Regressionsfläche (mrs) nahe seinem Top ist die T-R-Sequenz der Alloformation 2 (Posidonienschiefer Formation) entwickelt, mit einer maximalen Überflutungsfläche (mfs) am Übergang Falciferum/Commune-Subzone und nachfolgender regressiver Phase innerhalb der höheren Bifrons-Zone. Für die Commune-Subzone belegen eingeregelte Belemniten eine grundberührende Strömung aus südsüdwestlicher Richtung. Die nachfolgende maximale Regressionsfläche (mrs) liegt im Bereich der Bifrons/Variabilis-Zonengrenze. Die nächste Sequenz ist am untersuchten Profil nicht überliefert. Sie ist dagegen weiter östlich wie auch weiter westlich mit der transgressiven Dörnten-Subformation (Variabilis- und Thouarsense-Zone) erhalten geblieben. Die regressive Phase (Fallaciosum-Subzone) fehlt allerdings auch dort, angezeigt durch eine markante Sequenzgrenze mit Erosionsrelief an der Basis der Dispansum-Zone. Die Alloformation 3 (Jurensismergel- und tiefste Teile der Opalinuston-Formation) repräsentiert eine weitere T-R-Sequenz mit maximaler Überflutungsfläche (Basis Mactra/Aalensis-Subzone) und einer etwas längeren regressive Phase (Aalensis-Subzone). Die folgende maximale Regressionsfläche stellt die Grenze zur Alloformation 4 (Hauptteil der Opalinuston-Formation) dar, nachfolgend wieder mit kürzerer transgressiver Phase (Pseudolotharingicum-Subzone), Kondensationshorizont und längerer regressiver Phase (Opalinum-Zone).

Diese sequenzstratigraphischen Interpretationen stehen weitgehend in Einklang mit bisherigen Untersuchungen aus Nord- und Süddeutschland. Marginale zeitliche Abweichungen von maximalen Transgressions- oder Regressionsflächen spiegeln wahrscheinlich Effekte durch höhere Subsidenz bei variablen Sedimentationsraten im norddeutschen Becken wider. Für die am Untersuchungsort nur lückenhaft aufgeschlossene Opalinuston-Formation bedarf es weiterer Untersuchungen an vollständigen Kernprofilen.

Keywords

Ammonoidea, Jurensismergel Formation, Lower Jurassic, Northern Germany, Posidonienschiefer Formation, sealevel changes, stratigraphy

Schlüsselwörter

Ammonoidea, Jurensismergel-Formation, Meeresspiegel-Schwankungen, Norddeutschland, Posidonienschiefer-Formation, Stratigraphie, Unterer Jura

Introduction

The Lower Toarcian Posidonienschiefer Formation is considered as a fossil example of a climate change from cooler conditions with traces of glaciation to a greenhouse climate with increased temperatures, restricted ocean circulation, and oxygenation on shelf areas (i.e. the Toarcian Oceanic Anoxic Event T-OAE), with a consecutive extinction event (Jenkyns 1988; Palfy and Smith 2000; Dera and Donnadieu 2012; Ruebsam and Schwark 2021). For a further understanding of the T-OAE, the documentation of many individual Posidonienschiefer Fm. sections and, based on that, the reconstruction of palaeogeography, sea level fluctuations and seawater current pattern are of fundamental importance. In turn, for the understanding of the recovery phase and stepwise vanishing of anoxic seafloor conditions after the T-OAE, the investigation of the subsequent Jurensismergel Formation is required.

Contrary to Southern Germany (e.g., Dotternhausen: Riegraf 1985; Röhl et al. 2001; Frimmel et al. 2004; Röhl and Schmid-Röhl 2005; Maisch 2021) the knowledge on biostratigraphy and sedimentary sequences of the Posidonienschiefer Formation in Northern Germany is still incomplete, despite the fact that the type locality of the formation (Hildesheim; Roemer 1836) is in this region (Fig. 1). However, much progress was achieved by the sequence stratigraphic investigations of drill cores in Northern Germany by Zimmermann et al. (2015).

Overview sections of the Toarcian of the investigation area (Fig. 1) have already been published in the classical works of Denckmann (1887, 1892), who demonstrated the principal lithological succession of the Posidonienschiefer Formation including the "Dörntener Schiefer", as well as the distinct erosive discontinuity at the contact to the following Jurensismergel Formation. Based on numerous exploration drillings, later researchers focussed on the organic geochemistry and source rock properties of the Posidonienschiefer Formation but also on palaeogeography and facies distribution (Dorn 1936; Brockamp 1944; Hoffmann 1968a; Schmitz 1968). Ammonite biostratigraphy of the lower and middle Posidonienschiefer Formation is discussed in Denckmann (1892), Hoffmann and Martin (1960), Hoffmann (1968a, b) and Weitschat (1973). Remarkable is the fragmentary documentation of the Toarcian section in the famous open pit mine Haverlahwiese, with scattered information in Hiltermann et al. (1960), Lehmann (1966), Schmitz (1968), Hoffmann (1968a), and Weitschat (1973). However, one of the few sedimentologically and palynologically well documented sections is that of Hildesheim-Itzum by Maul (1984), Riegel et al. (1986) and Loh et al. (1986), who also provided a palaeoenvironmental model for the Posidonienschiefer Formation of this region. Likewise well documented is the Posidonienschiefer Fm. of the Braunschweig area (e.g. Wunnenberg 1928, 1950; Brockamp 1944), especially due to a new drill core at Schandelah (van de Schootbrugge et al. 2019; Visetin et al. 2022).

With respect to the Upper Toarcian Jurensismergel Formation, early lithologic and biostratigraphic descriptions of sections are available in Ernst (1923–1924), Heidorn (1928) and Althoff (1936), summarized in Kumm et al. (1941). The commonly discontinuous sections with condensation and highly fluctuating thicknesses as well as the differently handled boundary to the Opalinuston Formation (partly resulting from a poor outcrop conditions) do not yet reveal any conclusive thickness and facies distribution patterns. Furthermore, section correlations are hampered by changing opinions on the identity of biostratigraphically important ammonites, especially with respect to the Toarcian-Aalenian boundary (e.g., *Pleydellia buckmani* Maubeuge and *Leioceras opalinum* (Reinecke)).

In 1975 and 1976, an exploration project of the Lower Saxony State Office for Soil Research (NLfB) on bituminous shales provided a number of drill cores, documented in unpublished short reports (Ringelheim 1–9, Hildesheim 1–4). Unfortunately these drillings have only been superficially investigated. Likewise, only short reports of iron ore exploration drillings of the Salzgitter AG 1938–1939 are available („Hainberg" 1 to 7, „Küchenhai" 1 and 2). In any case, the new sequence stratigraphic interpretation of the Lower Jurassic succession in Northern Germany mentioned above (Zimmermann et al. 2015), based on numerous drillings of hydrocarbon companies, forms a valuable basis for the present work.

Construction work at the motorway A7 between Bockenem and the Salzgitter junction exposed in September 2011 a section from the top parts of the Amaltheenton (Upper Pliensbachian), through the Posidonienschiefer and Jurensismergel (Toarcian) to the Opalinuston Formations (uppermost Toarcian to Lower Aalenian) at the foothill of the Hainberg (Fig. 1).

The aim of the study is to document the sedimentary succession and biostratigraphy of this almost continuous section of the Toarcian at a classical location (i.e., Hainberg; Denckmann 1892) in Northern Germany and to discuss its implications for sealevel changes and palaeogeography.

Location and geological overview

The investigated section "Hainberg" is a motorway cutting located in Northern Germany, Lower Saxony, approximately 18 km ESE of Hildesheim (Fig. 1) at the motorway A7 (Hannover-Kassel) immediately south of the resting place "Sillium-Ost". The coordinates of the section, located on the topographic map 1:25000, sheet 3927 Ringelheim are 52°3.250781'N, 10°11.397949'E to 52°3.465281'N, 10°11.517376'E, at an elevation of ca. 150–155 m a.s.l. at the western foot of the "Hainberg". The exposure of the motorway cutting was about 350 m long, with up to 4 m height.

The Hainberg is situated in the northern foreland of the Harz Mountains at the southern margin of the North German Basin. The area is composed of gentle synclines and anticlines of Mesozoic sedimentary rocks, overlying Permian evaporites (Zechstein Group) and the Variscan basement of the deep subsurface (Fig. 1). The latter, at 2.0–2.3 km depth, is composed of folded Palaeozoic greywackes and shales, which are exposed further SE in the Harz Mountains. The Permian comprises minor continental siliciclastics (70–140 m Rotliegend Group) and a thick sequence of marine evaporites (600–1200 m Zechstein Group), which commonly form salt diapirs. The Mesozoic cover sequence starts with continental siliciclastics of

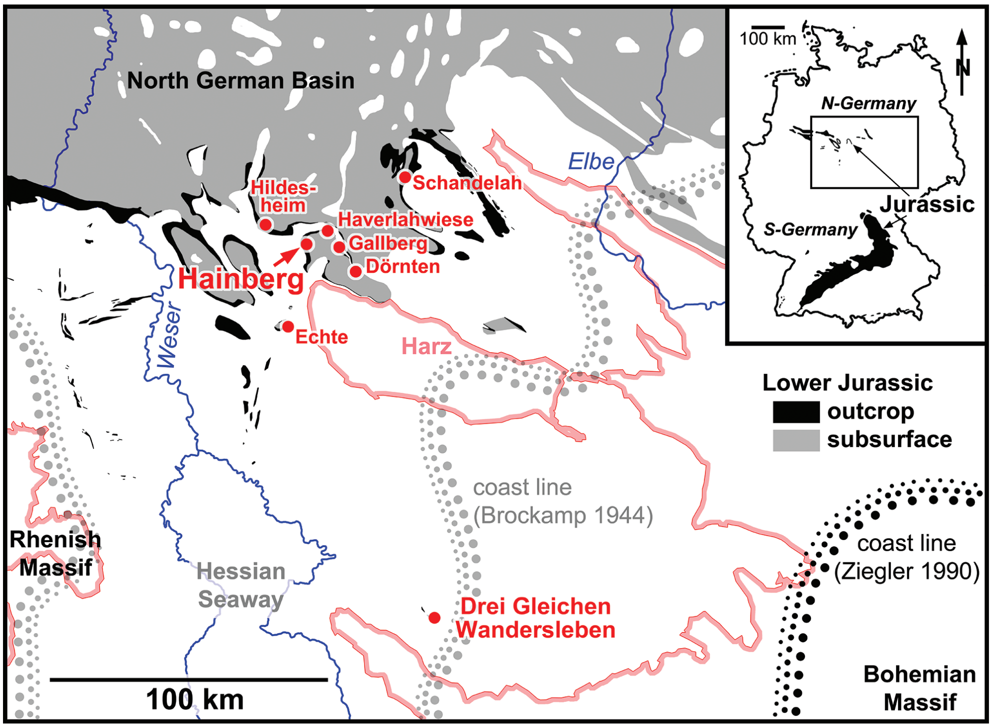


Figure 1. Geographic and geological overview with the location of the Hainberg section and further locations of Toarcian sections in Northern Germany. Outcrop and subsurface deposits of Lower Jurassic after Arnold et al. (1973), Duphorn et al. (1974), Motzka et al. (1979), Waldeck (1986), Kriebel et al. (1998), Motzka-Nöring (1998), Seidel et al. (1998), Radzinski et al. (1999), Knoth et al. (2000), Martiklos (2002), and Reinhold et al. (2008). Supposed former coastlines of the Toarcian after Brockamp (1944; outdated) and Ziegler (1990). Areas outlined in red are Variscan basement rocks, uplifted during the Cretaceous.

the Lower Triassic Buntsandstein Group (700–950 m), followed by marine carbonates of the Middle Triassic Muschelkalk Group (275–290 m) and again continental red beds of the Upper Triassic Keuper Group (ca. 350 m) (Schröder 1912; Dahlgrün 1939; Look et al. 1984, 1986; Jordan 1989).

At the western slope of the Hainberg, which is part of the Ringelheim Syncline, Lower Jurassic strata of the Schwarzjura Group (Franz et al. 2020) show a 300–350 m thick succession of dark calcareous claystones, with the 27–30 m thick Posidonienschiefer Fm. and a less than 1 m thick Jurensismergel Fm. at its top. Of the following Braunjura Group, up to 300 m dark marine claystones are preserved, cut at their top by an angular unconformity. Younger Jurassic strata as well as major parts of the Lower Cretaceous strata are absent. Albian to Santonian strata of the Hilssandstein Fm., Alfeld Fm., Plänerkalk Group, and Emscher Fm. (Hiss et al. 2005), together up to 520 m thick, follow from the top of the Hainberg to the centre of the Ringelheim Syncline, which is covered by Quaternary sediments (Look et al. 1984, 1986).

The folding of the Mesozoic strata into synclines and anticlines is due to a combination of tectonic faults in the Variscan basement and halotectonic movements of the Zechstein Group (Martini 1953; Jordan 1989). These combined ortho- and halotectonic movements were active during the Triassic, Late Jurassic and, with increasing intensity, during the Santonian to Campanian, when the Harz Mountains were uplifted (Voigt et al. 2004; von Eynatten et al. 2008). For the Early Jurassic, such tectonic movements in Northern Germany have been inferred from increased strata thickness at the margin of salt diapirs (e.g. drilling Etzel 24; Hoffmann 1968a; drilling Hamburg Allermöhe 1; Zimmermann et al. 2015) and thin, iron-oolitic deposits at salt pillows (e.g., Fallstein; Thomas 1924; Ott 1967). Indeed, the Hainberg section lies at the western margin of the Eichsfeld-Altmark High, a Permotriassic tectonic high (Paul 1993), which was active at least to Late Triassic times (Barnasch et al. 2005).

At the site of investigation, the strata were 10° inclined towards ENE (70°). Further uplift of the whole region, from a near sealevel position to the present day elevation took place after the Oligocene (e.g. Jordan et al. 1994: p. 68). The present-day geomorphology is essentially the result of an intense Miocene-Pliocene weathering, followed by Pleistocene erosion with frost wedging and solifluction (e.g. Brosche 1996), which also shaped the ridge of the Hainberg and covered its lower slopes with debris (Look et al. 1984, 1986; Heunisch et al. 2017).

Materials and methods

Fieldwork and sampling was carried out on three days in September 2011. Lithological descriptions are based on field observation and binocular observations on hand specimens, supplemented by eight thin sections of 28×48 mm and 7.5×10 cm in size, and about 50 µm thickness.

Total carbon (C_{tot}), total nitrogen (N_{tot}), and total sulphur (S_{tot}) of 50 bulk rock samples (Table 1) were analysed with a Euro EA 3000 Elemental Analyser (HEKAtech, Wegberg, Germany) applying 2,5-bis(5-tertbenzoxazol-2-yl) thiophene (BBOT) and atropine sulphate monohydrate (IVA Analysentechnik, Meerbusch, Germany) as reference material. Organic and carbonate carbon (C_{org}, C_{carb}) contents were determined by a LECO RC612 (Leco, St. Joseph, MI, USA) multi-phase carbon and water analyser. For calibration, Leco synthetic carbon (1 and 4.98 carbon %) and Leco calcium carbonate (12 carbon %) standards were used. All analyses were performed as duplicates. Analytical accuracy of all analyses was better than 3%. The carbonate-free fraction was calculated from the total weight minus the $CaCO_3$ and C_{org} content. Biostratigraphy is based on 24 determinable ammonites that were recovered *in situ*. Ammonite determinations were made using the descriptions of the type specimens and the systematic descriptions in Howarth (1992), Schulbert (2001), Rulleau (2007), Lacroix and Le Pichon (2011), Rulleau et al. (2013), and Di Cencio and Weis (2020). Belemnite determinations were made using Kolb (1942), Schlegelmilch (1998), Weis (1999), Riegraf (2000) and Arp (2010).

Orientation of belemnite rostra of two beds (n = 79 and 104) was measured in the field using a Freiberg Geological Compass. Graphical analysis was carried out using the program StereoNett Version 2.46 (Duyster 2000).

Repository: The material is stored in the Museum and Collection of the Geoscience Centre, University of Göttingen, under the numbers GZG.INV.866–GZG.INV.920.

Data Availability Statement: All data used in this publication, supplementary figures and tables are stored on the Göttingen Research Online Data repository (https://doi.org/10.25625/UEELUH).

Figure captions: unless otherwise noted, all specimen are coated by ammonium chloride prior to photography. Abbreviations: diameter (d), diameter of penultimate half whorl (d_i), umbilical width (u), whorl height (wh), whorl breadth (wb), primary ribs per half whorl (rb/2) (Howarth 1992). Shell parameters are given in brackets, when precise measurements were not possible due to poor preservation.

Results

Description of the section

Informal bed names are given in quotation marks. An overview of the section is provided in Fig. 2. Ammonites and belemnite findings are illustrated in Figs 3–26. The strata are described from bottom to top:

Amaltheenton Formation:

Bed 1: >100 cm medium-grey, well bedded claystone with white-grey quartz silt and fine-grained mica layers;

Bed 2: 1 cm rust-brown layer of siderite nodules;

Bed 3: 230 cm medium-grey, well bedded claystone with white-grey quartz silt and fine-grained mica layers (with small-scale cross stratification);

Bed 4: 2 cm rust-brown layer of siderite nodules;

Bed 5: 60 cm medium-grey, well bedded claystone with white-grey quartz silt and fine-grained mica layers;

Bed 6: 8 cm light-grey to white-grey, well bedded silty claystone with fine-grained mica.

Posidonienschiefer Formation:

Bed 7: 15 cm rust-brown/yellowish-brown varved, laminated clay with fine-grained mica and black manganese coatings on bedding planes and fractures;

Bed 8: 5 cm light-grey/middle-grey varved, laminated clay with yellow-brown weathered layers of former iron sulphides, abundant fine-grained mica on bedding planes;

Bed 9: 40 cm grey to yellow-brown weathered, laminated bendable clay with few fish scales and teeth; ammonoids: *Dactylioceras* cf. *crosbeyi* (Simpson) (compressed; Fig. 3);

Bed 10: 40 cm dark-grey bituminous calcareous claystone with even lamination and minor fish scale debris; ca. 10 above basis one 8 cm thick lenticular limestone concretion (“Elegantulum Concretion”); ammonoids: *Eleganticeras elegantulum* (Young & Bird) (in concretion; Fig. 27), 10 cm above basis *Eleganticeras* sp. (compressed); other fossils: *Lepidotes elvensis* (de Blainville) (Fig. 27), *Meleagrinella* (*Clathrolima*) sp.; *Coelodiscus minutus* (Schübler in Zieten);

Bed 11: 0–18 cm “Boreale Concretions”: medium grey laminated bituminous limestone concretions (pellet packstone) up to 50 cm width, with scattered mm-sized holoplanktonic gastropods in layers, fine-grained shell debris and minor fish scale debris; ammonoids: *Hildaites murleyi* (Moxon) (Fig. 4); other fossils: *Coelodiscus minutus* (Schübler in Zieten), abundant *Parainoceramya dubia* (Sowerby);

Bed 12: 150 cm dark-grey laminated bituminous marl to calcareous marl; minor fine-grained shell and fish scale debris; ammonoids: *Lytoceras* sp. (compressed; 75 cm above basis; Fig. 5); other fossils: *Meleagrinella* (*Clathrolima*) sp. (layers with poorly preserved specimens 10–15 and 140 cm above basis; *Parainoceramya dubia* (Sowerby) (75 cm above basis; Fig. 5);

Bed 13: 15 cm dark-grey laminated bituminous argillaceous limestone with fine-grained shell debris and minor fish scale debris; ammonoids: *Lytoceras* sp. (compressed), *Eleganticeras* sp. (compressed), other fossils: several bedding planes with abundant *Bositra buchi* (Roemer) up to 8 mm in size, few small *Parainoceramya dubia* (Sowerby), *Meleagrinella* (*Clathrolima*) sp.;

Bed 14: 25 cm dark-grey laminated bituminous calcareous marl with fine-grained shell debris and minor fish scale debris; fossils: *Meleagrinella* (*Clathrolima*) sp.;

Table 1. Carbon, sulphur, and nitrogen contents of sedimentary rocks of the Hainberg section.

Sample Number	Formation	Bed Number	Section meter [m] from top	Lithology	Remarks	C_{tot} mean [wt %]	C_{org} mean [wt %]	C_{carb} mean [wt %]	$CaCO_3$ calculated [wt %]	C_{org} carbonate-free [wt %]	N_{tot} mean [wt %]	S_{tot} mean [wt %]	S_{tot} carbonate-free [wt %]
sil1	Opalinuston	41	-0.25	weathered clay	affected by solifluction	1.98	1.95	0.03	0.25	1.95	0.10	0.75	0.75
sil2	Opalinuston	40	-1.7	claystone		1.20	0.97	0.23	1.92	0.99	0.07	0.05	0.05
sil3	Opalinuston	38	-2.65	claystone		0.67	0.56	0.11	0.92	0.57	0.06	0.05	0.05
sil4	Opalinuston	36	-2.77	calcareous claystone	matrix between concretions	3.25	0.51	2.74	22.8	0.66	0.05	0.04	0.05
sil5	Opalinuston	35	-3.1	claystone		1.03	0.66	0.37	3.08	0.68	0.06	1.40	1.45
sil6	Opalinuston	34	-13.35	claystone		1.16	0.59	0.57	4.75	0.62	0.06	0.04	0.04
sil7	Opalinuston	32	-13.7	marlstone	matrix between concretions and stromatolites	5.68	0.41	5.27	43.9	0.73	0.04	0.01	0.02
sil8	Opalinuston	31	-14.0	claystone		1.09	0.99	0.10	0.83	1.00	0.07	0.04	0.04
sil9	Opalinuston	31	-14.85	claystone		1.38	1.06	0.32	2.67	1.09	0.07	0.04	0.04
sil10	Opalinuston	31	-15.7	claystone		1.23	1.09	0.14	1.17	1.10	0.07	0.17	0.17
sil11	Jurensismergel	29	-16.2	calcareous marlstone	echinoderm packstone	8.24	0.36	7.88	65.7	1.05	0.03	0.08	0.23
sil12	Jurensismergel	28	-16.3	calcareous claystone	matrix of „zeta conglomerate"	2.36	0.97	1.39	11.6	1.10	0.07	0.03	0.03
sil13	Jurensismergel	27	-16.4	calcareous claystone	middle part of „oolite marl"	2.39	1.08	1.31	10.9	1.21	0.07	0.04	0.04
sil14	Jurensismergel	27	-16.5	calcareous claystone	lower part „oolite marl"	2.77	1.07	1.70	14.2	1.25	0.07	0.07	0.08
sil15	Jurensismergel	27	-16.55	marlstone	basis „oolite marl", matrix between belemnites	5.97	1.71	4.26	35.5	2.65	0.07	1.49	2.31
sil16	Posidonienschiefer	26	-16.6	calcareous marlstone	„fucoid bed equivalent"	10.9	2.43	8.44	70.3	8.19	0.07	0.05	0.17
sil17	Posidonienschiefer	25	-16.9	claystone	bituminous	12.1	12.0	0.07	0.58	12.1	0.34	3.78	3.81
sil18	Posidonienschiefer	24	-19.2	calcareous claystone	bituminous	12.6	9.96	2.67	22.2	12.8	0.27	0.95	1.22
sil19	Posidonienschiefer	24	-21.7	calcareous claystone	bituminous	14.3	11.8	2.47	20.6	14.9	0.34	2.72	3.42
sil20	Posidonienschiefer	24	-25.2	argillaceous marlstone	bituminous	12.5	8.38	4.14	34.5	12.8	0.24	2.04	3.11
sil21	Posidonienschiefer	24	-26.2	argillaceous marlstone	bituminous	12.8	9.19	3.61	30.1	13.1	0.26	1.29	1.84
sil22	Posidonienschiefer	24	-29.3	argillaceous marlstone	bituminous	12.5	8.77	3.68	30.7	12.6	0.26	1.26	1.81
sil23	Posidonienschiefer	24	-32.2	calcareous claystone	bituminous	14.1	11.3	2.78	23.2	14.7	0.31	1.96	2.55
sil24	Posidonienschiefer	24	-33.2	calcareous claystone	bituminous	16.1	13.4	2.71	22.6	17.3	0.36	2.70	3.49
sil25	Posidonienschiefer	24	-34.3	calcareous claystone	bituminous	14.4	11.6	2.72	22.7	15.0	0.31	0.73	0.95
sil26	Posidonienschiefer	24	-35.1	calcareous claystone	bituminous	13.8	11.2	2.56	21.3	14.2	0.28	0.78	0.99
sil27	Posidonienschiefer	23	-35.23	argillaceous marlstone	bituminous martix of belemnite accumulation	12.4	8.97	3.38	28.2	12.5	0.24	0.58	0.81
sil28	Posidonienschiefer	22	-35.25	argillaceous limestone	„Monotis event bed"	11.7	0.74	11.0	91.5	8.70	0.02	0.02	0.24
sil29	Posidonienschiefer	21	-35.3	marlstone	bituminous	13.8	7.07	6.73	56.1	16.1	0.22	1.07	2.42
sil30	Posidonienschiefer	21	-35.45	marlstone	bituminous	14.7	8.11	6.54	54.5	17.8	0.23	1.01	2.23
sil31	Posidonienschiefer	21	-35.6	argillaceous marlstone	bituminous	17.0	13.5	3.48	29.0	19.0	0.35	1.08	1.52
sil32	Posidonienschiefer	20	-35.7	argillaceous limestone	bituminous	14.1	5.16	8.96	74.7	20.4	0.13	1.56	6.15
sil33	Posidonienschiefer	19	-35.8	calcareous marlstone	bituminous	14.3	6.23	8.09	67.4	19.1	0.17	0.28	0.87
sil34	Posidonienschiefer	18	-36.0	argillaceous limestone	bituminous	13.9	4.40	9.48	79.0	21.0	0.11	0.51	2.42
sil35	Posidonienschiefer	17	-36.65	marlstone	bituminous	17.4	11.2	6.25	52.1	23.4	0.30	1.81	3.77
sil36	Posidonienschiefer	17	-37.25	marlstone	bituminous	18.6	13.3	5.28	44.0	23.7	0.34	1.64	2.93
sil37	Posidonienschiefer	17	-39.0	marlstone	bituminous	17.8	12.8	4.98	41.5	21.9	0.32	0.68	1.15
sil38	Posidonienschiefer	16	-39.65	argillaceous marlstone	bituminous	21.1	18.0	3.06	25.5	24.2	0.44	1.23	1.65
sil39	Posidonienschiefer	15	-40.0	argillaceous limestone	„Elegans Bed", bituminous	12.9	3.17	9.73	81.1	16.8	0.08	0.27	1.44
sil40	Posidonienschiefer	14	-40.35	calcareous marlstone	bituminous	13.8	5.65	8.10	67.5	17.4	0.14	0.21	0.66
sil41	Posidonienschiefer	13	-40.55	argillaceous limestone	bituminous	13.5	4.35	9.12	76.0	18.1	0.11	1.14	4.73
sil42	Posidonienschiefer	12	-40.75	marlstone	bituminous	14.5	7.45	7.09	59.1	18.2	0.19	0.53	1.29
sil43	Posidonienschiefer	12	-41.15	calcareous marlstone	bituminous	14.8	6.96	7.82	65.2	20.0	0.16	0.29	0.84
sil44	Posidonienschiefer	12	-41.65	argillaceous marlstone	bituminous	15.1	12.0	3.08	25.7	16.2	0.32	0.55	0.75
sil45	Posidonienschiefer	12	-42.0	argillaceous marlstone	bituminous	17.0	13.1	3.96	33.0	19.5	0.37	0.57	0.85
sil46	Posidonienschiefer	11	-42.25	argillaceous limestone	„Boreale Nodule", bituminous	12.7	1.33	11.3	94.3	23.5	0.04	0.20	3.58
sil47	Posidonienschiefer	10	-42.5	calcareous claystone	bituminous	23.4	22.1	1.23	10.2	24.7	0.56	1.67	1.86
sil48	Posidonienschiefer	9	-42.95	claystone		0.84	0.81	0.03	0.25	0.81	0.09	0.05	0.05
sil49	Posidonienschiefer	8	-43.15	claystone	with fine-grained mica	0.54	0.52	0.02	0.17	0.52	0.07	0.03	0.03

Sample Number	Formation	Bed Number	Section meter	Lithology	Remarks	C_{tot} mean	C_{org} mean	C_{carb} mean	$CaCO_3$ calculated	C_{org} carbonate-free	N_{tot} mean	S_{tot} mean	S_{tot} carbonate-free
			[m] from top			[wt %]	[wt %]	[wt %]	[wt %]	[wt %]	[wt %]	[wt %]	[wt %]
sil50	Posidonienschiefer	7	-43.25	claystone	rust-brown basal layer	0.84	0.82	0.02	0.17	0.82	0.07	0.07	0.07
sil51	Amaltheenton	6	-43.4	claystone	with quartz silt and fine-grained mica	0.30	0.28	0.02	0.17	0.28	0.05	0.31	0.31
sil52	Amaltheenton	3	-44.3	claystone	with quartz silt and fine-grained mica	0.34	0.32	0.02	0.17	0.32	0.05	0.13	0.13
sil53	Amaltheenton	3	-45.6	claystone	with quartz silt and fine-grained mica	0.56	0.54	0.02	0.17	0.54	0.05	0.31	0.31
sil54	Amaltheenton	1	-46.8	claystone	with quartz silt and fine-grained mica	0.72	0.69	0.03	0.25	0.69	0.07	0.31	0.31

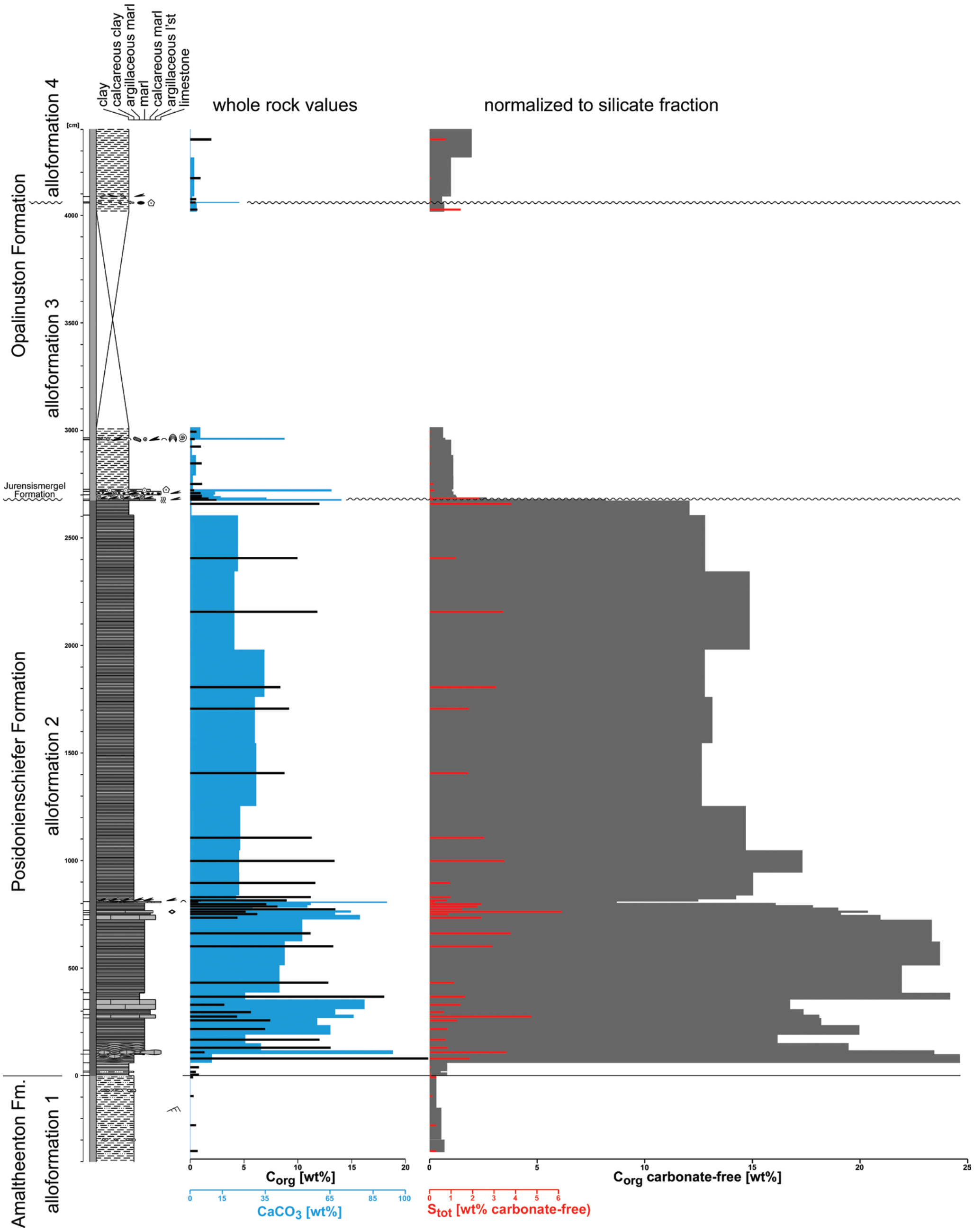


Figure 2. Overview on lithology and lithostratigraphy of the Hainberg section (top Amaltheenton Fm. to lower Opalinuston Fm.) with $CaCO_3$, organic carbon, and sulphur contents. For legend see Fig. 28.

Bed 15: 45 cm "Lower Elegans Bed": dark-grey laminated bituminous argillaceous limestone with fine-grained shell debris and rare fish scales; ammonoids: *Eleganticeras elegans* (Sowerby) (compressed; Fig. 6); other fossils: two aptychae, one fragmentary fish remain (*Tetragonolepis*?);

Bed 16: 30 cm dark-grey to black, highly bituminous laminated argillaceous marl with fine-grained shell debris; fossils: several bedding planes with pavements of *Bositra buchi* (Roemer) (up to 8 mm in size); one *Parainoceramya dubia* (Sowerby);

Bed 17: 340 cm dark-grey to black, bituminous laminated marl with fine-grained shell debris and rare fish scales; minor fine-grained carbonaceous plant debris; ammonoids: *Harpoceras* sp. (compressed fragment 50 cm above basis); other fossils: *Parainoceramya dubia* (Sowerby) (common 220 and 280 cm above basis);

Bed 18: 22 cm dark-grey, bituminous laminated calcareous limestone full of *Bositra* shell debris and abundant fish scales in layers; fossils: *Bositra buchi* (Roemer);

Bed 19: 10 cm dark-grey, bituminous laminated calcareous marl full of *Bositra* valves and shell debris; uneven bedding planes; fossils: *Bositra buchi* (Roemer);

Bed 20: 10 cm dark-grey, bituminous laminated calcareous marl to argillaceous limestone; fish scale debris in layers;

Bed 21: 40 cm dark-grey, bituminous laminated marl full of *Bositra buchi* valves up to 12 mm in size; uneven bedding planes;

Bed 22: 1 cm "Monotis Bed": medium-grey, microcrystalline argillaceous limestone composed of numerous *Meleagrinella* (*Clathrolima*) *substriata* (Münster) (see Lutikov and Arp 2022 for taxonomy);

Bed 23: 2 cm "Commune belemnite battlefield": dark-grey, rust-brown oxidized, bituminous laminated argillaceous marl with numerous, current-aligned belemnite rostra; belemnites poorly preserved due to pyrite oxidation; ammonoids: *Dactylioceras* sp. (compressed; Fig. 7); other fossils: *Acrocoelites* sp. (Fig. 8), *Dactyloteuthis irregularis* (Fig. 9), *Stenopterygius* sp. (rib fragments);

Bed 24: ca. 18 m dark-grey bituminous laminated calcareous claystone to argillaceous marl; scattered compressed marcasite nodules; even bedding planes; lower 10 m with bedding planes full of *Bositra* shell debris and few complete *Bositra buchi* valves (up to 5 mm in size); uppermost 8 m with decreasing fine-grained *Bositra* shell debris, increasing carbonaceous plant debris and mica flakes; partially fossil-free-layers; compressed ammonoids *Dactylioceras* cf. *commune* (Sowerby) (5 cm above basis); other fossils: *Bositra buchi* (Roemer), ostracods (uppermost 2 m), one mm-sized pellet composed of fish remains (2 m below top);

Bed 25: 60 cm medium-grey to brownish, bituminous laminated claystone; with minor fine-grained shell debris at its top;

Bed 26: 0–6 cm "fucoid bed equivalent": medium-grey, laminated lenticular to irregularly shaped calcareous marl to argillaceous limestone concretions with calcite or marcasite-filled burrows (0.5 cm diameter); thin layers with white, fine-grained shell debris; sharp upper boundary, with impressions of ooids from the bed above.

Jurensismergel Formation:

Bed 27: 20 cm "Oolite marl with belemnite accumulation": indistinctly bedded, medium-grey marl with numerous bioclasts, iron ooids and cm-sized white, ooid-bearing phosphorite nodules; iron ooids 1–2 mm in size and colonized by nubeculariid foraminifera; belemnite accumulation at the basis of the bed; ammonoids: *Osperleioceras* cf. *beauliziense* (Monestier) (5 cm above basis) (Fig. 10); *Perilytoceras* sp.; other fossils: *Dactyloteuthis irregularis* (Schlotheim) (mass accumulation), *Chlamys textoria* (Schlotheim), *Liostrea erina* (d'Orbigny), *Parainoceramya* sp., *Chladocrinus* sp., ostracods, *Chondrites* sp.;

Bed 28: 15 cm "Zeta Conglomerate": indistinctly bedded, medium-grey marl with iron ooids, bioclasts and numerous reworked rust-brown, cm-sized concretions (intraclast rudstone); abundant phosphoritic ammonite casts and reworked fragments; abundant nubeculariid foraminifera on ooids, echinoderm debris and other bioclasts; belemnite accumulation at the basis of the bed; ammonoids: *Phlyseogrammoceras dispansiforme* (Wunstorf) (Figs 11, 12), *Phlyseogrammoceras transiens* (Ernst) (Fig. 13), ?*Alocolytoceras* sp. (Fig. 14); *Dumortieria* sp. (juvenile, fragment from top of the bed); other fossils: *Dactyloteuthis similis* (Seebach) (mass accumulation), *Palaeonucula hammeri* (Defrance), *Sphenodus* sp.; bryozoan colonies on shell fragments;

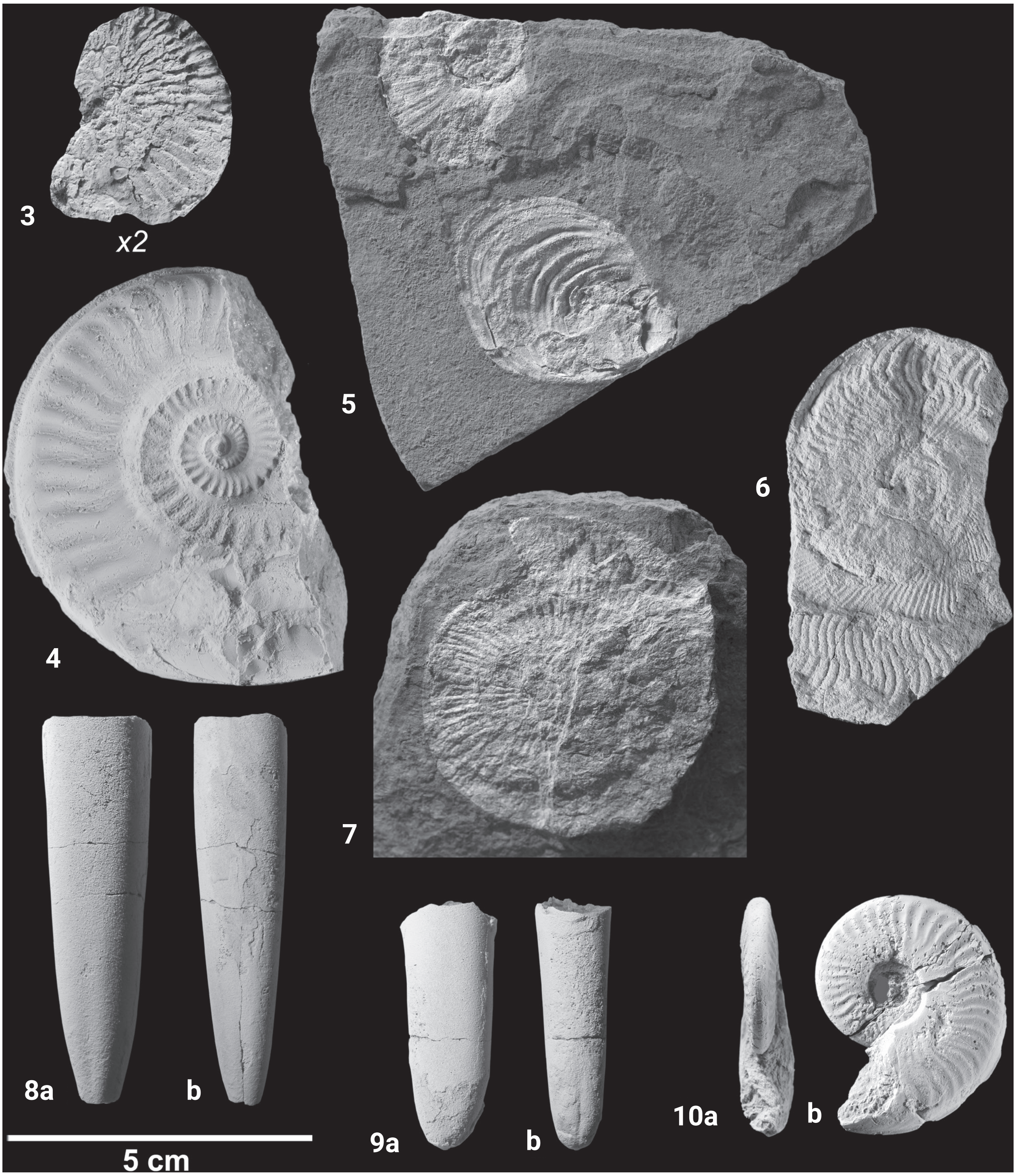
Bed 29: 10 cm medium-grey, massive calcareous marl full of echinoderm remains (echinoderm packstone with micritic matrix) with abundant iron as well as calcareous ooids, abundant nubeculariid foraminifera at the surface of ooids, echinoderm ossicles and rounded shell fragments, echinid spines, bivalve shell; indistinct lower boundary;

Bed 30: 2 cm fibrous calcite with cone-in-cone structures.

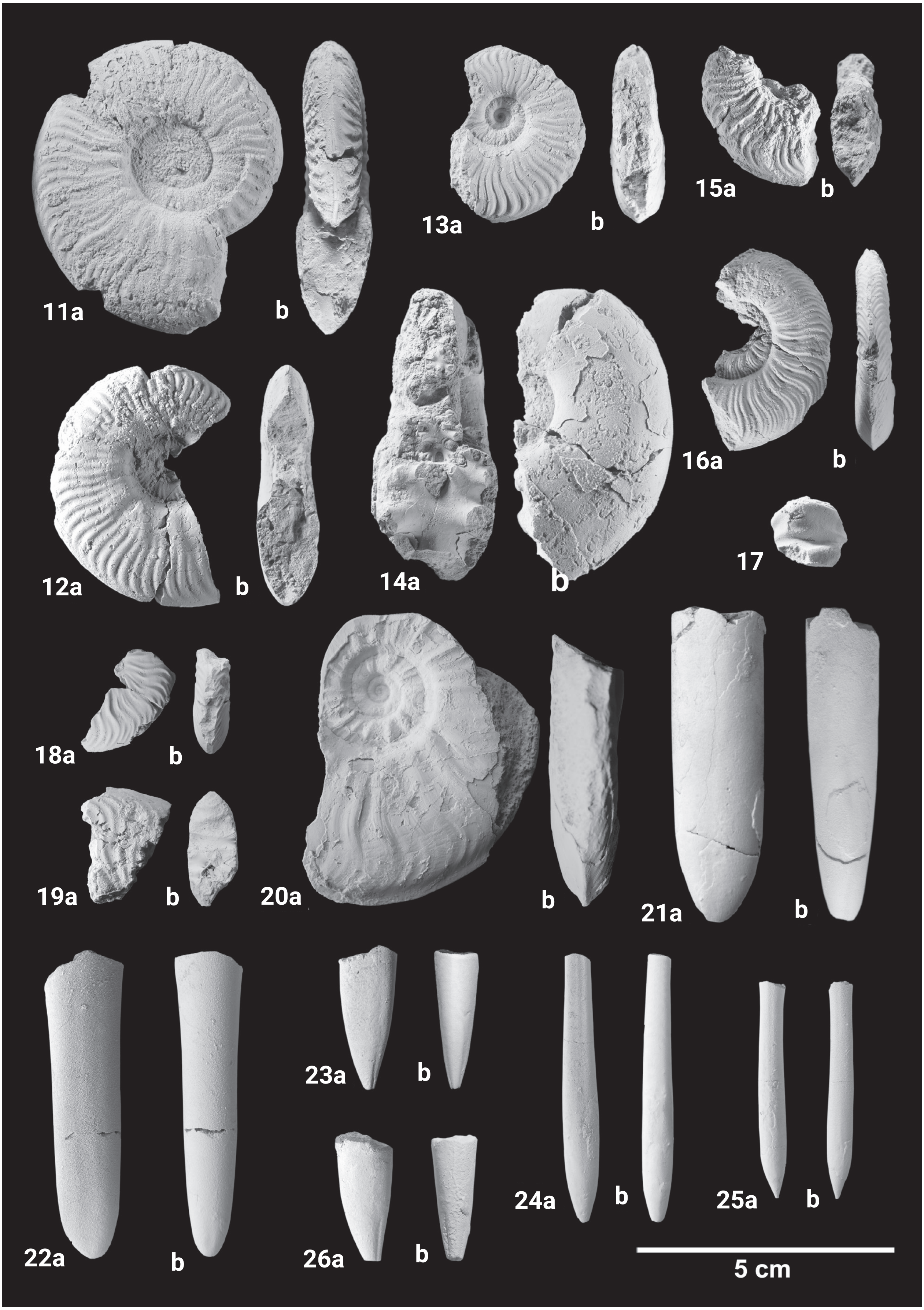
Opalinuston Formation:

Bed 31: 230 cm medium-grey, well-bedded claystone; few layers with fine-grained white shell debris of *Bositra* 25–40 cm and 120–140 cm above basis; thin marcasitic burrows; ammonoids: indeterminable compressed ammonite with bundled sinuous ribs; other fossils: *Bositra suessi* (Oppel) (25 cm above basis);

Bed 32: 6–8 cm dark-grey, well bedded marl full of fine-grained shell debris, abundant limonitic iron ooids, belemnite rostra and cm-sized white-grey, corroded phosphorite nodules; near the basis rust-brown irregular argillaceous limestone concretions and large compressed ammonite shell fragments (> 15 cm) with mm-thin stromatolitic crusts;



Figures 3–10. Ammonites and Belemnites of the Toarcian Hainberg section **3**. *Dactylioceras* cf. *crosbeyi* (Simpson), bed 9, Posidonienschieder Formation, Tenuicostatum Zone. GZG.INV.866: d = (21) mm, n = (7), wh = (8) mm, rb/2 = (20); **4**. *Hildaites murleyi* (Moxon), bed 11 "Boreale Concretions", Posidonienschiefer Formation, Exaratum Subzone. GZG.INV.867: d = 75 mm, di = 53 mm, u = 30 mm, wh = 23 mm, wb = (17) mm, rb/2 = (20); **5.** *Lytoceras* sp. und *Parainoceramya dubia* (Sowerby), bed 12, Posidonienschiefer Formation, Exaratum/Elegans Subzone. GZG.INV.868: d = (33) mm, u = (10) mm, wh = 14 mm; **6.** *Eleganticeras elegans* (Sowerby), bed 15, Posidonienschiefer Formation, Elegans Subzone. GZG.INV.869: d = 66 mm, di = (42) mm, u = (13) mm, wh = (36) mm; **7.** *Dactylioceras* (*Dactylioceras*) cf. *commune* (Sowerby), 5 cm above basis of bed 24, Posidonienschiefer Formation, Commune Subzone. GZG.INV.870: d = 53 mm, di = (42) mm, u = (27) mm, wh = (12) mm; **8.** *Acrocoelites* sp., left: lateral view, right: ventral view, bed 23, Posidonienschiefer Formation, Commune Subzone. GZG.INV.871: Length = 63.5 mm (incomplete: without alveolar region); **9.** *Dactyloteuthis irregularis* (Schlotheim) [syn.: *Dactyloteuthis digitalis* (Blainville)], left: lateral view, right: ventral view, bed 23, Posidonienschiefer Formation, Commune Subzone. GZG.INV.872: Length = 40.5 mm; **10.** *Osperleioceras* cf. *beauliziense* (Monestier), bed 27, Jurensismergel Formation, ?Thouarsense Zone. GZG.INV.873: d = 40 mm, di = (27) mm, u = 11 mm, wh = 18 mm, wb = 9.5 mm, rb/2 = 20.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Figures 11–26. Ammonites and Belemnites of the Upper Toarcian of the Hainberg section **11.** *Phlyseogrammoceras dispansiforme* (Wunstorf), bed 28 "zeta conglomerate", Jurensismergel Formation, Dispansum Subzone. GZG.INV.874: d = 55.5 mm, di = (38) mm, u = 17 mm, wh = 24 mm, wb = 14 mm, rb/2 = (30); **12.** *Phlyseogrammoceras dispansiforme* (Wunstorf), bed 28 "zeta conglomerate", Jurensismergel Formation, Dispansum Subzone. GZG.INV.875: d = 49.5 mm, di = 34.5 mm, u = 13 mm, wh = 23.5 mm, wb = 13 mm, rb/2 = 31; **13.** *Phlyseogrammoceras transiens* (Ernst), bed 28 „zeta conglomerate", Jurensismergel Formation, Dispansum Subzone. GZG.INV.876: d = 34 mm, di = (23) mm, u = 9.5 mm, wh = 15.5 mm, wb = 10 mm, rb/2 = 24; **14.** ?*Alocolytoceras* sp., bed 28, Jurensismergel Formation, Dispansum Subzone. GZG.INV.877: d = (59) mm, wh = 28 mm, wb = 24 mm; **15.** *Cotteswoldia aalensis* (Zieten), bed 32, Opalinuston Formation, Aalensis Subzone. GZG.INV.878: d = (34) mm, wh = 17 mm, wb = 9 mm; **16.** *Pleydellia subcompta* (Branco), bed 32, Opalinuston Formation, Aalensis Subzone. GZG.INV.879: d = 40 mm, di = (28) mm, u = 15 mm, wh = 14.5 mm, wb = 18 mm, rb/2 = (45); **17.** Fragment of *Pleurolytoceras* cf. *hircinum* (Schlotheim), dorsal view showing v-shaped constriction; bed 32, Opalinuston Formation, Aalensis Subzone. GZG.INV.880; **18.** *Pleydellia* cf. *pseudoarcuata* Maubeuge, bed 39, Opalinuston Formation, Pseudolotharingicum Subzone. GZG.INV.881: wh = 11.5 mm, wb = 7 mm; **19.** ?*Cotteswoldia* sp., bed 39, Opalinuston Formation, Pseudolotharingicum Subzone. GZG.INV.882: wh= 20 mm, wb = 10 mm; **20.** *Leioceras* cf. *goetzendorfensis* (Dorn), Opalinuston Formation, Opalinum Subzone. GZG.INV.883: d = (70) mm, di = (48) mm, u = 19 mm, wh = 31 mm, wb = 14 mm; **21.** *Dactyloteuthis irregularis* (Schlotheim) [syn.: *Dactyloteuthis digitalis* (Blainville)], left: lateral view, right: dorsal view; bed 27, Jurensismergel Formation, ?Thouarsense Zone. GZG.INV.884: Length = 61 mm; **22.** *Dactyloteuthis similis* (Seebach), left: lateral view; right: dorsal view; bed 28, Jurensismergel Formation, Dispansum Subzone. GZG.INV.885: Length = 59 mm; **23.** *Acrocoelites rostriformis* (Theodori in Bronn) [syn.: *Acrocoelites* (*Odontobelus*) *curtus* (d'Orbigny)], left: lateral view, right: dorsal view; bed 32, Opalinuston Formation, Aalensis Subzone. GZG.INV.886: Length = 28 mm; **24.** *Hastites subclavatus* (Voltz), left: lateral view, right: dorsal or ventral view; bed 32, Opalinuston Formation, Aalensis Subzone. GZG.INV.887: Length = 52 mm; **25.** *Hastites subclavatus* (Voltz), left: lateral view, right: dorsal or ventral view; bed 32, Opalinuston Formation, Aalensis Subzone. GZG.INV.888: Length = 42.5 mm; **26.** *Acrocoelites rostriformis* (Theodori in Bronn) [syn.: *Acrocoelites* (*Odontobelus*) *curtus* (d'Orbigny)], left: lateral view, right: dorsal view; bed 39, Opalinuston Formation, Pseudolotharingicum Subzone. GZG.INV.889: Length = 24.5 mm.

ammonoids: *Cotteswoldia aalensis* (Zieten) (Fig. 15), *Pleydellia subcompta* (Branco) (Fig. 16), *Pleurolytoceras* cf. *hircinum* (Schlotheim) (Fig. 17); other fossils: *Hastites subclavatus* (Voltz) (Figs. 24-25), *Acrocoelites rostriformis* (Theodori in Bronn) (Fig. 23); *Nicaniella voltzii* (Hoeninghaus in Roemer), *Palaeonucula hammeri* (Defrance), fragments of *Chlamys textoria*, *Costatrochus subduplicatus* (d'Orbigny), *Thecocyathus mactrus* (Goldfuss), one terebratulid brachiopod, one serpulid tube, driftwood (jet);

Bed 33: 1 cm fibrous calcite with cone-in-cone structures;

Bed 34: 50 cm medium-grey, yellow-brown weathered, well-bedded claystone; few thin shell fragments, oxidized lenticular marcasite nodules; ca. 10 m lack of exposure (claystones);

Bed 35: 40 cm medium-grey, well-bedded claystone with abundant fine-grained white *Bositra* shell debris on bedding planes; fossils: *Bositra suessi* (Oppel) (one complete valve);

Bed 36: 5 cm medium-grey calcareous claystone with reworked cm-sized, rounded to irregular siderite concretions; top of concretions corroded and covered by thin veneer of echinoderm and bivalve debris; ammonoids: one reworked phosphoritic fragment of a ?*Cotteswoldia* sp.; other fossils: *Hastites* sp. (three fragments), pectinid bivalve fragments, small gastropods, one serpulid tube fragment;

Bed 37: 1 cm fibrous calcite with cone-in-cone structures;

Bed 38: 25 cm medium-grey, well-bedded claystone with fine-grained *Bositra* shell debris on bedding planes; fossils: *Coelodiscus minutus* (Schübler in Zieten) (limonite cast);

Bed 39: 1 cm yellow-brown calcareous clay with reworked phosphorite nodules, siderite nodule fragments, belemnites and phosphoritic ammonite fragments; ammonoids: *Leioceras*/*Pleydellia* sp. (fragment), *Pleydellia* cf. *pseudoarcuata* Maubeuge (Fig. 18) , ?*Cotteswoldia* sp. (Fig. 19); other fossils: *Acrocoelites rostriformis* (Theodori in Bronn) (Fig. 26);

Bed 40: 200 cm medium-grey, well-bedded claystone; 80 cm above basis a layer with fine-grained *Bositra* shell debris; 100 and 120 cm above basis 1-cm-thin siderite nodule beds;

Bed 41: >50 cm medium-grey, yellow-brown weathered unstratified clay (solifluction deposit) with white-grey septarian nodules; few marcasitic burrows and mica flakes; ammonoids: *Leioceras* cf. *goetzendorfensis* (Dorn) (Fig. 20).

Carbonate, organic carbon and sulphur contents

The Amaltheenton Formation (beds 1–6) is characterized by very low $CaCO_3$ contents (0.2 wt%) as well as low C_{org} contents (0.3–0.7 wt%) (Table 1, Fig. 2). Similarly, carbonate-free S_{tot} contents are low (0.3 wt%).

The lowermost Posidonienschiefer Formation (beds 7–9) is still very low in $CaCO_3$ (0.2 wt%) and C_{org} (0.7 wt%), despite the onset of lamination. Carbonate-free S_{tot} is even lower (<0.1 wt%) than in the Amaltheenton Fm. (Table 1, Fig. 2). Only at the base of the middle Posidonienschiefer Fm., i.e. in beds 10 and 11 (horizon of Elegantulum and Boreale Concretions) a marked increase in all three parameters ($CaCO_3$: 10 wt%, C_{org}: 22.1 wt%, carbonate-free S_{tot}: 1.9 wt%) can be observed. Carbonate-free C_{org} contents reach their maximum here with 24.7 wt%. Farther up in the middle Posidonienschiefer Fm. (beds 12 to 17), $CaCO_3$ contents remain comparatively high (around 52 wt%). Likewise, C_{org} and carbonate-free S_{tot} fluctuate at elevated val-

Figure 27. Limestone concretion (“Elegantulum Concretion”) of bed 10 with *Lepidotes elvensis* (de Blainville) and *Eleganticeras elegantulum* (Young & Bird). GZG.INV.890ab: d = 28.7 mm, u = 8 mm, wh = 12 mm, wb = 7.8 mm.

ues (around 10 and 1.8 wt%, respectively). Normalised to the carbonate-free fraction, beds 16 and 17 again show similarly high C_{org} contents (around 23 wt%) as in beds 10 and 11. A cyclicity of the C_{org} contents, indicated by maxima in beds 10, 12, 16 and 17 with subsequent decreases, is unfortunately not provable due to the too low sample density. Beds 18–23, which include the “Monotis event bed” and “Commune Belemnite Battlefield”, again show increased $CaCO_3$ contents (around 60 wt%) and high carbonate-free S_{tot} contents (around 2.1 wt%), but with tending declines in carbonate-free C_{org} (from about 20 to 10 wt%).

The upper part of the Posidonienschiefer Fm., represented by beds 24–26, is characterised by only moderately high $CaCO_3$ contents (around 27 wt%) and consistently high carbonate-free S_{tot} contents (around 2.1 wt%), with C_{org} and carbonate-free C_{org} stabilising at values around 10 and 13.5 wt%, respectively. The uppermost, bioturbated bed 26 of the Posidonienschiefer Fm., however, already shows significantly reduced C_{org} (2.4 wt%) and S_{tot} contents (<0.1 wt%).

The Jurensismergel Formation with its strongly condensed, bioclastic and Fe-oolitic rocks (beds 27–29) shows clearly elevated $CaCO_3$ contents (up to 66 wt%) with now very low C_{org} (around 1 wt%) and S_{tot} (below 0.1 wt%) (Table 1, Fig. 2). Only the basal belemnite accumulation is still characterised by high S_{tot} contents (1.5 wt%, i.e., 2.3 wt% carbonate-free S_{tot}).

The Opalinuston Formation (beds 31–41) is composed of only slightly calcareous mudstones, with significant lower $CaCO_3$ values (around 2.0 wt%) compared to the Jurensismergel Fm. rocks, but slightly higher than the Amaltheenton Fm. rocks (0.2 wt%). Only the stromatolite-bearing condensed bed 32 and the conglomeratic bed 36 show increased $CaCO_3$ contents of 44 and 23 wt%, respectively. C_{org} and S_{tot} contents of the Opalinuston Fm. (total rock as well as carbonate-free fraction) are only 0.9 wt% and 0.3 wt%, respectively (Table 1, Fig. 2).

Belemnite accumulations

The orientation of the tip direction of belemnite rostra was measured in bed 23 (“Commune Belemnite Battlefield”) of the Posidonienschiefer Formation and bed 27 (“Oolite marl with belemnite accumulation”) of the Jurensismergel Formation (Suppl. material 1).

In bed 23, a total of 79 rostra with a length between 1 and 9 cm were analysed. The belemnite rostra tip direction pattern shows one maximum in the class 195–210° (i.e., 10.1%), a second and third maximum in the class 150–165° (i.e., 8.9%) and 105–120° (i.e., 8.9%). The average azimuth of all measurements is 156° (Fig. 28).

In bed 27, a total of 104 rostra with a length between 1 and 9 cm were analysed. While there is one maximum at 165–180° (i.e., 9.6%), several further maxima occur at 45–60° (i.e., 7.7%), 0–15° (i.e., 6.7%), 30–45°, 60–75°, 90–105°, 285–300°, and 300–315° (each 5.8%). The average azimuth of all measurements for bed 27 is 86° (Fig. 29).

Stromatolites

Up to 9 mm thick laminated, sulphide-rich stromatolitic carbonate crusts were detected on cm-sized ammonite shell fragments in bed 32 of the Opalinuston Formation (Fig. 30). The crusts are composed of slightly undulating to flat hemispheroids. Thin sections demonstrate that the lamination results from an alternation of 10–40 µm thick microcrystalline to microsparitic and 15–40 µm thick dark, iron-sulphide-rich layers (Fig. 30). The stromatolitic crusts neither show a fenestral fabric nor morphological traces of microbial filaments or coccoidal structures. The same type of stromatolites has been described from discontinuities in the South-German Schwarzjura-Group by Keupp and Arp (1990).

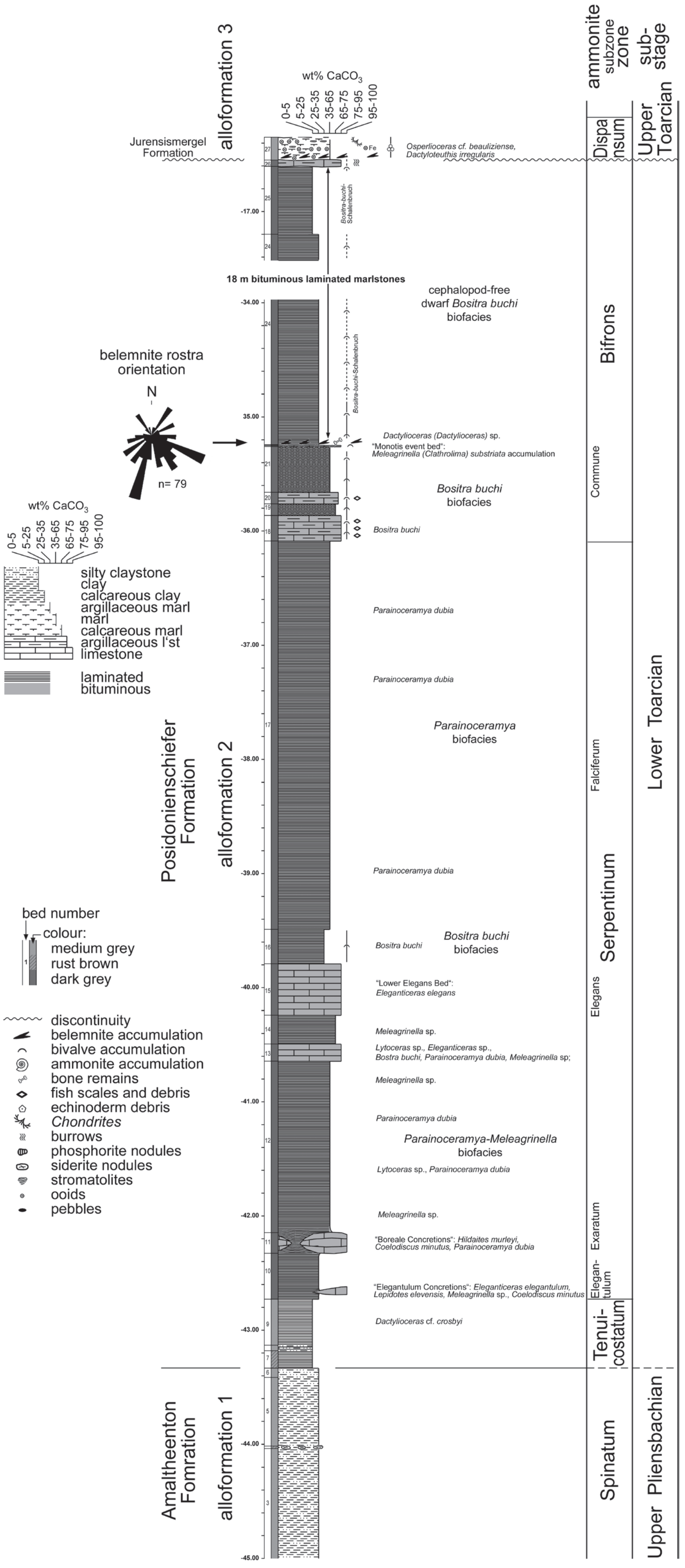

Figure 28. Lithostratigraphy, biostratigraphy and biofacies of the Posidonienschiefer Formation, Lower Toarcian, exposed at the Hainberg section.

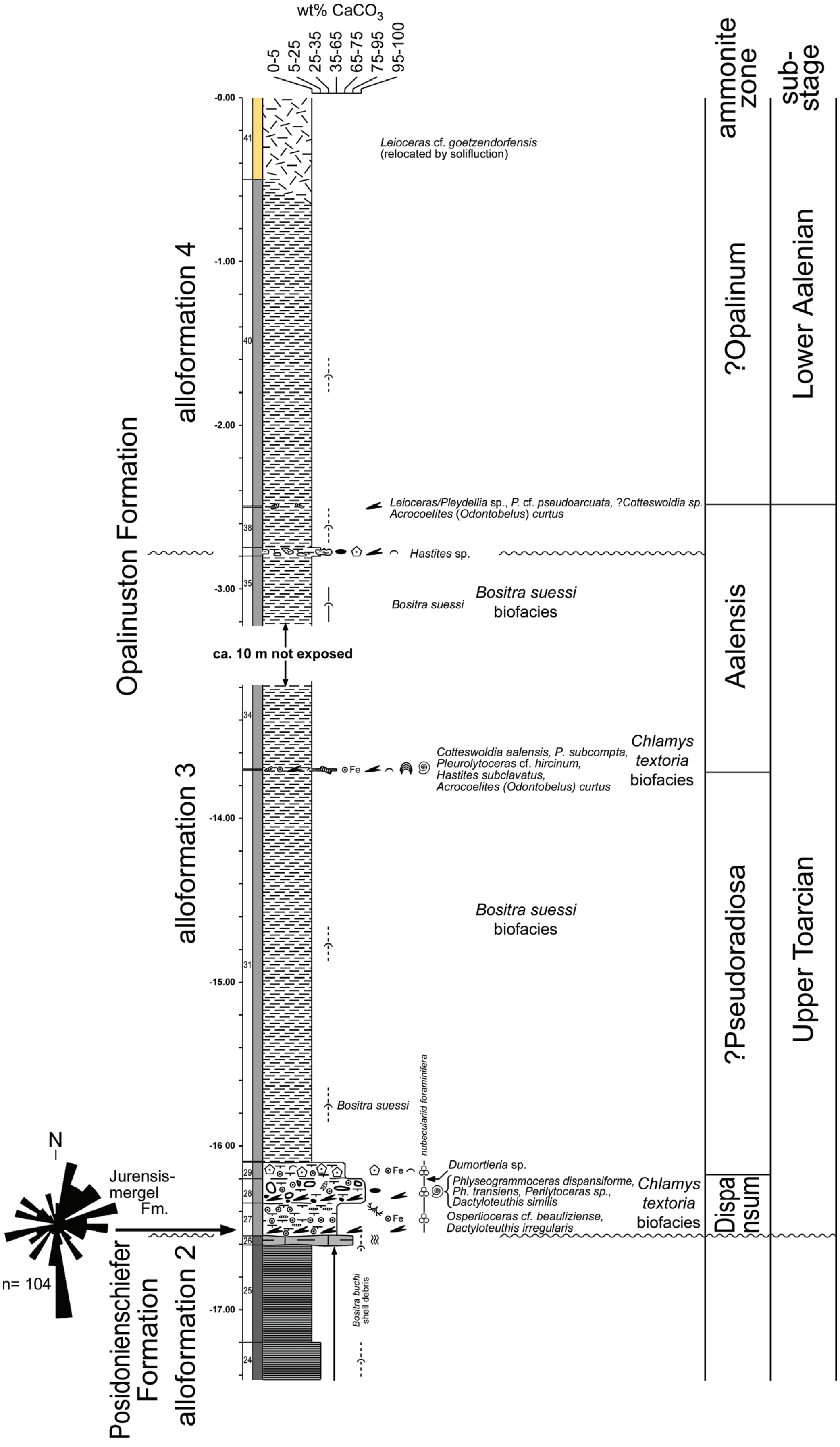

Figure 29. Lithostratigraphy, biostratigraphy and biofacies of the Jurensismergel Formation, Upper Toarcian, exposed at the Hainberg section. For legend see Fig. 28.

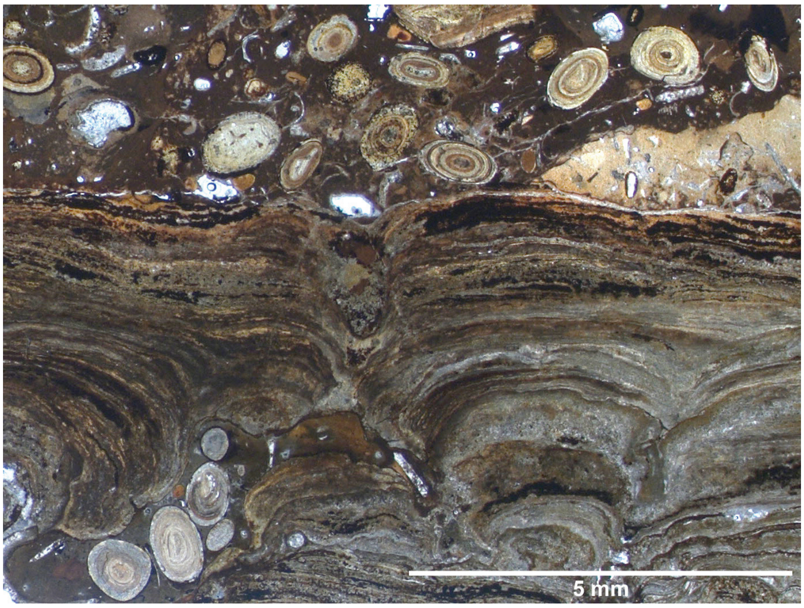

Figure 30. Thin section micrograph of a stromatolite crust of bed 32, Mactra/Aalensis Subzone, accompanied by marlstone with ooids showing mixed limonitic-calcareous cortices. Note the very dense lamination lacking a fenestral fabric and morphological microbial remains.

Bivalve assemblages

Although quantitative bivalve samples were not collected, qualitative descriptions provide some information on the general development of bivalve assemblages for the Toarcian along the section (Figs 28, 29; Suppl. material 2). No bivalves were recovered from the top parts of the Amaltheenton Fm. (beds 1–6) and lowermost parts (beds 7–9) of the Posidonienschiefer Fm. (i.e., gap of collection).

Lower parts of the middle Posidonienschiefer Fm. (beds 10–14) are dominated by *Parainoceramya dubia* (Sowerby) and *Meleagrinella* (*Clathrolima*) sp., which regularly occur on bedding planes. This "*Parainoceramya Meleagrinella* biofacies" is associated with cephalopods. Only in bed 13, first *Bositra buchi* (Roemer) covering single bedding planes were observed.

Further up in the middle Posidonienschiefer Fm., bed 16 is characterized by abundant bedding planes covered with *Bositra buchi* (Roemer) ("*Bositra buchi* biofacies"), while bed 17 regularly shows *Parainoceramya dubia* (Sowerby) but lacking *Bositra*. Beds 18–21 again show abundant bedding planes covered with *Bositra buchi* (Roemer) ("*Bositra buchi* biofacies"). The dense shell package results in a wrinkled pseudo-lamination of the rock.

Almost at the top of the middle Posidonienschiefer Fm., a monospecific *Meleagrinella* (*Clathrolima*) *substriata* (Münster) mass accumulation is developed, i.e. the "Monotis event bed" 22. Cephalopods are still present in this part of the section (Fig. 28).

Finally, the upper parts of the Posidonienschiefer Fm. (beds 24–25) are characterized by abundant beddings planes with *Bositra buchi* (Roemer) of reduced size (max. 6 mm) and its shell debris. Except for the immediate basis, this section is devoid of cephalopods ("cephalopod-free dwarf *Bositra buchi* biofacies") (Fig. 28).

After a stratigraphic gap, iron-oolitic marls (beds 27–28) of the Jurensismergel Formation commonly show valves of the epibyssate *Chlamys textoria* (Schlotheim), associated with scattered *Parainoceramya* sp., *Liostrea erina* (d'Orbigny) and rare *Palaeonucula hammeri* (Defrance) ("*Chlamys textoria* biofacies"), while claystones of the lower Opalinuston Formation are characterized by *Bositra suessi*, locally forming accumulations on bedding planes ("*Bositra suessi* biofacies"; Fig. 29). Further up in the Opalinuston Formation, *Bositra buchi* (Roemer) significantly decreases in abundance.

Discussion

Litho- and allostratigraphy

Distinct lithofacies changes, marker beds and discontinuities provide a good allostratigraphic framework, which partly corresponds to lithostratigraphic formations (Figs 2, 28, 29). The application of the terms "formation" and "alloformation" follows the recommendations in NACSN (1983, 2021), Lutz et al. (2006) and Pratt et al. (2023):

Alloformation 1 (equivalent to Amaltheenton Formation): Bedded medium-grey claystones with mica and silt-layers (beds 1–6) represent the top parts of the Amaltheenton Formation.

Alloformation 2 (equivalent to Posidonienschiefer Formation): The onset of fine-laminated medium-grey, rust-brown weathered claystones (beds 7–9) represents the lower boundary of the Posidonienschiefer Formation with its 60 cm thick lower, still non-bituminous part. An increase to high C_{org} values, marking the onset of the middle Posidonienschiefer Fm. with the T-OAE, is observed in bed 10. This 7.48 m thick middle, bituminous, part of the Posidonienschiefer

Fm. comprises beds 10 to 23, i.e. includes the Monotis event bed 22 and Commune Belemnite Battlefield (bed 23) at its top. The following upper part of the Posidonienschiefer Fm. (beds 24–26) consists of a 18.66 m thick monotonous succession of laminated bituminous marls with small *Bositra buchi* (Roemer) as almost the only fossils. The C_{org} contents are slightly lower than in the middle Posidonienschiefer Fm., similar to the trends in Southern Germany (Frimmel et al. 2004; Arp et al. 2021), but different from results in the Braunschweig area (Brockamp 1944). The top bed of the alloformation 2 is formed by bed 26, which is a laminated concretionary bed with distinct, straight burrows. This bed is considered as an equivalent of the "fucoid bed" at the top of the Posidonienschiefer Formation in Southern Germany (see e.g. Riegraf et al. 1984; Riegraf 1985). No deposits of the Dörnten Subformation with their fossiliferous limestone concretions were detected, consistent with former observations of Denckmann (1892: p. 107).

Alloformation 3 (corresponds to Jurensismergel and lowermost Opalinuston Formations): After a sharp boundary and discontinuity, the Jurensismergel Formation starts with a Fe-oolitic marls with a basal belemnite accumulation followed by a conglomeratic, Fe-oolitic calcareous clay bed with a second belemnite accumulation at its basis, and an echinoderm debris bed at its top. This rather marly, condensed and fossiliferous part of the Jurensismergel Fm. (beds 27–29) shows only 45 cm thickness. The higher, 13.3 m thick parts of this alloformation (beds 30–35) comprise medium-grey, bedded claystones, with more or less abundant *Bositra suessi* debris. This lithology already represents the Opalinuston lithofacies, so that earlier authors already assigned these beds in this region to the "Schichten des *Am. opalinus*" (von Seebach 1864), "Untere Zone des *Ammonites opalinus*" (Brauns 1865), or "Thone des *Harp. opalinum*" (Denckmann 1892). The thin bed 32 with reworked phosphorites and stromatolite crusts points to a minor discontinuity or condensation within this alloformation.

Alloformation 4 (corresponds to major parts of Opalinuston Formation): The lower boundary of this allostratigraphic unit is drawn with the erosional discontinuity of bed 36. Lithologically, the well-bedded carbonate-poor claystones are identical to those of the alloformation 3 top parts, except that *Bositra* shell debris layers are scarce. Only the lowermost 2.8 m of this formation were exposed.

Biostratigraphy

Only a limited number (24) of determinable ammonites were recovered from the investigated section (Figs 3–26). A number of them were compressed and poorly preserved. However, well-preserved uncompressed specimens have been found in limestone concretions in the Posidonienschiefer Fm. and phosphorite-bearing beds of the Jurensismergel and Opalinuston Formations. For the biostratigraphic scheme of ammonite zones and subzones, the reader is referred to Gabilly 1976a, Knitter and Ohmert 1983; Riegraf et al. 1984; Riegraf 1985; Ohmert et al. 1996; Elmi et al. 1997, and Cresta et al. 2001, summarized in Arp et al. (2021).

Upper Pliensbachian: Top parts of the alloformation 1 (≙ Amaltheenton Fm.) are devoid of biostratigraphic relevant fossils in the investigated section, but *Pleuroceras spinatum* has been recovered from a former clay pit near Sillium 1.5 km NNW of the investigated section (specimen in BGR collection: BGR-H-STGR-000290034 and -000290039; leg. R. Jordan 1956). The youngest, *in situ* collected *Pleuroceras spinatum* in this region comes from an 1.85 m thick interval at the top of the Amaltheenton Formation of the Friederike Mine near Bad Harzburg (Jordan 1960: his Abb. 14). No findings at the immediate lithostratigraphic boundary Amaltheenton-Posidonienschiefer are known. The precise boundary to the Toarcian, therefore, cannot be drawn with confidence.

Lower Toarcian: The lowermost recovered ammonite from alloformation 2 (≙ Posidonienschiefer Fm.), a poorly preserved, compressed *Dactylioceras* cf. *crosbeyi* (Simpson) with low umbilical width in bed 9 points to the presence of the Tenuicostatum Zone (Figs 3). Unfortunately, the Siemensi and Capillatum Concretions of the Tenuicostatum Zone, elsewhere present in this region (Wunnenberg 1950; Hoffmann 1968a, b; Weitschat 1973), are not developed at the investigated site. Their absence, however, rather reflects different early diagenetic conditions in the former porewater, not a stratigraphic gap (Hoffmann 1968b: p. 20). Clear evidence for the Tenuicostatum Zone, therefore, can only be given by *Dactylioceras semicelatum* (Simpson) from Heinde (BGR collection, e.g., BGR-H-STGR-000292526) and Haverlah (Hoffmann and Martin 1960), both locations with well developed limestone concretions. One *Dactylioceras* sp. is mentioned from 22–29 cm above basis of the Posidonienschiefer Formation, Friederike Mine near Bad Harzburg (Jordan 1960: p. 109). *Eleganticeras elegantulum* (Young & Bird) within the limestone nodule of bed 10 (Elegantulum Concretions; Fig. 27) indicates the Elegantulum Subzone, i.e. the basis of the Serpentinum Zone. The limestone nodules of bed 11 (Boreale Concretions) show well-preserved, uncompressed *Hildaites murleyi* (Moxon) (Fig. 4), indicating the Exaratum Subzone, while bed 15 (Lower Elegans Bed) belongs to the Elegans Subzone due to findings of compressed *Eleganticeras elegans* (Sowerby) (Fig. 6). The following beds 16 and 17 did only reveal indeterminable fragmentary imprints of *Harpoceras* sp. and likely represent higher parts of the Serpentinum Zone, while beds 18–21 probably already belong to the basal Bifrons Zone. No ammonite findings were made in these beds 18–21 of the present section.

However, Vinken (1971, p. 61 f.) provides a partial section from Listringen (9 km WNW of the Hainberg section), showing the "interval of Monotis limestones" (i.e., bituminous calcareous marls with wrinkled lamination due to *Bositra* and *Meleagrinella* shells) with a basal limestone bed containing *Dactylioceras commune* (Sowerby) and ?*Frechiella subcarinata* (Young & Bird) (Suppl. material 3). This bed corresponds to bed 18 of the Hainberg section.

Differing from that, Riegel et al. (1986) and Loh et al. (1986) draw the lower boundary of the Bifrons Zone at Hildesheim-Itzum (Suppl. material 4) several meters deeper, which corresponds approximately to the middle of bed 17 in the Hainberg section. They support their stratigraphic assignment by the replacement of *Harpoceras* by abundant *Dactylioceras* in their section. However, the genus *Dactylioceras* occurs throughout the Posidonienschiefer Fm. in varying abundances. Many of these dactylioceratids cannot be attributed with confidence to a specific species if compressed (such as *D. commune* of the Bifrons, and *D. toxophorum* Buckman of the Serpentinum Zone), a fact already noted by Hoffmann (1968a, p. 452). The identification of the basis of the Bifrons Zone, therefore, appears more reliable using *Frechiella subcarinata* (Young & Bird), which appears identifiable even if compressed or less well preserved.

Indeed, Weitschat (1973) places the boundary Serpentinum-Bifrons zone in the lower part of the "interval of Monotis limestones" (which he defines as a 0.4–1.0 m thick interval of bituminous limestone beds partially with left valves of *Meleagrinella* (*Clathrolima*) *substriata* (Münster)), because of a *Harpoceras falciferum* (Sowerby) [not figured] finding within the "basal Posidonia pavements". This bed corresponds to our bed 18 in the Hainberg section. It has to be noted, however, that *Harpoceras falciferum* (Sowerby) reaches into the Commune Subzone (Howarth (1992, p. 132 and text-figs. 2, 5 and 6), thus, overlaps with *Dactylioceras commune* (Sowerby) and *Frechiella subcarinata* (Young & Bird). We therefore place the basis of the Bifrons Zone, Commune Subzone at the basis of bed 18 in the Hainberg section.

In the present investigation, poorly preserved *Dactylioceras* (*Dactylioceras*) sp. were only found in the "Commune Belemnite Battlefield" (bed 23) and at the very basis of the upper Posidonienschiefer Fm. (i.e., near the lower boundary of bed 24; Fig. 7). No further ammonites were found in beds 24–26. Likewise, no ammonite findings are reported from the upper Posidonienschiefer Fm. in adjacent sections Haverlahwiese and Hildesheim-Itzum. While the presence of the Fibulatum Subzone is likely (*Hildoceras bifrons* (Bruguiere) from Dörnten; Ernst 1923–1924), the presence of the Semipolitum Subzone appears questionable.

Upper Toarcian: No indication of the Variabilis Zone was found at the Hainberg section, consistent with its absence already shown by Denckmann (1892) and similar to adjacent sections Haverlahwiese and Hildesheim-Itzum (Maul 1984; Loh et al. 1986; Riegel et al. 1986). However, the Variabilis Zone, which forms major parts of the Dörnten Subformation, is well documented in Dörnten and Gallberg (Denckmann 1892; Ernst 1923–24; Dahlgrün 1928). It is probably present at the city centre of Hildesheim (Bischofskamp), from which Denckmann (1892) reports "*Harp. quadratum* Quenst. und *Harp. bingmanni* Denckm." in the collection of the Roemer-Museum Hildesheim) (Fig. 32).

The stratigraphically lowest ammonite finding of alloformation 3 (≙ Jurensismergel and lowermost Opalinuston Formations) at Hainberg, an *Osperleioceras* cf. *beauliziense* (Monestier) in bed 27 ("oolite marl"; Fig. 10), points to the Fallaciosum Subzone (Lacroix and Le Pichon 2011). The specimen is probably reworked into the Dispansum Zone, although the latter cannot be proven for the bed 27 directly. Unfortunately, the belemnite *Dactyloteuthis irregularis* (Schlotheim) (Fig. 21), abundant in bed 27, also does not provide a precise biostratigraphic assignment, because it ranges from the Variabilis Zone into the Pseudoradiosa Zone (Kolb 1942; Riegraf 1996; Schlegelmilch 1998; Weis 1999; Arp 2010).

A clear assignment of bed 28 ("zeta conglomerate") to the Dispansum Zone was possible due to findings of well preserved *Phlyseogrammoceras dispansiforme* (Wunstorf) (Figs 11, 12) and *Phlyseogrammoceras transiens* (Ernst) (Fig. 13). The single finding of a ?*Alocolytoceras* sp. (Fig. 14) is consistent with this interpretation. Similarly, the co-occurring belemnite *Dactyloteuthis similis* (Seebach) (Fig. 22) is consistent with the Dispansum Zone (Kolb 1942; Riegraf 1996). One poorly preserved *Dumortieria* sp. at the top of bed 28 indicates the transition to the Pseudoradiosa Zone. Bed 31, forming the lowermost parts of the Opalinuston Formation, unfortunately revealed only indeterminable compressed ammonoids and may represent younger parts of the Pseudoradiosa Zone.

However bed 32, with reworked phosphorite nodules, some ooids, stromatolite crusts and abundant belemnites, clearly represents a condensed lowermost part of the Aalensis Zone due to findings of *Cotteswoldia aalensis* (Zieten) (Fig. 15), *Pleydellia subcompta* (Branco) (Fig. 16), *Pleurolytoceras* cf. *hircinum* (Schlotheim) (Fig. 17), *Hastites subclavatus* (Voltz) (Figs 24, 25) and *Acrocoelites rostriformis* (Theodori in Bronn) (Fig. 23). The following 10 m gap of exposure and beds 34 to 35 probably still represent the Aalensis Subzone.

While only few fragmentary ammonoid remains (Figs 18, 19: *Pleydellia* cf. *pseudoarcuata* Maubeuge, ?*Cotteswoldia* sp.) were recovered from beds 36–41 of alloformation 4 (≙ major parts of Opalinuston Formation), *Acrocoelites rostriformis* (Theodori in Bronn) from bed 39 (Fig. 26) indicates that this bed is still Upper Toarcian in age. This belemnite species is known to occur from the uppermost Pseudoradiosa Zone (i.e. Moorei Subzone) to the top of the Aalensis Zone (Riegraf 1996; Rulleau 2007), if its short variety "*Acrocoelits curtus* (d'Orbigny)" (e.g. Arp 2010) is included in this taxon. Pinard et al. (2014) indicate its range into the lowermost Opalinum Zone, but the assignment of corresponding findings (Dumortier and Fontannes 1876; Quenstedt 1845–1849) cannot unequivocally assigned to the Aalensis or Opalinum Zone.

Lower Aalenian: Clear indication of Lower Aalenian provides *Leioceras* cf. *goetzendorfensis* (Dorn) (ex *Leioceras comptum* (Reinecke); see Dietze et al. 2021) from nodules of bed 41 at the top of the Hainberg section (Fig. 20), which is affected by solifluction. The ammonite, therefore, probably originates from further up in the section. *In situ* evidence for the Opalinum Subzone has not been found at the Hainberg. *Leioceras opalinum* (Reinecke), however, has been mentioned from Dörnten by Brachmann (1991) and from Haverlahwiese, with several specimens are hosted in the collection of the BGR in Hannover (e.g., BGR-H-STGR-000241142; leg. Kolbe 1955, BGR-H-STGR-000241149: leg. R. Jordan 1958). Borgmann

(1990: p. 54, his Fig. 29) assigns a 15.4 m thick interval of claystones at Echte-Dögerode (30 km SSW of Hainberg) to the Opalinum Zone due to findings of *Leioceras opalinum lineatum* (Buckman). At Sehnde near Hannover, 30 km NNW of Hainberg, the Opalinum Zone is approximately 18 m thick (Hoffmann 1913).

In addition to the limited ammonite and belemnite findings discussed above, bivalve assemblages (Suppl. material 2) provide some supplementary information on the biostratigraphic position, when compared to the observations in Southern Germany (Röhl et al. 2001). The observations at Hainberg are also consistent with the distribution of bivalve assemblages mentioned in Maul (1984), Loh et al. (1986), and Riegel et al. (1986), except for *Steinmannia*, which has not been found at Hainberg. In Southern Germany, *Steinmannia radiata* (Goldfuss) is characteristic of the upper part of the Tenuicostatum Zone (Riegraf et al. 1984), i.e., and interval identical to the "*Bositra buchi* occurrence I" of Röhl et al. (2001).

With respect to the Serpentinum Zone (i.e., beds 10–17), bivalves are largely represented by *Parainoceramya dubia* (Sowerby) and *Meleagrinella* sp. As an intercalation, the *Bositra buchi* biofacies appears first in bed 16 of the Hainberg section, which corresponds to "occurrence II" of Röhl et al. (2001) in top parts of the Elegans Subzone in Dotternhausen. The *Bositra buchi* biofacies reoccurs in beds 18–21, which corresponds to the lower-middle Commune subzone in Dottenhausen (occurrence III of Röhl et al. 2001).

The Monotis event bed 22 corresponds to the Monotis bed in Southern Germany, i.e., a marker bed within Commune Subzone (Birzer 1936; Riegraf et al. 1984; Arp and Gropengießer 2016). From the sections Hainberg and Listringen it becomes clear that the Monotis event bed (i.e., the Monotis Bed s.str.) is located at the top of the "interval of Monotis limestones" sensu Weitschat (1973), which comprises a section of 40–100 cm thick shell-rich calcareous marls and marly limestones – possibly reflecting sediment condensation (Kaiser 2021). Finally, the cephalopod-free dwarf *Bositra buchi* biofacies is apparently time-equivalent to the *Bositra buchi* mass occurrence IV in Röhl et al. (2001) in the upper Commune and Fibulatum Subzones, however with cephalopods and normal-sized *Bositra* in Southern Germany. For the Upper Toarcian, with *Bositra suessi* dominating in bedded calcareous claystones and *Chlamys textoria* characterising condensed oolitic or conglomeratic beds, no ecostratigraphically relevant pattern has been recognized to date.

Sealevel changes and seawater currents

The investigated section Hainberg shows several discontinuities and condensed beds, separating continuous sediments with bedding or lamination, and beds with increased quartz silt and mica content (or even carbonaceous plant debris). Together with the biofacies and the comparison with sections along an offshore-coastal transect (Figs 1, 31), an interpretation of sequences controlled by sealevel changes can be made (Fig. 32). An important basis for comparison and discussion forms the sequence stratigraphic work of Zimmermann et al. (2015) for Northern Germany, as well as investigations from Southern Germany by Röhl and Schmid-Röhl (2005) and Arp et al. (2021) (Fig. 32). The transgressive-regressive sequences discussed here are considered to reflect changes in the shoreline trajectory, with the maximum regression surface at the end of a regression, and the maximum flooding surface at the end of a transgression (Embry and Johannessen 1992; Catuneau et al. 2009, 2011).

The Latest Pliensbachian sediments, i.e., the top of alloformation 1 (≙ Amaltheenton Formation) with quartz silt and mica, are considered as regressive, reflecting prograding siliciclastics of deltaic origin. This is in accordance with Zimmermann et al. (2015), who suggested a regression and mrs within Spinatum Zone. Seawater currents may have been directed from North to South, as indicated by the occurrence of cool water organisms (Arp and Seppelt 2012) and glendonites (Merkel and Munnecke 2023).

The following sequence boundary is located at or near the Amaltheenton/Posidonienschiefer Formation boundary, specifically within the lower Tenuicostatum Zone (Röhl and Schmid-Röhl 2005) or within the late Spinatum Zone (mrs Pli 2; Zimmermann et al. 2015). No sedimentological indication of a discontinuity is known from Hainberg and adjacent sections, so that a continuous sedimentation across the Pliensbachian-Toarcian transition appears likely. The lack of corresponding ammonites of the Paltum and Clevelandicum Subzones could reflect changing or reduced salinities during the lowstand conditions and proximity to deltaic influx.

For the 0.6 m thick Tenuicostatum and 6.6 m thick Serpentinum Zones, i.e. beds 7–17, a transgressive trend is indicated by first ammonites in bed 9, followed by ammonite-rich limestone concretions during the T-OAE (i.e., the negative $d^{13}C_{org}$ excursion in the Elegantulum and Exaratum Subzones; Hesselbo and Pieńkowski 2011; Xu et al. 2018) and continuing stagnant basin conditions with opportunistic bivalve assemblages during the Elegans and Falciferum Subzones (Röhl and Schmid-Röhl 2005).

Contrary to that, Zimmermann et al. (2015) suggest for the North-German Basin that this initial Toarcian transgression is followed by a maximum flooding surface (mfs Toa1) already within top parts of the Tenuicostatum Zone. This interpretation is based on a retrogradational shoreline shift of more than 200 km to the East (Zimmermann et al. 2015), with spreading of bituminous shale deposition to the Western Pomerania area (with *Dactylioceras* cf. *semicelatum*; Ernst 1967, 1991). Then, a regression from the latest Tenuicostatum to Bifrons Zone should follow, with the mrs Toa1 in the latest Bifrons Zone (Fig. 32).

Lowermost parts of the Bifrons Zone with the bivalve-shell-rich beds 18–22 (0.85 m "interval of Monotis limestones" sensu Weitschat 1973) can be interpreted as high-stand deposits with reduced rate of sedimentation (condensation according to Kaiser 2021), while the thin accumulation of *Meleagrinella* (*Clathrolima*) *substriata* (i.e., the Monotis bed s.str. at the top of this interval), trace-able along 500 km to Southern Germany, is considered as an event bed (Arp and Gropengießer 2016). Indeed, Röhl and Schmid-Röhl (2005) place a mfs at the Serpentinum/Bifrons zone boundary in Southern Germany (Fig. 32).

The belemnite accumulation on top of the Monotis event bed, also known from the Franconian Alb, might reflect a SSE to NNW directed seawater bottom current though the "Hessian Seaway" (Fig. 1), after the possibly tectonic-induced "Monotis bed event" (Arp and Gropengießer 2016). Current-aligned belemnites have also been mentioned and figured at the same stratigraphic bed from the open pit mine Haverlahwiese by Hoffmann (1968a: p. 496, his pl. 34). Likewise, Maul (1984: p. 30) shows a rose diagram of 500 measurements from the Commune Belemnite Battlefield at Hildesheim-Itzum with a clear maximum at 165°, i.e., confirming a bottom current directed from SSE to NNW (Suppl. material 4). Later parts of the Bifrons Zone, i.e., the 18.66 m upper Posidonienschiefer Fm. (i.e., beds 24–26) with its cephalopod-free dwarf *Bositra* biofacies and increasing content of fine-grained mica and plant debris, is best explained as the regressive phase of a sequence (Fig. 32), with increasing terrestrial influx and decreasing salinities, in accordance with Zimmermann et al. (2015) and Röhl and Schmid-Röhl (2005). The lowering of carbonate-free C_{org} contents from the upper Falciferum (ca. 23 wt%) to the Bifrons Zone bituminous shales (about 13.5 wt%) reflects a dilution effect by the increased sedimentation rate. Anoxic bottom water conditions, therefore, continued unchanged in this region proximal to deltaic influx.

For the Upper Toarcian, a sequence stratigraphic interpretation remains difficult for the investigated section, because the absence of the Variabilis Zone and major parts of the Thouarsense Zone, a 10-m-lack of exposure, and limited ammonite findings. A preliminary interpretation, however, can be given on basis of the comparison with adjacent sections (Figs 31, 32).

A sealevel lowstand is inferred for the basis of the Variabilis Zone, i.e. just prior to the deposition of the Dörnten Subformation. The latter, while preserved in its type region and some basinal sections (e.g. Echte; Hoffmann 1968a), obviously has been eroded in the area Haverlahwiese-Hainberg-Hildesheim (except for Hildesheim-Bischofskamp: Denckmann 1892: p. 101).

Contrary to Southern Germany, there is apparently no significant erosional discontinuity within (Arp et al. 2021) or at the top of the Variabilis Zone (Riegraf 1985; Jordan and Schmidt-Kaler 1985), because the presence of all its subzones is evident by corresponding ammonite findings at Dörnten (Denckmann 1892; Ernst 1923–1924; Brachmann 1991). This might be related to higher subsidence and sedimentation rates in Northern Germany. Likewise, the Thouarsense Zone at Dörnten is proven by *Pseudogrammoceras doerntense* (Denckmann), *Ps. bingmanni* (Denckmann), *Ps. struckmanni* (Denckmann), and *Grammoceras striatulum* (Sowerby), with only the Fallaciosum Subzone absent (Fig. 32). Continuous sedimentation with bituminous shales from the Bifrons to Variabilis Zone is also likely farther North in Schandelah (van de Schootbrugge et al. 2019: p. 272; Visetin et al. 2022). The precise nature of the sedimentological boundary Posidonienschiefer s.str. to Dörnten Member (i.e., sharp or gradationally) is, however, unknown.

In any case, after the regressive top of the Bifrons Zone (i.e., the top of the Posidonienschiefer Formation with cephalopod-free dwarf *Bositra* biofacies), the change to a cephalopod biofacies (with ammonite-rich limestone concretions at Dörnten, Gallberg, and corresponding relics at Hildesheim-Bischofskamp) could best be explained by a transgression. Deviating from that, Zimmermann et al. (2015) suggests transgressive conditions only during the early Variabilis Zone, with a maximum flooding surface (mfs Toa2) within the latest Variabilis Zone (Fig. 32).

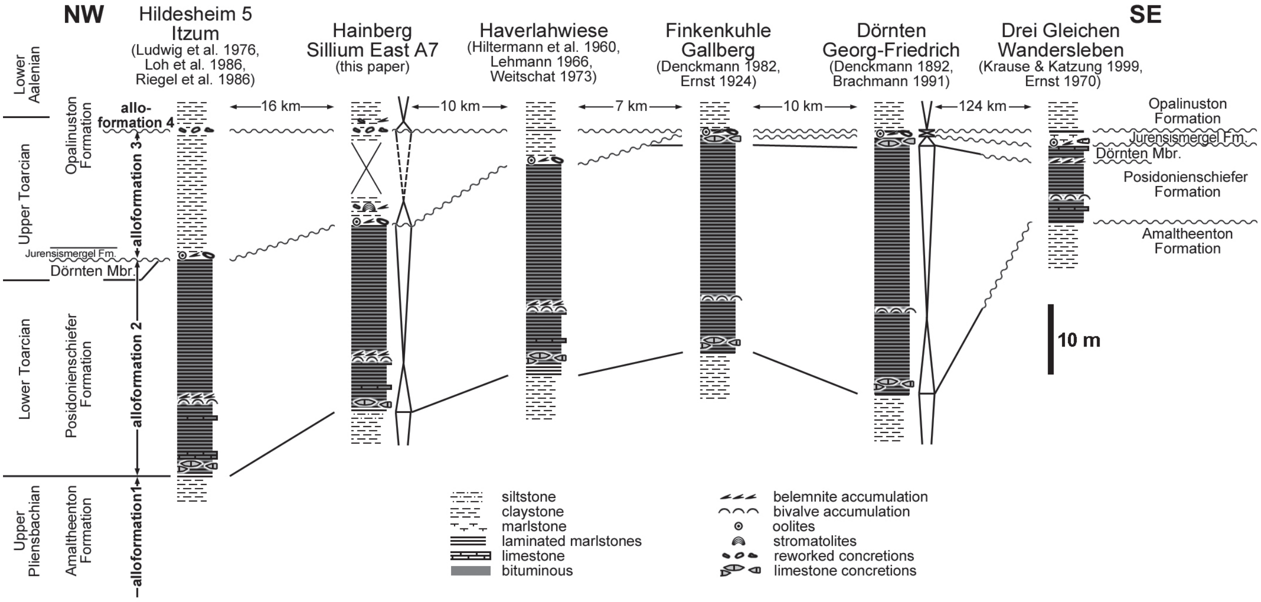

Figure 31. Correlation of the investigated section Hainberg with sections from Northern Germany and Thuringia, with suggested T-R cycles for the sections Hainberg and Dörnten.

The basis of the Dispansum Zone, i.e., the basis of alloformation 3, is the most obvious erosional sequence boundary in the working area, as indicated by conglomeratic oolitic marls and belemnite accumulations (i.e. beds 27–28) (Fig. 31). Indeed, submarine erosion removed the Variabilis and Thouarsense Zones as well as top parts of the Bifrons Zone in the area Haverlahwiese-Hainberg-Hildesheim, as already described by Denckmann (1892: p. 107). These conglomeratic deposits comprise reworked ammonites of the Variabilis and Thouarsense Zones (e.g. *Haugia* and *Grammoceras* sp. at Hildesheim-Itzum: Maul 1984; *Osperleioceras* cf. *beauliziense* (Monestier) at Hainberg), but are dominated by *Phlyseogrammoceras dispansum* (Lycett) and *Phl. dispansiforme* (Wunstorf), at least in their upper part (Hainberg). Unfortunately, no clear direction of potential bottom water currents was obtained from belemnite rostra alignment measurements (Fig. 29).

In accordance with that, Zimmermann et al. (2015) place their maximum regression surface mrs Toa2 within the latest Thouarsense Zone. Indeed, most of the described Jurensismergel Fm. sections in Northern Germany show a stratigraphic gap for the Fallaciosum Zone (Heidorn 1928), similar to Southern Germany, where a discontinuous Dispansum Zone belemnite accumulation overlies the Thouarsense Subzone with local erosion of the Fallaciosum Subzone (Arp et al. 2021). The conglomeratic-oolitic Dispansum Zone sediments themselves appear to be transgressive, with reworking at highly reduced siliciclastic influx.

The ongoing sealevel rise could be represented by strata dated to the Pseudoradiosa Zone, i.e., beds 29–31 of the Hainberg section. The condensed bed 32 with stromatolites might represent high-stand conditions, in analogy to the Pseudoradiosa/Aalensis zone transition in the Franconian Alb (Arp et al. 2021), if this correlation is correct. Unfortunately, the presence of this condensed bed has not yet been shown in adjacent sections due to limited detailed sedimentological observations (Fig. 31). Likewise, the following Aalensis Zone claystones (beds 34–35) are herein tentatively considered to represent a regressive phase. The discontinuity at bed 36 (i.e., the basis of alloformation 4), then possibly reflects a further sealevel lowstand and sequence boundary. Strikingly, a 1 m thick shelly carbonate bed has been reported from the Toarcian-Aalenian transition at Echte-Dögerode, 30 km SSW of the Hainberg (Borgmann 1990), where the Upper Toarcian is about 25 m thick (Hoffmann 1949, p. 122). Unfortunately, no definite ammonite proof of the presence and extent of the Pseudolotharingicum Subzone (i.e. top of Aalensis Zone) is available at the investigated section Hainberg. However, accepting *Acrocoelites rostriformis* (Theodori in Bronn) as an index fossil of the Upper Toarcian, the Pseudolotharingicum Subzone might cover the

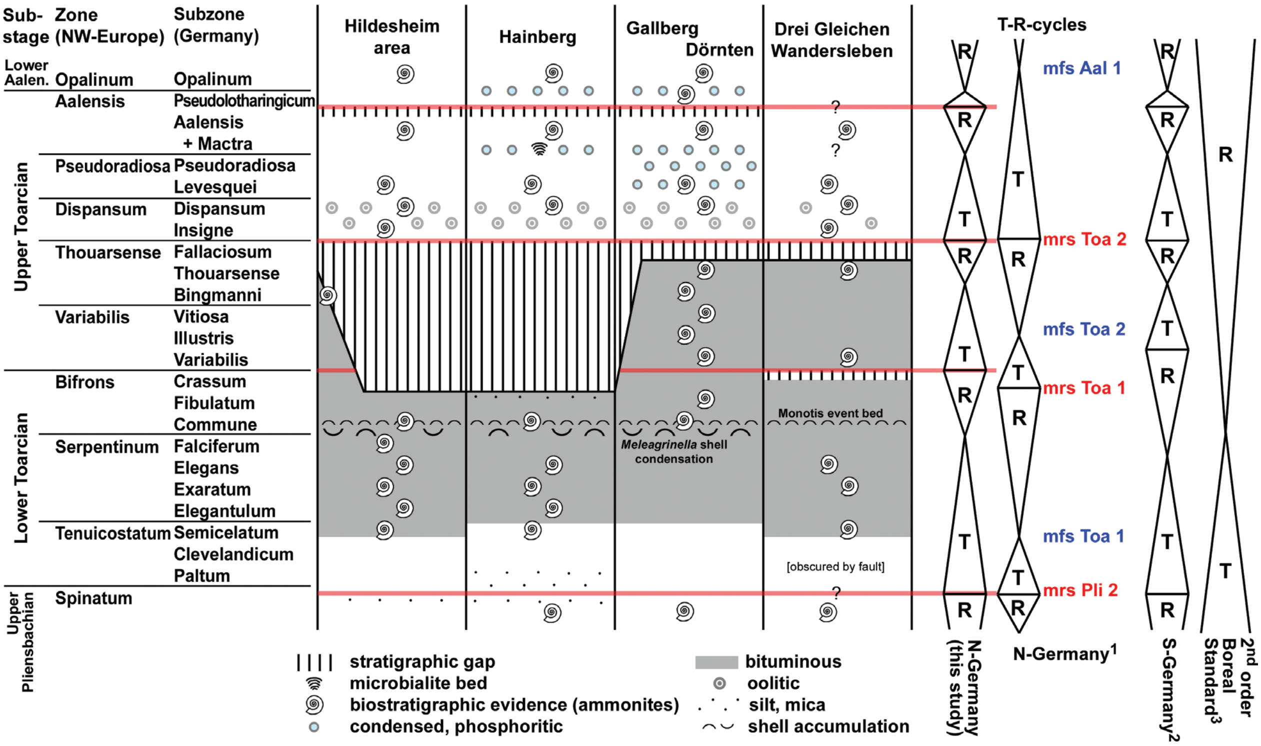

Figure 32. Sequence stratigraphic interpretation of the Toarcian succession in Northern Germany (including the Hainberg section) and Thuringia in comparison with 3rd order South-German and the 2nd order Boreal standard cycles. Sedimentary succession and ammonite biostratigraphic evidence according to Denckmann (1892), Ernst (1923–1924), Kumm (1941), Ernst (1970), Maul (1984), Brachmann (1991), Krause and Katzung (1999), and specimens from the BGR collection [https://gewis.bgr.de/, leg. K. Hoffmann, R. Jordan, K. Wiedenroth]. T-R cycles: [1] third order sequences Northern Germany (Zimmermann et al. 2015), [2] third order sequences Southern Germany (Röhl and Schmid-Röhl 2005; Arp et al. 2021); [3] second order sequences Boreal standard (de Graciansky et al. 1998; Jacquin et al. 1998).

thin transgressive interval of bed 38, followed by a condensed bed 39 and thicker regressive claystones (bed 40 and younger) of the Opalinum Zone. In any case, the sequence stratigraphic considerations on the Toarcian-Aalenian transition currently remain hypothetical and further complete sections with sufficient ammonite findings are required for testing and potential corrections.

Minor differences appear in the positions of maximum regression and maximum flooding surfaces between Toarcian sections of the central North-German Basin to Poland (Zimmermann et al. 2015), southern part of Northern Germany (this paper) and Southern Germany (Röhl and Schmid-Röhl 2005; Arp et al. 2021). These may reflect limitations of biostratigraphic high-resolution dating in the ammonoid-poor North-German deposits proximal to deltaic foresets, and corresponding interpolations in stratigraphic dating and correlation (Fig. 32).

Furthermore, the high thickness of sections in the Northern Germany and Poland (i.e. 82 to 231 m Toarcian for Usedom to Hamburg; Baermann et al. 2000; Zimmermann et al. 2015; e.g. ca. 90 m Toarcian at Nowa Wieś 12-Praszka 1/81: Pienkowski 2004) indicates significant higher subsidence and sedimentation rates, if compared to the Hainberg-Hildesheim area. Significantly increased clastic deposition (delta front and prodelta) during eustatic sealevel fall and (forced) delta progradation may have caused an apparent earlier onset of relative sealevel fall, if compared to the low subsidence and low sedimentation rate areas in Southern Germany. In turn, stratigraphic gaps covering intervals longer than subzones obscure the precise timing of maximum regression in areas of low subsidence, while ammonoid findings in thicker but more proximal positions are rare.

A further complication for interpreting thickness pattern and sedimentary sequences in the working area may result from possible synsedimentary ortho- and halotectonic movements during the Lower Jurassic at the Eichfeld-Altmark-High. Indeed, the available thickness data for alloformation 2 (Posidonienschiefer Fm. exclusive Dörnten Member) show short-distance variations between 29.7 and 33.4 m in the Hildesheim area, between 23.3 and 30.4 m at the Hainberg (unpublished drilling reports BGR), and between 30 and 37 m at the Salzgitter anticline (Gallberg: Ernst 1923–1924; Schröderstollen: Dahlgrün 1928) (Fig. 31). Larger thickness variations have been reported from the Hils Syncline (16 to 40 m; Littke and Rullkötter 1987), while the Braunschweig area shows rather uniform thickness pattern (Brockamp 1944) around 36.5 m (Schandelah; Visetin et al. 2022). For the lower and middle Posidonienschiefer Fm. a minor reduction in thickness is evident for the Hainberg, Haverlah and Gallberg sections, if compared to the Hildesheim area (NW) and Dörnten area (SE) (Fig. 31), as well as the Braunschweig area (Wunnenberg 1950; Visentin et al. 2022). These data, however, may rather point to minor local halotectonic movements or erosion at the top of the formation. Nonetheless, reduced thicknesses of 12 m at Wefensleben (67 km ENE of the Hainberg section; Koert 1923), possibly 3 to 7 m at Bad Harzburg (30 km SE of the Hainberg section; Kumm et al. 1941; Brockamp 1944), and 12–16 m in the Altmark area (Bauss 1976) may point to a structural zone of reduced subsidence farther East, i.e. the Eichsfeld-Altmark-High.

For alloformation 3 and 4 (i.e., Dörnten Member and Jurensismergel plus lower Opalinuston Fm.), spatial thickness pattern are even less well known due to poor outcrop conditions and difficulties in recognizing lithostratigraphic boundaries in drillings. Thus, the relation of condensed sections of these allostratigraphic units (e.g., in the Gallberg-Dörnten area) to structural elements remains to be investigated.

Conclusions

- Construction work at the A7 motorway cutting at the Hainberg, Lower Saxony, temporarily exposed a 40.81 m thick section of the Toarcian, with a 10 m gap within the Upper Toarcian Aalensis Zone.
- Above quartz silt bearing claystones of the Pliensbachian Amaltheenton Formation (alloformation 1), the 26.74 m thick Toarcian Posidonienschiefer Formation (alloformation 2) starts with 0.6 m laminated, C_{org}-poor claystones, followed by 6.6 m bituminous laminated marlstones with limestone beds, and the 0.85 m thick "interval of Monotis limestones". The C_{org} (carbonate-free) maximum of 24.5 wt% lies within the Elegantulum Subzone, while average C_{org} (carbonate-free) contents are about 19 wt%. The upper, 18.66 m thick part of the Posidonienschiefer Formation is characterised by varying, generally lower C_{org} contents (carbonate-free) around 13.5 wt%.
- Above an erosive discontinuity, the 13.76 m thick alloformation 3 comprises the 0.45 m thin Jurensismergel Formation with iron-oolitic marls including belemnite accumulations, and a 13.31 m interval (lowermost Opalinuston Formation) of C_{org}-poor carbonate clays with an intercalated ammonite condensation layer. The latter shows thin, non-cyanobacterial stromatolitic crusts. The boundary to the alloformation 4 (major parts of Opalinuston Formation) is drawn with an erosional layer of corroded geodes and echinoderm debris.
- With respect to biostratigraphy, ammonite findings indicate for the Lower Toarcian Posidonienschiefer Formation the presence of the Tenuicostatum Zone, Elegantulum-Subzone, Exaratum-Subzone, Elegans Subzone, and Commune Subzone. The presence and extent of the Falciferum Subzone is delimited by a first *Bositra buchi* maximum and the "interval of Monotis limestones". The upper Posidonienschiefer Formation is devoid of ammonites and might represent the late Commune and Fibulatum subzones. With respect to the Upper Toarcian Jurensismergel Formation, the Variabilis Zone is absent. One reworked *Osperleioceras* cf. *beaulizieuse* (Monestier) likely represents a relic of the Thouarsense Zone within thin condensed iron oolitic marls of the Dis-

pansum Zone at the discontinuous basis of the formation. The following calcareous claystones comprise the Pseudoradiosa and Aalensis zones, with their upper limit indicated by the last *Acrocoelites rostriformis* (Theodori in Bronn) in a thin layer of reworked fossils. Evidence for the Lower Aalenian, i.e. *Leioceras* cf. *goetzendorfensis* (Dorn), is found at the solifluction affected top bed of the section.

- With respect to sequence stratigraphy, three 3rd order transgressive-regressive cycles are recognized for the Toarcian succession in the investigated area, largely in accordance with previous studies in Northern (Zimmermann et al. 2015) and Southern Germany (Röhl and Schmid-Röhl 2005; Arp et al. 2021). After a regression during late Pliensbachian, a sequence boundary is evident at the Amaltheenton-Posidonienschiefer transition (mrs Pli 2 sensu Zimmermann et al. 2015). A transgressive phase is represented by the Elegantulum to Falciferum subzones, with highstand conditions and reduced sedimentation during Commune Subzone, superimposed by the Monotis bed event. A belemnite battlefield indicates seawater bottom currents from SSE. The corresponding regressive phase with increased sedimentation is developed during late parts of the Bifrons Zone. The cephalopod-free dwarf *Bositra* biofacies with increasing mica and plant debris reflects distant effects of prograding deltas and reduction of salinities. The following sequence boundary, not preserved at the site of investigation, is located at the Bifrons/Variabilis transition (mrs Toa 1 sensu Zimmermann et al. 2015).

  For the Upper Toarcian, the following tentative interpretation is given: The Variabilis to Thouarsense Zone represented by the Dörnten Member is likely a transgressive phase and highstand of the second Toarcian T-R cycle. The following regressive phase (Fallaciosum Subzone) is rarely preserved in Northern Germany. A major sequence boundary with significant erosion at Thouarsense-Dispansum zone boundary (mrs Toa 2 sensu Zimmermann et al. 2015) is associated with the removal of the Dörnten Member in the Hainberg-Hildesheim area. The following Dispansum Zone iron oolitic marls and Pseudoradiosa Subzone clays possibly form a transgressive phase of a third Toarcian T-R cycle, with highstand at the Pseudoradiosa-Aalensis zone transition. Aalensis Subzone claystones may represent the regressive phase, with a minor erosional sequence boundary at their top. The poorly delineated Pseudolotharingicum Subzone might be transgressive, with highstand condensations at its top, followed by a regressive phase of the Lower Aalenian Opalinum zone claystones.
- Minor deviations in the timely position of maximum flooding and regression surfaces between the different studies (Zimmermann et al. 2015; Röhl and Schmid-Röhl 2005; Arp et al. 2021) likely reflect effects of a higher subsidence at variable sedimentation rate in the North German Basin.

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Supplementary material 1

Measurements of belemnite alignments in the Posidonienschiefer and Jurensismergel Formations, Toarcian, Hainberg section

Authors: Gernot Arp, Yagmur Balmuk, Stephan Seppelt, Andreas Reimer

Data type: xls

Link: https://doi.org/10.3897/zitteliana.97.110677.suppl1

Supplementary material 2

Selected biofacies of the Toarcian to lowermost Aalenian succession, Hainberg section

Authors: Gernot Arp, Yagmur Balmuk, Stephan Seppelt, Andreas Reimer

Data type: jpg

Explanation note: (1) *Parainoceramya* biofacies, bed 11 "Boreale Concretions", middle Posidonienschiefer Formation. GZG.INV.891. (2) *Bositra buchi* biofacies, bed 21, middle Posidonienschiefer Formation. GZG.INV.892. (3) Cephalopod-free dwarf *Bositra buchi* biofacies, 9 m above basis of bed 24, upper Posidonienschiefer Formation. GZG.INV.893. (4) *Chlamys textoria* biofacies, bed 27 "oolite marl", Jurensismergel Formation. GZG.INV.894. (5) Nubeculariid foraminifera on bioclasts of the *Chlamys textoria* biofacies. Bed 29, Jurensismergel Formation. GZG.INV.895. (6) *Bositra suessi* biofacies, 80 cm above basis of bed 40, Opalinuston Formation. GZG.INV.896.

Link: https://doi.org/10.3897/zitteliana.97.110677.suppl2

Supplementary material 3

Columnar section from the middle part of the Posidonienschiefer Formation at Listringen

Authors: Gernot Arp, Yagmur Balmuk, Stephan Seppelt, Andreas Reimer

Data type: jpg

Explanation note: According to Vinken (1971).

Link: https://doi.org/10.3897/zitteliana.97.110677.suppl3

Supplementary material 4

Columar section of the lower and middle Posidonienschiefer Formation at Hildesheim-Itzum

Authors: Gernot Arp, Yagmur Balmuk, Stephan Seppelt, Andreas Reimer

Data type: jpg

Explanation note: According to Maul (1984), Loh et al. (1986), and Riegel et al. (1986).

Link: https://doi.org/10.3897/zitteliana.97.110677.suppl4

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On Paleozoic platycerate gastropods

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Abstract

The platycerate gastropods *Orthonychia yutaroi* Ebbestad, **sp. nov.** (Ordovician, Boda Limestone, Sweden), *O. enorme* (Silurian, Sweden, Gotland), *O. parva* (Pennsylvanian, Finis Shale Member, USA), and *Orthonychia* sp. (Mississippian, Imo Formation, USA) are studied including their protoconch morphology. *Orthonychia yutaroi* is the oldest known species in *Orthonychia*. Platycerates contain species with both, openly and tightly coiled protoconchs. This is the first report that tightly coiled protoconchs occur in *Orthonychia*. This and previously published observations blur the diagnostic difference between orders Cyrtoneritimorpha (openly coiled protoconch) and Cycloneritimorpha (tightly coiled protoconch). We suggest to treat Cyrtoneritimorpha and Cycloneritimorpha as synonyms of Neritimorpha. The monotypic Devonian genus *Pragoserpulina* is morphological so close to the *Orthonychia* species reported herein that synonymy of both genera seems to be possible (and thus of the families Pragoserpulinidae and Orthonychiidae). Protoconch morphology and dimensions suggest that the studied platycerate species had planktotrophic larval development. By contrast, two studied Carboniferous euomphaloid species (one with an openly and the other with tightly coiled protoconch) have paucispiral, large protoconchs indicating non-planktotrophic larval development. We assume that openly and tightly coiled protoconchs were present in various Paleozoic gastropod clades and that selection acted against the openly coiled protoconch morphology. It has previously been proposed that increasing predation pressure in the plankton was the reason for the demise of openly coiled protoconchs (Paleozoic plankton revolution). The presence of larval planktotrophy in platycerates excludes the possibility that they belong to extant basal gastropod clades such as Patellogastropoda, Cocculiniformia, and Vetigastropoda. However, a previously proposed close relationship to Neritimorpha is corroborated.

Keywords

Mollusca, Gastropoda, Neritimorpha, Ordovician, Silurian, Carboniferous, Sweden, USA, protoconchs, systematics, larval development

PENSOFT.

Introduction

Platyceras, *Orthonychia* and other similar genera are more or less limpet-shaped Paleozoic gastropods that occur often abundantly from the Ordovician to the Permian. Such *Platyceras*- and *Orthonychia*-like gastropods are informally called platycerates herein. They are best known for their association with crinoids and there are numerous reports of them still being attached to their crinoid host (e. g., Baumiller and Gahn 2002) although by far most specimens are known isolated (unattached to crinoids). Simplified, *Platyceras* is more strongly bent and coiled, and becomes limpet-shaped with a widened aperture only late in ontogeny. By contrast, *Orthonychia* shows strong coiling of the teleoconch only in its early ontogeny whereas the late shell is almost straight conical and tube-like. These morphologies are unusual in Gastropoda and are interpreted as adaptations to their sedentary life on crinoids (e. g., Frýda et al. 2008b and references therein). Phylogeny and systematic placement of platycerates have been a matter of debate. Wenz (1938) placed Platyceratidae in Archaeogastropoda: Trochonematoida, Knight et al. (1960) in Archaeogastropoda: Trochina, and Bouchet et al. (2005, 2017), based on Bandel and Frýda (1999) in Neritimorpha. Close phylogenetic links to euomphalids (Wagner 2002; Kaim 2004) and patellids (Sutton et al. 2006, see Frýda et al. 2009 for a discussion) have been discussed.

Simplified current classification of *Platyceras* and *Orthonychia* based on Bouchet et al. (2005, 2017):

Subclass Neritimorpha Koken, 1896
    Order uncertain
        Superfamily Platyceratoidea Hall, 1879
            Family Platyceratidae Hall, 1879
    Order Cyrtoneritimorpha
            Family Orthonychiidae Bandel & Frýda, 1999
            Family Vltaviellidae Bandel & Frýda, 1999

Orthonychia was commonly used as a subgenus of *Platyceras* and even synonymy of both genera has been discussed. For instance, Rollins and Brezinski (1988: 209) stated: "Even the distinction between *Platyceras* (*Platyceras*) and *Platyceras* (*Orthonychia*) is most likely no more than a morphological convenience (Yochelson 1969; Keyes 1894). The differentiation of the two subgenera depends entirely upon the nature of the juvenile whorls; they are in contact in the subgenus *Platyceras* and disjunct in the subgenus *Orthonychia*" (it is unclear as to whether "juvenile whorls" includes the protoconch here). However, based on the presence of openly coiled protoconchs, *Orthonychia* was placed in the family Orthonychiidae and in the order Cyrtoneritimorpha (Bandel and Frýda 1999). Thus, these character states had been considered diagnostic at a high level in systematics i. e, for the order Cyrtoneritimorpha (including *Orthonychia*) (Bandel and Frýda 1999). But then, Frýda et al. (2009) reported that Platyceratoidea contain both, members with uncoiled and with tightly coiled larval shells. This could suggest, that Cyrtoneritimorpha are not monophyletic or that this character is not (or at least not always) diagnostic at high systematic levels i. e., both character states may be present in a single superfamily, family or genus.

Well-preserved high-conical limpet-shaped gastropods of the *Orthonychia*-type from the Late Ordovician Boda Limestone, Sweden (Fig. 2), the Silurian of Gotland, Sweden (Figs 3–8), the Pennsylvanian Finis Shale, Texas, USA (Figs 9–12), and the Mississippian Imo Formation, Arkansas, USA (Fig. 13) are reported in the present contribution. They provide new morphological details about this gastropod group that may help to better understand its evolutionary history.

Teleoconch morphology

Probably due to their sedentary, parasitic or commensal life style, shell plasticity and intraspecific variability are pervasive in platycerates including *Orthonychia* making alpha taxonomy and systematics particularly difficult (Knight 1934; Yochelson 1956; Frýda et al. 2008b and references therein). As outlined above, *Platyceras* species are more strongly coiled, cap-shaped with wide apertures. The teleoconch of *Orthonychia* is only initially coiled and later uncoiled, often forming an almost straight tube. Most of these cap-shaped gastropods lack shell ornaments but commonly have irregular co-marginal rugae and longitudinal folds towards the aperture probably reflecting the morphology of their substratum, namely their crinoid hosts. The Devonian *Crossoceras* Boucot & Yochelson, 1966 (originally placed in Platyceratidae) has the shape of *Platyceras* but is ornamented with co-marginal sharp ribs (frills, lamelllae) and a fine spiral lineation. This type of teleoconch ornament is also present in *Orthonychia yutaroi* sp. nov. and *Orthonychia enorme* from the Silurian of Gotland as is reported in the following. A similar shell ornament is also present in the Devonian *Pragoserpulina* Frýda, 1998a which also has disjunct late teleoconch whorls (Frýda 1998a, b). Pronounced frills are also present in "*Platyceras* (*Platyceras*) *cornutum loricatum* Lindström, 1884" as reported by Rohr et al. (1981) from the Silurian of the Canadian Arctic. Some platycerate shells have pronounced hollow spines (e. g., Blodgett et al. 1988; Blodgett and Frýda 1999; Cook and Jell 2016). The taxonomic and systematic relevance of such ornaments in *Orthonychia* and similar forms is obscured by the fact that the Devonian type species of *Orthonychia* is known from steinkerns only (Knight 1941) and hence its ornament type is unknown.

Shell mineralogy

Platyceras and *Orthonychia* have calcitic shells (Knight 1934; Yochelson and Kriz 1974; Batten 1984; Carter and Hall 1990). Carter and Hall (1990) reported chiefly crossed semi-foliated and complex crossed semi-foliated shell microstructures. As to whether shells were bi-mineralic with an inner aragonitic layer (as is found in Recent Neritimorpha) is unclear. Thin sections of Silurian specimens from Gotland provided herein support that *Orthonychia* has a primarily calcitic, foliated shell micro-structure (Fig. 6). Thin calcitic outer shell layers are also present in Mesozoic and modern Neritimorpha and also in Paleozoic/Mesozoic Naticopsidae which would corroborate the assumption that these groups are closely related.

Operculum

Opercula have not been reported for *Platyceras*- and *Orthonychia*-like gastropods which seems unsurprising considering their attached lifestyle. However, mineralized opercula are well-known in other Neritimorpha including Paleozoic Naticopsidae (e. g., Kaim and Sztajner 2005; Nützel and Nakazawa 2012).

Protoconch morphology

Protoconch morphology may yield crucial information for gastropod taxonomy, systematics and larval ecology. Unfortunately, protoconchs are unknown for the majority of Paleozoic gastropods due to insufficient preservation (Nützel 2014). Protoconchs of a few platycerates have been reported (Knight 1934; Yochelson 1956; Bandel and Frýda 1999; Frýda et al. 2009). Knight (1934), Bandel and Frýda (1999), and Frýda et al. (2009) showed that the Pennsylvanian *Orthonychia parva* has an openly coiled protoconch, that is partly even straight and elongated. Yochelson (1956: 259) stated that “It may be that the vermiform protoconch represents a free living stage, and as soon as the specimen became attached to a crinoid calyx it expanded rapidly to increase the area of attachment.” However, he did not consider the possibility that the hook-like protoconch is a larval shell of the planktotrophic type. Yochelson (1969: 31) stated: “Species of *Platyceras* that have a curved horn shape to the body whorl may or may not have the protoconch coiled. The presumed distinction between *Platyceras* in a restricted sense, with half a whorl or more in contact, and the subgenus *Orthonychia*, without any of the juvenile shell in contact, may be artificial, especially in those forms where the area of contact is extremely small compared to the size of the mature shell.” Thus, Yochelson (1969) was aware of the fact that both, openly coiled and tightly coiled protoconchs are present in platycerates.

Many Ordovician and Silurian internal molds of gastropod protoconchs (many from micro-samples dissolved with acid for conodonts) display open coiling resulting in almost straight to fish-hook-like morphologies as was also reported for *Orthonycha parva* (Nützel and Frýda 2003; Nützel et al. 2006, 2007a). In some cases, such a morphology might represent a preservational artifact (Dattilo et al. 2016) but this is clearly not so in all cases. Rarely the openly coiled morphology has also been found in Paleozoic protoconchs with preserved shells (and not as steinkerns) and more of such rare examples are reported herein. The openly coiled protoconch morphology gradually vanished until the Late Triassic (Nützel and Frýda 2003; Nützel et al. 2006, 2007a; Nützel 2014; Seuss et al. 2012; Dzik 2020). In the Late Paleozoic, such uncoiled protoconchs are present only in a small minority of species for which the protoconchs are known. However, the large majority of Late Paleozoic gastropods with preserved protoconchs have tightly coiled larval shells (Nützel and Frýda 2003; Nützel 2014) as is also usual for modern marine gastropods (only some modern holoplanktonic gastropods have elongated protoconchs). Here, we report openly coiled protoconchs for two Carboniferous taxa and we will discuss whether these protoconchs reflect planktotrophic larval development.

Repository, institutional abbreviations

The studied material is reposited in the following institutions:

NRM	Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.
PMU	Palaeontological collections, Museum of Evolution, Uppsala University, Sweden.
SNSB-BSPG	Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany

Material and methods

As mentioned, well-preserved high-conical limpet-shaped gastropods of the *Orthonychia*-group from the Late Ordovician Boda Limestone, the Silurian of Gotland (both Sweden), the Mississippian Imo Formation, Arkansas, USA, and the Pennsylvanian Finis Shale, Texas, USA are reported in the present contribution. Details about the four localities from which the studied gastropods stem are provided in the material section for each of the taxa.

The **Boda Limestone** is represented by large carbonate mud mounds of Late Ordovician (Katian) age, exposed in several quarries in the Siljan district of central Sweden (Fig. 1A). The mound fauna is exceptionally diverse and well-preserved (Ebbestad and Högström 2007). More than 50 species of gastropods are present but although several species are described the main gastropod fauna remains to be studied (e. g., Angelin and Lindström 1880; Koken 1897; Koken and Perner 1925; Wängberg-Eriksson 1964, 1979; Ebbestad 1999; Gubanov et al. 1999; Ebbestad and Peel 2001). Case studies of failed predatory attacks on Boda Limestone gastropods were given by Ebbestad and Peel (1997). A number of platycerate gastropod species occur in the Boda Limestone but no one shows obvious

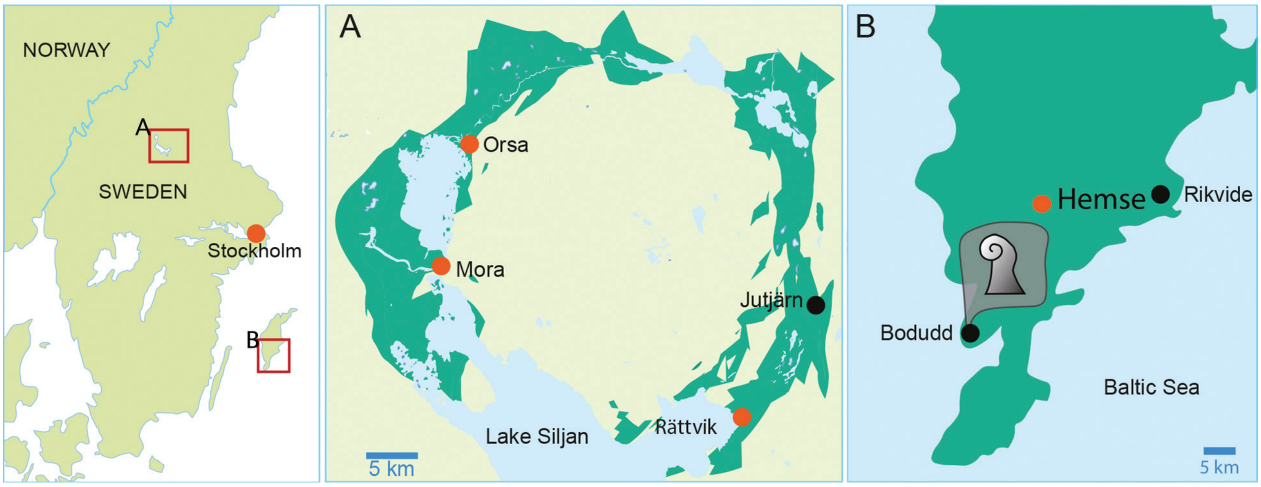

Figure 1. Locations of the studied material of the Ordovician Boda Limestone **(A)** and the Silurian Eke Formation, Gotland **(B)**.

morphological modifications of the shape of the aperture during growth, which would otherwise indicate obligatory attachment to a substrate or host (e. g., Baumiller and Gahn 2002). Furthermore, one cannot assume that this mode of life applied to all platycerates or cyrtoconic platycerates. Crinoidal packstone is common as flank deposits but nearly absent in the main mound facies, so any crinoidal hosts are not obvious. Fossils in the Boda Limestone are mainly preserved in shell accumulations in deep and often large and complex synsedimentary fissures (Suzuki and Bergström 1999; Kröger et al. 2016). The main constituency of the accumulations consist of trilobite remains, typically made up of only one specific taxon where *Stenopareia linnarssoni* and *Eobronteus laticauda* are the two most common. Only one accumulation consisting of gastropods is known, represented by a block made up of *Subulites* specimens (Thorslund 1936, fig. 9). Gastropods are otherwise found as scattered remains within the trilobite accumulations and mostly only one or two specimens are known of the more uncommon species.

The gastropod fossils presented here from the **Silurian of Gotland** stem from the Eke Formation (Ludlow, South Gotland, localities Rikvide and Bodudd). The island of Gotland, Sweden, is situated in the Baltic Sea (Fig. 1B). The Silurian deposits of Gotland comprise a section of latest Llandovery- to Ludlow-aged deposits representing remnants of a former extended carbonate platform complex and the erosional leftovers create a succession that is up to 700 m thick (Calner et al. 2004). Late diagenetic alteration and tectonic disturbance of the rock sequences are rarely observed (Calner et al. 2004). The youngest strata occur in the southeast of the island and become older towards the northwest (compare Calner et al. 2004; Calner 2008). Deposits show a distinct difference in distribution: while the NE is dominated by sediments representative of shallow marine settings, the western part of Gotland is characterized by argillaceous limestones and marls of an open marine shelf (Samtleben et al. 1996; Hede 1960; Jeppsson 1994; Calner et al. 2004; Jeppsson et al. 2006).

Gastropods from the Silurian of Gotland are mainly known from the classic monograph of Lindström (1884) who reported more than 160 species from this island. Since then, few taxonomic studies about this gastropod fauna have been conducted. A washed residue from marls of the Eke Formation (Ludlow, South Gotland) has yielded a fossil assemblage with numerous small vermiform, horn-shaped gastropods, here identified as *Orthonychia enorme*. This gastropod species is described and reported in detail herein. The samples also have yielded abundant oncoids, some of which are also cone-shaped and might have these gastropods as a substrate.

The Eke Formation contains deposits from the Lau event with its strong positive $\delta^{13}C$ excursion, the highest in the entire Phanerozoic (Samtleben et al. 1996; Calner 2008). The Formation can be subdivided into three conodont zones, the Lower, Middle and the Upper Icriodontid Subzone (Jeppsson 2005). The Eke Fm. on western Gotland is characterized by a heterogeneous succession of oncoid-rich wacke-, pack-, and grainstones. Deposits studied derive from a section characterized by a micritic limestone-marl alternation from the Bodudd locality that is extremely rich in oncoids, microbial mats and crusts.

Samples were collected during a student field course in 2013 (Fig. 1C). The deposits containing oncoids and the studied mollusks derive from a topographically flat peninsula running from east to west. Along this into the Baltic Seas protruding headland the samples were collected at three localities (Eke A: 57°04'11.9"N, 18°11'19.2"E / Eke B: 57°04'10.9"N, 18°11'00.8"E / Eke C: 57°04'05.8"N, 18°11'34.7"E). At this locality, the Eke Formation is exposed as limestone-marl-alternations consisting of almost horizontal layers that fall in flat steps towards the Baltic Sea. Eke A and Eke B originate from the lower, Eke C from the upper part of the formation. The samples were dissolved in H_2O_2, sieved (>2 mm, >500 µm, >250 µm) and the residues were picked.

Besides the common *Orthonychia enorme* reported herein, a large number of oncoids, brachiopods and echinoderm remains (especially crinoid remains) are present as well as rostroconchs and a few bivalves. Ostracods are rather common while remains of blastoids, tentaculites and trilobite fragments are less abundant. To very rare elements belong fragments and teeth of tube worms and bryozoans. The sample also yielded the gastropod *Euomphalopterus* sp. Samtleben et al. (2000) reported the presence of orthoceratids and rugose corals from this locality. According Samtleben et al. (2000) crinoid remains are rare whereas they are abundant in the studied samples. The cauliflower-shaped oncoids contain biogenic components as core and including the here reported *Orthonychia enorme* as core (Fig. 6G–I).

Few well-preserved specimens of *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow) were recovered from of the **Finis Shale** Member of the Graham Formation (Pennsylvanian, Virgillian, North Central Texas, USA). The Finis Shale is a poorly lithified grey shale that has yielded an abundant and commonly well-preserved marine invertebrate fauna that is rich in brachiopods, bivalves, gastropods, and others. Several groups of gastropods from the Finis Shale have been studied (e.g., Nützel 1998; Nützel et al. 2000; Bandel 2002a, b; Nützel and Pan 2005; Karapunar et al. 2022a) although a comprehensive monograph on the entire gastropod fauna is pending. Case studies of failed predatory attacks on Finis Shale gastropods were given by Vermeij et al. (1981) and Lindström (2003).

Finally, two well-preserved specimens representing *Orthonychia* sp. are reported from the Mississippian (Chesterian) **Imo Formation** of Arkansas, USA. The Imo Formation consist of dark shales that yielded a diverse bivalve (Hoare et al. 1989) and gastropod (Jeffery et al. 1994) fauna as well as other marine invertebrates.

Results

Systematic Paleontology

Class Gastropoda

Family Orthonychiidae Bandel & Frýda, 1999

Remarks. Bandel and Frýda (1999) erected this family for limpet-shaped Paleozoic gastropods formerly included in Platyceratidae. Based on the openly coiled fishhook-like protoconch of the Pennsylvanian limpet-shaped species *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), they placed Orthonychiidae in their new order Cyrtoneritimorpha. However, the protoconch of the Devonian type species of *Orthonychia* is yet unknown (see Knight 1941). The Ordovician family Pollicinidae resembles some members of Orthonychiidae but these shells are bilaterally symmetrical and their early ontogeny is largely unknown (see Peel 2020a, b).

Genus *Orthonychia* Hall, 1843

Type species. *Platyceras subrectum* Hall, 1859; by subsequent monotypy by Hall (1859).

Remarks. *Orthonychia* is a cap-shaped or elongate tube-like mollusk which has traditionally been placed in the in the Paleozoic gastropod family Platyceratidae and was also considered a subgenus of *Platyceras* (Knight et al. 1960). The Devonian type species of *Orthonychia*, *O. subrecta* (Hall, 1859), is known from steinkerns only (Knight 1941) and therefore, the status of shell ornamentation and protoconch morphology cannot be assessed. The general habitus (elongated slightly curved shell with only the early teleoconch being coiled) is close to that of *Orthonychia enorme* (Lindström, 1884) and *Orthonychia yutaroi* Ebbestad, sp. nov. as described below, especially regarding the tube-shaped, stretched late teleoconch. Based on an openly coiled fish-hook-like protoconch, present in the Pennsylvanian species *O. parva*, Bandel and Frýda (1999) erected the family Orthonychiidae and placed it in a new order Cyrtoneritimorpha, forming the fossil sister group of modern Neritimorpha (Cycloneritimorpha).

The tall shell morphology of some *Orthonychia* species including *O. yutaroi* and *O. enorme* as reported herein superficially resembles that of the Ordovician archaeogastropod *Pollicina*, described by Peel (2020a, b). This genus can reach a height of at least 3 cm, has a thick shell, with even co-marginal ribs, and an apex truncated by septa. The shell is bilaterally symmetrical, in contrast to that of *Orthonychia*.

Orthonychia yutaroi Ebbestad, sp. nov.

https://zoobank.org/595BAF12-C8B3-4219-B528-657BAF5EEA0B
Fig. 2

Material. Only the holotype (PMU 37146) is known, from the Late Ordovician (Katian) Boda Limestone at Jutjärn quarry, Siljan district, Dalarna.

Derivation of name. After Dr Yutaro Suzuki, Shizuoka University, Japan, who found the specimen and who has made extensive studies of fossils and the mound ecology of the Boda Limestone.

Diagnosis. Shell tall, teleoconch forming a weakly cyrtoconic tube, open coiled with apex coiled through half a whorl; supra-apical surface formed by raised and convex median section; teleoconch ornamentation consist of densely spaced, slightly undulating, strong co-marginal ribs on initial parts, widening later in ontogeny to distinct growth increments that end in a flared lamellae; growth lines corrugated, laterally forming two or three spaced flutes, across the median part only weakly undulating; last part of protoconch without visible ornament and abrupt transition to teleoconch; early protoconch whorls poorly preserved as imprint, possibly tightly coiled consisting of ca. two whorls.

Description. Shell tall, weakly cyrtoconic, open coiled with apex coiled through at least half a whorl before shell coiling ends and a straight tube forms, widening gradually with length at base about 45% of total height (= 20 mm). Shell nearly planispiral but with weak translation down the axis if viewed with aperture in normal right-handed

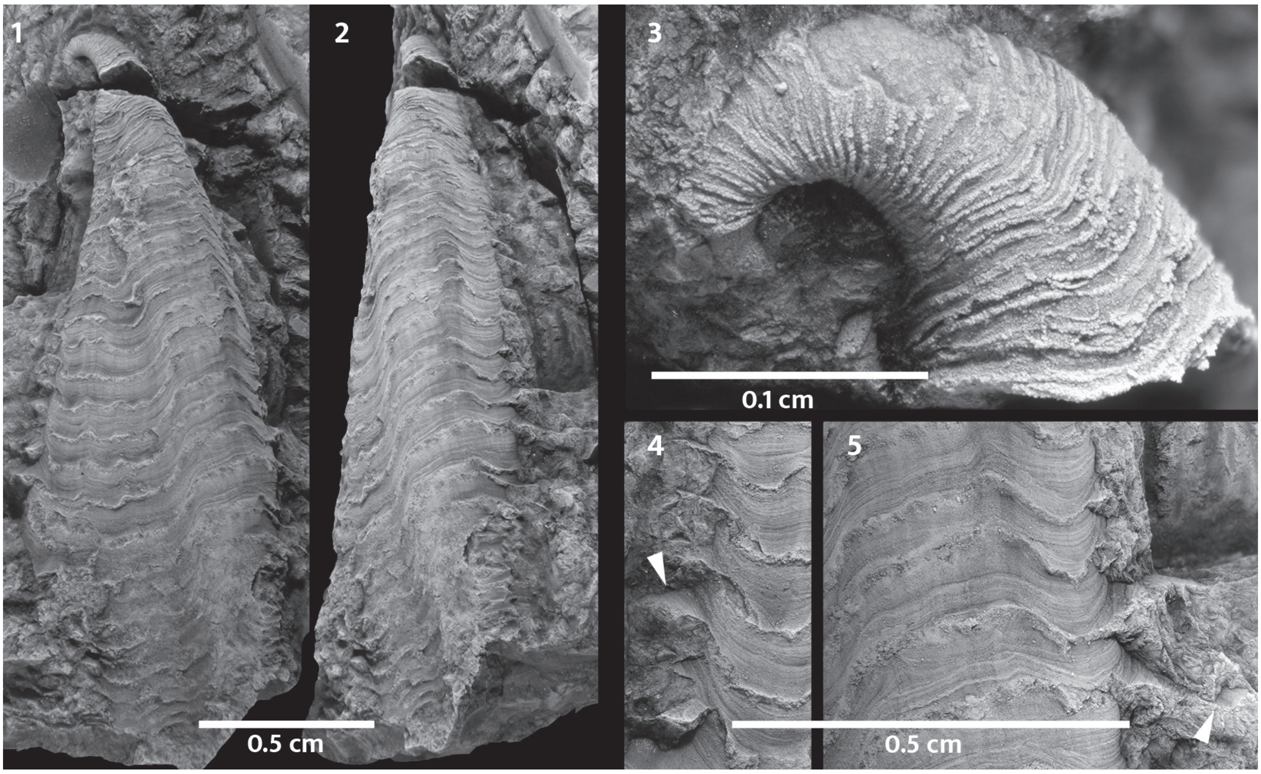

Figure 2. *Orthonychia yutaroi* Ebbestad, sp. nov., holotype PMU 37146. **(1, 2)** Right lateral and anterior views. **(3)** Detail of initial whorls. **(4)** Detail of left periphery with arrow pointing to lamella. **(5)** Detail of left periphery with arrow pointing to lamella.

position. Apex overhang sub-apical margin. Supra-apical surface of shell forms a raised and convex median section, with concave transition to lateral surfaces. Ornamentation on initial conch consist of densely spaced, slightly undulating, strong co-marginal ribs. A couple of millimeters from the apex, the space between the ribs widens gradually and distinct growth increments (here taken as the growth accumulated in the space between subsequent lamellae) become apparent. Increments are spaced no more than 1 mm apart, consist of fine co-marginal growth lines and end with a lamella that extends prominently and nearly horizontal from the shell (arrows in Fig. 2A4, A5). Near the aperture the space between the increments again becomes narrower. The growth lines are corrugated, laterally forming two or three spaced flutes that have a pointed bell-shaped, whereas the growth lines across the median part only are weakly undulating. Ornamentation on inner margin obscured by matrix. Medially the growth-lines form a broad low-relief U-shape.

Last part of protoconch without visible ornament and abrupt transition to teleoconch; width of last protoconch whorl at termination about 200 μm; early protoconch whorls poorly preserved as imprint, possibly tightly coiled consisting of ca. two whorls.

Remarks. The conch of *Orthonychia yutaroi* resembles an orthonychian shell morphology in the tall elongated tube-like shell and has a similar crenulated teleoconch ornamentation as the Silurian *O. enorme* (see below). Compared with *O. enorme* it differs markedly in attaining an open coiled shell earlier, as the initial shell of *O. enorme* coils more tightly. However, the teleochonch in *O. yutaroi* expands more slowly in late ontogeny than that of *O. enorme* and the shell of the Dalarna species is proportionally taller and straighter (less pronounced supra-apical curvature). The periodic flaring lamellae in *Orthonychia yutaroi* are much more extensive and more pronounced, and ribbing is much denser, especially in the early teleoconch, than in *O. enorme*. Furthermore, *O. yutaroi* has stronger crenulations forming flutes laterally, whereas the longitudinal flutes are weak or absent in *O. enorme*. But both species share the development of periodic growth increments that end with a crenulated lamella.

The protoconch of *Orthonychia yutaroi* is incompletely preserved but it is clear that it lacks visible ornament and has an abrupt transition to the teleoconch. It seems to be possible that the protoconch is tightly coiled and consists of ca. 2.5 whorls, similar to what we have found in *O. enorme* (see below).

Orthonychia enorme (Lindström, 1884)

Figs 3–8

1884 *Platyceras enorme* sp. nov. – Lindström: 69, pl. 2, figs 59–72.
cf. 1976 *Platyceras* (*Orthonychia*) cf. *P.* (*Orthonychia*) *enorme* Lindström, 1884 – Peel and Yochelson: 17.

Lectotype. Selected here, NRM Mo 38219 from the Eke Formation at Rikvide, Gotland, illustrated by Lindström (1884, pl. 2, figs 60, 61, re-illustrated here in Fig. 3A. The

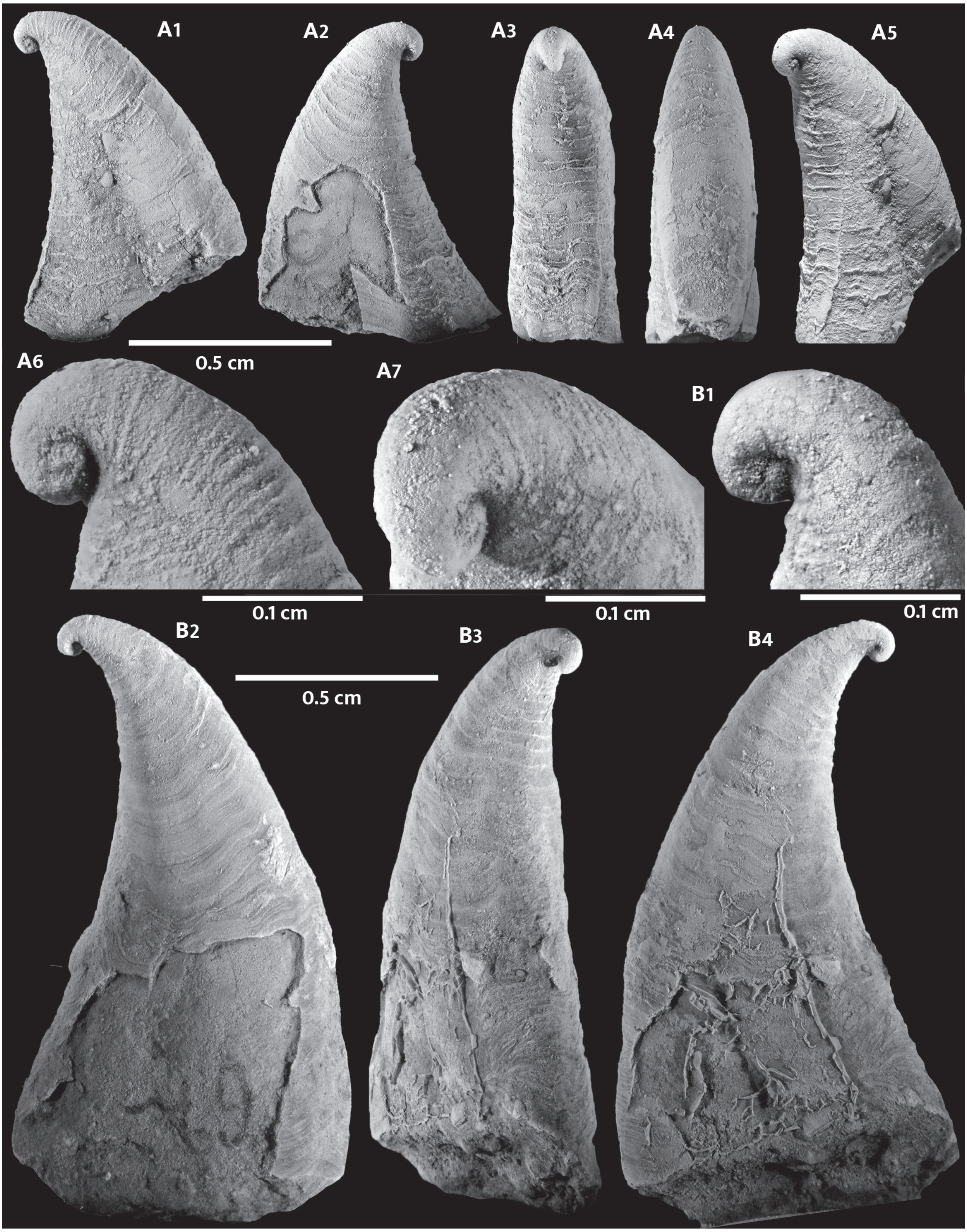

Figure 3. *Orthonychia enorme* (Lindström, 1884) **(A)** Lectotype NRM 38219. **(A1–A5)** Right lateral, left lateral, posterior, anterior, and posterior oblique views. **(A6, A7)** Details of apex; illustrated by Lindström (1884 pl. 2, figs 60, 61). **(B)** Paralectotype NRM 38220. **(B1)** Detail of apex. **(B2–B3)** Left lateral, posterior oblique and right lateral views; illustrated by Lindström (1884, pl. 2, figs 62, 63). Scale bar: 0.5 mm (**A1–A5, B2–B4**).

specimen is laterally compressed and incomplete when it comes to height but shows the early ontogeny, the tube-like expansion of the shell and the distinct ornamentation.

Other type material. Lindström (1884) illustrated an additional six specimens from the same locality as the lectotype, and these are here considered paralectotypes

(NRM Mo 38218, Mo 38220–Mo 38324); see Figs 3B–5B. The identity of specimens listed by Lindström (1884) from other localities cannot be established, with the exception of the specimen from Slite which is not conspecific with *O. enorme* (see below). The other localities mentioned by Lindström (1884) span older strata (Djupvik and Klinteberget = Slite beds of Sheinwoodian/Homerian age; Havdhem and Hammar in Kräklingbo = Hemse beds of Gorstian/Ludfordian age) and younger strata (Burgsvik = the Burgsvik Sandstone just overlying the Eke Formation).

Additional material. Ca. 240 juvenile shells (illustrated material SNSB-BSPG 2023 X 1–15). from the Eke Formation at Bodudd (S Gotland, Sweden, 57°04'05.8"N, 18° 11'34.7"E, compare Calner et al. 2004, fig. 2) which is Ludfordian (Ludlow, upper Silurian) in age.

Description of type material (Figs 3–5, Table 1). Largest shell 16.5 mm tall and 7.5 mm in apertural length (in lateral view). On average the shell is twice as tall as long (in lateral view). NRM Mo 38219 (Fig. 3A) deviates by length of aperture being 75% of height, but the shell is laterally compressed. NRM Mo 38222 (Fig. 5B) has an aperture length that is only about 40% of shell height. Rate of expansion high when viewed in a lateral perspective, but less when viewed anteriorly/posteriorly, making aperture sub-oval. Growth lines irregularly crenulated, but overall attitude is straight across posterior section of shell (Figs 3A3, 4A4), gently arched on lateral surfaces and curved into broad median sinus anteriorly. Here the growth lines are sinusoid with two asymmetrical crenulations of which the left has greater amplitude (Figs 3A4, 4A3). Although the intensity and irregularity of the crenulations vary, there are no major deviations from the overall co-marginal alignment. The co-marginal ribs or frills seen in early ontogeny widens into distinct growth increments, spaced less than 1 mm apart and ending in seemingly short lamellae. Fine radial striae may be present within each growth increment. Specimen NRM 38220 appears to have a mostly smooth shell with fine growth lines only, but increments with lamellae are visible on the initial part of the shell (Figs 3B3, B4). Space between increments get narrower in late ontogeny (Fig. 4A, B). Radial ornamentation is absent.

Description of additional material from sieved bulk samples (juvenile and encrusted shells, Figs 6–8). Shell with tightly coiled ca. 1.5–2.5 initial whorls including protoconch and early teleoconch; largest shell studied with SEM 4.1 mm long, 1.9 mm wide; encrusted specimens (forming cores of oncoids) probably belonging to the present species up to 20 mm long; protoconch with round, convex whorls and slightly elevated spire, lacking ornament (but re-crystallized); encrusted (oncoid) specimens possibly belong to this species up to 20 mm long; diameter of first whorl 0.17–0.25 mm, diameter of protoconch 0.37–0.68 mm (two measurements); protoconch/teleoconch-transition indistinct due to preservation (re-crystallization) but apparent by sudden onset of co-marginal ribs (may also appear as frills or lamellae) and rapid increase of expansion rate of whorl diameter; later teleoconch detaches and becomes uncoiled, bent to slightly elongated, slowly increasing in diameter, forming a cap-shaped tube; teleoconch ornamented by sharp, narrow co-marginal ribs separated by wide interspaces; strength of ribs and density of ribbing variable; ribs can also form lamellae; ribs appear much longer (lamellae) in specimens studied in thin sections than ribs in specimens from bulk samples suggesting that such lamellar ribs broke off during processing of sample; teleoconch also ornamented by thin spiral lirae, much weaker than co-marginal ribs; shell having a calcitic layer as suggested by thin sections.

Remarks. Lindström (1884, p. 69) mentioned several specimens from various localities on Gotland, but figured only specimens from Rikvide. In the NRM collection only specimens from Rikvide and Burgsvik are registered, but specimens from the latter locality were not available for study. The specimen from Slite in the PMU collections, mentioned by Lindström (1884), is illustrated here in Fig. 5B. It comes from the much older Slite Group sediments and is here treated as *Orthonychia* sp. The species was also listed from the Slite Beds by Manten (1971, table 11). However, it differs markedly from *O. enorme* in the initial shell having higher rate of coiling, possibly more coiled whorls before extending into the tubular shell, the shell is proportionally broader at the aperture, the W/H ratio is higher (0.65), it lacks clear growth increments and lamellae, and have a distinct radial ornamentation crossing the fine co-marginal growth lines thus creating a fine reticulate pattern. Furthermore, the shell reverses curvature during growth.

Lindström (1884, p. 69, pl. 2, fig. 71) described and illustrated a fine radial ornamentation. Some faint striations may be discerned in NRM 38218 (Fig. 4B2) but similar ornamentation is not seen in other macro-specimens. Fine and widely spaced lirae are present in early ontogeny (Gotland Ortho 1, C2). The two-element illustration in Lindström (1884) cannot readily be linked to any of the available specimens.

Peel and Yochelson (1976, p. 17) listed *Platyceras* (*Orthonychia*) cf. *P.* (*Orthonychia*) *enorme* Lindström, 1884 from the Telychian of Norway.

Table 1. Measurements of type specimens of *Platyceras enorme* Lindström, 1884.

	Height [cm]	Width at aperture [cm]	W/H
NRM Mo 38219	0.82	0.6	0.73
NRM Mo 38220	1.5	0.83	0.55
NRM Mo 38221	1.4	0.73	0.52
NRM Mo 38222	1	0.42	0.42
NRM Mo 38223	1.65	0.75	0.45

The present material from the bulk samples closely resembles the type material of *Platyceras enorme* Lindström, 1884 as described and illustrated above. The type specimens are much larger (more than 16 mm long)

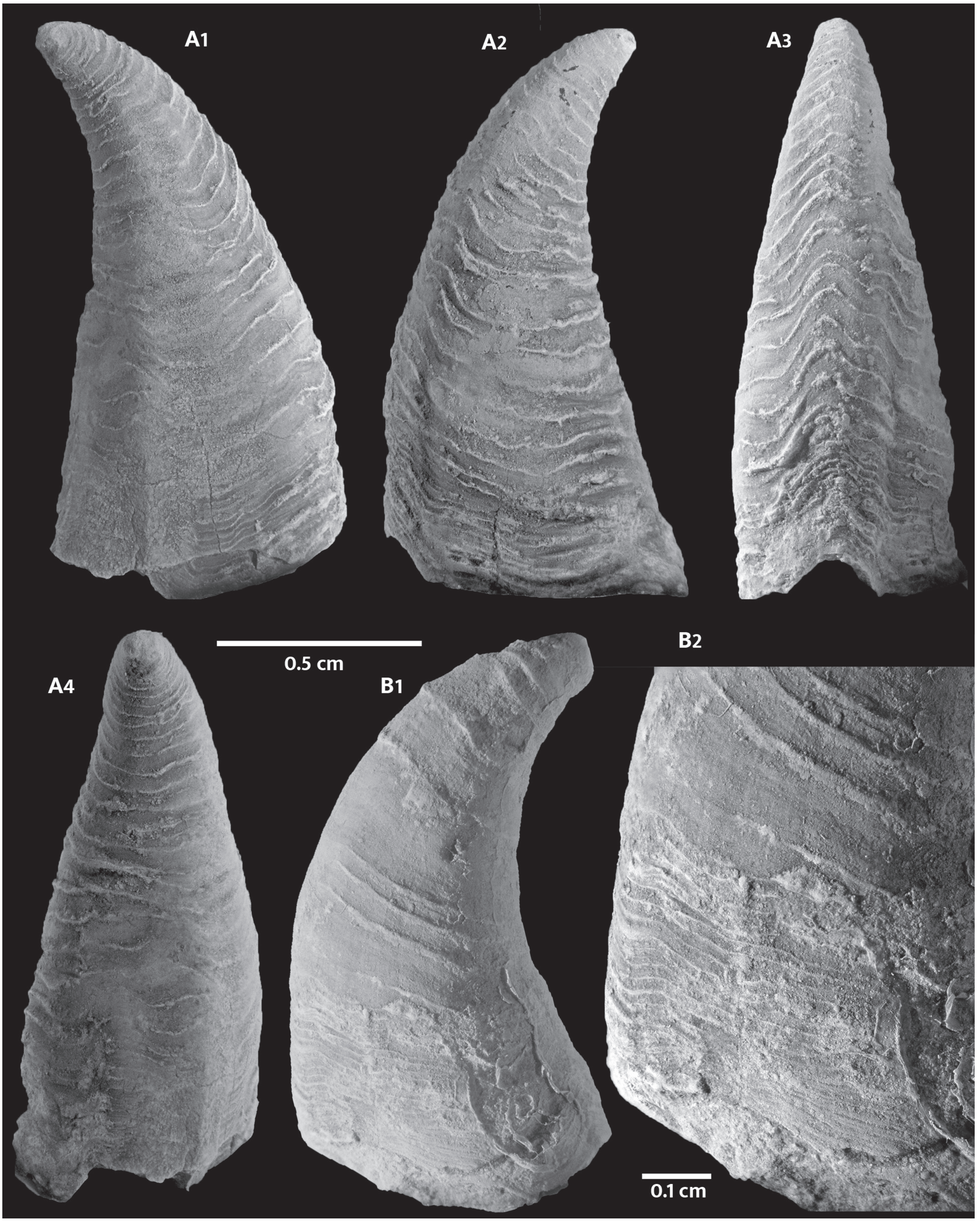

Figure 4. (A, B) *Orthonychia enorme* Lindström (1884). **(A)** Paralectotype NRM 38221. **(A1–A4)** Right lateral, left lateral, anterior, and posterior views; illustrated by Lindström (1884, pl. 2, figs 64–66). **(B)** Paralectotype NRM 38218. **(B1)** Left lateral view. **(B2)** Detail of ornamentation near the aperture. The museum label indicates that this is the specimen illustrated by Lindström (1884, pl. 2, fig. 59), but the specimen does not match the illustration particularly well. Scale bar: 0.5 cm (**A, B1**).

than the specimens from the washed residue reported here. However, strongly encrusted specimens studied by Schugmann (2015) and herein (Fig. 6) are also in this larger size range suggesting that the specimens from the residues are juveniles. *Platyceras cornutum* from the upper Silurian of Gotland as illustrated by Lindström (1884)

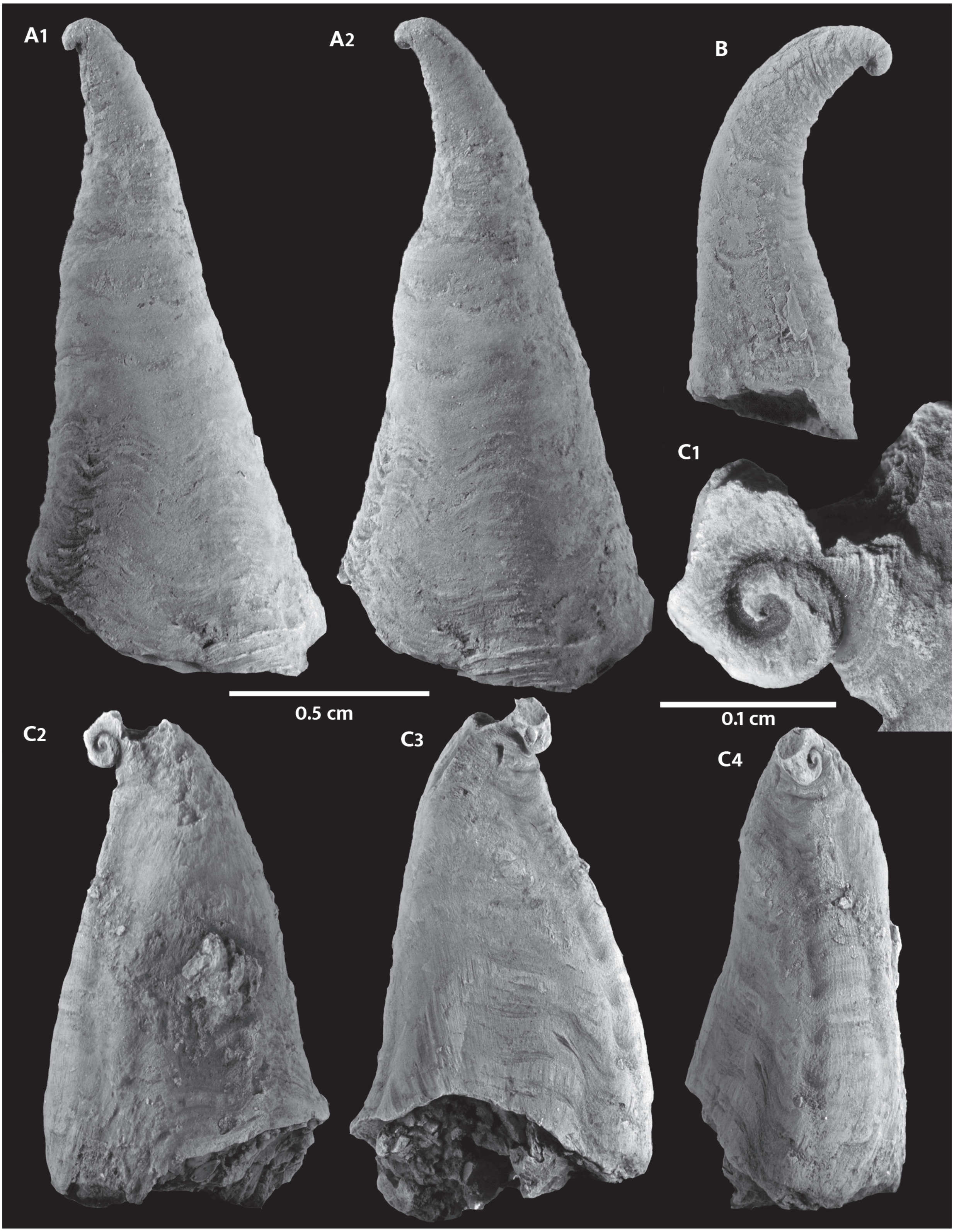

Figure 5. (A, B) *Orthonychia enorme* Lindström (1884). **(A)** Paralectotype NRM 38223. **(A1, A2)** Right lateral and anterior oblique views; illustrated by Lindström (1884, pl. 2, figs 69, 70). **(B)** Paralectotype NRM 38222. Left lateral view; illustrated by Lindström (1884), pl. 2, fig. 68. **(C)** *Orthonychia* sp., PMU 21576. **(C1)** Detail of apex. **(C2–C4)** Right lateral, left lateral and posterior views. Specimen collected by Cleve and mentioned by Lindström (1884, p. 69). Scale bar: 0.5 cm (**A, B, C2–C4**).

is similar but lacks ornamentation of axial ribs/frills and spiral lirae; instead it has co-marginal irregular bulges. Moreover, the teleoconch of *Platyceras cornutum* is generally more curved.

The Devonian *Crossoceras* Boucot & Yochelson, 1966 (Platyceratidae) is ornamented with co-marginal sharp ribs (frills) and a fine spiral lineation similar to the ornament of *Platyceras enorme*. However, *Crossoceras* has a

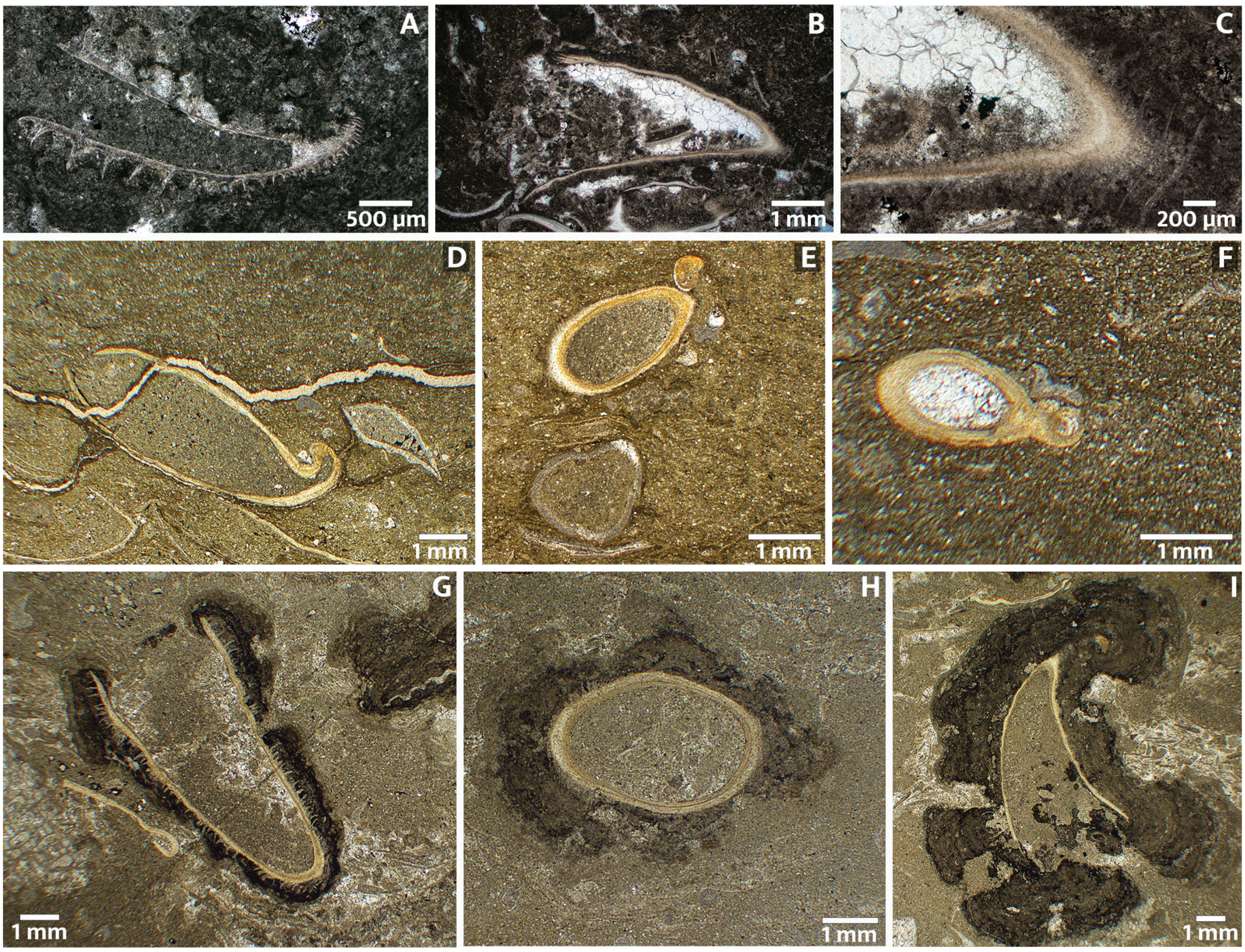

Figure 6. *Orthonychia enorme* (Lindström, 1884) in thin sections, Silurian Eke Formation, Gotland; the type of preservation of the shells suggests that they were primarily calcitic with foliated micro-structures; some of the shells have very long frills; these frills are much longer than those on specimens from the type series (Figs 3–5) and washed samples (Figs 7–8) suggesting they broke off during weathering and the processing of the samples. Thin sections reposited Friedrich-Alexander-Universität Erlangen-Nürnberg, GeoZentrum Nordbayern, Erlangen, Germany. **(A)** Shell in longitudinal section, specimen with pronounced frills. **(B, C)** Shell in longitudinal section, specimen with pronounced frills in apical portion (C). **(D)** Shell in longitudinal section, specimen shows coiling in its apical portion. **(E)** Upper portion of image, shell in transverse section of one whorl (large oval) and tangential to earlier whorl (round). **(F)** Middle left portion of image, shell in transverse section of one whorl (left large oval) and earlier whorl (right circular). **(G)** Shell in longitudinal section, specimen shows pronounced frills covered by a thick microbial crust. **(H)** Shell in transverse section, covered by a thick microbial crust. **(I)** Shell in longitudinal section, covered by a thick microbial crust.

stronger curvature of the teleoconch and is thus close to *Platyceras* in this respect. A close phylogenetic relationship of *Crossoceras* and *Orthonychia enorme* seems to be likely. The protoconch of *Crossoceras* is unknown; judging from the illustration given by Boucot and Yochelson (1966, pl. 3, fig. 11) it could be tightly coiled as in *Orthonychia enorme* but the preservation is insufficient to be sure.

Pragoserpulina tomasi Frýda, 1998a, type species of *Pragoserpulina* Frýda, 1998a, family Pragoserpulinidae Frýda, 1998a, from the Early Devonian of the Czech Republic (Dvorce-Prokop Limestone, Praha Formation, Pragian, Czech Republic) closely resembles *O. enorme* in teleoconch morphology and in having the same type of tightly coiled protoconch. However, the uncoiled teleoconch of *P. tomasi* is more bent, its ribbing is denser, the co-marginal ribs are stronger; the ribs are rounded and not as sharp (no frills). Bouchet et al. (2005, 2017) classified Pragoserpulinidae as a Paleozoic taxon that certainly belongs to gastropods, unassigned to superfamily – it is possible that *Pragoserpulina* is platycerate.

The tightly coiled protoconchs shown here for *Orthonychia enorme* and that illustrated by Frýda (1998a) for *Pragoserpulina tomasi* are clearly not of the vetigastropod type (see e. g., Bandel 1982; Haszprunar et al. 1995; Nützel 2014). They probably were produced by larvae with a short-termed planktotrophic phase. Similar protoconchs were reported for the Paleozoic neritimorph *Naticopsis* (Nützel and Mapes 2001; Nützel et al. 2007b) and *Platyceras* (Frýda et al. 2009). The same type of protoconch was found in Devonian and early Carboniferous gastropods with a cap-shaped teleoconch placed in the family Pragoscutulidae Frýda, 1998a (Cook et al. 2008). They were classified as Caenogastropoda but a neritimorph relation seems also possible. Pragoscutulidae are much stouter i.e., they have a much wider apical angle.

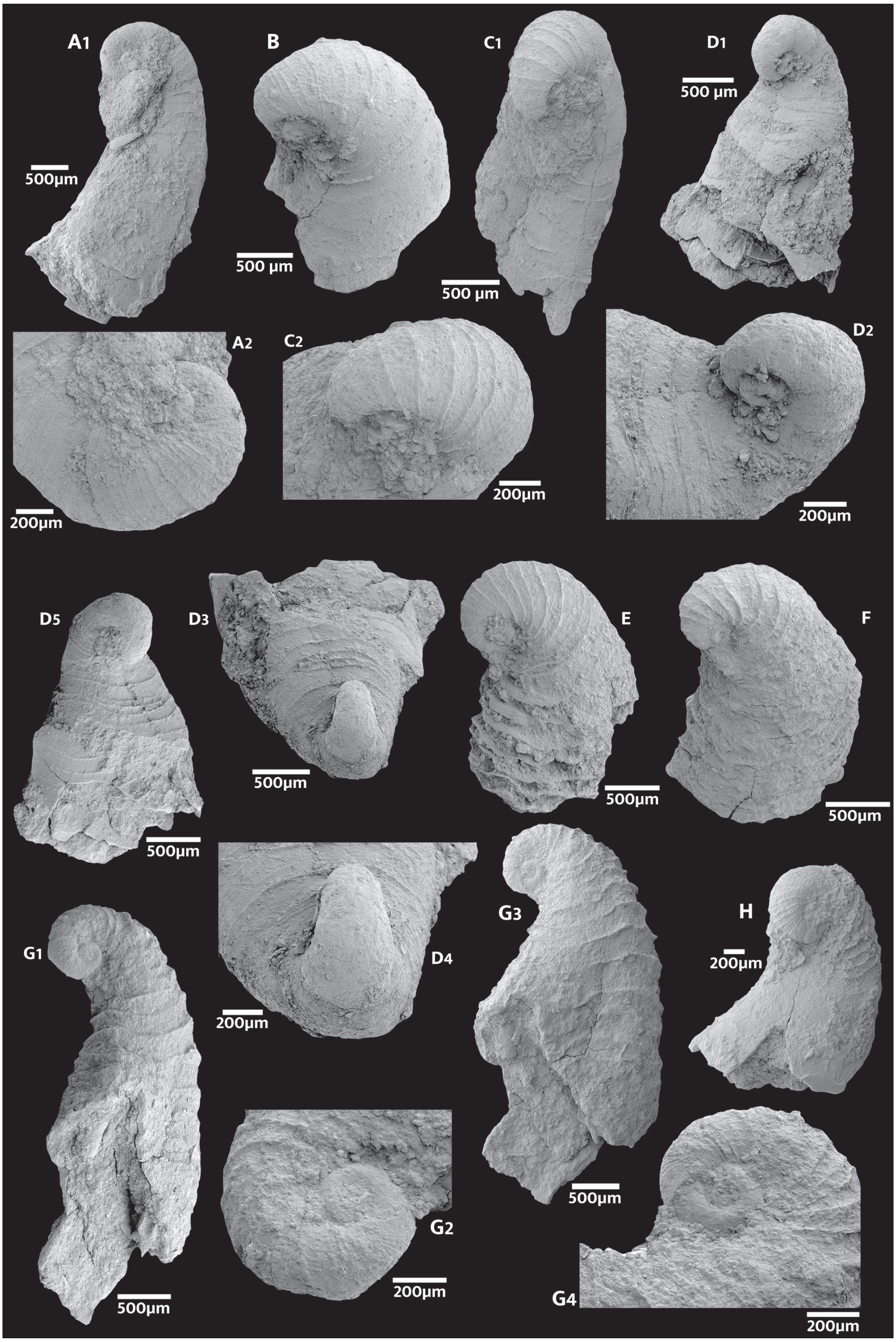

Figure 7. *Orthonychia enorme* (Lindström 1884), Silurian Eke Formation, Gotland. **(A)** SNSB-BSPG 2023 X 1. **(A1)** Lateral view. **(A2)** Initial whorls in oblique apical view. **(B)** SNSB-BSPG 2023 X 2, juvenile specimen in lateral view. **(C)** SNSB-BSPG 2023 X 3. **(C1)** Lateral view. **(C2)** Early teleoconch with distinct axial ribs/frill and faint spiral lirae. **(D)** SNSB-BSPG 2023 X 4. **(D1)** Juvenile specimen in lateral view. **(D2)** Initial whorls in oblique apical view including tightly coiled protoconch without visible ornament. **(D3, D4)** Dorsal views including last smooth whorl of protoconch. **(E)** SNSB-BSPG 2023 X 10, juvenile specimen with strong frills in lateral view. **(F)** SNSB-BSPG 2023 X 6, juvenile specimen with strong frills in lateral view. **(G)** SNSB-BSPG 2023 X 11. **(G1)** Lateral view. **(G2)** Initial whorls including tightly coiled protoconch without visible ornament in oblique apical view. **(G3)** Lateral view. **(G4)** Initial whorls including tightly coiled protoconch without visible ornament in apical view. **(H)** SNSB-BSPG 2023 X 12, juvenile specimen in lateral view.

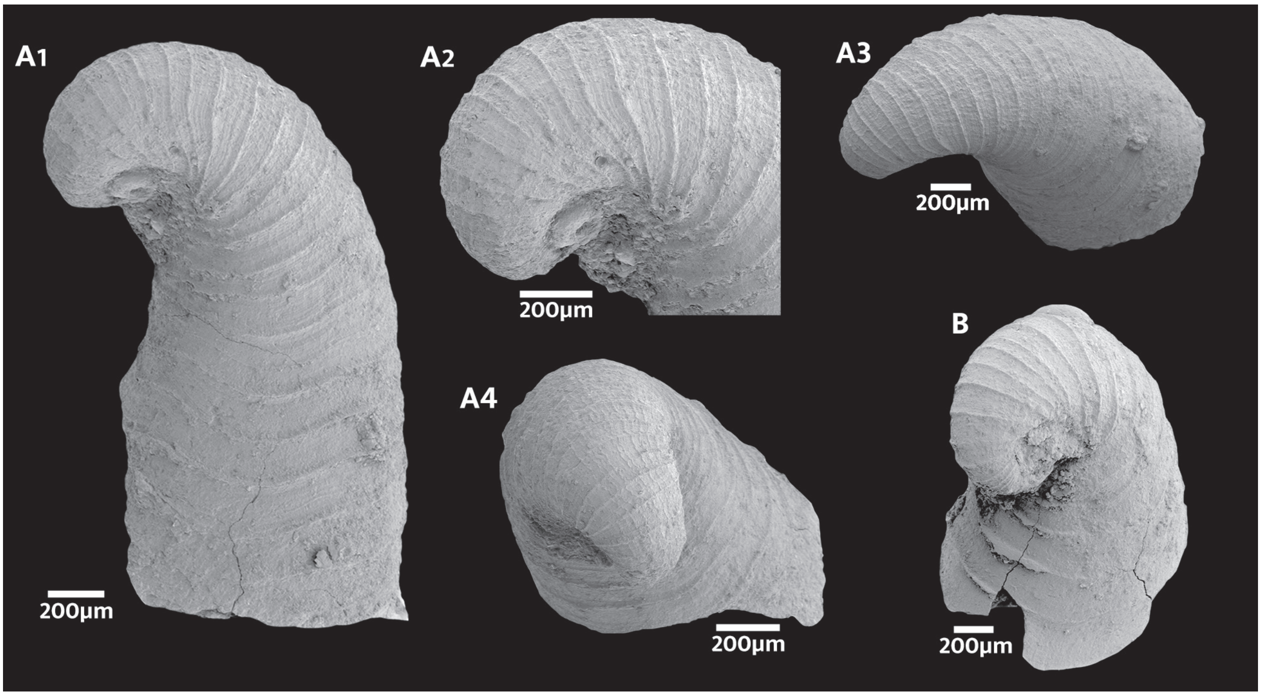

Figure 8. *Orthonychia enorme* (Lindström, 1884), Silurian Eke Formation, Gotland. **(A)** SNSB-BSPG 2023 X 13, specimen with distinct co-marginal ribs and longitudinal lirae. **(A1)** Lateral view. **(A2)** Initial whorls in oblique apical view. **(A3)** Dorsal lateral view. **(A4)** Dorsal view. **(B)** SNSB-BSPG 2023 X 15, lateral view.

Orthonychia parva (Swallow, 1858 in Shumard and Swallow)

Figs 9–12

*1858 *Capulus parvus* sp. nov. - Swallow (in Shumard and Swallow): 205.
1967 *Platyceras* (*Orthonychia*) *parvum* (Swallow, 1858) - Yochelson and Saunders: 173 [additional synonymy and chresonymy therein].
1999 *Orthonychia parva* (Swallow, 1858) - Bandel and Frýda: text-fig. 1, pl. 2, figs 5–8, pl. 3 figs 1–2.
2005 *Orthonychia parva* - Frýda: 382, fig. 3D.
2008a *Orthonychia parva* - Frýda et al.: 254, fig. 10.8E, G.
2009 *Orthonychia parva* (Shumard & Swallow, 1858) - Frýda et al.: 112, 116, fig. 5C–D.
2012 *Orthonychia parva* - Frýda et al.: 417, fig. 14E, M.
2014 *Pseudorthonychia* - Nützel: 491, fig. 14E, H.

Material. 6 specimens (SNSB-BSPG 2020 XCI 117–122) from the Finis Shale Member of the Graham Formation (late Pennsylvanian, Virgillian, North Central Texas, USA) at the locality TXV–200: Lost Creek Lake emergency spillway at dam, approximately 4 km northeast of Jacksboro, Jack County, Texas on Texas Highway 59. AMNH Locality 5562, 33°14'11.17"N, 98°07'11.33"W, 33.230, -98.136.

Description. Shell limpet-shaped; protoconch (description largely based on SNSB-BSPG 2020 XCI 117, Figs 9A, 12) with an initial bulb (Fig. 12 I) slightly elongated, 100–120 µm long, 70–75 µm wide, terminating in a slight constriction; width of initial bulb at 100 µm shell length 70–80 µm; shell after initial bulb forming a straight tube slowly increasing in width (Fig. 12 II); dextral coiling starts at 270–360 µm shell length and coiling comprises 100–180° (Fig. 12 III) until strong co-marginal ribs develop on the shell; the smooth initial shell has the form of a hook that encloses a central gap i. e., it is openly coiled; terminal width of whorl of initial smooth shell 0.5–0.6 mm; smooth initial whorl followed by rapidly expanding shell portion with strong collabral ribs (Fig. 12 IV); ribs separated by wider interspaces, prosocyrt in apical view and prosocline in lateral view; initial smooth shell part resting on axially ribbed shell; shell part with strong axial ribs has width of 0.8–1 mm at termination; shell distinctly and abruptly widening after initial shell with axial ribs resulting in a cap-shaped morphology (Fig. 12 V), transition at an angle; following shell cap-shaped with variable co-marginal ornament; one specimens shows fine longitudinal lirae on the teleoconch (Fig. 10B6).

Discussion. *Orthonychia parva* is widely distributed throughout the Carboniferous of the US (Yochelson and Saunders 1967). It has also been reported from the Pennsylvanian of North Central Texas (Mineral Wells Fm.) (Plummer and Moore 1921) although not from the Finis Shale. To our knowledge, Knight (1934, figs 1d–g) reported the only specimens (four) with preserved protoconchs. Two of these specimens were also illustrated in detail (SEM) by Bandel and Frýda (1999, pl. 2 figs 5–8): (reproduced by Frýda 2005, fig. 3D; Frýda et al. 2008a, fig. 10.8 E, G; Frýda 2012, fig. 14E,M; Nützel 2014, fig. 14E, H, erroneously as *Pseudorthonychia*). The same type of protoconch with stretched initial part and open coiling has been reported for the Devonian *Praenatica cheloti* by Frýda et al. (2009).

The present shell displays considerable ontogenetic change. There can be little doubt that the initial bulb rep-

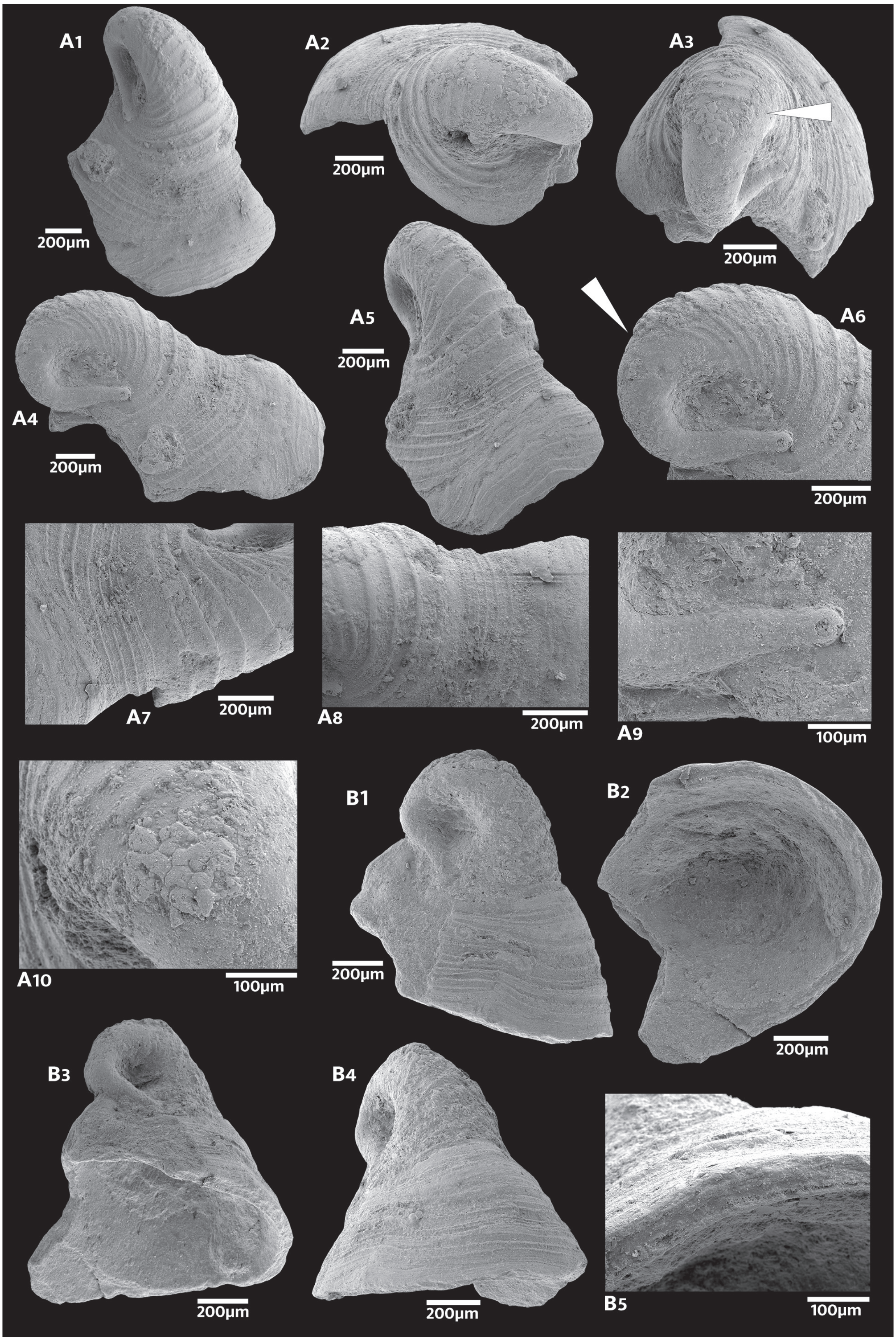

Figure 9. *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), two juvenile specimens with uncoiled, hook-like protoconchs in various views; Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. **(A)** SNSB-BSPG 2020 XCI 117. **(A1)** Oblique anterior view. **(A2)** Oblique dorsal view. **(A3)** Dorsal view. **(A4)** Lateral view, openly coiled protoconch well visible. **(A5)** Oblique lateral view. **(A6)** Detail initial whorl including openly coiled protoconch. **(A7, A8)** Detail early teleoconch at rapid widening of shell, openly coiled protoconch well visible. **(A9)** Detail of straight part of openly coiled protoconch including initial bulb. **(A10)** Detail encrustation at transition from smooth protoconch to ribbed early teleoconch. **(B)** SNSB-BSPG 2020 XCI 118. **(B1)** Lateral view, openly coiled protoconch well visible. **(B2)** Apertural view. **(B3)** Oblique lateral view, openly coiled protoconch well visible. **(B4)** Oblique anterior view. (**B5)** Detail of shell to show foliated micro-structure.

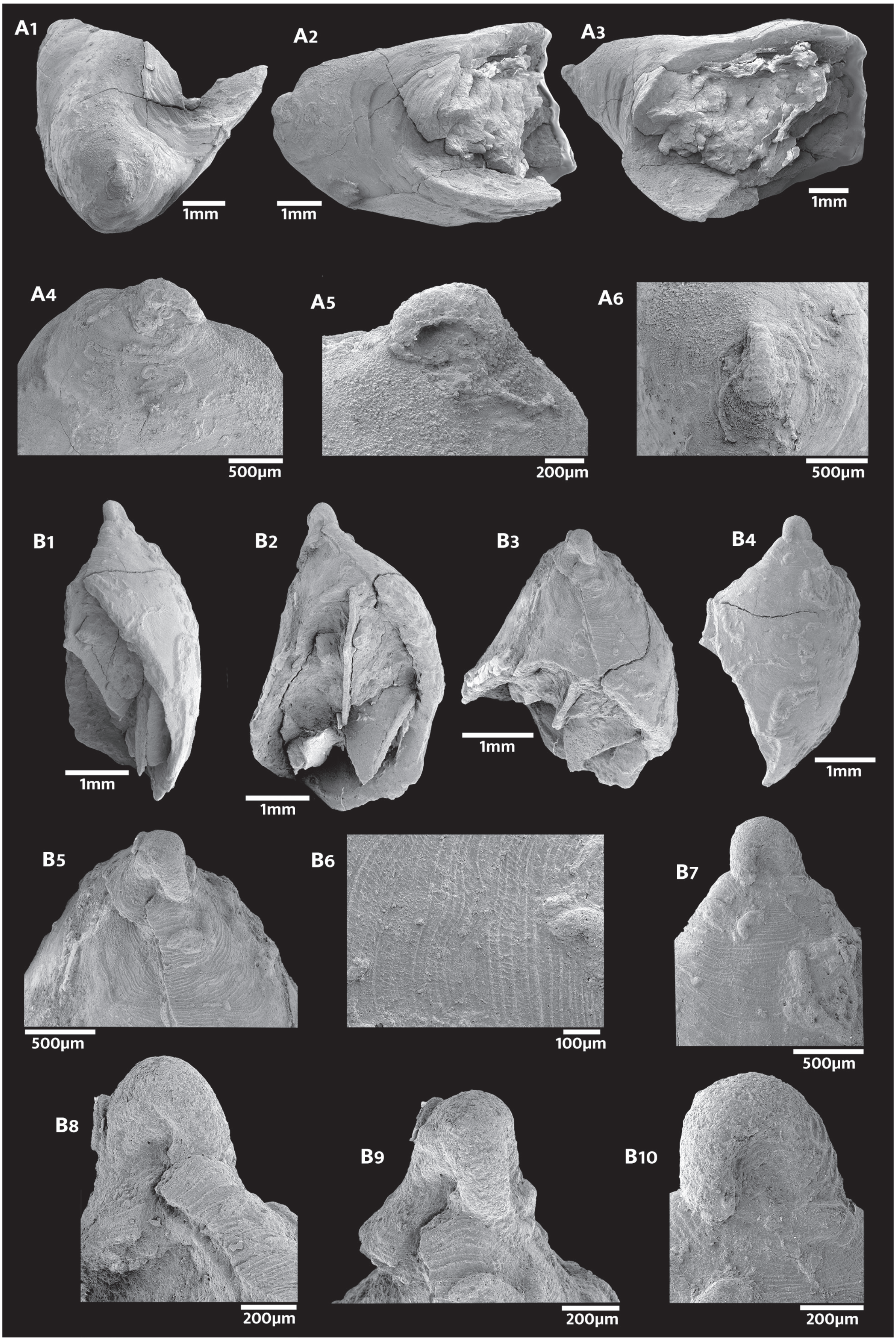

Figure 10. *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. **(A)** SNSB-BSPG 2020 XCI 121. **(A1)** Apical view. **(A2, A3)** Apertural views at different angles. **(A4, A5)** Protoconch remains in lateral view. **(A6)** Protoconch remains in apical view. **(B)** SNSB-BSPG 2020 XCI 122. **(B1, B2)** Apertural views at different angles. **(B3, B4)** Lateral views at different angles. **(B5, B7)** Protoconch remains and early teleoconch with strengthened growth lines. **(B6)** Detail of early teleoconch ornament consisting of strengthened growth lines and very delicate longitudinal lirae. **(B8–B10)** Protoconch remains in lateral views.

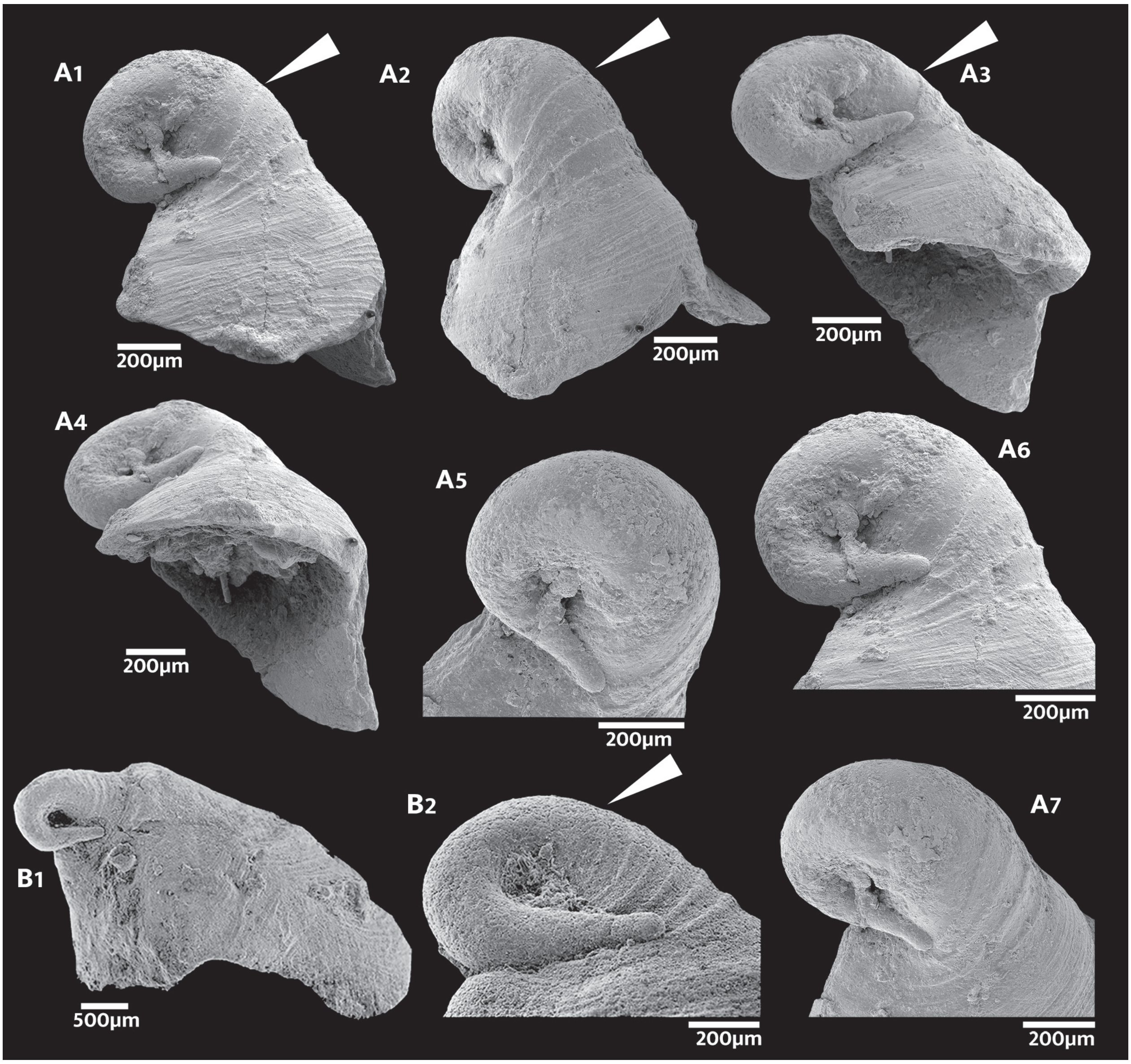

Figure 11. *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow). **(A)** SNSB-BSPG 2020 XCI 119, juvenile shell portion, Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. **(A1)** Lateral view, openly coiled protoconch well visible. **(A2)** Oblique anterior view. **(A3)** Oblique lateral view. **(A4)** Oblique apertural view. **(A5)** Openly coiled, smooth protoconch. **(A6)** Openly coiled, smooth protoconch in apical view and early teleoconch in lateral view. **(A7)** Openly coiled, smooth protoconch and early teleoconch. **(B)** From Bandel and Frýda 1999, pl. 2, figs 6, 8, Pennsylvanian Labette Shale, Saint Louis, Missouri, USA. **(B1)** lateral view, openly coiled protoconch well visible. **(B2)** Openly coiled protoconch well visible including initial bulb, straight and coiled parts followed by early teleoconch with so-marginal ribbing.

resents the embryonic shell as was also concluded by Bandel and Frýda (1999), Frýda et al. (2008b), and Frýda (2012). Its small size of 100–120 µm × 70 µm suggests indirect, planktotrophic larval development. The question is at which stage the larval shell terminates and the teleoconch starts. Knight (1934) for the first time reported and described this type of protoconch and noticed its morphology which is unusual for gastropods (‘curious vermiform nuclei’). He described the ‘nucleus’ as a narrow vermiform hook of one smooth revolution. The abrupt expansion of the shell which then bears co-marginal ribs was called by him ‘neanic’ i. e., as representing the early juvenile teleoconch. By contrast, based on the restudy of Knight’s (1934) material from the Labette Shale, Bandel and Frýda (1999) and Frýda (2012) assumed that the axially ribbed part following the smooth hook-like shells belongs to the larval shell. Here, we follow Knight’s (1934) interpretation because the smooth shell terminates abruptly and the size of the following axially ribbed portion of the shell (here Fig. 12 IV) has a width of ca. 2 mm at its termination which is too large for a larval shell. Hence the larval shell of *O. parva* comprises portions I–III as given in Fig. 12.

The change from a straight narrow tube to a coiled tube (Fig. 12 II to III) is readily explained: it would be highly disadvantageous for the pediveliger to settle with an entirely

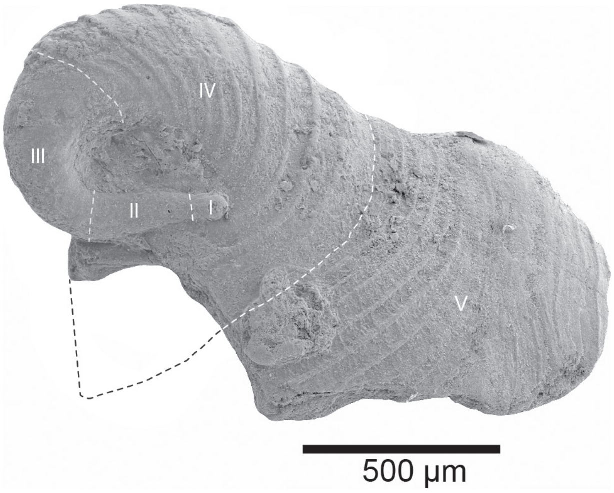

Figure 12. *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), SNSB-BSPG 2020 XCI 117, juvenile specimen with uncoiled, hook-like protoconch (same as Fig. 9A4); Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. I–III smooth protoconch consisting of initial bulb formed within the egg (I), straight part of larval shell (II) coiled part of larval shell (III) first portion of teleoconch with strong ribbing (IV) second portion of teleoconch with rapidly widening (V).

straight narrow tube (stretched, uncoiled shell tube would probably be vulnerable and hinder locomotion) and therefore coiling in the last period of larval life does make sense as a preparation for benthic life. The early axially ribbed teleoconch was probably formed by the crawling juvenile and the sudden widening of the shell could indicate the start of the sedentary life on crinoids.

Orthonychia sp.

Fig. 13A, B

Material. Two specimens from the Upper Mississippian (Chesterian) Imo Formation, Arkansas (SNSB-BSPG 2023 I 89, SNSB-BSPG 2023 I 90). The material was sampled by R. H. Mapes (ARC-02, samples Imo-6 and Imo-8.) at the Location #1 as given by Jeffery et al. (1994), figs 1 and 2). This location, the Peyton Creek Roadcut, was also described in detail by Manger (1977) who measured a section in the outcrop (Manger 1977, fig. 1). The sample Imo-6 sample came from position 20 in this section, approximately 110 feet above the base of his measured section and the Imo-8 sample came from position 24, which is about 135 feet above the base of his measured section. NE1/4 sec. 11 and NW1/4 sec. 12, T. 13 N., R. 15 W. Van Buren County, Arkansas

Description. Juvenile shell 0.66 mm wide, 0.52 mm high; shell starts with a slightly elongated initial bulb with a length of 87 µm and a width of 63 µm; width of shell at shell length 100 µm is 66–68 µm; initial bulb is bent slightly adapically in relation to the following straight shell-tube; following shell is an entirely straight, smooth tube that increases slowly in diameter. At a total shell length of 320 µm the tube starts a sharp coiling in a dextral direction and at the same time, it is strongly expanding in diameter; shell is smooth except of a faint micro-striation visible on the coiled part of the first whorl.

Remarks. We suppose that approximately the first openly coiled whorl represents the larval shell and that the faint micro-striation is the larval shell ornament. The protoconch of this species resembles the above described

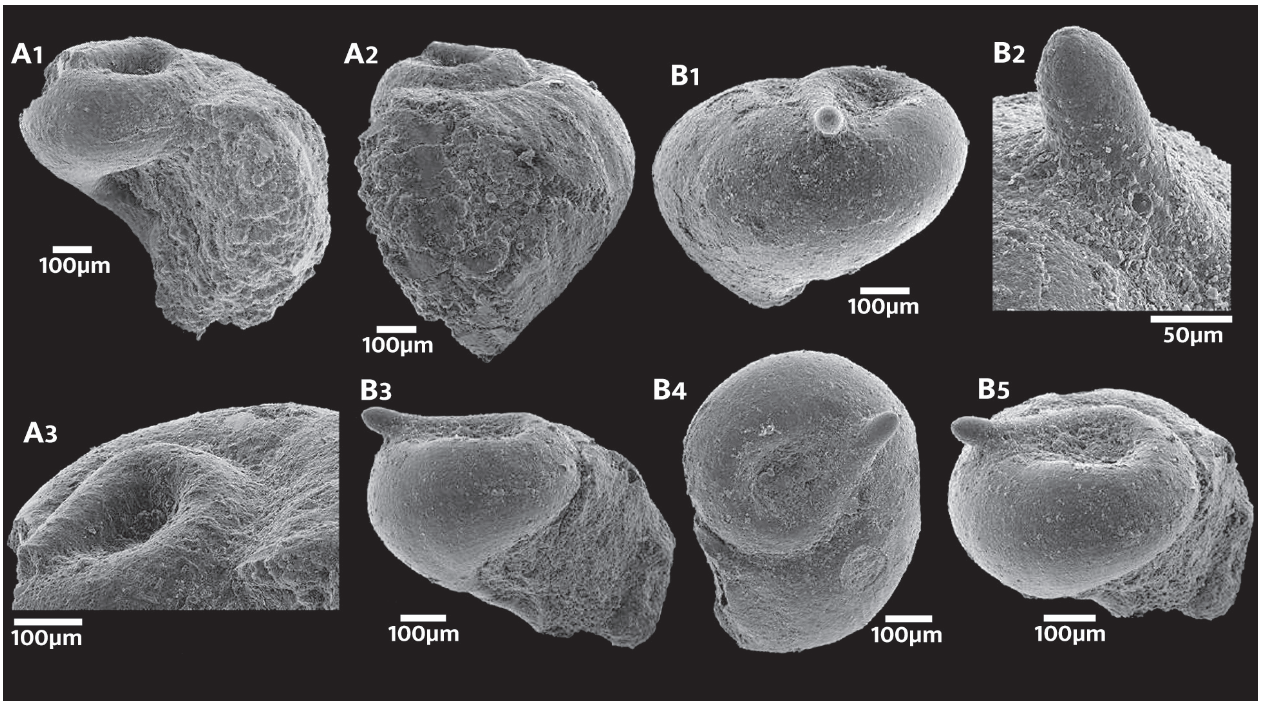

Figure 13. *Orthonychia* sp., with openly coiled larval shell; Mississippian (Chesterian) Imo Formation, Arkansas, USA. **(A)** SNSB-BSPG 2023 I 89. **(A1)** Apertural view. **(A2)** Lateral view. **(A3)** Oblique lateral view on openly coiled protoconch. **(B)** SNSB-BSPG 2023 I 90. **(B1)** Lateral view. **(B2)** Detail initial bulb of protoconch. **(B3)** Apertural view. **(B4)** Apical view. **(B5)** Oblique lateral view.

Orthonychia parva by having an initial bulb, representing most likely the embryonic shell (protoconch 1) and a following straight tube. However, the early shell of *Orthonychia* sp. lacks any strong co-marginal ribs or frills. Among the gastropod species described from the Imo Formation by Jeffery et al. (1994), *Platyceras* (*Orthonychia*?) sp. is the most likely candidate to be conspecific with the two juvenile specimens studied herein. They reported a single specimen from their rich collections and thus the species is very rare in this fauna.

Discussion

With this contribution, more evidence has been provided that openly coiled and tightly coiled protoconchs occur in platycerate gastropods as was already illustrated by Yochelson (1956), noted by Yochelson (1969), and shown by Frýda et al. (2009). If openly coiled protoconchs are diagnostic on family (Platyceratidae and Orthonychiidae) or higher (order Cyrtoneritimorpha) systematic levels, then these taxa would be probably polyphyletic in their current composition (i. e., species with tightly coiled protoconch would have to be removed). Previously, Karapunar et al. (2022b) argued against placing *Orthonychia* and *Platyceras* in distinct families or orders, because the protoconch of *Platyceras* has not been documented yet. Openly coiled and tightly coiled protoconchs are also present in other clades such as Paleozoic Caenogastropoda (Nützel et al. 2000; Nützel and Cook 2005), and Euomphaloidea (Bandel and Frýda 1998; Nützel 2002). The gradual decline of gastropods with openly coiled protoconchs during the Paleozoic and the absence of openly coiled protoconchs in extant gastropods (except of some holoplanktonic species) was described and quantified by Nützel and Frýda (2003) who interpreted this decline as a trend driven by increasing predation pressure in the plankton that selected against this probably vulnerable larval shell morphology. According to the meaning of the openly coiled protoconch morphology for phylogeny and systematics, these authors formulated two hypotheses:

1) Paleozoic gastropod clades with openly coiled protoconchs became extinct selectively during the Paleozoic and all modern gastropods are exclusively descendants of Paleozoic gastropods that had tightly coiled protoconchs.
2) Openly coiled protoconchs were present in the stem lines of most extant gastropod clades, but were differentially lost across major clades.

Given our new data and the current state of knowledge, we favor the second hypothesis: the trend against the openly coiled protoconch morphology persisted within various gastropod clades including platycerates. If true, Cyrtoneritimorpha and Cycloneritimorpha are synonyms of Neritimorpha.

Regarding the systematic placement of platycerate gastropods it is crucial to infer whether they contained species with planktotrophic larval development or not because extant members of basal gastropod clades such as Patellogastropoda, Neomphaliones, and Vetigastropoda obligatorily lack planktotrophic larval development (Bandel 1982; Haszprunar et al. 1995; Nützel 2014). As mentioned, the tightly coiled protoconch with up to more than two whorls and a small initial whorl reported for *Orthonychia enorme* herein is clearly unlike those in the mentioned basal gastropod clades and reflect larval planktotrophy. In gastropods with tightly coiled protoconchs, small initial whorls and a high number of protoconch whorl are diagnostic for larval planktotrophy (Nützel 2014). However, this does not work for openly coiled protoconchs and for protoconch steinkerns from micro-samples. Nützel et al. (2006, 2007a) introduced a method to overcome this problem: the measurement of the width of the shell at a length of 100 µm (measured from the zenith of the initial cap). This measurement serves as a proxy for the size of the embryonic shell, thus also for egg size and thus the amount of yolk. The smaller this value is, the higher is the likelihood that the measured shell was produced by a planktotrophic larva. Conversely, if the shell is very wide at a shell length of 100 µm, non-planktotrophy is likely. Table 2 shows values for eight platycerate species from the Silurian and Carboniferous and six values for Carboniferous Euomphaloidea - in both groups tightly and openly coiled protoconchs were measured (see Fig. 14 for two examples of Carboniferous euomphaloid species with well well-preserved protoconchs. The results show that the measured platycerates have much smaller values than Euomphaloidea (Tables 2, 3). The protoconchs of well-preserved Euomphaloidea consist of slightly less than one whorl (in species with tightly coiled protoconchs) and the shell is much wider at a shell length of 100 µm; this suggests non-planktotrophic early ontogeny like that of extant members of basal gastropod clades (see also Nützel 2002).

The shell width at 100 µm shell length of the investigated platycerate specimens are relatively small and are in the range of Ordovician/Silurian protoconch steinkerns from conodont samples measured by Nützel et al. (2006) that were interpreted as larval fall out communities of planktotrophic larvae. Besides these measurements, the protoconch morphology, as discussed in the systematic section, also supports the assumption of larval planktotrophy for the studied platycerate species.

The presence of larval planktotrophy shows that platycerates do not belong to Patellogastropoda and Vetigastropoda (extant members lack planktotrophic larval development), or Euomphaloidea as was previously assumed (e. g., Wenz 1938; Knight et al. 1960; Ponder and Lindberg 1997; Wagner 2002). The assumption that platycerates are Neritimorpha (Knight 1934; Bandel 1992; Bandel and Frýda 1999; Frýda et al. 2009) is corroborated herein by our new protoconch data. The Neritimorpha-hypothesis is also supported by the pres-

Table 2. Shell width at 100 µm shell length of the investigated platycerate and euomphaloid specimens, measured from SEM-images. The values for platycerates are much smaller indicating larval planktotrophy.

	Width at 100 µm shell length	Protoconch coiling	Age	Country	Specimen
Platyceratoids					
Orthonychia enorme	82 µm	tight	Silurian	Sweden	SNSB-BSPG 2023 X 6
Orthonychia enorme	80 µm	tight	Silurian	Sweden	SNSB-BSPG 2023 X 13
Orthonychia parva	71 µm	open	Pennsylvanian	USA	SNSB-BSPG 2020 XCI 117
Orthonychia parva	74 µm	open	Pennsylvanian	USA	SNSB-BSPG 2020 XCI 119
Orthonychia parva	82 µm	open	Pennsylvanian	USA	Bandel and Frýda (1999)
Orthonychia parva	76 µm	open	Pennsylvanian	USA	Bandel and Frýda (1999)
Orthonychia sp.	68 µm	open	Mississippian	USA	SNSB-BSPG 2023 I 89
Orthonychia sp.	66 µm	open	Mississippian	USA	SNSB-BSPG 2023 I 90
Euomphaloids					
Euomphalus sp.	136 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 91
Euomphalus sp.	117 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 92
Euomphalus sp.	150 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 93
Amphiscapha catilloides	160 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 88
Amphiscapha sp.	147 µm	tight	Mississippian	USA	SNSB-BSPG 2023 I 94
Euomphalus sp.	127 µm	open	Mississippian	Australia	SNSB-BSPG 2023 I 87

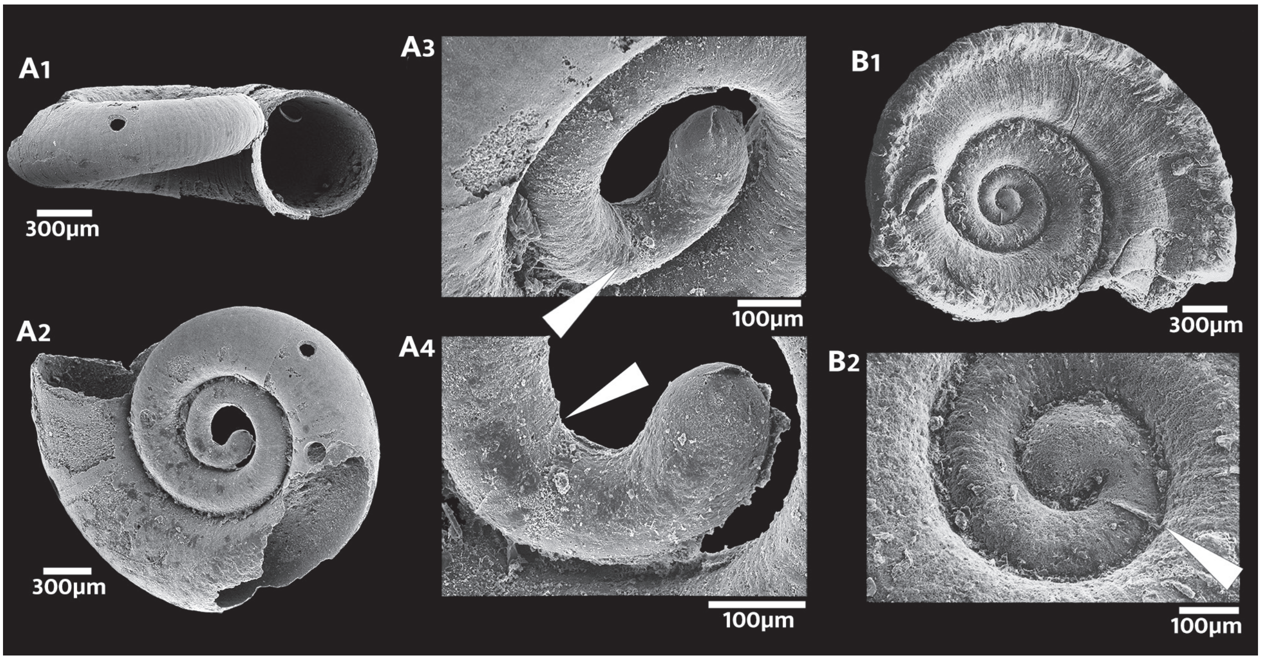

Figure 14. Carboniferous euomphaloids with preserved protoconch (one openly coiled **(A)**, one tightly coiled **(B)**) reflecting non-planktotrophic early ontogeny. **(A)** *Euomphalus* sp. SNSB-BSPG 2023 I 87, Locality 28 (Marohn) of Yoo (1994): Scone 1:25,000, GR 084544. Bioclastic limestone in the upper part of the Dangarfield Formation, 150 m west of 'Marohn' homestead, 4 km south-west of Gundy, Early Carboniferous, Tournaisian. **(A1)** Apertural view. **(A2)** Umbilical view. **(A3, A4)** Detail of openly coiled initial whorl; arrows mark end of protoconch. **(B)** *Amphiscapha catilloides* (Conrad, 1842), SNSB-BSPG 2023 I 88, Graham Formation, Finis Shale Member, Pennsylvanian, Texas, USA. **(B1)** Umbilical view. **(B2)** Protoconch of less than one whorl, demarcated by a ledge (arrow).

ence of a calcitic teleoconch and by the neritoid shape of many platycerates. Modern marine Neritimorpha have a characteristic highly convolute larval shell (e. g., Robertson 1971; Bandel 1982; Nützel et al. 2007b). However, Paleozoic forms have a larval shell that is similar to those present in Caenogastropoda (Nützel and Mapes 2001; Nützel et al. 2007b). In limpets with a tightly coiled larval shell, such as the Devonian *Pragoscutula* Frýda, 1998a and the Mississippian *Australoscutula* Cook, Nützel & Frýda, 2008, a decision as to whether they belong to Neritimorpha or Caenogastropoda remains difficult. It is possible that these taxa also belong to platycerate gastropods.

Table 3. Average and range of shell width at 100 µm shell length of the investigated platycerate and euomphaloid specimens. The values for platycerates are much smaller indicating larval planktotrophy.

	Average	Range	Stdv.	n
Platyceratoids	75 µm	66–82 µm	6.2	8
Euomphaloids	140 µm	117–160 µm	15.9	6

Conclusions

Based on the data presented here and previous publications (mainly Bandel and Frýda 1999; Frýda et al. 2009) we conclude the following:

- We are reporting the oldest well-preserved *Orthonychia* species from the Late Ordovician.
- In each, *Platyceras*- and *Orthonychia*-like gastropods, openly coiled and tightly coiled protoconchs occur.
- Thus, either both groups or genera are polyphyletic or openly coiled and tightly coiled protoconchs occur in closely related taxa; in the latter case, the order Cyrtoneritimorpha that was based on the presence of an openly coiled protoconch cannot be maintained. We suggest to treat Cyrtoneritimorpha and Cycloneritimorpha as synonyms of Neritimorpha as was previously suspected by Karapunar et al. (2022b).
- The monotypic Devonian genus *Pragoserpulina* and family Pragoserpulinidae are morphological so close to the *Orthonychia* species reported herein that synonymy of both genera seems to be possible.
- Morphology and dimensions of the known protoconchs of *Platyceras*- and *Orthonychia*-like gastropods suggest that they had planktotrophic veliger larvae. These protoconchs are unlike those of Vetigastropoda, Patellogastropoda, and Euomphalina which all have obligatory non-planktotrophic early ontogeny with a protoconch consisting of ca. one whorl.
- By contrast, the protoconch of *Orthonychia enorme* has distinctly more than one whorl (up to ca. 2) and that of *Orthonychia parva* has a small initial bulb (hatchling) followed by a much longer, elongated larval shell; both protoconchs reflect larval planktotrophy.
- The protoconch of *Orthonychia enorme* resembles that of Naticopsidae and those of some caenogastropods.
- The morphology of tightly coiled protoconchs, the teleoconch morphology of genera like *Platyceras* and the presence of a calcitic shell suggest that *Platyceras*- and *Orthonychia*-like gastropods belong to Neritimorpha and are probably closely related to Naticopsidae.

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The Early Pleistocene freshwater mollusks of the Denizli Basin (Turkey): a new long-lived lake fauna at the crossroads of Pontocaspian and Aegean-Anatolian realms

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Abstract

We describe here a newly discovered, diverse fossil fauna of freshwater gastropods and bivalves from the Denizli Basin in SW Turkey. The material was collected from the Kolankaya Formation, for which latest chronostratigraphic and magnetostratigraphic data indicate an Early Pleistocene age, which is much younger than previously assumed for the fossil-bearing strata of the Denizli Basin. The fauna consists of at least 27 species (25 gastropods, 2 bivalves) and includes a new genus, *Harzhauseria* **gen. nov.**, and 6 new species within the Hydrobiidae: *Falsipyrgula*? *coronata* **sp. nov.**, *Graecoanatolica*? *alcicekorum* **sp. nov.**, *Harzhauseria schizopleura* **gen. et sp. nov.**, *Iraklimelania minutissima* **sp. nov.**, *Iraklimelania submediocarinata* **sp. nov.**, and *Xestopyrguloides*? *sagitta* **sp. nov.** Additionally, we define lectotypes for *Staja orientalis* (Bukowski, 1896) and *Valvata orientalis* Fischer, 1866, as well as a neotype for *Theodoxus percarinatus* (Oppenheim, 1919). Nine of the recovered species (33.3%) are only known from the Denizli Basin. Almost half of the fauna (44.7%) is endemic to the Aegean–Anatolian region, with biogeographical affinities to the Pliocene–Early Pleistocene faunas of Rhodes, Kos, and mainland Greece, as well as the Çameli and Eşen Basin in Turkey. On the genus level, the fauna also contains several typical Pontocaspian elements. The composition points toward a typical long-lived lake environment with oligohaline conditions.

Zusammenfassung

Wir beschreiben hier eine neu entdeckte, diverse fossile Fauna von Süßwassergastropoden und -Bivalven aus dem Denizli-Becken im Südwesten der Türkei. Das Material stammt aus der Kolankaya-Formation, für die neueste chronostratigraphische und magnetostratigraphische Daten auf ein frühpleistozänes Alter hindeuten, das viel jünger ist als bisher für die fossilführenden Schichten des Denizli-Beckens angenommen. Die Fauna besteht aus mindestens 27 Arten (25 Gastropoden, 2 Bivalven) und umfasst eine neue Gattung, *Harzhauseria* **gen. nov.**, und 6 neue Arten innerhalb der Hydrobiidae: *Falsipyrgula*? *coronata* **sp. nov.**, *Graecoanatolica*? *alcicekorum* **sp. nov.**, *Harzhauseria schizopleura* **gen. et sp. nov.**, *Iraklimelania minutissima* **sp. nov.**, *Iraklimelania submediocarinata* **sp. nov.**, und *Xestopyrguloides*? *sagitta* **sp. nov.** Zusätzlich definieren wir Lektotypen für *Staja orientalis* (Bukowski, 1896) und *Valvata orientalis* Fischer, 1866, sowie einen Neotypus für *Theodoxus percarinatus* (Oppenheim, 1919). Neun der gefundenen Arten (33,3%) sind nur aus dem Denizli-Becken bekannt. Fast die Hälfte der Fauna (44,7%) ist endemisch für die ägäisch-anatolische Region, mit biogeografischen Verbindungen zu den pliozänen und frühpleistozänen Faunen von Rhodos, Kos und dem griechischen Festland sowie dem Çameli- und Eşen-Becken in der Türkei. Auf der Gattungsebene enthält die Fauna auch einige typische pontokaspische Elemente. Die Zusammensetzung deutet auf das Milieu eines typischen Langzeitsees mit oligohalinen Bedingungen hin.

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Keywords

Taxonomy, biogeography, Pontocaspian biota, Anatolia, Quaternary

Introduction

The late Neogene to Quaternary non-marine mollusk faunas of Anatolia have attracted scientists since the 19th century. Early geological and geographical expeditions by Spratt and Forbes (1847) and Fischer (1866) yielded the first species records, already from a series of different basins and faunas. The first milestone work was published by Oppenheim (1919), who described numerous species from various basins and time horizons all over western Anatolia. The species inventory of the region grew further through contributions by Bukowski (1930), Taner (1974a, 1974b, 1980, 1983), Becker-Platen and Kuiper (1979, Schütt and Kavusan (1984), Schütt (1985b, 1991, 1992, 1994, 1997), Kapan Yesilyurt and Taner (2002), Wesselingh et al. (2008), Wesselingh and Alçiçek (2010), Vasilyan et al. (2014), van den Hoek Ostende et al. (2015), Alçiçek et al. (2017), Büyükmeriç and Wesselingh (2018), and Rausch et al. (2019). These contributions witness a heterogeneous species composition across different basins and time intervals, with a high degree of endemic developments. The earlier paleontological studies were put into context by the stratigraphical, tectonic, and paleoenvironmental studies of the 21st century (Becker-Platen 1970; Bering 1971; Becker-Platen et al. 1975, 1977; Alçiçek et al. 2005, 2007, 2013, 2015, 2019; Alçiçek 2007, 2010), which provide an important baseline to unravel the evolution and paleobiogeography of the Anatolian mollusks faunas.

Partly related faunas of similar age were detected especially in Greece. As for Turkish faunas, a wealth of contributions was published on Late Miocene to Early Pleistocene (and partly related) faunas of mainland Greece (Fuchs 1877; Neumayr 1880a; Oppenheim 1890, 1891; Papp 1947, 1953, 1955, 1979, 1980; Kühn 1951, 1963; Papp and Psarianos 1955; Schütt 1976, 1985a, 1986, 1988; Kaouras and Velitzelos 1985; Schütt et al. 1985; Rust 1997; Esu and Girotti 2015, 2020), the Aegean islands (Neumayr 1880b; Bukowski 1892, 1893, 1896; Schütt and Besenecker 1973; Willmann 1977, 1980, 1981, 1982, 1985; Schütt and Velitzelos 1991) and the Marmara Sea region (Hoernes 1876; Calvert and Neumayr 1880; Neumayr 1883; Gillet et al. 1978; Taner 1982, 1997; Rückert-Ülkümen et al. 2006).

Of all Anatolian faunas, the Denizli Basin contains probably the most diverse species inventory, which is partly owed to its long stratigraphic record (Figs 1, 2; Alçiçek et al. 2007, 2015; Wesselingh et al. 2008). Since the first description of a species by Fischer (1866), 43 species and another 13 subspecies (22 bivalves, 33 freshwater gastropods, 1 land snail) have been described from the Denizli Basin (not including species that have been reported from the basin but were first described elsewhere). Already Oppenheim (1919) recognized two different faunas with completely different species compositions and ecological implications, a “lower, more lacustrine type” and an “upper brackish type”. The younger, brackish fauna was studied in detail by Wesselingh et al. (2008). It contains elements typical of Pleistocene to modern Pontocaspian faunas, such as bivalves of the subfamily Lymnocardiinae.

The ages of the two faunas have a long history of debate. For the older fauna, age estimates range from Middle Miocene or Sarmatian (Oppenheim 1919) to Maeotian (Taner 1975, 2001). The younger, Pontocaspian-type fauna was assumed to be Pontian by Oppenheim (1919) and Taner (1975, 2001) and Messinian by Wesselingh et al. (2008), respectively. Taner (1975) referred both faunas to the “Lower Pliocene” but she correlated it with the Maeotian/Pontian strata of the Paratethys.

Because of the presumed latest Miocene age, the younger fauna was previously considered to be among the oldest Pontocaspian-type faunas, serving as potential source of origin for Pliocene to Quaternary species lineages (Wesselingh et al. 2008). Latest chronostratigraphic and magnetostratigraphic data, however, indicate a much younger, Early Pleistocene age for both fossil-bearing deposits (S. Lazarev, pers. comm.). More precisely, the older (“Kolankaya I”) fauna is classified as Gelasian (> ~1.8 Ma), the younger (“Kolankaya II”) one as Calabrian (< ~1.8 Ma). These new ages call for a revised assessment of biogeographic relationships.

In contrast to the well-studied Kolankaya II fauna, a modern assessment of the older Kolankaya I is largely missing. Here we report a newly collected fauna from the southern margin of the Denizli Basin. We provide a comprehensive taxonomic study, along with paleoecological and paleobiogeographical interpretations.

Geological setting

The Denizli Basin in SW Turkey is a 70 × 50 km graben-type basin trending WNW–ESE (Alçiçek et al. 2007, 2015; Figs 1, 2). The Neogene–Quaternary basin infill is bordered by the Paleozoic–Mesozoic metamorphic rocks of the Menderes Massif in the southwest and northwest and Lycian nappes in the eastern part, both of which form the bedrock of the basin. In the northwest, the basin is split into two subbasins by an intrabasinal high known as Buldan Horst (Alçiçek et al. 2007, 2015; and references therein). The study area is located in the SW subbasin.

The Neogene–Quaternary infill, referred to as the Denizli Group, attains a thickness of up to 1300 m and consists of a complex succession of alluvial, fluvial, and lacustrine deposits. Following the stratigraphic and paleo-

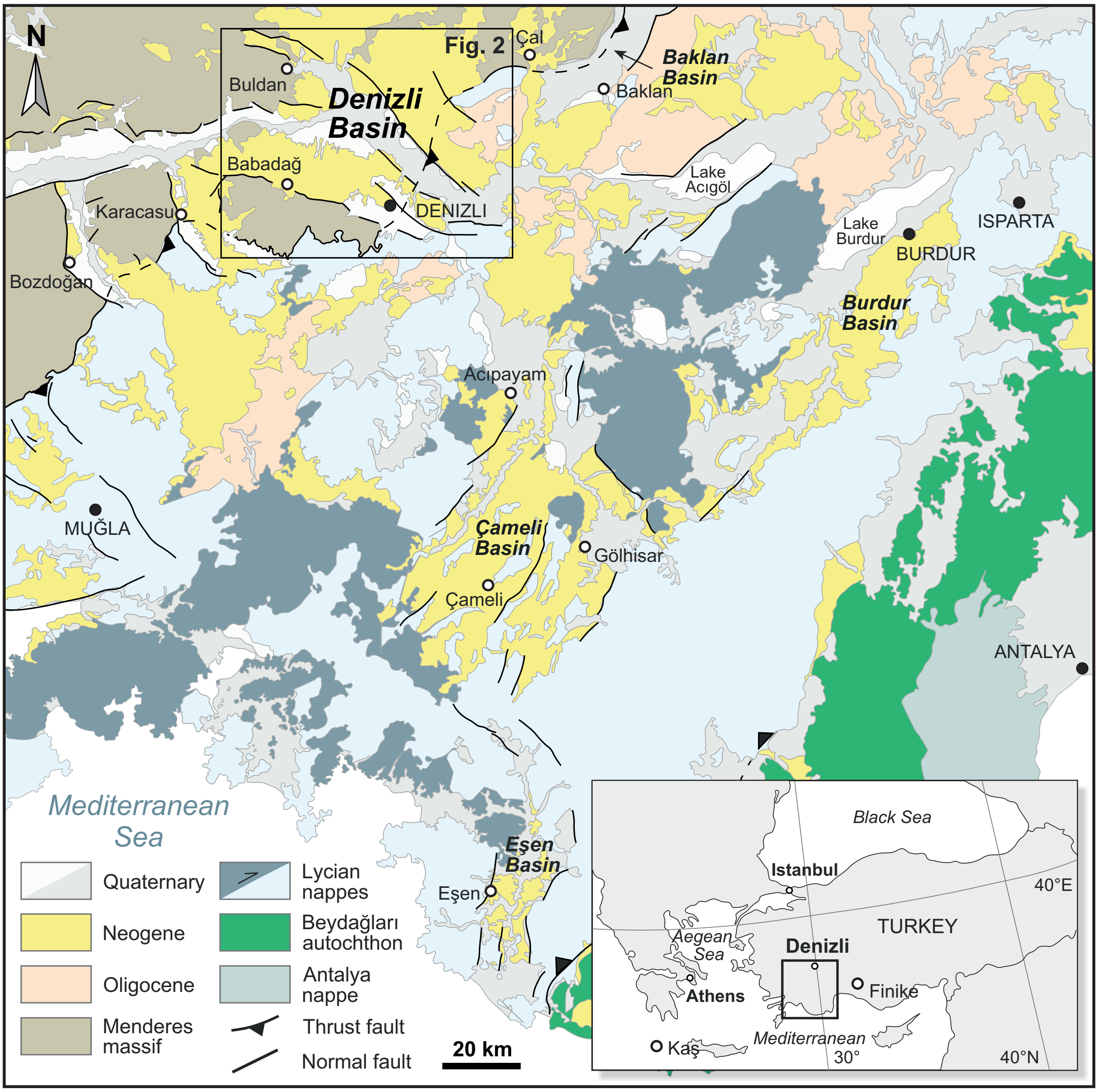

Figure 1. Geographical and geological overview of the study area in SW Turkey (modified from Alçiçek et al. 2015).

environmental studies of Alçiçek et al. (2007, 2015), four formations are recognized: 1) the Kızılburun Formation, unconformably overlying the bedrock, covers up to 450 m thick alluvial-fan to river deposits and represents a wetland type environment with small lakes, rivers, and mires; 2) the Sazak Formation, which gains a thickness of 300 m, comprises marls, claystones, mudstones, siltstones, limestones, dolostones, as well as gypsum and halite deposits in the upper part, and corresponds to the development of a marginal to shallow and finally saline lake; 3) the Kolankaya Formation, containing the here described mollusk fauna, reaches a thickness of up to 500 m and overlies conformably the Sazak Formation and unconformably metamorphic bedrock in the northern part of the basin, respectively. It represents a balanced-filled, shallow to deep-water lake; 4) the up to 150 m thick Tosunlar Formation, which rests unconformably on the Kolankaya Formation, consists of alluvial-fan and fluvial deposits.

The stratigraphic ages of the formations are currently subject of revision with radiometric age-constrained paleomagnetic approaches (S. Lazarev, pers. comm.). The new age estimates strongly deviate from earlier age estimates that were poorly constrained and show that the Kolankaya Formation is of a Pleistocene age rather than a Neogene age. The new age data also imply that the ages of the Sazak and Kızılburun formations will need re-evaluation. The older Kolankaya I fauna subject of this paper is very likely to be of a Gelasian age with an upper limit for this fauna of approximately 1.8 Ma (S. Lazarev, pers. comm.).

Material and methods

Mollusks representing the Kolankaya I fauna were collected in three shell rich levels in the Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of

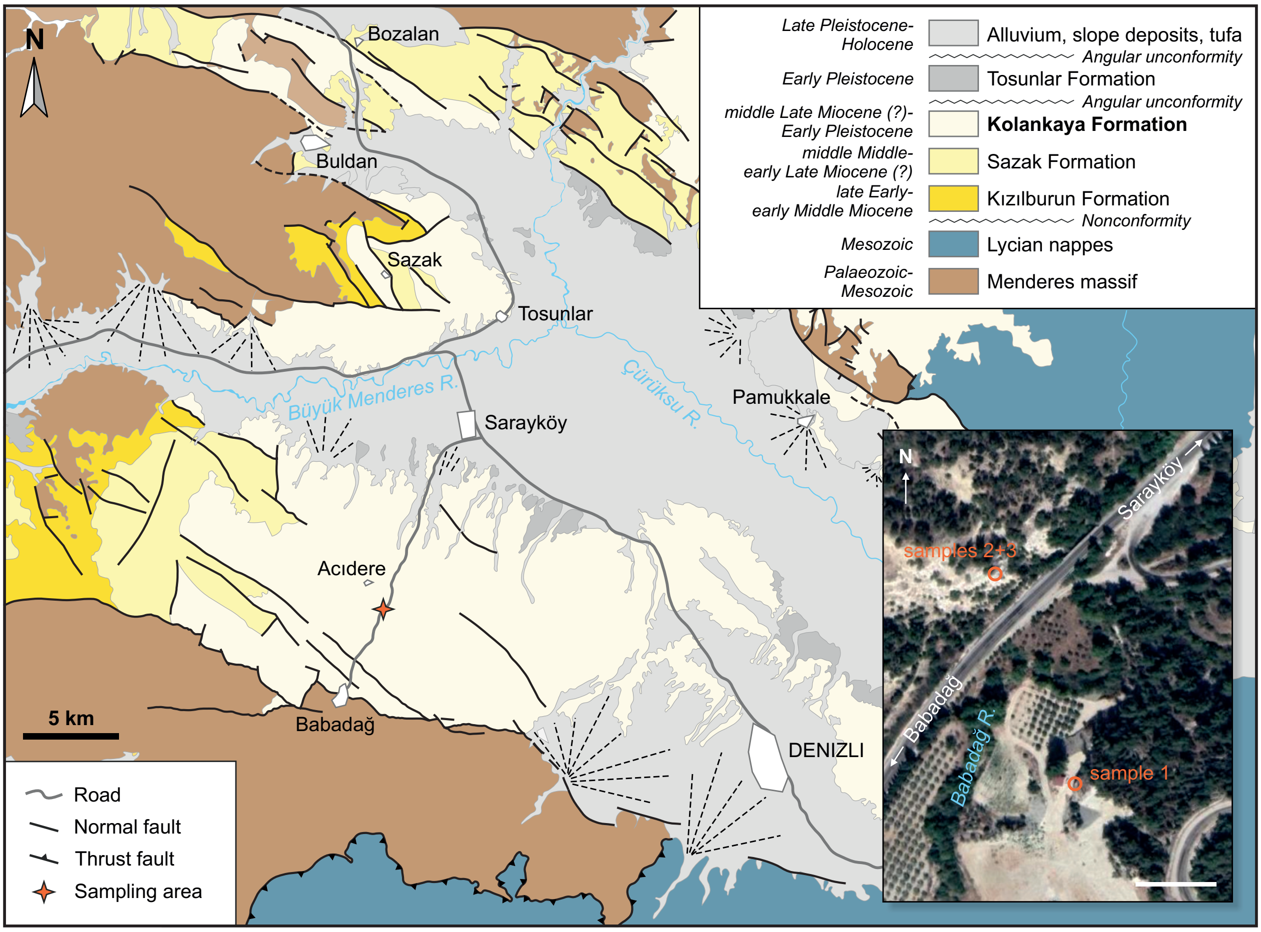

Figure 2. Geology of the Denizli Basin with indication of the sampling area (modified from Alçiçek et al. 2015). The insert shows the sampling locations in the Babadağ river valley along the Babadağ-Sarayköy road. Underlying satellite image © Google Maps 2023, CNES/Airbus, Maxar Technologies.

Babadağ. Sample 1 was taken from a small wall-cut behind a shed on the east side of the valley, from an interval with olive brown parallel-stratified siltstones and the scree zone around (37°50'40.3"N, 28°52'53.3"E, WGS84). Here, larger specimens were hand-picked and a few hundred grams of sediment was sampled and washed over a 0.5 mm sieve. Sample 2 was obtained at the top of a small cliff on the west side of the road (37°50'44.5"N, 28°52'51.3"E), at the contact between brown sandy siltstones and white limestones on top. About 3 kg of sediment was obtained and washed over 0.5 mm. Sample 3 refers to hand-picked material from scree deposits within a few meters radius of sample 2. The three samples were taken from the upper part of the lower Kolankaya Formation, below a major lithological transition toward a gravel interval that marks the transition to the overlying Kolankaya II interval (S. Lazarev, unpublished data). The stratigraphic levels of the bulk samples correspond to approximately 200 m (sample 1) and 230 m (sample 2) from the base of the Kolankaya Formation, respectively (S. Lazarev, pers. comm. 11/2023).

Preservation of shells varies, ranging from specimens with excellently preserved shell surface, protoconch sculpture, and even color patterns to fragmentary or abraded individuals. Especially larger specimens and those collected from the surface typically show signs of abrasion and ornament obliteration.

Photos were taken with a Keyence VHX-7000 digital microscope at SNSB-BSPG and a Leica M165C stacking microscope at Naturalis. Scanning electron microscopy photographs were taken with a ZEISS LEO-1430 VP with 20 kV at the Bavarian State Collection for Zoology, Munich (SNSB-ZSM) and a Tescan Vega\\xmu with 5 kV at the Department of Palaeontology at Friedrich-Alexander-Universität Erlangen-Nürnberg. For that purpose, specimens were sputter coated with gold with a Quorum Q150R S at BSPG and a Polaron SC510 at ZSM. Photos were edited with Adobe Photoshop CC, figures were arranged with CorelDRAW Graphics Suite X8.

For gastropods, dimensions are given as shell height × width and were measured based on frontal views with specimens arranged vertically along their axis (as illustrated on the figures). To calculate the proportion of the last whorl, the whorl's height was measured at the shell axis. For the dreissenid bivalves (all of which are fragmented), length is measured with the dorsal margin horizontally placed, height is measured perpendicularly, and the semidiameter is the shell width measured when the shell is put on a horizontal surface.

The material is stored at Naturalis Biodiversity Center (coll. no. RGM 962606–962621, 962689–962704, 1310375–1310377, 1310796–1310799, 1310837–1310861, 1365347–1365352) and the Bavarian State

Collection for Palaeontology and Geology (coll. no. SNSB-BSPG 2023 XII 1–24).

We aimed to compare our material with that of Oppenheim (1919), who described many species from the Denizli Basin. However, the material could be found neither in the Museum für Naturkunde Berlin (M. Aberhan, pers. comm. 09/2022), where Oppenheim himself originally deposited the specimens, nor in the Hebrew University of Jerusalem (R. Rabinovich, H.K. Mienis, pers. comm. 11/2022), which contains large parts of Oppenheim's collection. We contacted several other institutions in Europe for further information (Natural History Museum Vienna, Muséum national d'Histoire naturelle in Paris, Natural History Museum London, Moravské zemské muzeum in Brno, Masaryk University in Brno), but no hint on the whereabouts of the type material could be obtained. Hence, we have to assume it got lost, perhaps in the course of the relocation of the Berlin collection during and after World War II (Neumann et al. 2018).

Material from Pliocene to Pleistocene strata of Rhodes (Bukowski 1893, 1896) stored at the Department of Geology at the University of Vienna (IGUW) and of mainland Greece (Fuchs 1877) housed at the Geological-Paleontological Department of the Natural History Museum (NHMW) was studied for comparison. An updated stratigraphy of the relevant deposits on Rhodes was recently published by Schneider et al. (2023).

Systematic paleontology

We follow the higher classification scheme of Bouchet et al. (2017) for Gastropoda and Carter et al. (2011) for Bivalvia. Synonymy/chresonymy lists include first descriptions, records where a taxon was illustrated or discussed in detail, as well as references to Wenz' (1923–1930) fossil catalogue (which may list further mentions of taxa in question).

Class Gastropoda Cuvier, 1795
Subclass Neritimorpha Golikov & Starobogatov, 1975
Order Cycloneritida Frýda, 1998 emend. Bouchet et al. 2017
Superfamily Neritoidea Rafinesque, 1815
Family Neritidae Rafinesque, 1815
Subfamily Neritininae Poey, 1852

Genus *Theodoxus* Montfort, 1810

Type species. *Theodoxus lutetianus* Montfort, 1810 [unnecessary substitute name for *Theodoxus fluviatilis* (Linnaeus, 1758)]; by original designation.

Theodoxus percarinatus (Oppenheim, 1919), comb. nov.

Fig. 3A–T

*1919 *Neritina percarinata* sp. nov. – Oppenheim: 128–129, pl. 9, fig. 7.

Material. Sample 1: c. 500 specimens (RGM 1310838) and 1 specimen (SNSB-BSPG 2023 XII 1); sample 2: 1 specimen tentatively attributed to the species (RGM 962606), 1 specimen (RGM 962607), 1 specimen (RGM 1310797), 123 specimens (RGM 1310839), 2 fragments and fragmented opercula (RGM 1310840), 1 specimen (SNSB-BSPG 2023 XII 2); sample 3: 53 specimens (RGM 1310841).

Neotype. Oppenheim's type material could not be found despite considerable efforts and is presumably lost (see Material and Methods section). To ensure nomenclatural stability and link the name to a type specimen, we herewith designate a neotype. The original type locality includes two localities, Giralan near Pamukkale and Bozalan near Buldan ("Abstieg nach Giralan.—Bosalan bei Bulladan.") in the Denizli Basin (Fig. 1). No material from those localities is available to us, but considering the geographic vicinity of the newly collected material as well as the distinct morphological features, there can be no doubt that our material represents the same species as the one described by Oppenheim (1919). We select as neotype the specimen illustrated on Fig. 3I–L, which comes from sample 2 (RGM 962607).

Description. Globular neritid with short, flattened spire and up to 3.3 whorls. Characteristic keel is observed in part of the material. In well preserved, keeled specimens narrow, distinct keel develops early in ontogeny. In first whorl it aligns with suture, but as shell growth becomes slightly more abapically oriented, keel emerges more clearly and separates whorl top and whorl flank. Expression and extent of keel varies, it may appear and disappear within 0.2 whorls or range until last whorl; however, no specimen is found with keel covering entire shell. Strength of keel very variable, ranging from robust and well delimited to almost obsolete. In much of the material the keel is worn. Aperture broadly semicircular with broad, smooth callus that is weakly thickened especially in its center (see lateral views). Coloration variable, including fully black, white with dark stripes, irregular mix of dark and white, white blotches arranged in spiral bands or entirely white.

Dimensions. 6.64 × 7.76 mm (neotype, RGM 962607; Fig. 1I–L), 10.66 × 10.51 mm (RGM 1310797; Fig. 1A–D), 6.72 × 7.24 mm (SNSB-BSPG 2023 XII 1; Fig. 1M–P).

Remarks. The species has not been treated in the literature since the original description. It was neither included in the Fossilium Catalogus by Wenz (1930), perhaps because he considered this form not to be a freshwater taxon, nor was it listed by Taner (1974a, 1975). The combination with the genus *Theodoxus* appears for the first time in Alçiçek (2010), but without discussion. Here, we formalize the classification and re-describe the species.

The diagnostic character of this species is its name-giving thin keel at the transition between whorl top and flank, which distinguishes the species from most others. A similarly keeled species is *Theodoxus carinatus* (Fuchs, 1877) from the Lower Pleistocene (Calabrian) of Livonates (mainland Greece). It differs in the flattened whorl flanks, the weakly raised spire, the broader keel and the color pattern consisting of wavy axial lines.

In addition to the majority of keeled specimens of *Theodoxus percarinatus*, shells occur that lack the

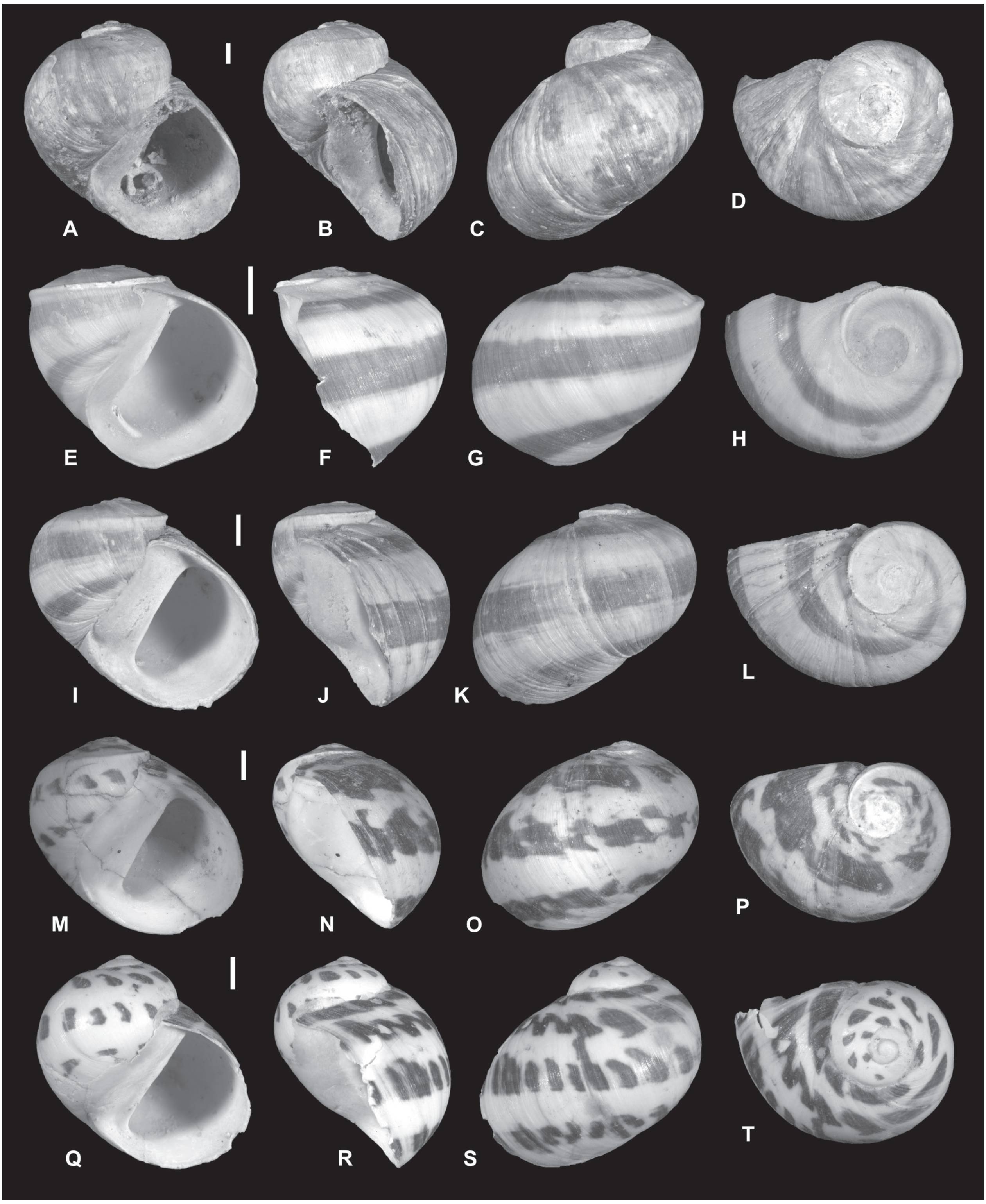

Figure 3. Neritidae of the Kolankaya I fauna. **A–D.** *Theodoxus percarinatus* (Oppenheim, 1919), RGM 1310797, sample 2. **E–H**. *T. percarinatus*, SNSB-BSPG 2023 XII 2, sample 2. **I–L.** *T. percarinatus*, Neotype, RGM 962607, sample 2. **M–P.** *T. percarinatus*, SNSB-BSPG 2023 XII 1, sample 1. **Q–T.** *T.* cf. *percarinatus*, RGM 962606, sample 2. Scale bars: 1 mm.

keel entirely and have a slightly more elevated spire (Fig. 3Q–T). In terms of size, general shape, and color patterns these specimens fall well within the range of *T. percarinatus*. Many *Theodoxus* species are known to have highly variable shells (Sands et al. 2020), which complicates a taxonomic decision about the status of these specimens. Apparent intermediate specimens occur in our material, but the worn nature of much of the material, the small numbers of specimens, and the general variability of the genus preclude confirmation whether it concerns untypically unkeeled representatives of *T. percarinatus* or constitute a separate, rare, and potentially new species.

Distribution. Only known from the Denizli Basin.

Theodoxus aff. *pilidei* (Tournouër, 1879)

Fig. 4A–H

Material. 2 specimens (RGM 962608, RGM 1310796), 2 specimens and 1 fragment (RGM 1310842), 1 specimen (SNSB-BSPG 2023 XII 3); all from sample 2.

Dimensions. 1.97 × 2.69 mm (RGM 962608; Fig. 4A–D, H), 3.66 × 3.88 mm (RGM 1310796; Fig. 4E–G).

Remarks. Our material contains two moderately preserved specimens that exhibit a high variability in spire height and angulation. The low-spired morphotype (Fig. 4A–D, H) resembles *Theodoxus pilidei* (Tournouër, 1879), originally described from Pliocene or Lower Pleistocene strata of the Dacian Basin (Wenz 1942; Pană et al. 1981; Pană 2003; Papaianopol and Marinescu 2003), in terms of the general ovoid shell shape with depressed spire and the strong, papery lamellae. The illustrations of Pană et al. (1981) show quite some variability in the morphology of *T. pilidei*, including the expression of sculpture, which can be weak or nearly absent in some specimens. However, our material differs from that species particularly in the presence of a distinct angulation, which results in a nearly flat, apical plane. Specimens with elevated spire even show two angulations separated by a concave whorl flank (Fig. 4E–G). From the little material we have available it is difficult to judge the species' range of variability as well as make a taxonomic assignment. The distinct angulation present in our material, however, makes an affiliation with *T. pilidei* unlikely.

Another similar species is *Theodoxus boteani* (Porumbaru, 1881), which has a similar type of sculpture but more globular shells (Pană 2003). The extant, allegedly subterranean *Theodoxus gloeri* Odabaşi & Arslan, 2015 from Eskişehir region (Turkey), which also exhibits papery lamellae, differs in a slightly higher spire and the absence of an angulation (Odabași and Arslan 2015; Sands et al. 2020). Possibly our material signifies a new species.

Subclass Caenogastropoda Cox, 1960
Order unassigned
Superfamily Cerithioidea Fleming, 1822
Family Melanopsidae H. Adams & A. Adams, 1854

Genus *Esperiana* Bourguignat, 1877

Type species. *Melanopsis esperi* Férussac, 1823; by original designation.

Esperiana esperi (Férussac, 1823)

Fig. 5A–F

*1823 *Melanopsis Esperi*, nobis – Férussac: 160.

1974a *Melanopsis* (*Melanopsis*) cf. *bergeroni* Stefanescu – Taner: 116, pl. 9, figs 16–21.

2018 *Esperiana esperi* (Férussac, 1823) – Neubauer et al.: 89. fig. 17N.

2012 *Esperiana esperi* (Férussac, 1823) – Welter-Schultes: 35, unnumbered textfig.

2019 *Esperiana* (*Esperiana*) *esperi* (A. Férussac, 1823) – Glöer: 83, textfig. 83.

Material. Sample 1: 3 specimens (RGM 962691–962693), 10 specimens (SNSB-BSPG 2023 XII 4), ca. 300 specimens (RGM 1310843); sample 3: 13 specimens (RGM 1310844), 1 specimen (RGM 1365348).

Dimensions. 16.25 × 7.78 mm (RGM 962691; Fig. 5A–C), 14.44 × 7.47 mm (RGM 962692; Fig. 5D, E).

Remarks. The present material matches well the extant *Esperiana esperi* concerning the elongate, smooth shell with adpressed whorls, lanceolate aperture with thickened inner lip and the slight concavity between base of the last whorl and base of the aperture (Welter-Schultes 2012; Glöer 2019). Even the color pattern, consisting of dissected

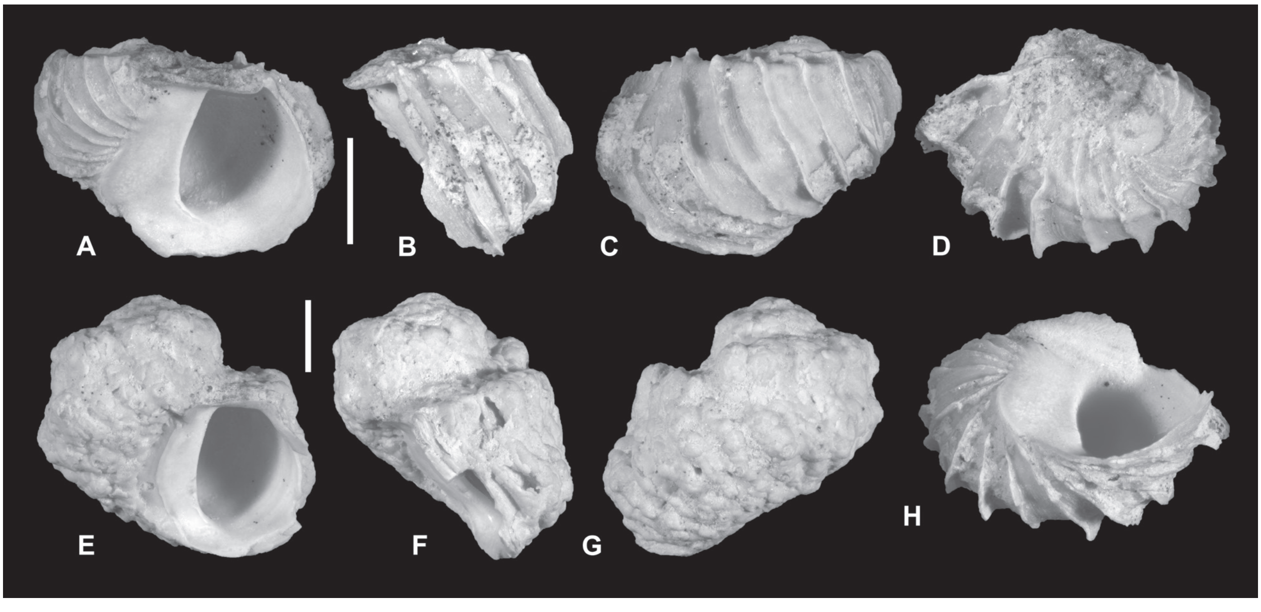

Figure 4. Neritidae of the Kolankaya I fauna. **A–D, H**. *Theodoxus* aff. *pilidei* (Tournouër, 1879), RGM 962608, sample 2. **E–G**. *T.* aff. *pilidei*, RGM 1310796, sample 2. Scale bars: 1 mm.

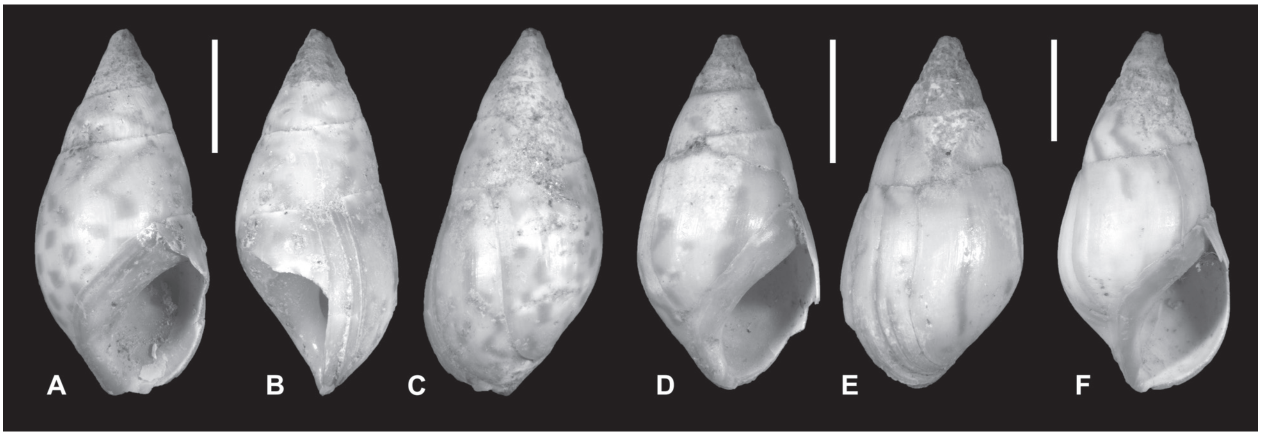

Figure 5. Melanopsidae of the Kolankaya I fauna. **A–C.** *Esperiana esperi* (Férussac, 1823), RGM 962691, sample 1. **D, E.** *E. esperi*, RGM 962692, sample 1. **F.** *E. esperi*, RGM 962693, sample 1. Scale bars: 5 mm.

zigzag lines to a chess-like arrangement of orange spots, and the corroded apex are typical of the modern species.

Shape, apertural characteristics and color pattern are also found in the Plio-Pleistocene species *Melanopsis bergeroni* Stefanescu, 1896 from the Dacian Basin (Romania) (Stefanescu 1896; Pană et al. 1981; Pană 2003). The same is true for *Melanopsis esperioides* Stefanescu, 1896 from the same region, which seems to be only slightly more slender and larger on average than *M. bergeroni* (Stefanescu 1896). It might well be that both species range within the morphological variability of *E. esperi*, but a final verdict on their status requires comparison with topotypic material from the Dacian Basin. In case of synonymy, the subgenus *Melanopsis* (*Calodiona*) Stefanescu, 1896, of which *M. bergeroni* is the type species, would become a synonym of *Esperiana*.

The specimens from the Denizli Basin studied by Taner (1974a) and identified as *M.* cf. *bergeroni* falls well into the range of *E. esperi* and considered conspecific herein.

Distribution. Today in central to southeastern Europe (western Black Sea region to Hungary, Slovakia, Austria, and Slovenia) and northwestern Anatolia (Welter-Schultes 2012; Glöer 2019). Also found in Pleistocene strata of the North Caspian Basin (Neubauer et al. 2018).

Superfamily Truncatelloidea Gray, 1840
Family Hydrobiidae Stimpson, 1865
Subfamily Caspiinae B. Dybowski, 1913

Genus *Graecoanatolica* Radoman, 1973b

Type species. *Hydrobia vegorriticola* Schütt, 1962; by original designation.

Graecoanatolica alcicekorum sp. nov.

https://zoobank.org/DF386B7C-64EC-4328-B6C6-8DBC765BB6E0
Fig. 6A–E

Etymology. Named in honor of Hülya and M. Cihat Alçiçek, esteemed Turkish geologists with long research background in the Denizli Basin, for their continuing support and friendship.

Holotype. RGM 962617 (Fig. 6A–E). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

Additional material. None (holotype only).

Diagnosis. Slender, weakly ovoid shell with slightly tapered last whorl, adnate whorls with thin suture, faint subsutural concavity in late ontogeny, sinuate outer lip, and sigmoidal growth lines.

Description. Slender, ovoid hydrobiid shell, with 4.75 whorls. Protoconch consisting of c. 1 whorl, low domed with broad nucleus, weakly, finely-meshed malleate surface; sculpture fades out toward P/T transition; transition indicated by growth stop and onset of growth lines. Whorls moderately convex in early ontogeny; penultimate whorl exhibits nearly straight-sided upper whorl half and regularly convex lower half; last whorl, portion below suture weakly concave, producing weak constriction and slightly irregularly convex whorl profile. Last whorl attains 60% of shell height. Base ~45°, straight-sided. Aperture drop-shaped, tightly coiled, leaving no umbilicus; peristome not thickened or notably expanded; outer lip distinctly sigmoidal in lateral view. Growth lines sigmoidal, with opisthocyrt upper half and slightly weaker, prosocyrt lower half.

Dimensions. 2.21 × 0.97 mm (holotype, RGM 962617; Fig. 6A–E).

Remarks. The species' shell shape and size, the protoconch size, the subsutural concavity, the ovoid aperture with thin, sinuate peristome, and the sigmoidal growth lines are characteristics typical of extant members of the genus *Graecoanatolica*. The co-occurring species of *Iraklimelania* share many of these attributes, but they both have more slender shells with relatively smaller last whorls and larger protoconchs (1.2 whorls compared to 1 whorl).

The only fossil species of the genus was previously reported as *G. denizliensis* (Taner, 1974a) by Wesselingh et al. (2008) from the overlying "*Didacna* Beds" (= Kolankaya II fauna). The specimens, however, differ from true “*Hydrobia*” *denizliensis* in the much smaller, ovoid shell with strongly convex whorls. The original species described by Taner is a large hydrobiid (7 mm) with moderately convex whorls and elongated aperture. The species of Wesselingh et al. (2008), which is currently without a name but fits well in the genus *Graecoanatolica*, differs from the new species in the slightly broader shell, the more convex whorls, and the presence of a narrow umbilicus.

Graecoanatolica alcicekorum sp. nov. resembles several extant representatives of the genus. Shells of the North Macedonian *Graecoanatolica macedonica* Radoman & Stankovič, 1979 and the Greek *G. vegorriticola* (Schütt, 1962) are similarly slender, but whorls have a regularly convex profile. The Turkish *G. dinarica* Kebapçı, Koca & Yıldırım, 2012 has a shell with highly convex whorls, a slightly irregularly shaped last whorl and a smaller aperture (Kebapçı et al. 2012). *Graecoanatolica lacustristurca* Radoman, 1973b (the type species) and *G. tenuis* Radoman, 1973b, both also described from Turkey, have conical shells with broad, blunt apex and a narrow umbilicus (Kebapçı et al. 2012).

The genus was recently placed in Caspiinae by Delicado et al. (2023) based on a comprehensive phylogenetic analysis.

Distribution. So far only known from the Early Pleistocene of the Denizli Basin.

Graecoanatolica? sp.

Fig. 6F–I

Material. 1 specimen (RGM 1365349) from sample 1.

Remarks. At first glance, this shell reminds of *Iraklimelania minutissima* sp. nov. (see below) in terms of the very small, slender shell with convex whorls. However, the protoconch of *Graecoanatolica*? sp. is higher, whorls are more regularly convex, the aperture is oblique in lateral view, and the umbilicus is clearly visible. In all these characteristics it closely resembles extant *Graecoanatolica dinarica* Kebapçı, Koca & Yıldırım, 2012, for which we have studied topotypical material from İncirlipınar in Afyonkarahisar region. That species differs from *Graecoanatolica*? sp. in the larger size, the comparatively larger apex, the faster whorl expansion rate, and the often irregular growth (Kebapçı et al. 2012). Yet, the growth lines of *Graecoanatolica*? sp. are nearly orthocline, which has not been observed in any *Graecoanatolica* species, which is why we only tentatively associate the species with this genus.

Genus *Iraklimelania* Willmann, 1981

Type species. *Iraklimelania levis* Willmann, 1981; by original designation.

Remarks. The revised attribution of *Iraklimelania*, originally tentatively placed in “Micromelaniidae” by Willmann (1981), to Caspiinae is based on two pillars. First, the protoconch sculpture, with the malleate surface bearing faint spiral striae and a thickened terminal portion, reminds of species of Caspiinae (Anistratenko et al. 2021). Extant Pontocaspian members are typically characterized by an increasing sculpture intensity toward the end and

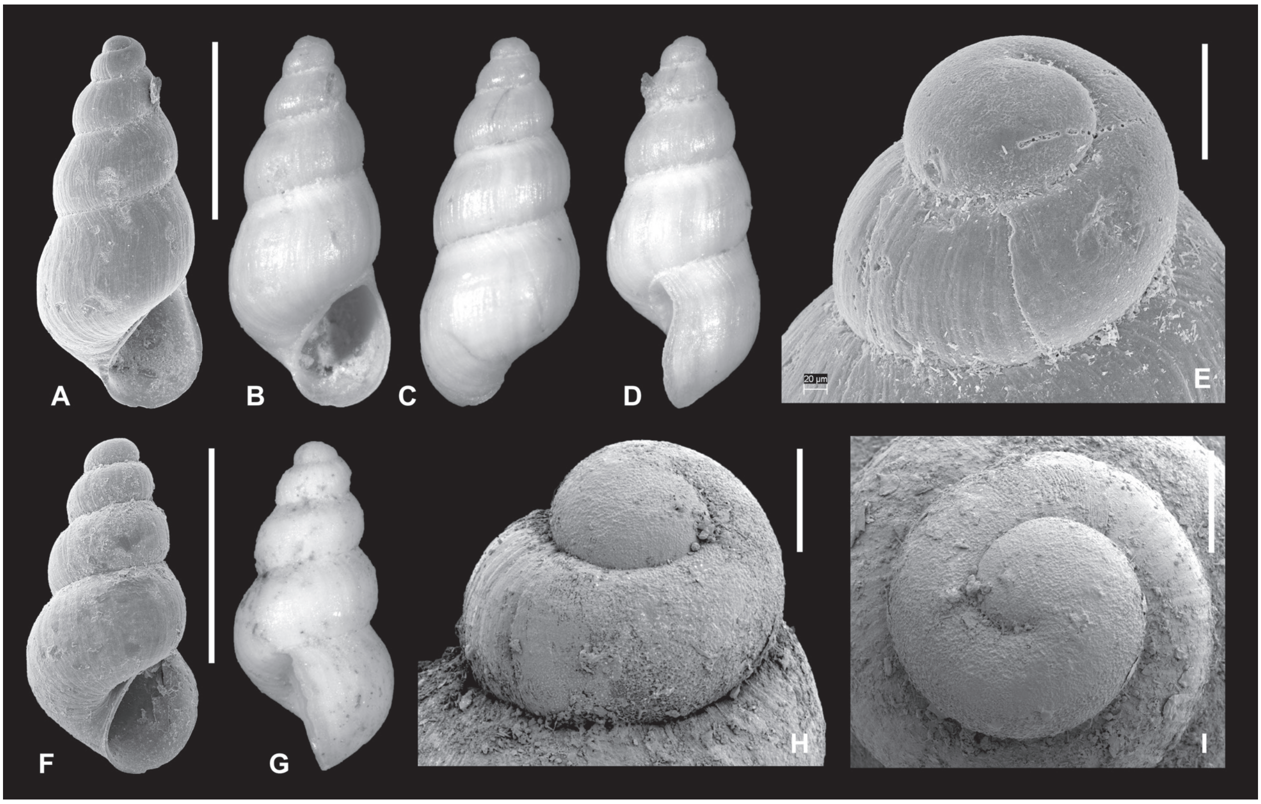

Figure 6. Caspiinae (Hydrobiidae) of the Kolankaya I fauna. **A–E.** *Graecoanatolica alcicekorum* sp. nov., holotype, RGM 962617, sample 2. **F–I.** *Graecoanatolica*? sp., RGM 1365349, sample 1. Scale bars: 1 mm (**1–D, F, G**); 100 µm (**E, H, I**).

the upper whorl half of the protoconch, as well as sculpture-free triangle at the P/T boundary (Anistratenko et al. 2021), which is missing though in the Turkish material. Second, the close morphological similarity to species of *Graecoanatolica*, recently placed in Caspiinae as well, supports a classification in that subfamily.

Iraklimelania minutissima sp. nov.

https://zoobank.org/90224404-5C1A-443C-B219-D83B2A467FF4

Etymology. Referring to the exceptionally small shell size.

Holotype. RGM 962617 (Fig. 7A–E). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

Additional material. One juvenile or subadult form (SNSB-BSPG 2023 XII 5; Fig. 7F–J) from sample 2.

Diagnosis. Very small, slender hydrobiid with highly convex and slowly growing whorls that show weak subsutural concavity in late ontogeny, small aperture with weak bulge at columella, and sigmoidal growth lines.

Description. Exceptionally small, slender hydrobiid shell, with slightly less than 5 whorls that slowly expand in width and height. Protoconch consisting of c. 1.2 whorls; low domed with broad nucleus, malleate surface, with initially tiny mesh-size, which becomes coarser toward P/T

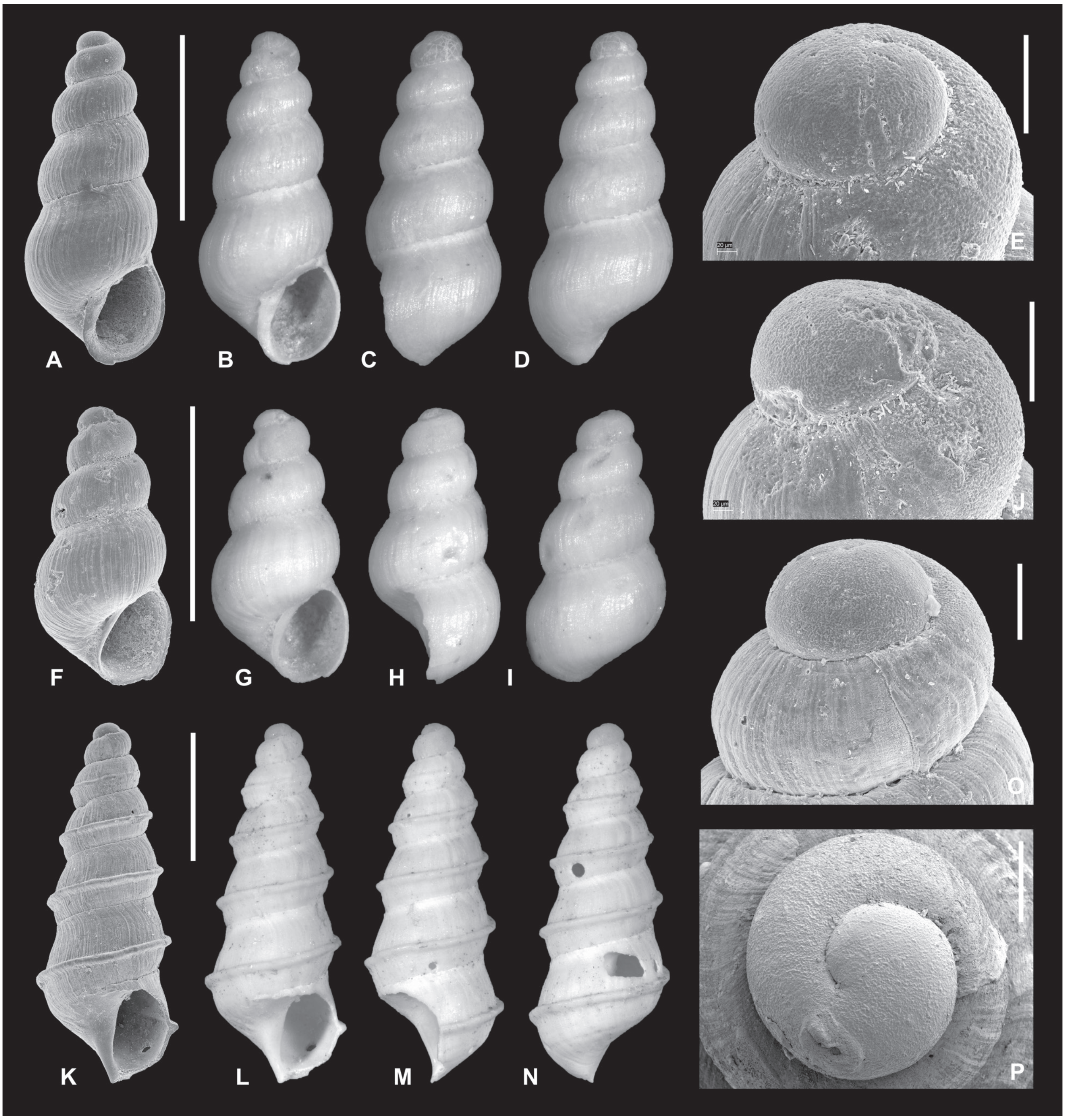

Figure 7. Caspiinae (Hydrobiidae) of the Kolankaya I fauna. **A–E.** *Iraklimelania minutissima* sp. nov., holotype, RGM 962618, sample 2. **F–J.** *Iraklimelania minutissima* sp. nov., juvenile or subadult form, SNSB-BSPG 2023 XII 5, sample 2. **K–P.** *Iraklimelania submediocarinata* sp. nov., holotype, RGM 962689, sample 1. Scale bars: 1 mm (**A–D, F–I, K–N**); 100 µm (**E, J, O, P**).

transition; P/T transition indicated by growth stop and onset of growth lines. Whorls highly convex throughout ontogeny; in last two whorls, faint concavity forms below suture. Last whorl attains c. 53% of total shell height. Base ~45°, straight-sided. Aperture small, elliptical; weak bulge occurs at columella. Inner lip covers sheet-like base of penultimate whorl, slightly expanded across columella, leaving very narrow umbilicus; outer lip not preserved. Growth lines distinct, sigmoidal, with opisthocyrt upper half and prosocyrt lower half.

Dimensions. 1.93 × 0.83 mm (holotype, RGM 962618; Fig. 7A–E).

Remarks. We attribute the new species to the genus *Iraklimelania* based on the following characters matching the type species, *I. levis* Willmann, 1981, from the Lower Pleistocene Irakli Formation of Kos Island: the small size; the small, simple aperture, having a slight bulge at the columella; the highly convex whorls, characterized by a narrow, faint constriction below the suture ("weak, concave sulcus" of Willmann 1981); the sigmoidal growth lines; the faint spiral striae. Our species can be distinguished by the even smaller size, the exceptionally slender shape and the narrower subsutural constriction. The only other species known for that genus, ?*Iraklimelania coa* Willmann, 1981 from the Lower Pleistocene Tafı Formation of Kos, differs in the conical shell and the presence of a blunt keel near the lower suture.

In addition to the holotype, a juvenile or subadult specimen is considered to belong to the new species (Fig. 7F–J). In that shell, the sigmoidality of the growth lines is not yet fully expressed, but the other features fit well to the holotype.

Distribution. So far only known from the Early Pleistocene of the Denizli Basin.

Iraklimelania submediocarinata sp. nov.

https://zoobank.org/21403AD8-AA28-49B9-972F-AA7CECA9C827

Etymology. Named with respect to the keel below the whorl center.

Holotype. RGM 962689 (Fig. 7K–P). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 1 (37°50'40.3"N, 28°52'53.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

Additional material. None (holotype only).

Diagnosis. Small, slender hydrobiid with distinct, blunt keel below whorl center, slowly growing whorls that show weak subsutural concavity in late ontogeny, small aperture, and sigmoidal growth lines.

Description. Small, slender hydrobiid shell, with 6 whorls that slowly expand in width and height. Protoconch consisting of c. 1.2 whorls; low domed with broad nucleus, finely-meshed malleate surface with 6–7 widely, but more or less regularly, spaced, weak spiral striae; terminal phase thickened, devoid of surface sculpture; P/T transition indicated by growth stop and onset of growth lines. Distinct, blunt, relatively broad keel develops on about 2nd teleoconch whorl; becomes quickly more pronounced toward 3rd whorl; originally almost in whorl center, keel becomes successively shifted toward lower suture; on last whorl, it is placed between lower third and upper two thirds of whorl height. Keel leaves weak furrow inside shell, at least on last whorl (Fig. 7K). Disregarding keel, whorls are regularly convex in early whorls, but convexity decreases during ontogeny; whorl portion above keel in last whorl almost straight-sided, with faint concavity below upper suture. Last whorl attains c. 49% of total shell height. Base ~45°, grading from straight-sided upper part into concave neck. Aperture not preserved, but whorl cross-section suggests small, elliptical shape. Growth lines distinct, sigmoidal, with opisthocyrt upper half (above keel) and weakly prosocline lower half (below keel).

Dimensions. 2.83 × 1.13 mm (holotype, RGM 962689; Fig. 7K–P).

Remarks. As for the previous species, we consider this one to belong in *Iraklimelania*. It matches both *I. minutissima* sp. nov. and the type species in terms of the small, slender shell with convex whorls and narrow subsutural concavity, the small aperture with slight bulge and the sigmoidal growth lines. The main difference to both species is the blunt keel below the center of the whorls. This feature reminds of ?*Iraklimelania coa*, which differs however in the distinctly conical shell with nearly straight-sided whorls.

Distribution. So far only known from the Early Pleistocene of the Denizli Basin.

Subfamily Hydrobiinae Stimpson, 1865

Genus *Ecrobia* Stimpson, 1865

Type species. *Turbo minutus* Totten, 1834 [= *Ecrobia truncata* (Vanatta, 1924)]; by original designation.

Ecrobia sp.

Fig. 8A–F, Q

Material. 1 specimen (RGM 962612), 4 specimens (RGM 1310850), 1 specimen SNSB-BSPG 2023 XII 6); all from sample 2.

Dimensions. 5.54 × 3.55 mm (RGM 962612; Fig. 8A–C, Q), 4.61 × 3.01 mm (SNSB-BSPG 2023 XII 6, Fig. 8D–F).

Remarks. The shape of the shell and the aperture and the type of growth lines are typical of the genus *Ecrobia*. The protoconch includes ~1.1 whorls and appears to be smooth (the preservation of the apex is, however, rather poor). The P/T boundary is marked by the onset of growth lines. Shape-wise our specimens fall well into the morphological range of extant *E. grimmi* (Clessin in Dybowski, 1887) from the Caspian Sea, but it also resembles stout forms of the widespread European *E. ventrosa* (Montagu, 1803) and the Black Sea/eastern Mediterranean species *E. maritima* (Milaschewitsch, 1916). Only, our material is exceptionally large for *Ecrobia* and has a slightly thickened aperture, which is untypical as well. It might well represent

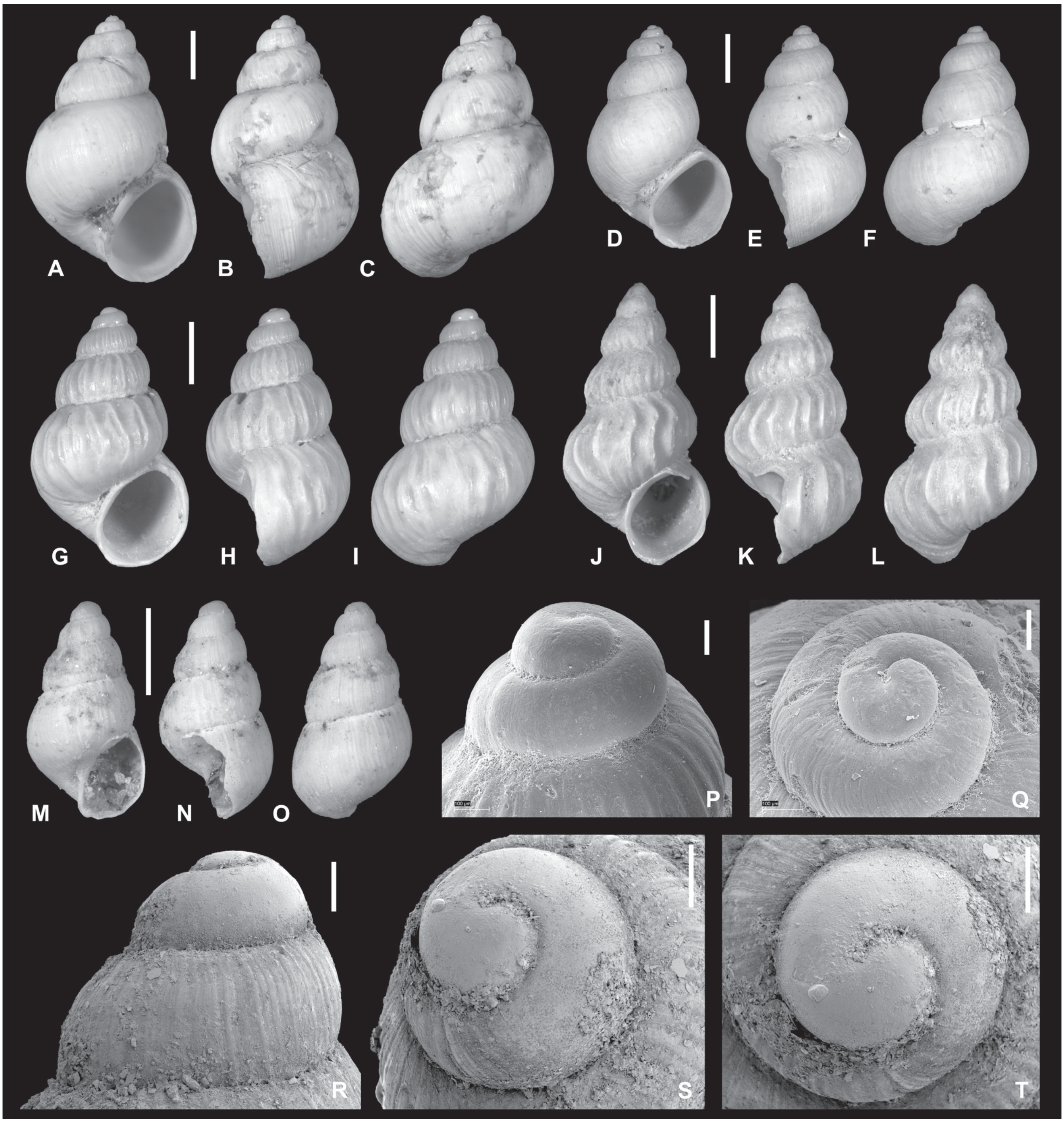

Figure 8. Hydrobiinae (Hydrobiidae) of the Kolankaya I fauna. **A–C, Q.** *Ecrobia* sp. RGM 962612, sample 2. **D–F.** *Ecrobia* sp. SNSB-BSPG 2023 XII 6, sample 2. **G–I.** P. *Harzhauseria schizopleura* gen. et sp. nov., holotype, RGM 962613, sample 2. **J–L.** *Harzhauseria schizopleura* gen. et sp. nov., paratype, RGM 962614, sample 2. **M–O, R–T.** Hydrobiinae sp. indet., RGM 1365350, sample 1. Scale bars: 1 mm (**A–O**); 100 µm (**P–T**).

an undescribed species, but since *Ecrobia* species are known to be extremely variable (Kantor and Sysoev 2006; Neubauer et al. 2018; Vandendorpe et al. 2019) and we have only limited material available for comparison, we refrain from introducing a new species.

Genus *Harzhauseria* gen. nov.

https://zoobank.org/C9177CC8-F0D6-4C9C-9032-3A33BF833F25

Type species. *Harzhauseria schizopleura* gen. et sp. nov.; designated herewith.

Etymology. Named in honor of Mathias Harzhauser for his many contributions on fossil Mollusca, pan-Tethyan biogeography, and a long friendship.

Diagnosis. As for the type species (so far only the type species is known).

Description. As for the type species.

Remarks. The shell shape, convex whorls, and round, large aperture remind of species of *Ecrobia*, such as the co-occurring *Ecrobia* sp. The presence of ribs, however, makes the species unique and clearly distinguishes it from any other known species or genus of Hydrobiinae (or other Hydrobiidae for that matter).

Harzhauseria schizopleura gen. et sp. nov.

https://zoobank.org/86156305-C9F6-41C3-BDD0-459193B1346E

Etymology. Derived from the Ancient Greek syllables σχίζω (skhízō) and πλευρόν (pleurón), referring to the extraordinary sculpture, occasionally showing diverging ribs.

Holotype. RGM 962613 (Fig. 8G–I, P). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

Paratypes. RGM 962614, SNSB-BSPG 2023 XII 7, SNSB-BSPG 2023 XII 8; all from the type locality and stratum.

Additional material. Sample 1: 1 specimen with traces of intense growth lines rather than distinct ribs (SNSB-BSPG 2023 XII 9); sample 2: 6 nearly complete specimens, lacking aperture or last whorl, plus 13 fragments (RGM 1310851), 1 specimen with fragmented aperture and 2 fragments (SNSB-BSPG 2023 XII 10).

Diagnosis. Small hydrobiine, conical, slender to slightly broader shell, with highly convex whorls that bear conspicuous irregular (straight to wavy, partly interfingering) ribs and large elliptical aperture.

Description. Shell conical, slender to slightly broader, with 5 highly convex whorls. Protoconch smooth, consisting of c. 1.25 regularly coiled whorls; P/T transition marked by distinct growth stop. Numerous, weak, regularly shaped axial ribs develop on first teleoconch whorl. Ribs soon become irregular, variably spanning full whorl height or only parts, partly interfingering with each other (Fig. 8G–I) or they become sigmoidal (Fig. 8J–L). Distance and intensity of ribs also varies across specimens. Sometimes, rib tops are abraded, creating illusion of two ribs merging near upper and lower suture, leaving narrow concavity in between. Last whorl attains 60–64% (n = 2) of total shell height. Base ~45°, straight-sided. Aperture relatively large, well-rounded, elliptical; peristome weakly and equally thickened; umbilicus narrow. Growth lines faint.

Dimensions. 3.50 × 2.23 mm (holotype, RGM 962613; Fig. 8G–I, P); 3.69 × 1.96 mm (paratype, RGM 962612; Fig. 8J–L).

Remarks. There is considerable morphological variability in the little material available to us. This concerns both shell shape and the expression of the ribs. However, it is well known that species of Hydrobiinae, such as the (probably related) genus *Ecrobia*, are morphologically highly variable, which often complicates establishing species boundaries (e.g., Wesselingh et al. 2019; Andreeva et al. 2022).

Distribution. So far only known from the Early Pleistocene of the Denizli Basin.

Hydrobiinae sp. indet.

Fig. 8M–O, R–T

Material. 1 specimen (RGM 1365350) from sample 1.

Dimensions. 2.52 × 1.37 mm.

Remarks. A single specimen is available, characterized by a small, white, conical shell with convex whorls, simple aperture, and distinct, orthocline growth lines. The protoconch is low domed, forming a bulbous cap of ~1.2 whorls, and apparently smooth, but this might be a result of the moderate preservation. The available features suggest placement in Hydrobiinae, but at present an attribution to genus or species cannot be made.

Subfamily Pyrgulinae Brusina, 1882

Genus *Laevicaspia* Dybowski & Grochmalicki, 1917

Type species. *Rissoa caspia* Eichwald, 1838; by subsequent designation (Logvinenko and Starobogatov 1969).

Laevicaspia sp.

Fig. 9A–C

Material. 1 specimen (RGM 962609) from sample 2.

Dimensions. 8.21 × 4.10 mm.

Remarks. The size and shape of the shell and the oblique, large, and slightly thickened aperture leaving a narrow umbilicus are characteristic of the Pontocaspian genus *Laevicaspia*. The species reminds of the Quaternary–extant species *L. lincta* (Milaschewitsch, 1908) from the Black Sea. That species is known for its high variability, which has led previous authors to introduce numerous species names (Wesselingh et al. 2019). The Denizli specimens differ from that species by a slightly broader shell with convex, spruce-like whorl profile. *Laevicaspia lincta* has mostly straight-sided whorls, sometimes convex ones; only some specimens approach this type of morphology [see lectotype illustrated by Kantor and Sysoev (2006: pl. 45, fig. D) as well as the holotype of *Pyrgula iljinae* Golikov & Starobogatov, 1966, now considered a synonym of *L. lincta* in Kantor and Sysoev (2006: pl. 49, fig. D)]. Also, the broad shell shape is approached by the holotype of the synonym *Pyrgula* (*Laevicaspia*) *milachevitchi* Golikov & Starobogatov, 1966 depicted in Kantor and Sysoev (2006: pl. 45, fig. C).

Another similar species is *Prososthenia sublaevis* Oppenheim, 1919, described from "Laodicäa", an ancient city 6 km north of Denizli. It differs in the flattened whorls and

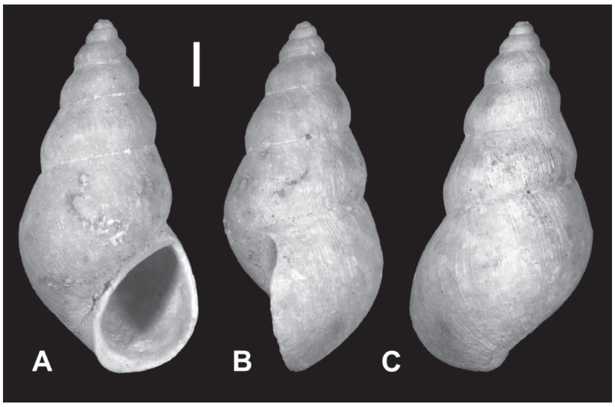

Figure 9. Pyrgulinae (Hydrobiidae) of the Kolankaya I fauna. **A–C.** *Laevicaspia* sp., RGM 962609, sample 2. Scale bar: 1 mm.

the presence of a weak subsutural band. *Prososthenia gregaria* (Fuchs, 1877) from the Early Pleistocene of mainland Greece is more slender and has low-convex whorls (see also Esu and Girotti 2020, fig. 9A–F).

Potentially our specimen represents an undescribed species, but given the limited material availability and the high morphological variability of related taxa, we do not introduce a new name.

Genus *Prososthenia* Neumayr, 1869

Type species. *Prososthenia schwartzi* Neumayr, 1869; by subsequent designation (Herbich and Neumayr 1875).

Prososthenia cf. *sturanyi communis* Willmann, 1981

Fig. 10A–J

cf. 1981 *Prososthenia sturanyi communis* ssp. nov. – Willmann: 160, pl. 6, figs 10, 11 (cum syn.).

Material. 1 specimen (RGM 962615), 7 specimens, 2 apertural fragments, and 2 apical fragments (RGM 1310852), 1 specimen (SNSB-BSPG 2023 XII 11); all from sample 2.

Type locality. Valley between Vokasia and Sefto valley, c. 3.5 km SW of Kos, Kos Island, Greece; lower Kos Formation, Lower Pleistocene.

Description. Shell elongate, ovoid, with 5 whorls that decrease in convexity. Early whorls regularly convex; penultimate to last whorl weakly convex to flattened in whorl center; last whorl occasionally has faint concavity below faintly expressed subsutural bulge; suture moderately incised. Base weakly convex to straight-sided. Aperture typically drop-shaped, relatively broad, only weakly inclined; slightly offset in fully grown specimen; peristome weakly and equally thickened, faintly expanded; umbilicus very narrow. Growth lines rather weak, weakly prosocline in upper half to nearly orthocline in lower half, crossed by faint spiral furrows. Protoconch consisting of ~0.9 whorls, with broad nucleus, covered by fine-meshed malleate sculpture.

Dimensions. 2.86 × 1.33 mm (RGM 962615; Fig. 10A–E), 2.77 × 1.20 mm (SNSB-BSPG 2023 XII 11; Fig. 10F–J).

Remarks. *Prososthenia sturanyi* encompasses shells with highly variable shapes and sizes (Willmann 1981). Slender specimens of *P. s. communis* from Kos Island match the Denizli material in terms of general shape, the flattened whorl flanks, the presence of a weak subsutural band, and faint spiral furrows, as well as the shape of the aperture (compare Willmann 1981, pl. 6, fig. 11). Yet, the Kos specimens are slightly larger and the apex appears to be smaller. Considering the otherwise close similarity, the generally great variability of the species, and the similar age and geographic vicinity, we tentatively refer the Denizli material to *Prososthenia sturanyi communis*.

Prososthenia sturanyi sturanyi (Bukowski, 1896) from Plio–Pleistocene formations of Rhodes has a stouter shell with a shorter spire (Willmann 1981). *Prososthenia gregaria* (Fuchs, 1877) from the Early Pleistocene of mainland Greece is much larger and has a slender, elongate shell with regularly, low-convex whorls. A particularly similar species is *Prososthenia eburnea* Brusina, 1897 from Middle Miocene (Langhian) strata of Miočić, Croatia, regarding the decreasing degree of whorl convexity through ontogeny. The species is, however, much larger and more regularly ovoid. The malleate protoconch (Fig. 10E), prosocline-orthocline growth lines, and the presence of spiral furrows also agree with a placement in the genus *Prososthenia* (compare Neubauer et al. 2020).

The taxon is also surprisingly similar to "*Caspia*" *laevigata* Jekelius, 1944 (p. 123–124, pl. 45, figs 9, 10) from the Early Pannonian (Early Tortonian) of Soceni in Romania. That species has a similarly slender, ovoid shell with straight-sided whorls, an angulation on the last whorl toward the straight base, and a slender ovoid aperture. It differs in the early whorls being also nearly straight-sided, where the Denizli species has convex whorls. Furthermore, there seems to be no umbilicus in the Romanian species. On a side note, despite the superficial similarity, it is questionable whether that species is a member of the genus *Caspia* and the Caspiinae. Shells of that group are characterized by a broad and rounded, dome-like protoconch. The Romanian species rather suggests a placement in Pyrgulinae, perhaps even *Prososthenia*. If, however, the species was transferred to *Prososthenia*, the species name *Prososthenia laevigata* Volkova, 1953 would be become a secondary homonym.

Distribution. Late Pliocene to Early Pleistocene (Phoka, Sefto, and Kos formations) of Kos Island (Willmann 1981) and, tentatively, Early Pleistocene of the Denizli Basin (this study).

Genus *Xestopyrguloides* Willmann, 1981

Type species. *Xestopyrguloides neumayri* Willmann, 1981; by original designation.

Xestopyrguloides? *sagitta* sp. nov.

https://zoobank.org/F8829057-B9CB-4F19-B7E4-29AF916C0FCB

Etymology. After the Latin sagitta meaning "arrow", referring to the slender, pointy shape reminding of an arrowhead (noun in apposition).

Holotype. RGM 962616 (Fig. 10K–Q). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

Paratype. SNSB-BSPG 2023 XII 12, specimen lacking aperture and apex; from type locality and stratum.

Additional material. 1 almost complete specimens and 5 fragments (RGM 1310853), 1 apertural fragment and 1 apical fragment (SNSB-BSPG 2023 XII 13); all from sample 2.

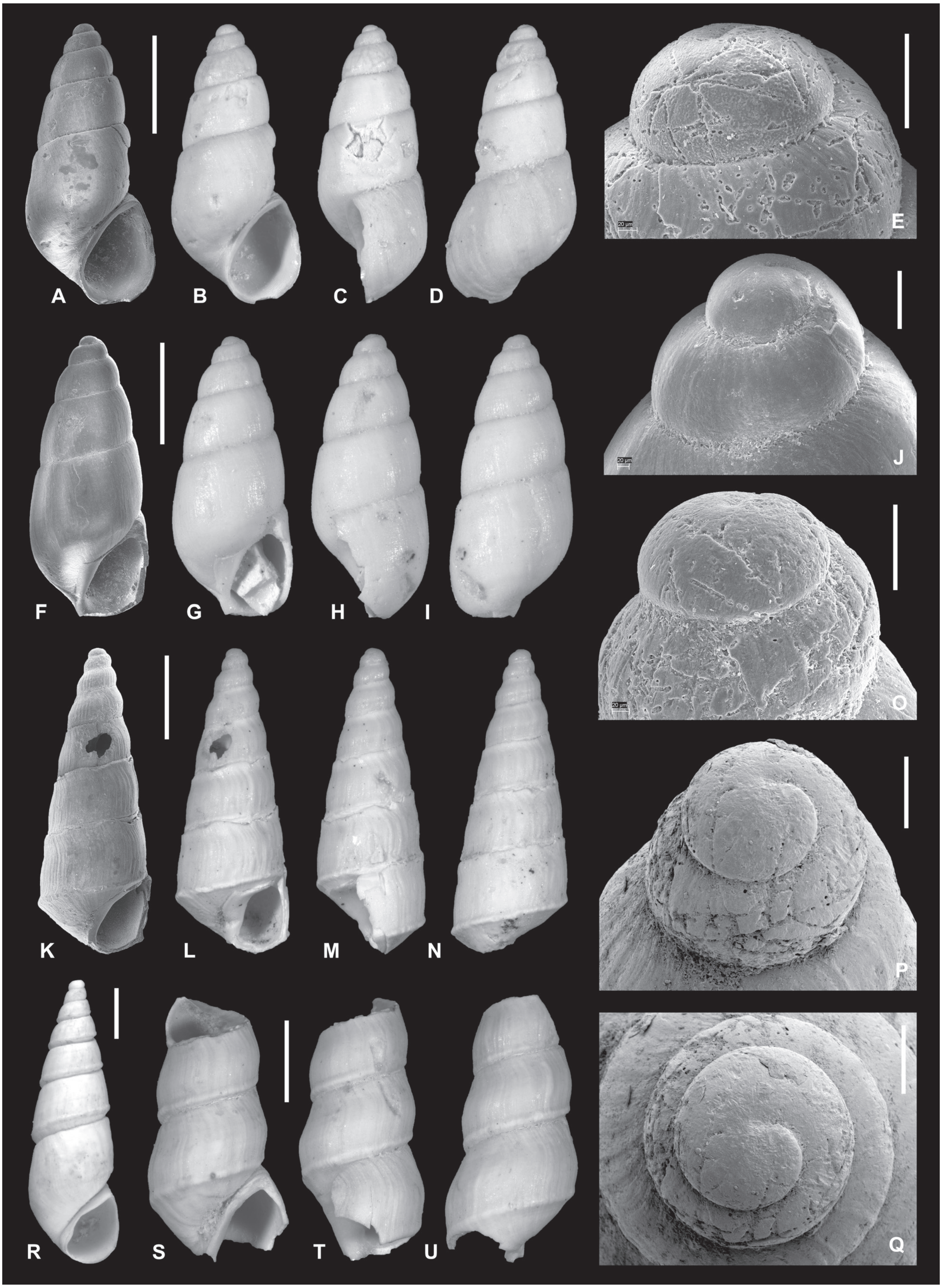

Figure 10. Pyrgulinae (Hydrobiidae) of the Kolankaya I fauna. **A–E.** *Prososthenia* cf. *sturanyi communis* Willmann, 1981, RGM 962615, sample 2. **F–J.** *P.* cf. *sturanyi communis*, SNSB-BSPG 2023 XII 11, sample 2. **K–Q.** *Xestopyrguloides*? *sagitta* sp. nov., holotype, RGM 962616, sample 2. **R**. *Xestopyrguloides*? *heldreichii* (Fuchs, 1870), lectotype (designated by Willmann 1981), NHMW 1878 XX 28, Megara, Pliocene. **S–U**. *Xestopyrguloides*? sp., RGM 1365347, sample 2. Scale bars: 1 mm (**A–D, F–I, K–N, R–T**); 100 µm (**E, J, O–Q**).

Diagnosis. Very slender, weakly ovoid pyrguline shell characterized by small last whorl, small aperture, narrow but distinct basal keel, and whorl convexity decreasing through ontogeny.

Description. Shell slender, elongate, faintly ovoid, almost conical, consists of about 7 whorls. Protoconch low domed, no sculpture discernible (perhaps because of poor preservation; Fig. 10O–Q); P/T boundary not visible. Initial teleoconch whorls are convex, but convexity decreases rapidly around 3rd to 4th whorl. Following whorls are straight-sided or nearly so, with only faint convexity remaining in center of whorls. Whorls bear thin keel directly at lower suture. Keel produces slight swelling at upper suture of following whorl where it overgrows keel. Onset of keel in ontogeny uncertain due to near full overlap; keel visible in parts on at least last four whorls, matching approximately change in convexity. Last whorl relatively small, attaining 43% of shell height. Keel there produces sharp angle toward straight-sided shallow base (~55° to shell axis). Aperture not full preserved, but appears to be narrow ovoid. Inner lip covers umbilicus. Growth lines opisthocyrt, but more distinctly in upper half of whorls.

Dimensions. 3.65 × 1.37 mm (holotype, RGM 962616; Fig. 10K–Q).

Remarks. Only two other *Xestopyrguloides* have been described so far: the type species *X. neumayri* (Willmann, 1981) from the Early Pleistocene of Kos Island and *X.*? *heldreichii* (Fuchs, 1877) from the Pliocene of Megara, whereas the second species is only tentatively referred to the genus (Willmann 1981, p. 202–203, textfig. 67). Both species have elongated shells with straight whorl flanks and distinct keel close to lower suture (or sometimes directly above it). Below the keel occurs a marked constriction toward the suture, which results in a weakly spruce-like appearance. *Xestopyrguloides*? *heldreichii* has in addition a slightly thickened peristome, especially at the inner lip. The lectotype designated by Willmann (1981, p. 203; NHMW 1878 XX 28) is illustrated on Fig. 10R.

The straight-sided whorls and keel at the lower suture are also present in *Xestopyrguloides sagitta* sp. nov. The aperture is, however, much smaller and the base is more shallow than in the other species of that genus, which is why we only tentatively allocate the Turkish species there.

A *Xestopyrguloides* sp. was mentioned by Schütt and Kavusan (1984) from supposedly Miocene deposits of the area around Harmancık but not illustrated. Judging from the brief description, referring to a rather stout form with lower height and a sharp keel right above the suture, it is a different species than the one we describe herein.

The new species also reminds of representatives of the genus *Falsipyrgula* Radoman, 1973a, many of which have a keel near the lower suture as well (Schütt and Yildirim 1999). The type species, *Falsipyrgula pfeiferi* (Weber, 1927), also shares the slender shape and the straight whorl flanks (Radoman 1973a). On average, however, *Falsipyrgula* species are broader and have larger and broadly ovoid apertures.

The placement in Pyrgulinae is preliminary and based on the comparison with Pontocaspian *Turricaspia* and *Laevicaspia*, with which *Xestopyrguloides*? *sagitta* sp. nov. shares the elongate, multi-whorled shell and the flattened, often smooth or faintly ornamented protoconch (Neubauer et al. 2018; T.A.N., pers. obs.).

Distribution. So far only known from the Early Pleistocene of the Denizli Basin.

Xestopyrguloides? sp.

Fig. 10S–U

Material. 1 fragment (RGM 1365347) from sample 2.

Remarks. A second species is tentatively referred to the genus *Xestopyrguloides*. A single incomplete shell is available, containing the last 2.5 whorls and the upper part of the aperture. The shell is similarly elongate as *Xestopyrguloides*? *sagitta* sp. nov. and also bears a narrow basal keel, as well as the same type of growth lines. However, the shell is larger, the whorls are moderately convex, and the aperture is larger and drop-shaped. The basal keel and shape of the aperture, as well as the size, would also fit to the Greek *X. neumayri* and *Xestopyrguloides*? *heldreichii* (Fig. 10R), but both species have straight-sided whorls.

The *Staja*–*Falsipyrgula* species complex

Remarks. The enormous morphological variability of the Denizli specimens, as well as other material from Turkey and Greece assigned to the genus *Staja* (e.g., Willmann 1982), makes a systematic classification incredibly difficult. This concerns variation in shell shape, size, and presence and expression of sculpture, which – if our assessment is correct – varies even within single species. The keeled representatives remind of and are considered to belong in the Pyrgulinae genus *Falsipyrgula*, while the smooth morphotypes are classically assigned to *Staja*, a genus that is originally described from the Late Miocene of the Pannonian Basin.

A full revision of the Greek–Turkish *Staja*–*Falsipyrgula* species complex is beyond the scope of this study. We follow the literature for the genus classifications of the known species, yet being aware of the unresolved genus concepts. A new species is placed in *Falsipyrgula* due to the close similarities to extant congeners.

Genus *Staja* Brusina, 1897

Type species. *Staja adiaphora* Brusina, 1897; by subsequent designation (Cossmann 1898).

Staja lycica (Oppenheim, 1919)

Fig. 11A–I, S, T

*1919 *Fluminicola* (*Gillia*) *lycica* sp. nov. – Oppenheim: 117–119, pl. 5, fig. 2, 2a.

1923 *Amnicola* (*Staja*) *lycica* (Oppenheim) – Wenz: 2086.

1982 *Pseudamnicola* (*Staja*) *lycica* (Oppenheim 1919) – Willmann: 313–314.

? 2008 *Pseudamnicola orientalis* (Bukowski, 1895) – Wesselingh et al.: 865, fig. 5(8a–c).

Material. Sample 1: 21 specimens and 5 fragments (RGM 1310854), 1 specimen (RGM 1365351), 2 specimens (SNSB-BSPG 2023 XII 14); sample 2: 1 specimen (RGM 962619), 1 specimen (SNSB-BSPG 2023 XII 15).

Type locality. Tlos (an ancient city in Muğla Province near Seydikemer), Turkey; probably Eşen Formation (Kocaçay Member), Zanclean, Lower Pliocene.

Description. Ovoid, slender to slightly broader shell with up to 5 moderately convex whorls. Protoconch low-domed, consisting of c. 1.2 apparently smooth whorls; P/T boundary marked by growth rim and onset of growth lines. Last whorl attains 79–82% (n = 3) of total height. Aperture oblique, ovoid to almost elliptical, weakly inclined in lateral view. Inner lip touches base of penultimate whorl but weakly detaches in some specimens near adapical tip and base, leaving very narrow umbilicus; latter occasionally opens into narrow canal that runs along inner lip toward base and is demarcated by weak fasciole. Shell surface smooth except for numerous faint spiral furrows detected in well-preserved specimens.

Dimensions. 6.08 × 4.24 mm (Fig. 11A–C, S; RGM 962619), 3.90 × 2.76 mm (SNSB-BSPG 2023 XII 15; Fig. 11D, T), 4.41 × 2.83 (Fig. 11G–I; RGM 1365351).

Remarks. Here, we combine a variety of morphologies under the name *Staja lycica*. This includes a comparatively large, broad morphotype with highly convex whorls (Fig. 11A–C, S; RGM 962619), which matches

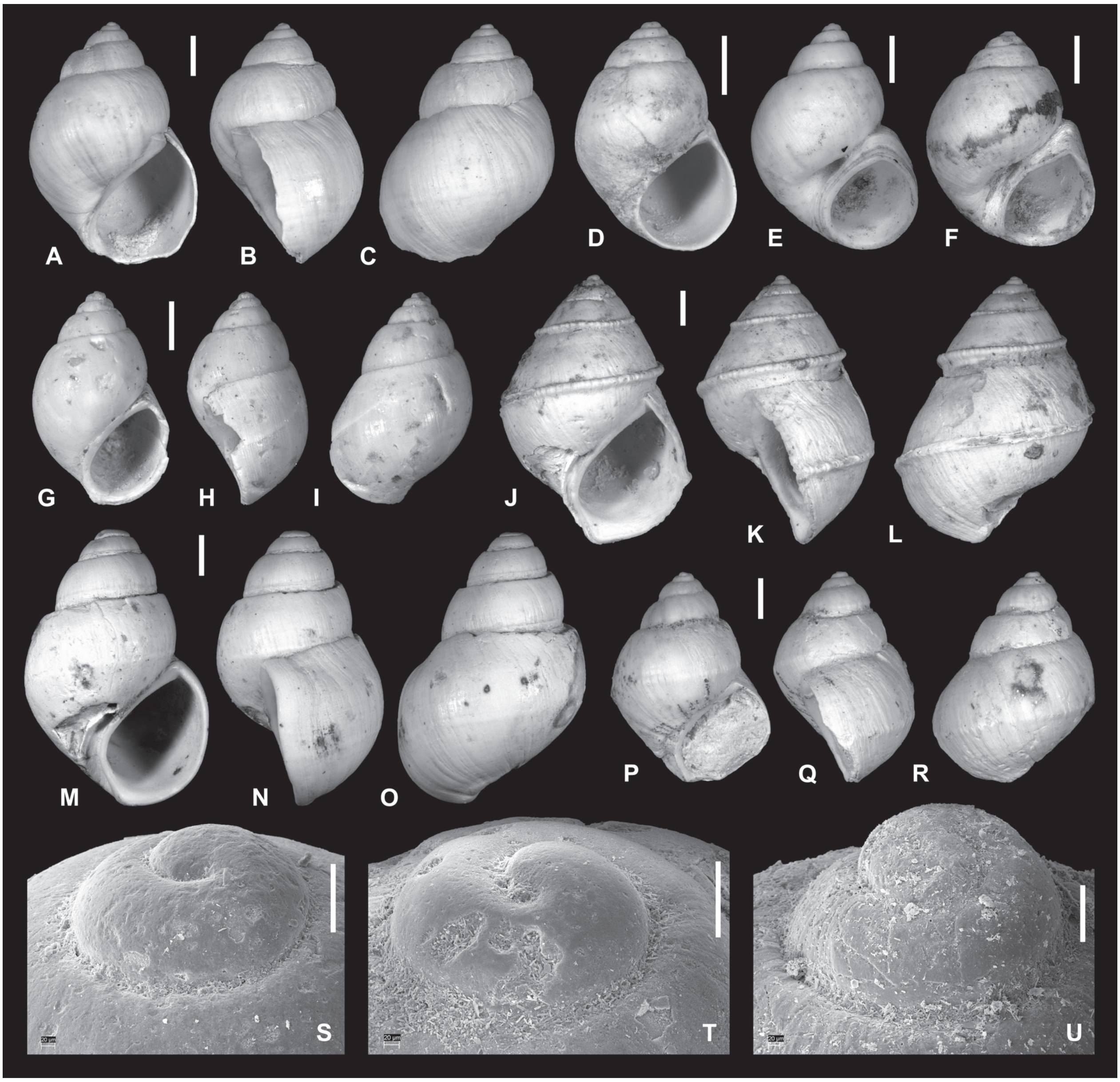

Figure 11. The *Staja*–*Falsipyrgula* species complex of the Kolankaya I fauna. **A–C.** S. *Staja lycica* (Oppenheim, 1919), RGM 962619, sample 2. **D, T.** *S. lycica*, SNSB-BSPG 2023 XII 15, sample 2. **E.** *Staja orientalis* (Bukowski, 1896), lectotype (designated herein), IGUW 1895 XII/45, between Profilia and Istrios, Rhodes, Greece, Istrios Formation (Pliocene). **F.** *S. orientalis*, paralectotype, IGUW 1895 XII/46, same locality and stratum. **G–I.** *S. lycica*, RGM 1365351, sample 1. **J–L, U.** *Staja*? *cibyratica* (Spratt & Forbes, 1847), RGM 962621, sample 2. **M–O.** *S.*? *cibyratica*, RGM 962620, sample 2. **P–R**. *S.*? *cibyratica*, SNSB-BSPG 2023 XII 16, sample 2. Scale bars: 1 mm (**A–R**); 100 µm (**S–U**).

the features illustrated by Oppenheim (1919). Also the overall size, the faint spiral furrows indicated by Oppenheim, as well as the slightly inclined aperture fit well. The very weak detachment of the aperture from the base of the last whorl and the "layered peristome" referred to by Oppenheim and shown in his illustrations match a morphotype that is more slender and smaller but otherwise fits the original description and illustration and cannot be reasonably distinguished (Fig. 11G–I). Since Oppenheim's type material seems to be lost, topotypic material from the Eşen Basin is needed to clarify the identity and variability of this species.

Staja orientalis (Bukowski, 1896) from the Pliocene Istrios Formation of Rhodes differs from *S. lycica* in the even broader shape, larger size, and presence of an umbilicus (Fig. 11E, F). However, some specimens of *S. orientalis* from Attica (mainland Greece) illustrated by Willmann (1982, fig. 3i–l) closely resemble *S. lycica*. Willmann (1982) even hypothesized that both species might be synonymous. A thorough revision of the *Staja lycica–orientalis* species group is required to settle these uncertainties. To fix the identity of *S. orientalis*, we hereby designate the specimen illustrated by Bukowski (1896, pl. 10, fig. 1) as the lectotype (IGUW 1895 XII/45; Fig. 11F).

The specimen from the Kolankaya II fauna of the upper Kolankaya Formation attributed to *S. orientalis* by Wesselingh et al. (2008) rather range within *S. lycica*; they even show the slightly detached aperture as mentioned by Oppenheim.

Distribution. So far only known from the type locality in the Eşen Basin (Oppenheim 1919), which is of Late Pliocene age according to (Alçiçek et al. 2019), and the Early Pleistocene of the Denizli Basin (this study).

***Staja*? *cibyratica* (Spratt & Forbes, 1847)**

Fig. 11J–R, T

*1847 *Paludina Cibyratica* – Spratt and Forbes: 177, textfig. b.
1928 *Viviparus cibyraticus* (Forbes) – Wenz: 2304.
? 1982 *Pseudamnicola* (*Staja*?) *cibyratica* (Forbes 1847) – Willmann: 315–318, textfigs 6, 7, 9g–h.

Material. Sample 2: 1 specimen (RGM 962620), 1 specimen (RGM 962621), 23 mostly poorly preserved specimens (RGM 1310855), 35 mostly poorly preserved specimens and a few fragments (RGM 1310856), 1 specimen (SNSB-BSPG 2023 XII 16); sample 3: 10 mostly poorly preserved specimens (RGM 1310857), 4 mostly poorly preserved specimens and 1 fragment (SNSB-BSPG 2023 XII 17).

Type locality. Between Altınyayla (former Dirmil) and the ancient city Kibyra ("between Tremeely and Cibyra"), Çameli Basin, Burdur, Turkey; Çameli Formation (Değne Member), Upper Pliocene; and Minare, Eşen Basin, Muğla; Eşen Formation (Kocaçay Member), Lower Pliocene.

Description. Large, bulky shell with up to 5.5 whorls. Apex raised, but top of protoconch depressed; protoconch consists of c. 1.2 whorls without discernible sculpture; P/T boundary marked by growth rim and onset of growth lines. Teleoconch whorls moderately convex to almost straight-sided; latter type creates nearly perfectly conical profile. Teleoconch bears keel close to or directly at lower suture. Expression of keel highly variable, ranging from distinct, blunt crest, typically with irregular surface (such as fused nodules), to almost absent, only with faint trace. Additionally, numerous fine spiral furrows cover well-preserved specimens. Last whorl attains 75–80% (n = 3) of total shell height; final portion occasionally grows stronger in adapical direction, creating slightly irregular shape and "raises" keel above whorl base (Fig. 11J–L). Base steep and straight-sided or weakly convex and passing into concavity toward neck. Aperture ovoid, pointed adapically, weakly inclined in lateral view. Peristome thin or occasionally thickened, with adnate inner lip. Umbilicus narrow, opens into narrow canal that runs along inner lip toward base, bordered by distinct, sharp fasciole.

Dimensions. 7.79 × 5.57 mm (RGM 962621; Fig. 11J–L, U), 11.02 × 7.28 mm (RGM 962620; Fig. 11M–O), 5.20 × 3.96 mm (SNSB-BSPG 2023 XII 16; Fig. 11P–R).

Remarks. This species covers a great variety of shell shapes and sizes, which complicates establishing species boundaries. The morphological variability is even larger when including Willmann's (1982) material from the Çameli Basin, which shows much thicker, bulkier shells with a thickened peristome and a keel that is blunt or entirely absent. Our specimens correspond more to the original, but rather poor illustrations by Spratt and Forbes (1847) showing shells bearing a slender keel and a thin peristome. Regarding size, the nearly conical spire, and the laterally oblique aperture, as well as the presence of a fasciole, our specimens correspond well to Willmann's.

The systematic placement of this species has proven difficult in the past. Because of its relatively large size and bulky morphology it was originally attributed to viviparids (Neumayr 1880b; Wenz 1923). Neumayr (1880b, footnote on p. 266) stated that he could not distinguish the species from juveniles of *Viviparus vukotinovicii* (Frauenfeld, 1862) ["die ich von jungen Exemplaren von *Viv. Vukotinovici* [sic] Frfld. aus Slavonien nicht unterscheiden kann"].

The species is classified in *Staja* following the opinion of Willmann (1982), but shell shape and keel remind of the genus *Falsipyrgula*, also in comparison with the co-occurring *F.* cf. *sieversi* and *F.*? *coronata* sp. nov. (see below). As stated above, the species complex and genus classifications therein may need reconsideration after a thorough revision.

Distribution. Known from several localities with Pliocene strata in the Çameli and Eşen basins (Spratt and Forbes 1847; Willmann 1982) and the Early Pleistocene of the Denizli Basin (this study).

***Falsipyrgula*? *coronata* sp. nov.**

https://zoobank.org/B3E4BA51-6674-436A-8F43-A3EF5A686A56

Etymology. The species epithet means "crowned" in Latin and refers to the beaded keel.

Holotype. RGM 1310837 (Fig. 12A–C). Babadağ river valley along the Babadağ-Sarayköy road, c. 2.4 km NW of the town of Babadağ, Denizli, Turkey; sample 2 (37°50'44.5"N, 28°52'51.3"E). Kolankaya Formation, Lower Pleistocene, Gelasian.

Paratypes. RGM 962611 (Fig. 12J–L) from sample 2; SNSB-BSPG 2023 XII 18 (Fig. 12D–F, T) from sample 2; SNSB-BSPG 2023 XII 19 (Fig. 12I) from sample 3.

Additional material. Sample 2: 1 specimen (RGM 1310377), 27 partly incomplete specimens and 10 fragments (RGM 1310858); sample 3: 4 specimens and 2 fragments (RGM 1310859).

Diagnosis. Conical pyrguline shell characterized by central to subcentral, typically beaded keel, topped by shallow, straight-sided subsutural whorl profile, convex portion below keel, grading into straight-sided base, thin peristome, and narrow umbilicus.

Description. Moderately sized conical shell with up to 6 whorls. Protoconch poorly preserved in all studied specimens; surface and P/T boundary unknown. Already on approximately first to second teleoconch whorl a central to subcentral keel appears, which increases continuously in strength through ontogeny. Also in cases with early keel placed at whorl center, keel becomes distinctly subcentral in later ontogeny. Keel typically bears nodules (Fig. 12D–F), which are sometimes not visible, probably due to abrasion (Fig. 12A–C, I–L). Whorl portions above and below keel straight-sided. Last whorl attains ~68–71% (n = 3) of total shell height; passes over weak convexity into moderately steep (~45°), straight-sided base. Aperture broadly ovoid, with rather thin peristome and adnate inner lip; umbilicus narrow.

Dimensions. 7.82 × 5.26 mm (holotype, RGM 1310837; Fig. 12A–C), 10.02 × 6.35 mm (paratype, RGM 962611; Fig. 12J–L), 6.73 × 3.78 mm (paratype, SNSB-BSPG 2023 XII 19; Fig. 12I), 4.05 × 2.84 mm (paratype, juvenile, SNSB-BSPG 2023 XII 18; Fig. 12D–F, T).

Remarks. As for other members in the *Staja–Falsipyrgula* species complex, the shell of this species exhibits a certain degree of variability. Occasionally, species with a more slender shell (Fig. 12I) or a narrower, non-beaded keel (Fig. 12J–L) are observed. The latter feature may, however, be the result of poor preservation, in many cases shell surfaces and sculptural elements are abraded. Common to all specimens is the conical shell, the comparatively shallow and straight-sided whorl profile above the keel, the thin and edgy peristome, and the narrow umbilicus. These features distinguish *Falsipyrgula*? *coronata* sp. nov. from similar species of *Falsipyrgula*, including the co-occurring *F.* cf. *sieversi*. The latter species shares the beaded keel, which is, however, consistently weaker and slightly lower positioned on the whorl, but the shell is ovoid, smaller, and has a stronger inclined, regularly ovoid aperture. Extant *Falsipyrgula* species have a lower positioned keel or multiple keels or otherwise differ in shape (Schütt and Yildirim 1999).

Prososthenia attica Fuchs, 1877 sensu Schütt and Besenecker (1973, pl. 1, fig. 7) from the Late Miocene (?) of Chios resembles *F.*? *coronata* in terms of overall shell shape and presence of a subcentral keel, but the last whorl is tapered and the whorl profile above the keel is convex. Original *P. attica* from the Pliocene of Megara is more elongate and has only a week keel near the whorl base (Fuchs 1877) and is probably a different species as the Chios specimens.

Distribution. Known only from the Early Pleistocene of the Denizli Basin.

Falsipyrgula cf. *sieversi* (Boettger, 1881)

Fig. 12G, H, M–R, U

cf. *1881 *Hydrobia Sieversi* Bttg. sp. nov. – Boettger: 246–247, pl. 9, fig. 23.
cf. 2014 *Falsipyrgula sieversi* (Boettger, 1881) – Vasilyan et al: 297, fig. 2k.
cf. 2016 *Pyrgula* (?) *sieversi* (O. Boettger, 1881) – Vinarski and Kantor: 242–243.
cf. 2018 *Hydrobia sieversi* O. Boettger, 1881 – Sitnikova et al.: 74, 75, fig. 4j [as *Falsipyrgula* in the discussion].

Material. Sample 2: 1 specimen (RGM 962610), 1 specimen (RGM 1310376), 27 partly incomplete specimens and fragments (RGM 1310861), 1 specimen (SNSB-BSPG 2023 XII 20); sample 3: 1 specimen (RGM 1310375).

Type locality. Bank deposits of the Araks River near Nakhichevan' Town, Azerbaijan (approximately 39°10'30"N, 45°21'41"E); extant.

Description. Small, ovoid hydrobiid with 5 whorls. Protoconch consists of ~1 whorl, without discernible sculpture but clear P/T boundary (Fig. 12U). First teleoconch whorl smooth, soon weak, beaded keel with round, equally spaced nodules appears slightly below whorl center. Nodules increase slightly in intensity throughout ontogeny and form keel-like appearance on last whorl. Whorl profile weakly convex above nodules, convex below them, grading into weakly convex base. Last whorl attains ~70–76% (n = 3) of total shell height. Aperture ovoid, strongly inclined, faintly detached, leaving narrow umbilicus. Peristome continuous, not thickened or expanded, but weakly intensified abapical growth in final ontogeny typical of hydrobiids exposes shell layers at adapical tip.

Dimensions. 4.66 × 2.97 mm (RGM 962610; Fig. 12M–O, U), 3.54 × 2.43 mm (RGM 1310376; Fig. 12G, H), 3.60 × 2.56 mm (SNSB-BSPG 2023 XII 20; Fig. 12P–R).

Remarks. The available material shows high similarities and is perhaps conspecific with the extant *Falsipyrgula sieversi* (Boettger, 1881) from the Aras river in Nakhchivan (Azerbaijan). Sitnikova et al. (2018) recently studied and illustrated the holotype, which matches our specimens in terms of shell shape, size, whorl convexity, the position of the keel, the slightly convex base, and the shape and tilt of the aperture. The only difference is that the keel is not beaded as in the Denizli specimens. However, Sitnikova et al. (2018) also reported keel-less, fossil specimens of that species, confirming the variability of this trait in the *Staja–Falsipyrgula* species complex. Shells

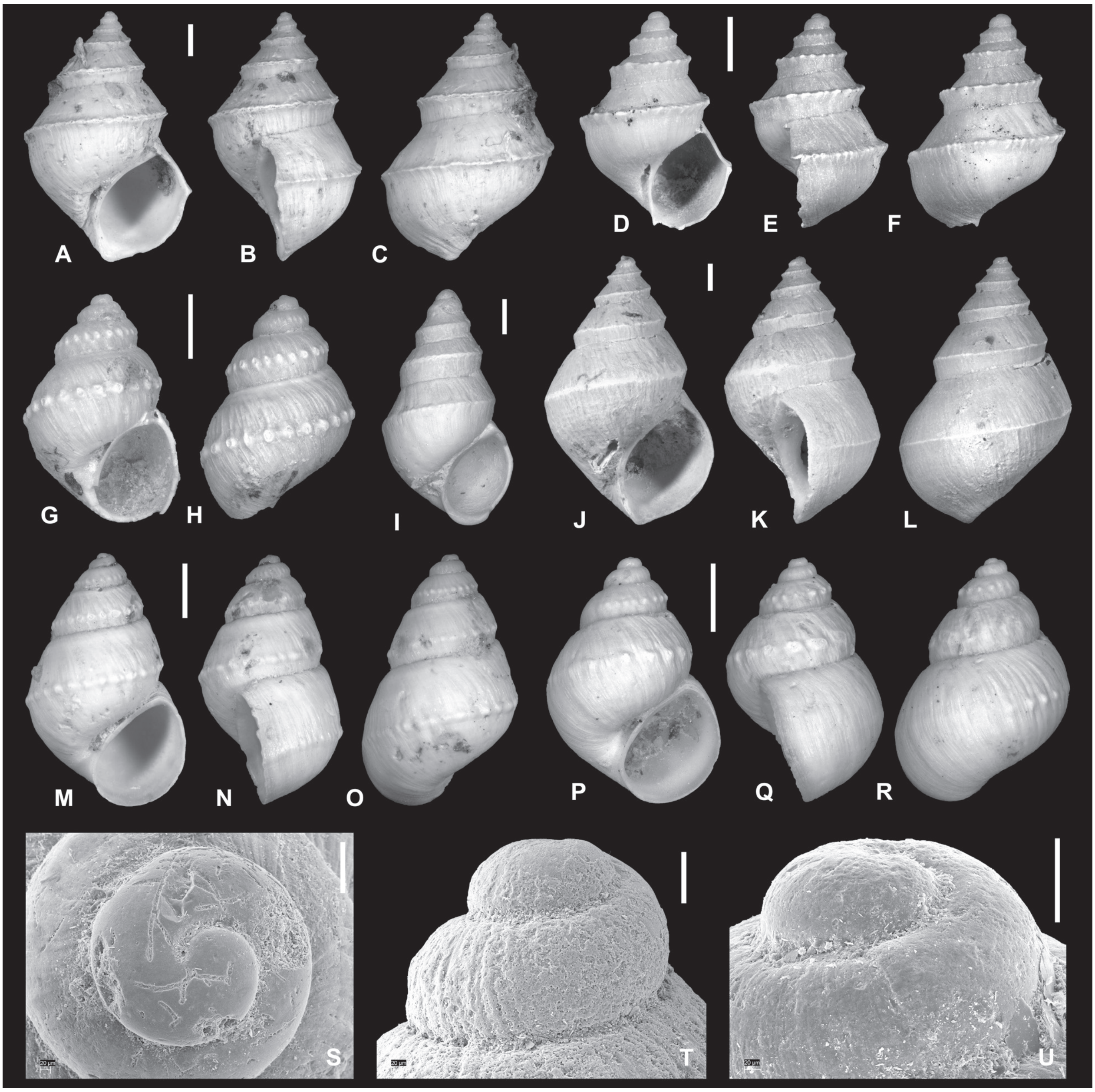

Figure 12. The *Staja–Falsipyrgula* species complex of the Kolankaya I fauna. **A–C.** *Falsipyrgula*? *coronata* sp. nov., holotype, RGM 1310837, sample 2. **D–F, T.** *F.*? *coronata* sp. nov., SNSB-BSPG 2023 XII 18, sample 2. **G, H.** *Falsipyrgula* cf. *sieversi* (Boettger, 1881), RGM 1310376, sample 2. **I.** *F.*? *coronata* sp. nov., SNSB-BSPG 2023 XII 19, sample 3. **J–L.** *F.*? *coronata* sp. nov., RGM 962611, sample 2. **M–O, U.** *F.* cf. *sieversi*, RGM 962610, sample 2. **P–R.** *F.* cf. *sieversi*, SNSB-BSPG 2023 XII 20, sample 2. **S.** *F.*? *coronata* sp. nov., RGM 1310377, sample 2. Scale bars: 1 mm (**A–R**); 100 µm (**S–U**).

reported from the Early Pleistocene of the Pasinler Basin are considerably broader, nearly conical, and bear the keel at the base of the whorl (Vasilyan et al. 2014).

Other similar species include *F. osmana* (Bukowski, 1930) from the Quaternary of Burdur and *Kirelia carinata* Radoman, 1973b (classified as *Falsipyrgula* by Schütt and Yildirim 1999), both of which differs in the stronger, continuous keel and the slightly more elongate shell (Schütt and Yildirim 1999).

Distribution. *Falsipyrgula sieversi* is known living and from Quaternary strata in Nakhchivan (Azerbaijan) (Sitnikova et al. 2018), the Early Pleistocene of Armenia (Tesakov et al. 2019), and the Pasinler Basin (Vasilyan et al. 2014).

Subfamily indet.

Hydrobiidae sp. indet.

Fig. 13A–C

Material. 1 shell (RGM 1310799) from sample 2.

Dimensions. 4.25 × 2.56 mm.

Remarks. The single specimen from Denizli closely resembles the extant *Radomaniola caputlacus* (Schütt & Şeşen, 1993), originally described as a species of *Orientalina* from eastern Anatolia. Both share the conical shape with weakly convex whorls and the simple ovate aperture. However, *Radomaniola caputlacus* is with 2.2 mm shell height (Schütt and Şeşen 1993) only about half the size of the Denizli shell. Larger species (up to 4 mm) of that genus are known from the Balkan Pensinula, where it is considerably more diverse, but these species differ clearly from the Denizli shell (Delicado and Hauffe 2022).

Another similar species is the fossil *Bithynia giralanensis* Oppenheim, 1919 (pl. 10, fig. 1), described from the Denizli Basin. However, that species is much larger (10 × 8 mm) at about the same number of whorls and bears a weak subsutural band; also, the shell is slightly broader and has a shallower base. Given these features, classification in the genus *Bithynia* is unlikely. Considering the poor preservation of Oppenheim's material as cast and the apparent loss of the type material (see Introduction), the name *Bithynia giralanensis* Oppenheim, 1919 should be considered a nomen dubium.

Yet another similar species is *Bania urosevici* (Pavlović, 1931) from the middle Miocene of Serbia in terms of general shape, the angulation, and the tilt of the aperture (Neubauer et al. 2020). The Denizli shell is, however, much larger (height of *B. urosevici* ~1.8 mm). Moreover, no *Bania* species is known until now from Turkey or deposits younger than Tortonian. The shell similarity may rather be due to convergence.

Finally, the species shares similarities with species of Shadiniinae, e.g., *Persipyrgula saboori* (Glöer & Pešić, 2009), which has a similar size, number of whorls, and shell shape, but more rounded whorls and a larger aperture (Delicado et al. 2016).

Given the poor preservation of our material and the overall difficulty of assigning fossil hydrobiids with few morphological characteristics to genera and even subfamilies, we refrain from a tentative placement in any of the abovementioned taxa.

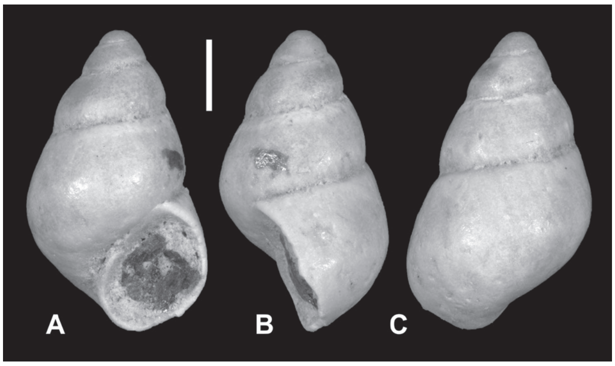

Figure 13. Hydrobiidae of the Kolankaya I fauna. **A–C.** Hydrobiidae sp. indet., RGM 1310799, sample 2. Scale bar: 1 mm.

Subclass Heterobranchia Burmeister, 1837
Informal group "Lower Heterobranchia" sensu Bouchet et al. 2017
Superfamily Valvatoidea Gray, 1840
Family Valvatidae Gray, 1840

Genus *Valvata* Müller, 1773

Type species. *Valvata cristata* Müller, 1774; by subsequent monotypy.

Valvata piscinalis (Müller, 1774)

Fig. 14A–D

*1774 *Nerita piscinalis* – Müller: 172.

1928 *Valvata* (*Cincinna*) *piscinalis piscinalis* (Müller) – Wenz: 2443–2445.

2002 *Valvata* (*Cincinna*) *piscinalis piscinalis* (O. F. Müller 1774) – Glöer: 190–191, textfig. 2019.

2012 *Valvata piscinalis* (Müller, 1774) – Welter-Schultes: 44, unnumbered textfig.

2019 *Valvata* (*Cincinna*) *piscinalis piscinalis* (O. F. Müller, 1774) – Glöer: 204–205, textfig. 256.

Material. 1 specimen (RGM 962694) from sample 3.

Dimensions. 6.25 × 6.15 mm.

Remarks. This well-known extant species is a typical representative of Quaternary freshwater mollusk faunas. It is known for its morphological variability, especially concerning the outline shape, ranging from nearly conical to broadly ovoid, being a result of an inflated penultimate whorl (Glöer 2002, 2019; Welter-Schultes 2012). The apex is depressed, the aperture is nearly circular and the umbilicus is wide. All these features match well the Turkish specimen, which also shows an expanded penultimate whorl. Only, it is slightly larger than the average extant members of the species (up to 4.5 mm high and 5 mm broad; Glöer 2019).

The material also resembles the depressed morphotype of the extant *Valvata lilljeborgi* Westerlund, 1897 in terms of the inflated penultimate whorl. That species comprises a broader range of morphologies, also including unusually high-spired forms (Vinarski et al. 2013). The species is today restricted to cold-temperate regions of the Baltic Sea Basin, the Dnieper Basin, and Western Siberia (Vinarski et al. 2013; Glöer 2019). Considering the above, we consider an identification with the more common *V. piscinalis* more likely.

Distribution. Today present throughout the Palearctic, also introduced to North America (Welter-Schultes 2012; Glöer 2019). Common in Upper Miocene to Pleistocene deposits across Europe (Wenz 1923).

Valvata sp. 1

Fig. 14E–L, U–W

Material. Sample 1: 1 specimen (RGM 1365352), 1 specimen (SNSB-BSPG 2023 XII 21); sample 2: 1 specimen (RGM 962695), 1 specimen (SNSB-BSPG 2023 XII 22).

Dimensions. 1.60 × 2.48 mm (RGM 962695; Fig. 14I–L, W), 1.48 × 2.18 mm (RGM 1365352; Fig. 14E–H, U, V).

Remarks. This species is characterized by a small, low-trochiform shell with relatively large, nearly circular aperture, slightly raised, bulbous apex, wide umbilicus, and moderately distinct growth lines. The protoconch bears the typical valvatid pattern, with numerous distinct spiral ridges crossed by weaker axial, u-shaped ridges, creating a wavy impression (Fig. 14U, V).

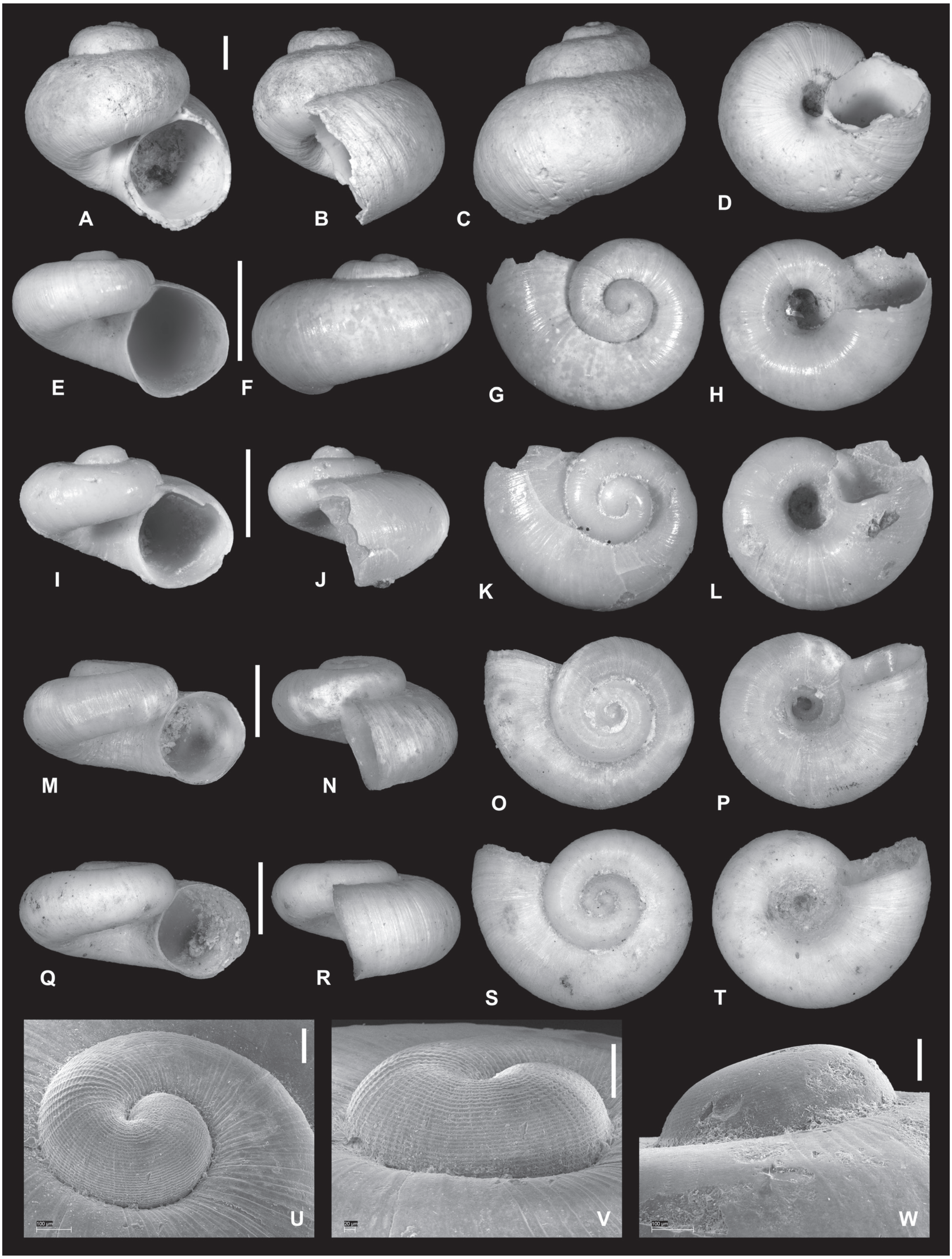

Figure 14. Valvatidae of the Kolankaya I fauna. **A–D.** *Valvata piscinalis* (Müller, 1774), RGM 962694, sample 3. **E–H, U, V.** *Valvata* sp. 1, RGM 1365352, sample 1. **I–L, W.** *Valvata* sp. 1, RGM 962695, sample 2. **M–P**. *Valvata gregaria* Bukowski, 1896, lectotype (designated by Willmann 1981), IGUW 1895 XII/25, Skiadhi Monastery, Rhodes, Greece, Istrios Formation (Pliocene). **Q–T.** *Valvata gregaria* Bukowski, 1896, paralectotype, IGUW 1895 XII/26, same locality and stratum. Scale bars: 1 mm (**A–T**); 100 µm (**U–W**).

The material closely resembles the Pliocene *Valvata gregaria* Bukowski, 1896 (p. 25–28, pl. 8, figs 7, 8) from Rhodes in terms of the shell size and shape, the relatively large aperture, and low number of whorls (see also Willmann 1981, p. 77, textfig. 25). However, the lectotype and paralectotype of that species (designated by Willmann 1981) show a depressed and unevenly coiled spire (Fig. 14M–T), while the Denizli specimens has a bulbous, almost pointy apex and a slightly more ovoid aperture.

Given the low amount of specimens available for comparison and assessing morphological variability, the perhaps not fully adult state of the specimens, as well as the low number of features, we do not describe a new species, although we could not detect any extant or late Cenozoic species that matches our material.

Valvata sp. 2

Fig. 15A–D, H

Material. 1 specimen (RGM 962690) from sample 1.

Dimensions. 4.60 × 4.97 mm.

Remarks. Only a single specimen for that species is available. It closely resembles *V. monachorum* Bukowski, 1896 from the Pliocene Istrios Formation of Rhodes, which Willmann (1981) considered (together with *V. aberrans* Bukowski, 1896) as a synonym of *V. skhiadica* (Fig. 15I–P). Our specimen matches this species regarding the conical, high-spired but apically flattened shell with the typical, adapically flattened whorls and the moderately wide umbilicus. However, the Turkish specimen bears distinct riblets, has a more pronounced convexity at the transition between whorl flank and base, and the base is straight-sided. In addition, our material is stratigraphically younger by several million years.

Another similar species is *Valvata hellenica* Tournouër in Fischer, 1877 from Rhodes (Fischer 1877, p. 55), probably from the Lower Pleistocene Kritika Formation (Willmann 1981, p. 133, pl. 3, figs 8–17). Willmann (1981) included a great variety of morphologies under that name and it is unlikely that all belong to the same species. The morphotype from the Lower Pleistocene Tafı Formation of Kos illustrated by Willmann (1981, pl. 3, fig. 9) resembles our specimen regarding the general shape, but like *V. skhiadica* above Tournouër's species has a more depressed spire (see also Bandel 2010, pl. 4, figs 49–51).

Valvata orientalis Fischer, 1866, which was also found in the Denizli Basin (Fischer 1866), has a similarly bulbous apex but a higher spire and a relatively smaller aperture. We illustrate for comparison the syntype of that species from Quaternary strata at Lake Buldur stored at Muséum national d'Histoire naturelle (MNHN.F.B41478; Fig. 15E–G). The syntype from Denizli could not be located at MNHN and might be lost (J.-M. Pacaud, pers. comm. 12/2022). To settle the taxonomic status of *Valvata orientalis* we hereby designate the illustrated specimen as lectotype.

Valvata sp. 3

Fig. 15Q–T

Material. 1 specimen (RGM 962697) from sample 2.

Dimensions. 2.79 × 2.92 mm.

Remarks. As for the previous species, this one is only known from a single specimen. It is characterized by a relatively small, globular shell with short apex and bulbous, regularly convex body whorl. The aperture is broken but appears to be nearly circular, the umbilicus is wide and the shell surface bears distinct orthocline growth lines. The protoconch is about half a whorl, weakly heterostrophic and bears weak signs of an originally spiral sculpture. The transition to the teleoconch is marked by a broad, shallow furrow and the onset of regular coiling.

The spherical shape with short apex and distinct growth lines reminds of the extant *Valvata montenegrina* Glöer & Pešić, 2008 from Lake Skadar and Podgorica (Montenegro). The Balkan species is, however, much larger (6–7 mm high, 6.2–6.8 mm wide; Glöer 2019) and slightly less broad than the Turkish specimen. Our specimen also reminds of juvenile *V. piscinalis*, but the shape is too conical and the umbilicus to wide with a too long straight upper flank. Given the generally large variability of *Valvata piscinalis* we cannot exclude the option that the specimen belongs to that species, but we consider it unlikely. The Turkish Quaternary species *Valvata orientalis* Fischer, 1866 (see above) shares the broad shape but has a higher apex and a relatively smaller aperture (Fig. 15E–G).

Although we could not find any species with which this one can be identified, we refrain from introducing a new name because of the low amount of material available, the incompleteness of the shell, and the small number of distinct morphological features.

Infraclass Euthyneura Spengel, 1881
Superorder Hygrophila Férussac, 1822
Superfamily Lymnaeoidea Rafinesque, 1815
Family Lymnaeidae Rafinesque, 1815
Subfamily Amphipepleinae Pini, 1877

Genus *Corymbina* Bukowski, 1892

Type species. *Corymbina rhodensis* Bukowski, 1892; by subsequent designation (Wenz 1923).

Corymbina elegans (Cantraine, 1841)

Fig. 16A–C

* 1841 *Ad.*[*elina*] *elegans*. Nob. – Cantraine: 156, pl. 5, fig. 12, 12a.
1847 *Limneus Adelina* – Spratt and Forbes: 177, textfig. a.
? 1877 *Lymnaeus Adelinae* [sic] Forbes [sic] – Fuchs: 5, pl. 1, fig. 4.
? 1877 *Lymnaeus Adelinae* [sic] Cantr. – Fuchs: 37, pl. 4, figs 1–6.
1923 *Radix* (*Adelinella*) *elegans* (Cantraine) – Wenz: 1319–1320.

1973 *Radix* (*Adelinella*) *elegans* (Cantraine) – Schütt and Besenecker: 16, pl. 1, figs 19, 20.

1981 *Corymbina elegans* (Cantraine) – Willmann: pl. 13, figs 18–20.

? 2022 *Corymbina elegans* (Cantraine, 1841) – Neubauer: fig. 6.7k, l.

Material. 1 juvenile specimen (RGM 962696) from sample 2.

Type locality. Italy; no further details known—Cantraine wrote: “Je ne connais cette espèce qu’à l’état fossile, le seul individu que je possède m’a été donnée par mon ami M. Rossi de Livourne, qui a’en connaissait pas exactement la provenarco.” [I only know this species in the fossil state, the only individual I have was given to me by my friend

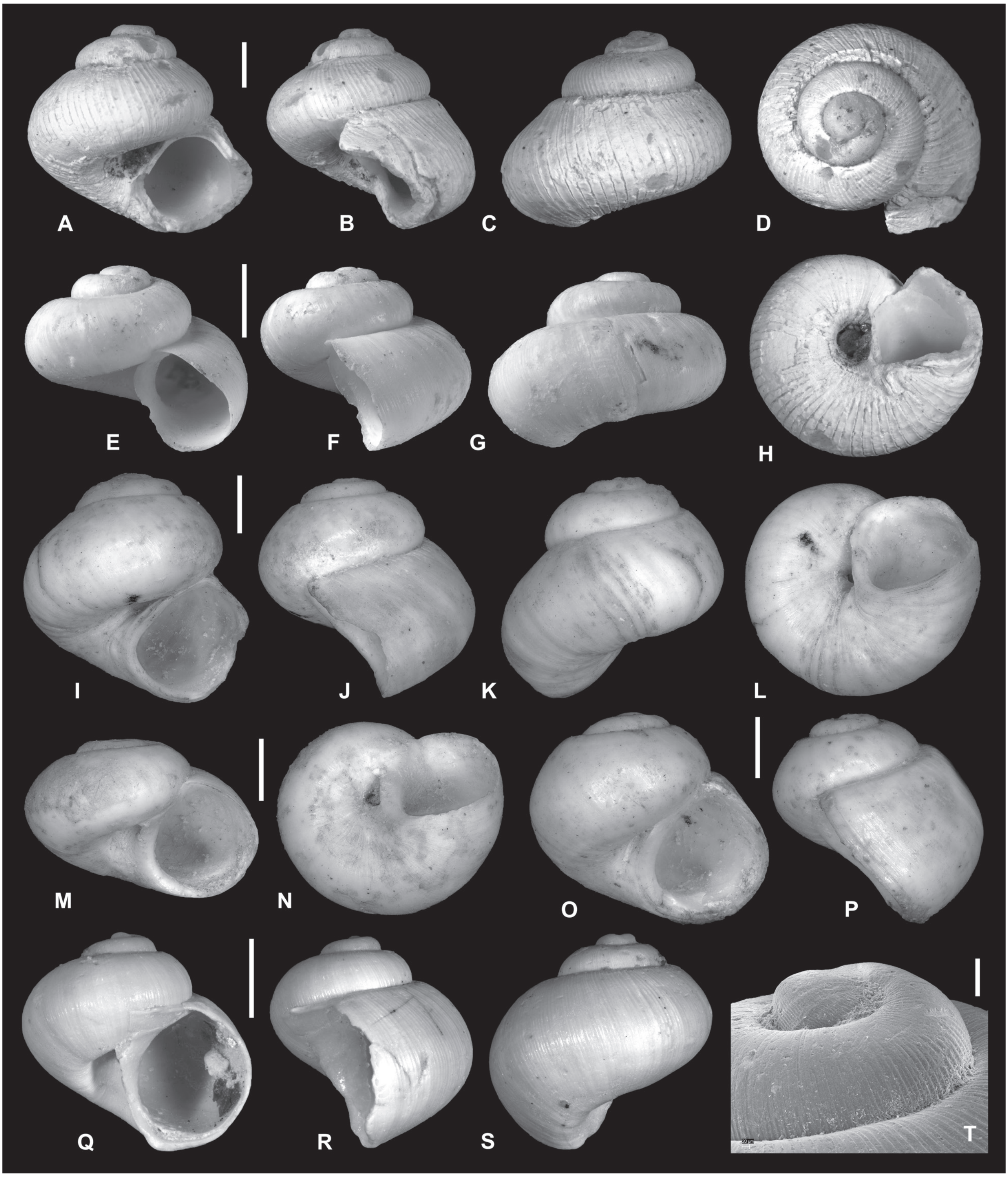

Figure 15. Valvatidae of the Kolankaya I fauna. **A–D, H.** *Valvata* sp. 2, RGM 962690, sample 1. **E–G.** *Valvata orientalis* Fischer, 1866, lectotype (designated herein), MNHN.F.B41478, Lake Buldur, Quaternary. **I–L.** *Valvata skhiadica* Bukowski, 1896, lectotype of *V. monachorum* Bukowski, 1896 (designated by Willmann 1981), IGUW 1895 XII/30, Skiadhi Monastery, Rhodes, Greece, Istrios Formation (Pliocene). **M–P.** *V. skhiadica*, lectotype (designated by Willmann 1981), IGUW 1895 XII/27, same locality and stratum. **Q–T.** *Valvata* sp. 3, RGM 962697, sample 2. Scale bars: 1 mm (**A–S**); 100 µm (**T**).

Mr. Rossi from Livorno, who didn't know exactly where it came from.].

Description. Shell comprises protoconch and about 0.75 teleoconch whorls. Initial part of protoconch smooth, followed by quarter whorl bearing faint riblets. P/T boundary not clearly visible, but probably coincides with weak angulation and onset of growth lines. Soon distinct, sharp ribs develop, which soon become broader and bulgier, leading to an irregular, wavy surface. Aperture fragmented, parts of outer lip missing; originally apparently elliptical. Umbilicus narrow.

Remarks. Spratt and Forbes (1847) mentioned the name *Limneus* [sic] *adelina* along with an illustration, making the name available. However, they clearly referred it to be the same species as *Adelina elegans* Cantraine, 1841, rendering *Lymnaea adelina* a junior objective synonym of *Corymbina elegans*. The specimen they illustrated has a much larger aperture, but the species has an extremely variable shell (see also Willmann 1981).

Corymbina bicarinata (Fuchs, 1877) from the Early Pleistocene of Livanates (Phthiotis, Greece) has a *Radix*-like appearance, with broad ovoid, attached aperture, an angulated last whorl, slender ribs, and small, pointy spire (Neubauer 2023b). Specimens from the same deposits identified by Fuchs (1877) as *L. adelinae* [= *C. elegans*] differ considerably from the phenotypes shown by Cantraine (1841), Spratt and Forbes (1847), and Willmann (1981). They rather resemble *C. bicarinata*, yet with a keel at the angulation. More data on the variability of both species is needed to disentangle their taxonomy and synonymies. We tentatively associate our single juvenile specimen with *C. elegans* given the general match in shell shape and sculpture as well as the known stratigraphic and geographic distribution of the species.

The Late Miocene *Corymbina rhodensis* Bukowski, 1892 is smaller and has a more slender shell, often with reduced sculpture (Willmann 1981). In both *C. elegans* and *C. rhodensis* specimens occur with the last whorl partly or entirely uncoiled (Willmann 1981). *Corymbina aegaea* (Oppenheim, 1919) from Upper Miocene (?) deposits near Harmancık (NW Turkey) has a more elongated shell (Schütt and Kavusan 1984). The Early Sarmatian (Serravallian, Middle Miocene) *Corymbina coronata* (Marinescu, 1992) from Romania differs from *C. elegans* in the more angulated body whorl and the ribs being reduced to elongated knobs at the uppermost whorl portion.

Corymbina rhodensis senestris İnal, 1975 from supposedly Pliocene sediments at Gürleyik SE Afyonkarahisar (c. 170 km ENE Denizli) shows a similar type of sculpture, but it is a rare case of a sinistral representative (İnal 1975). It is questionable, however, if it represents a distinct species or simply an aberrant morphotype of an existing species.

Distribution. *Corymbina elegans* has been reported from the Pliocene of the Denizli, Eşen, and Çameli basins in Turkey (Spratt and Forbes 1847; Oppenheim 1919; Wenz 1923), the Early Pliocene of central Italy (Esu and Girotti 2018), and the Pliocene–Pleistocene of Greece (Wenz 1923; Schütt and Besenecker 1973; Gillet et al. 1979). Records from the Late Miocene (Chios Island; Schütt and Besenecker 1973) are probably based on an outdated stratigraphy.

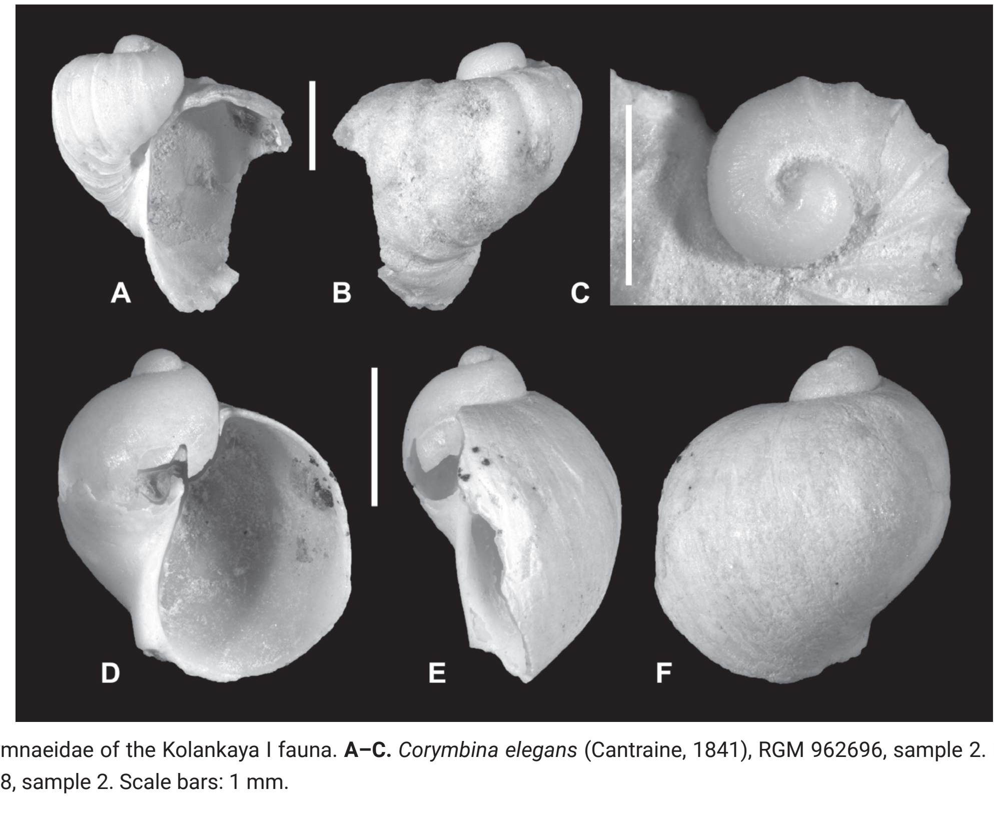

Figure 16. Lymnaeidae of the Kolankaya I fauna. **A–C.** *Corymbina elegans* (Cantraine, 1841), RGM 962696, sample 2. **D–F.** *Radix* sp., RGM 1310798, sample 2. Scale bars: 1 mm.

Genus *Radix* Montfort, 1810

Type species. *Radix auriculatus* Montfort, 1810 [unnecessary substitute name for *Radix auricularia* (Linnaeus, 1758)]; by original designation.

Radix sp.

Fig. 16D–F

Material. 1 juvenile specimen (RGM 1310798) from sample 2.

Remarks. The single available specimen contains about 2 whorls, with a small, bulbous protoconch and a large, inflated, and convex body whorl. The aperture is broad and semi-circular. Although a more precise identification is not possible, these features suggest a classification in the genus *Radix*.

Class Bivalvia Linnaeus, 1758
Infraclass Heteroconchia Gray, 1854
Order Cardiida Férussac, 1822
Superfamily Dreissenoidea Gray, 1840
Family Dreissenidae Gray, 1840
Subfamily Dreisseninae Gray, 1840

Genus *Dreissena* Van Beneden, 1835

Type species. *Mytulus* [sic] *polymorphus* Pallas, 1771; by monotypy.

Remarks. The dreissenid material at hand is very much broken and displays huge variability in shape and ornamentation. We have found it nearly impossible to distinguish species within the material. Our distinction of two morphotypes below will require confirmation by further designated collecting of entire specimens and populations in the region.

Dreissena kairanderensis (Oppenheim, 1919)

Fig. 17A–J

*1919 *Congeria* (?) *kairanderensis* sp. nov. – Oppenheim: 126–127, pl. 6, fig. 11.

? 1919 *Dreissensia* (?) *phrygica* sp. nov. – Oppenheim: 124–125, pl. 6, figs 1–3.

? 1919 *Dreissensia* (?) *hierapolitana* sp. nov. – Oppenheim: 127–128, pl. 6, fig. 12.

Material. Sample 2: 5 valves (RGM 962698–962702), c. 690 valves (RGM 1310845), 2 valves (SNSB-BSPG 2023 XII 23); sample 3: 28 valves (RGM 1310846).

Type locality. "Kairandere zwischen Bosalan und Buldan" [Kairandere between Bozalan and Buldan], Denizli Basin, Turkey.

Description. Variably shaped *Dreissena* with outlines ranging from mytiliform to flat, wide, and broad with apparent intermediate shapes. Dorsal margin usually curved but in some specimens can be straight. Ventral margin slightly curved, lacks byssate inflection. Semidiameter located toward ventral margin in adult stages. External ornamentation remarkably variable. Most specimens contain some sort of fanning out (axial) ribs. Number, shape, and length of these ribs highly variable; smooth specimens also occur. Typically 1–3 ribs develop almost immediately below umbo; often most prominent rib located at dorsal margin forms distinct dorsal angle. Ribs can fade within short distance or run entire shell length. Irregular small secondary ribs occur in some specimens. Hinge plate variable in strength. Plane of symmetry appears to be flat.

Dimensions. All material is broken, but measurements from cracked specimens in the field gave maximum dimensions of approximately 25 × 21 × 9.5 mm (width × height × semidiameter) for adult valves.

Remarks. Our material concerns a hugely variably shaped species for which additional study is required to determine whether it is a single species or consists of multiple species. Our juvenile and broken adult material does not enable making such a distinction. The flat plane of symmetry, the lack of a byssate inflexion on the shells exterior, and the relative prominence of the posterodorsal ridge in many of the specimens makes a close relationship with the *Dreissena polymorpha* Pallas, 1771 species group possible.

The species differs from the co-occurring *Dreissena* sp. 1 particularly in the shifting position of the semidiameter through ontogeny, which runs with an almost straight line 45° from the umbo toward the posterior margin, and the generally more curved shell. *Dreissena phrygica* Oppenheim, 1919 and *D. hierapolitana* Oppenheim, 1919, both also described from the Denizli Basin, seem to differ from *Dreissena kairanderensis* mostly in size, shell curvature, and/or the presence of additional keels. Given the variability we observe in our material, these names probably only signify morphological varieties of a single, polymorphic species. However, further studies are required to verify their taxonomic status. The same applies to other Denizli dreissenids, i.e., *Dreissena lycophila* Oppenheim, 1919, *Dreissena filifera* Andrusov, 1893, sensu Taner, 1974b, *Congeria prekairenderensis* Taner, 1974b, and *C. spathulata minor* Taner, 1974b [non *Congeria minor* Fuchs, 1877], all of which require investigation.

Distribution. Endemic to the Denizli Basin.

Dreissena sp. 1

Fig. 17K–N

Material. Sample 2: 2 valves (RGM 962703, 962704), 49 valves (RGM 1310847), 2 valves (SNSB-BSPG 2023 XII 24); sample 3: 6 valves (RGM 1310848).

Description. Shell large, wide, and distinctly flat. Exterior smooth, apart from fine growth lines. Dorsal margin long, almost straight, with robust but rounded posterodorsal angle. Through ontogeny, semidiameter shifts with al-

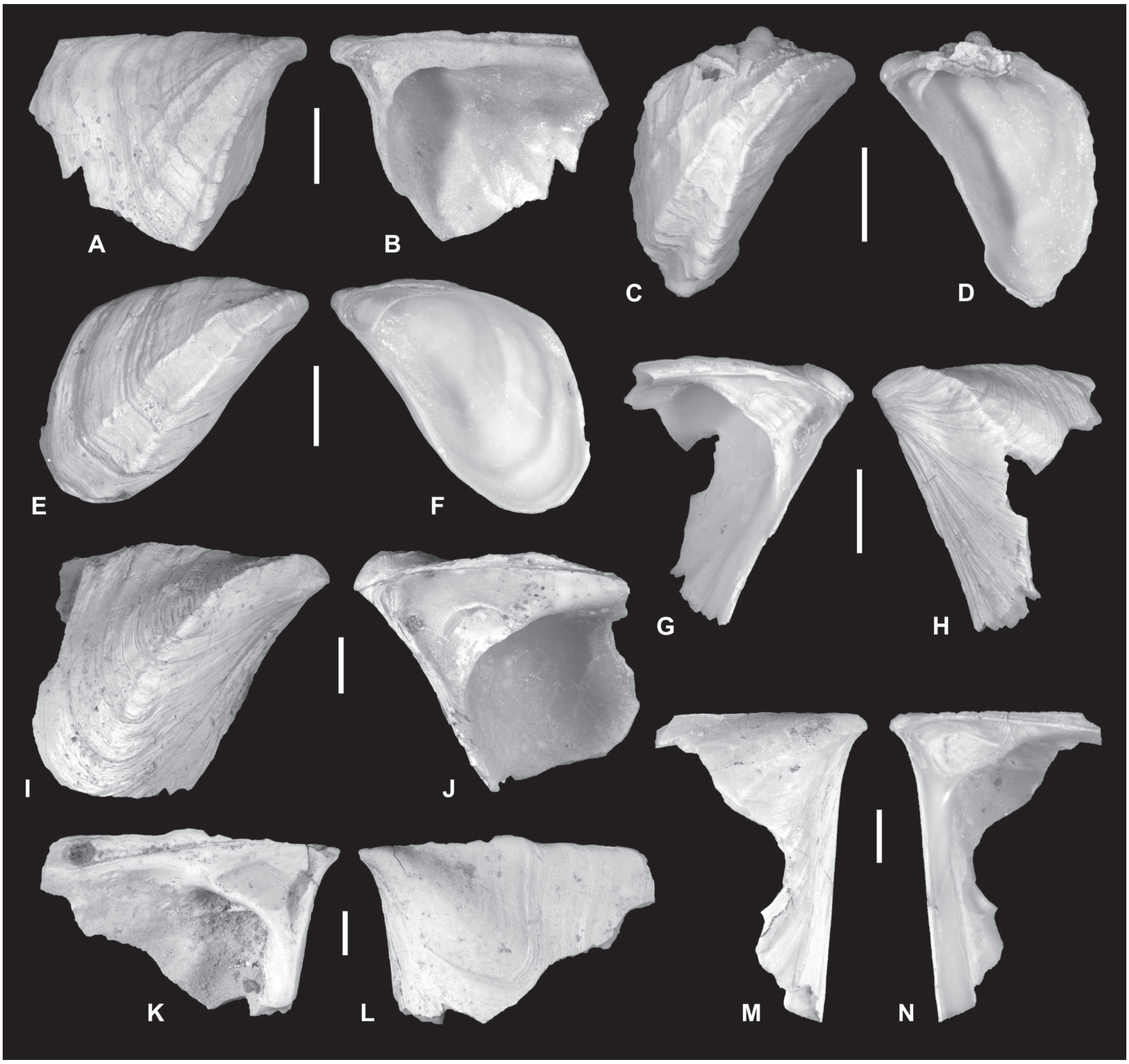

Figure 17. Dreissenidae of the Kolankaya I fauna. A, B. *Dreissena kairanderensis* (Oppenheim, 1919), RGM 962699, sample 2. **C, D.** *D. kairanderensis*, RGM 962701, sample 2. **E, F.** *D. kairanderensis*, RGM 962702, sample 2. **G, H.** *D. kairanderensis*, RGM 962700, sample 2. **I, J.** *D. kairanderensis*, RGM 962698, sample 2. **K, L.** *Dreissena* sp. 1, RGM 962703, sample 2. **M, N.** *Dreissena* sp. 1, RGM 962704, sample 2. Scale bar: 2 mm.

most straight line 45° from umbo toward posterior margin (which is broken in all specimens). In some specimens, slight byssal inflection may be developed on ventral margin, which is otherwise almost straight. Plane of symmetry between valves appears to be not entirely flat. Hinge plate robust, wide, and flat.

Dimensions. Length c. 20 mm (all material is broken).

Remarks. The smooth appearance and the presence of a very slight byssate inflection are characters that may point to a relationship with the Pontocaspian *Dreissena rostriformis* Deshayes, 1838 species group (Wesselingh et al. 2019). However, the very wide nature of specimens is unknown from this group and resembles superficially *Congeria* species.

Distribution. *Dreissena* sp. 1 is only known from the Lower Pleistocene Kolankaya Formation of the Denizli Basin.

Discussion

The Kolankaya I fauna described here contains 27 species (25 gastropods, two bivalves) in six families (Table 1). Six species and one genus (all among Hydrobiidae) are new to science. The composition, including endemic species, many hydrobiids, melanopsids, and comparatively few pulmonate species, is typical of a long-lived lake, which fits to previous reconstructions of the paleoenvironment of Lake Denizli (Alçiçek et al. 2007, 2015). Similar compositions featuring neritids, melanopsids, hydrobiids, pulmonates, and dreissenids are known from other long-lived lake faunas from late Cenozoic strata of Europe (e.g., Neubauer et al. 2013, 2016, 2020).

The fauna containing *Ecrobia*, *Dreissena*, *Theodoxus*, and Pyrgulinae/Caspiinae is typical of a Pontocas-

Table 1. Species inventory of the here described fauna, with indication of family attribution, samples, and status as endemic (to the Denizli Basin and the Aegean-Anatolian region, respectively). The Aegean-Anatolian region follows here the definition by Neubauer et al. (2015) based on Pliocene faunas.

Species	Family	Sample 1	Sample 2	Sample 3	Denizli endemic	Aegean-Anatolian endemic
Theodoxus percarinatus (Oppenheim, 1919)	Neritidae	x	x	x	x	x
Theodoxus aff. *pilidei* (Tournouër, 1879)	Neritidae		x			
Esperiana esperi (Férussac, 1823)	Melanopsidae	x		x		
Graecoanatolica alcicekorum sp. nov.	Hydrobiidae		x		x	x
Graecoanatolica? sp.	Hydrobiidae	x				
Iraklimelania minutissima sp. nov.	Hydrobiidae		x		x	x
Iraklimelania submediocarinata sp. nov.	Hydrobiidae	x			x	x
Ecrobia sp.	Hydrobiidae		x			
Harzhauseria schizopleura gen. et sp. nov.	Hydrobiidae	x	x		x	x
Hydrobiinae sp. indet.	Hydrobiidae	x				
Laevicaspia sp.	Hydrobiidae		x			
Prososthenia cf. *sturanyi communis* Willmann, 1981	Hydrobiidae		x			x
Xestopyrguloides? *sagitta* sp. nov.	Hydrobiidae		x		x	x
Xestopyrguloides? sp.	Hydrobiidae		x			
Staja lycica (Oppenheim, 1919)	Hydrobiidae	x	x			x
Staja? *cibyratica* (Spratt & Forbes, 1847)	Hydrobiidae		x	x		x
Falsipyrgula? *coronata* sp. nov.	Hydrobiidae		x	x	x	x
Falsipyrgula cf. *sieversi* (Boettger, 1881)	Hydrobiidae		x	x		
Hydrobiidae sp. indet.	Hydrobiidae		x			
Valvata piscinalis (Müller, 1774)	Valvatidae			x		
Valvata sp. 1	Valvatidae	x	x			
Valvata sp. 2	Valvatidae	x				
Valvata sp. 3	Valvatidae		x			
Corymbina elegans (Cantraine, 1841)	Lymnaeidae		x			
Radix sp.	Lymnaeidae		x			
Dreissena kairanderensis (Oppenheim, 1919)	Dreissenidae		x	x	x	x
Dreissena sp. 1	Dreissenidae		x	x	x	x

pian-type assemblage (Wesselingh et al. 2019). Pyrgulinae and Caspiinae are adapted to a wide range of salinities, from freshwater to mesohaline, but typically are dominant in oligohaline and lower mesohaline Pontocaspian faunas (Anistratenko 2008; Anistratenko et al. 2021). *Ecrobia* is distinctly euryhaline. Modern representatives are found under low oligohaline conditions (<1 psu for *E. maritima*; Kevrekidis and Wilke 2005), but usually occur at higher salinities. *Dreissena* and *Theodoxus* are typically found at oligohaline as well as freshwater conditions, while *Graecoanatolica*, *Falsipyrgula*, *Esperiana*, *Valvata*, and *Radix* are typical for freshwater settings, but many species do tolerate oligohaline conditions (e.g., Yildirim et al. 2006; Kebapçı et al. 2012; Verbrugge et al. 2012; van de Velde et al. 2019, 2020; Karatayev and Burlakova 2022).

The taxonomic composition of the fauna, with rare pulmonate gastropods and without clear freshwater indicators such as unionid and sphaeriid bivalves, suggests an oligohaline setting.

Comparing different sampling localities (here considering bulk samples 1 and 2 only), there is a certain degree of variation in the species compositions. Samples 1 and 2 share a number of taxonomic groups, i.e., Neritidae, Caspiinae, Hydrobiinae, Pyrgulinae, and Valvatidae, but Dreissenidae and Lymnaeidae are missing in sample 1, while sample 2 lacks Melanopsidae (in the surrounding scree deposits they have been found however). Also missing in sample 1 is the ecological indicator *Ecrobia*, but that sample contains the assumed sister taxon *Harzhauseria* gen. nov., which supposedly lived under similar environmental conditions. Hence, we assume that the observed compositional differences are only partly owed to variation in the local ecological conditions. Differences in stratigraphic position of the sampling levels and/or sampling/preservation bias probably played additional roles.

Biogeographically, the fauna is typical of the Aegean–Anatolian region, which has been a hotspot for freshwater mollusk diversity since the Neogene (Neubauer et al. 2015; Neubauer 2023a). Many of the here recovered genera are typical or even endemic to this region. *Theodoxus*, *Esperiana*, *Falsipyrgula*, *Valvata*, *Radix*, and *Dreissena* are widespread genera of little biogeographic significance but are also documented from extant Anatolian freshwater faunas (Radoman 1973a, 1973b; Yildirim 1999, 2004; Yildirim et al. 2006; Kebapçı et al. 2012; Karatayev and Burlakova 2022). *Graecoanatolica* and the fossil genera *Iraklimelania* and *Xestopyrguloides* are endemic to the Aegean–Anatolian region (Willmann 1981; Kebapçı et al. 2012). The fossil, enigmatic genus *Corymbina* is commonly found in Pliocene–Pleistocene deposits of many Greek and Turkish freshwater environments, but it also occurs in Italy and Romania (Marinescu 1992; Esu and Girotti 2018).

As mentioned above, the Denizli fauna also contains several elements typical of Pontocaspian assemblages, such as *Theodoxus*, *Ecrobia*, *Laevicaspia*, and *Dreissena* (Wesselingh et al. 2019). Although most of them are widespread genera today, they have a long evolutionary history in the Pontocaspian realm (Andrusov 1897; Roshka 1973; Babak 1983; Anistratenko and Gozhik 1995; Neubauer et al. 2018; Wesselingh et al. 2019). Also *Esperiana* has been found in Pleistocene strata of the Caspian Sea (Neubauer et al. 2018). The current assignment of the genera *Graecoanatolica* and *Iraklimelania* to Caspiinae, a typical Pontocaspian group (Anistratenko et al. 2021), also contributes to the biogeographical affinity to that realm.

On the species level, the fauna is characterized by a moderate degree of endemism – a third of all species (33.3%), including all new species, is endemic to the Denizli Basin. Almost half of the fauna (44.7%, if cf.-records are considered) is restricted to the Aegean–Anatolian region, with three species (11.1%) being shared with the Eşen Basin and two with the Çameli Basin (7.4%). Although only 1–2 species (*Prososthenia* cf. *sturanyi communis*, *Corymbina elegans*) are shared with Pliocene–Early Pleistocene Greek faunas, the similarities observed between several Denizli species (*Theodoxus percarinatus*, *Iraklimelania minutissima*, *I. submediocarinata*, *Xestopyrguloides*? *sagitta*, *Xestopyrguloides*? sp., *Staja lycica*, *Valvata* sp. 1, *Valvata* sp. 2) and those from Kos, Rhodes, and mainland Greece (Fuchs 1877; Willmann 1981; Esu and Girotti 2015) suggest they are closely related lineages.

Three species (11.1%) are still among the living European fauna, including two widely distributed species (*Esperiana esperi*, *Valvata piscinalis*) (Welter-Schultes 2012; Glöer 2019) and, if our identification proves correct, a species nowadays restricted to the Caucasus region (*Falsipyrgula sieversi*) (Sitnikova et al. 2018). *Corymbina elegans* has been documented from various Pliocene–Pleistocene sites in Greece, Turkey, and Italy (Spratt and Forbes 1847; Oppenheim 1919; Wenz 1923; Schütt and Besenecker 1973; Esu and Girotti 2018, 2020). *Theodoxus* aff. *pilidei* has similarities with a species from the Pliocene–Early Pleistocene of Romania and possibly the Late Miocene–Early Pliocene (?) of Kosovo (Wenz 1942; Atanacković 1959; Papaianopol and Marinescu 2003), but it is potentially an unrelated, new species.

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Supplementary material 1

Complete list of specimens, with indication of inventory numbers and samples

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Middle Cenomanian coral fauna from the Roßsteinalmen (Northern Calcareous Alps, Bavaria, Southern Germany) – a revised and extended version

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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 lower Turonian) crop out and contain locally abundant corals. The fauna described here derives from Middle Cenomanian sediments. This study complements a former revision. In total, the fauna includes 98 species in 46 genera, belonging to 16 scleractinian superfamilies and two octocorallian families. One species – *Enallhelia octasepta* – is 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 Basque-Cantabrian Basin, the Prebetic zone, the Pelagonium, and the Quillan Basin, indicating stronger connections to Tethyan rather than Boreal faunas. The fauna also shares species with Aptian and Albian, but also with Late Cretaceous faunas of the Gosau Basin. Eight genera experienced a range extension; five genera have their last occurrence in the Middle Cenomanian fauna, and three genera have their first occurrence. Although the fauna presents numerous genera that became widespread in the Late Cretaceous, its generic composition is more closely related to late Early Cretaceous corals than to post-Cenomanian corals. The faunal turnover at the Cenomanian/Turonian boundary was not marked by the sudden appearance of new faunal elements, but rather by the disappearance of taxa. Some faunal elements that constitute post-Cenomanian faunas already existed in the Cenomanian, but they were very rare. The increase of taxa after the Cenomanian/Turonian boundary took place during the Coniacian and Santonian.

Keywords

Cretaceous, Hexacorallia, Octocorallia, Branderfleck Formation, Taxonomy, Palaeobiogeography

Introduction

Only shortly after the appearance of the first publication on the corals from the Northern Calcareous Alps (Löser et al. 2013c), additional material from the same locality was discovered in the Bayerisches Landesamt für Umwelt - Geologie collections, and some further specimens were found in the collections of the Berliner Naturkundemuseum. The material in Berlin was collected by Josef Bruckmair and given to Werner Quenstedt (1893–1960) who worked as geologist and palaeontologist at the Friedrich-Wilhelms-Universität

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in Berlin. The Munich specimens come from the same collector, Otto Hölzl, who also sold and donated material to the Bayerische Staatssammlung für Paläontologie und Geologie. Surprisingly, the material recently discovered at the Bayerisches Landesamt für Umwelt - Geologie encompasses material that is taxonomically different from that described in Löser et al. (2013c). It is impossible to speculate about the reasons. One reason may be that some individual picked out the material (that is now at the Bayerisches Landesamt für Umwelt - Geologie, formerly Bayerisches Geologisches Landesamt) from a larger collection, and that the Bayerische Staatssammlung für Paläontologie und Geologie has received the rest of the material. Within the new collection, there are very attractive and well-preserved specimens, whereas, the material at the Bayerische Staatssammlung für Paläontologie und Geologie is, for a large part, represented by bulk samples. Among the new material there are multiple genera and species that are not yet reported. In this compilation, we include, therefore, all species, and also the material described in Löser et al. (2013c), but species described in the first paper are not figured, described and provided with dimensions. The discussion encompasses all species.

Our first contribution to the Middle Cenomanian coral fauna from the Northern Calcareous Alps was published more than ten years ago, and since then much more data about Cenomanian coral faunas became available. In Löser (2014b), the Boreal coral fauna from the Elbtal-Group (Saxony, Germany) of Cenomanian age was revised and completed with more data. In Löser (2015a), the Cenomanian coral fauna from the Le Mans area was briefly revised. Löser and Bilotte (2017) described a Cenomanian platy coral association from Southern France. Löser et al. (2018) report a lower Cenomanian coral fauna from Central Greece with nearly 80 species. Löser and Callapez (2022) present small coral faunas from the Cenomanian/Turonian boundary of Portugal. Löser and Wilmsen (2022, 2023) recently began publication of a lower Cenomanian coral fauna from Cantabria (Spain) that encompasses around 140 coral species. Another contribution that helps to link the Cenomanian coral faunas to other upper Cretaceous faunas constitutes the taxonomic revision of the Coniacian-Santonian coral fauna from the Gosau Basin (Löser et al. 2019), with descriptions and illustrations of 360 coral species. The new taxonomic data shed a different light on Cenomanian coral faunas and the evolution of this group during the Cretaceous.

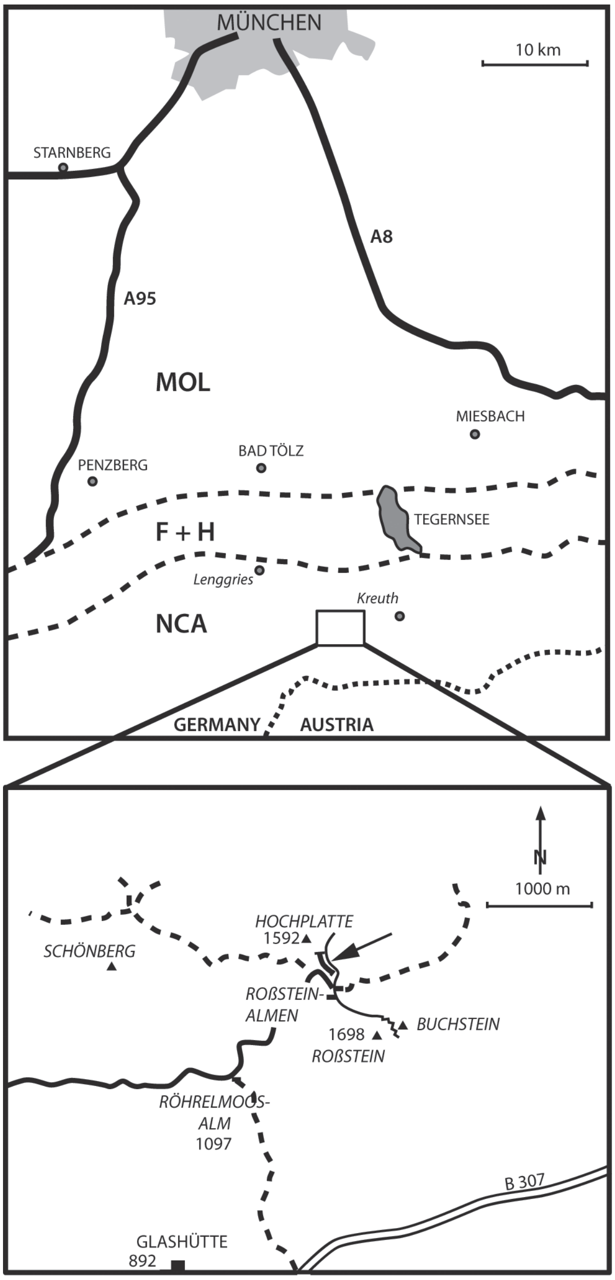

Figure 1. Location of the section Roßsteinalmen and tectonic units. NCA, Northern Calcaerous Alps, F + H, Flysch and Helvetic unit, MOL, Molasse. From Löser et al. (2013c).

Geological setting

The Roßsteinalmen locality is situated in the Alpine Mountains about 50 km south of Munich, 9 km SE of the Lenggries community and 5 km W of the Kreuth community (Fig. 1). At this locality, a small series of mainly siliciclastic Cretaceous sediments crop out, 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 Northern Calcareous Alps. They represent relics of a formerly more widely distributed facies, which have been protected from erosion by their tectonic position within synclinal structures. The "Cenoman Serie" is subdivided into two different formations, (1) the Losenstein Formation of Middle Albian to Lower Cenomanian age, consisting of silty marls, turbitic sandstones and deep water conglomerates with exotic pebbles, and (2) the Branderfleck Formation, consisting mainly of marls, calcareous sandstones, and breccias (?Upper Albian to Turonian; Gaupp 1980, 1982; Weidich 1984a, b; Faupl and Wagreich 2000). The Roßsteinalmen area belongs, tectonically to the northern part of the Lechtal nappe and here the Branderfleck Formation overlies Upper Jurassic radiolarites and limestones 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 (Fig. 2; 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* (Morrow, 1934)), 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 orbitolinid foraminifera (Steinberg 1980). This important index fossil family did not reach the Late Cenomanian (Schroeder and 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 and Wagreich (2005). Orbitolinids were collected in the marls but thin sections revealed their poor state of conservation. The marls and sandstones are, therefore, of a Middle Cenomanian age.

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 and Wagreich 2000; Pfiffner 2010). For the clastics of the lower Branderfleck Formation, palaeocurrent data give 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 nascent 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).

The corals described in the first part (Löser et al. 2013c) come from the lower part of the section (Fig. 2). Only specimen 2012 X 1 originates from a higher level and probably has a lower Upper Cenomanian age. The labels of the new coral material described and depicted for the first time in this study do not indicate the exact position within the Roßsteinalmen section; however, based on the preservation and a general rareness of fossils in the upper part of the section, these corals certainly do all come from the lower part of the section.

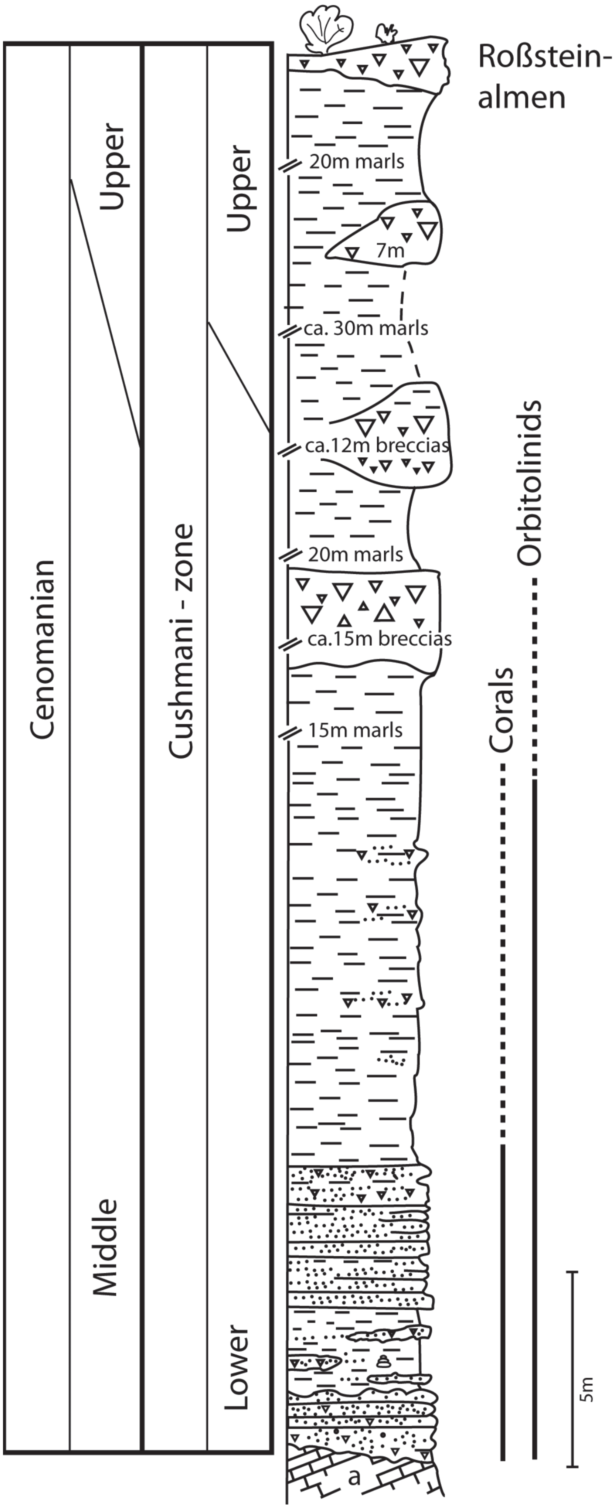

Figure 2. Section at the Roßsteinalmen. Planktonic foraminifera stratigraphy after Weidich (1984a, b), occurrence of corals and orbitolinid foraminifers after Steinberg (1980), Weidich (1984b), and personal observations. Scale only valid for the lower part of section. From Löser et al. (2013c).

Material and methods

In total, 240 coral specimens were included in this extended study; 220 of them could be identified at the species level. Nearly 200 thin sections in both transversal and longitudinal orientation were prepared. The coral material varies in its state of preservation, with exceptionally well-preserved specimens and others that are strongly recrystallised or fragmented.

Thin sections were scanned by passing light through them using a flatbed scanner with an optical resolution of

6,400 dpi. Scanned images were then transferred to 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, corallite dimensions of each specimen were systematically measured. To achieve statistical significance, the largest number of possible measurements was taken. This number was mainly controlled by the size and quality of the thin section and the size of the single corallites in relation to the size of the thin sections. Septa were counted for numerous corallites where the septal symmetry was not regular (in corals with a regular symmetry the number of septa is the same in all corallites). For each type of measurement (corallite diameter and distance, width and distance of corallite row) and count (principally septal counts) in one thin section, the following values were obtained:

n	number of measurements or counts;
min–max	lowest and highest measured or counted values (mm for measurements);
µ	arithmetic mean (average);
s	standard deviation;
cv	coefficient of variation according to K. Pearson
µ±s	first interval.

Measurements are always in millimetre. Thin sections were measured and values were calculated using the Palaeontological Database System PaleoTax, module PaleoTax/Measure (https://www.paleotax.de/measure); for details on the mathematical background, see Löser (2012b). Morphometric data of the corals were compared against the morphometric data of specimens in worldwide fossil coral collections, and an associated image database. The database encompasses approximately 28,920 coral specimens from Triassic to modern forms. Approximately 8,200 of them are type specimens, and 16,800 specimens are illustrated. The database is located in the Estación Regional de Noroeste (Instituto de Geología, UNAM), 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 3,100 worldwide coral localities with coral indications was used (Löser et al. 2002, 2005). To simplify the analysis, localities of the same age, belonging to the same basin, on the same continental margin or the same interoceanic platform, were grouped together into one palaeo-province (a type of large faunule, sensu Johnson 2007). Altogether, this produced 440 provinces, reaching from the Jurassic into the Palaeogene. Only firmly dated localities were assigned to a province in order to ensure that the subsequent analysis was valid, and that the studied locality was not included in any existing province. For the study area, an independent province was created to allow a clear comparison between the existing provinces and the new material. Interregional comparisons were carried out between the new province and existing provinces having at least three species in common with the fauna of the studied area. The comparisons were carried out using, exclusively, specimens that were available to the first author (H.L.), but not the indications in the literature. The literature does not offer precise morphometric data, that are necessary to separate species and to compare them to each other. For details, see also Löser (2008), and Löser and Minor (2007). Data analysis, statistics, and the creation of charts were all carried out using the Database System PaleoTax and the graphic module PaleoTax/Graph (www.paleotax.de). The material is kept in the Bayerisches Landesamt für Umwelt - Geologie/Paläontologie (Hof), the Bayerische Staatssammlung für Paläontologie und Geologie (Munich), and the Museum für Naturkunde der Humboldt-Universität (Berlin), all of which are located in Germany.

Systematic description

The distribution data (as reflected in the synonymy lists) are almost entirely based on material examined by the first author (H.L.). Material only mentioned in the literature, material not available, or insufficiently described and/or poorly illustrated in the literature, was not taken into account. To obtain better insight into the distribution patterns of the studied coral fauna, much unpublished material was included. Therefore, distribution data indicated under 'Other occurrences' could also be provided for species remaining in open nomenclature. As mentioned above, we include here all species, and also those species that are described in detail in Löser et al. (2013c), but measurements, descriptions, remarks, and illustrations are not repeated.

In scleractinian corals, the separation of superfamilies, families, and genera is based on qualitative characteristics, whereas the species are separated on the basis of morphometric data (corallite dimensions, septal counts, and septal density). The species of one genus are, more or less, alike and differ only in their measurements. For this reason descriptions of species are not given here. We provide for the taxonomic levels from superfamily to genus detailed descriptions, without repeating characteristics in lower levels. When a superfamily is characterised by large trabeculae, perforate septa, and the presence of synapticulae, this is also the case for all families and all genera. There are rare exceptions, but these are mentioned in the descriptions. When a superfamily encompasses only one family, the description is not repeated with the family.

The abbreviations used in the synonymy lists follow Matthews (1973): *****, earliest valid publication of the species name; **non**, the citation is excluded from the species; **p**, the described material belongs only in part to the species concerned; **v**, the specimen was observed by the first author (H.L.). The abbreviation **cf** indicates that the present species is similar to the species indicated in the concerned reference, but the assignment remains uncertain. A year in italics indicates that the quotation is provided with neither a description nor an illustration.

The following abbreviations are used to describe the dimensions of the corals: **c**, corallite diameter (outer diameter); **ccd**, distance between corallite centres; **clmax**, large lumen; **clmin**, small lumen; **cmax**, larger outer corallite diameter; **cmin**, smaller outer corallite diameter; **crd**, distance of corallite series; **crw**, width of corallite series; **md**, distance between crests in a hydnophoroid colony.

Collection abbreviations are as follows: **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany; **LFU**, Bayerisches Landesamt für Umwelt - Geologie, Hof, Germany; **NHMW**, Naturhistorisches Museum, Wien, Austria; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **PU**, Museo di Geologia e Paleontologia dell' Università di Torino, Torino, Italy; **MB**, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

Class Anthozoa Ehrenberg, 1834
Subclass Hexacorallia Haeckel, 1866
Order Scleractinia Bourne, 1900

Fossil scleractinian corals are described since the end of the 18th century. Since the late 20th century, they are examined using thin sections, leading to the discovery of hitherto unknown morphological elements and to changes in the classification. During former systematic revisions (Vaughan and Wells 1943; Alloiteau 1952; Wells 1956; Alloiteau 1957), the order Scleractinia was subdivided into suborders and families. The subdivision into suborders is now, up to 80 years later, not considered practical for various reasons, as explained by Löser et al. (2018), Löser and Callapez (2022), and Löser and Wilmsen (2023). Therefore, the classification system that was introduced by Löser (2016c) does not apply suborders, but rather applies superfamilies which group families together. This practical approach has the advantage that superfamilies are covered by the International Code of Zoological Nomenclature (ICZN 1999) and follow the type principle. This is not the case for the taxonomic level of orders, including suborders. Superfamilies clearly refer to a family, genus, type species, and a type. The characteristics of a superfamily are thus connected to a physical specimen that more precisely limits the characteristics of this higher rank taxon. Practically, suborders are, at the present time, replaced by superfamilies. Currently, 27 superfamilies with 56 families (or informal groups) are distinguished, that range from the Middle Jurassic to the Palaeogene, partly to the Neogene, and extant (Löser 2016c). Contrary to the former classification system based on suborders, the superfamilies may constitute monophyletic groups. The basic characteristics for the distinction of the superfamilies is the size of the trabeculae relative to the septa. Further distinction is based on the presence or absence of synapticulae and septal perforation.

Superfamily Actinastreoidea Alloiteau, 1952

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

Family Actinastreidae Alloiteau, 1952

Actinastrea d'Orbigny, 1849

Type species. *Actinastrea goldfussi* d'Orbigny, 1850.

Description. Plocoid colony with narrow coenosteum that is made of large isolated trabeculae. Corallites circular or polygonal. Septa in a regular radial symmetry, rarely bilateral. Septa of the first and second generation can be connected to the columella, younger septa can be connected to older septa. Columella styliform and large. No pali.

Actinastrea limbata Alloiteau, 1954b

*1954b *Actinastrea limbata* nov. sp. – Alloiteau: 89, text-fig. 17, pl. 2, fig. 5, pl. 10, fig. 7.

v2013 *Stelidioseris minima* (de Fromentel, 1857) – Löser, Werner and Darga: 44, pl. 1, figs 3, 4.

v2019 *Actinastrea limbata* Alloiteau, 1954 – Löser, Heinrich and Schuster: 42, figs 50a–c.

Material. BSPG 1947 XVI 26, 1947 XVI 61; two thin sections.

Remarks. The material does not belong to the genus *Stelidioseris* because it shows isolated trabeculae in the coenosteum as it is typical for *Actinastrea*. Therefore, the species name has been changed, compared to our publication from 2013.

Other occurrences. Upper Turonian of the Western Tethys (France), Coniacian to Santonian of the Central Tethys (Austria), lower Campanian of the Western Tethys (France), lower Maastrichtian of the Western Atlantic (Mexico).

Actinastrea polygonata Alloiteau, 1954b

Plate 1: figs 1–3

*v1954b *Actinastrea polygonata* nov. sp. – Alloiteau: 43, pl. 4, fig. 11, pl. 7, fig. 5.

v1989 *Actinastrea schizoformis* nov. sp. – Reig Oriol: 21, pl. 2, fig. 4, pl. 6, fig. 2.

v2019 *Actinastrea polygonata* Alloiteau, 1954 – Löser, Heinrich and Schuster: 45, figs 54a–c.

Material. LFU 8336SG015004#1; one thin section.

Dimensions. (LFU 8336SG015004#1).

	n	min–max	μ	s	cv	μ±s
clmin	20	1.25–1.60	1.44	0.09	6.6	1.35–1.54
clmax	20	1.53–2.06	1.70	0.14	8.7	1.56–1.85
ccd	27	1.37–2.02	1.73	0.18	10.6	1.54–1.91
septa	10+10					

Other occurrences. Upper Turonian of the Western Tethys (France), Coniacian to Santonian of the Central Tethys (Austria), Santonian of the Western Tethys (Spain).

Actinastrea subdecaphylla **(Oppenheim, 1930)**

v*1930 *Astrocoenia subdecaphylla* n. sp. – Oppenheim: 460, pl. 15, fig. 9.

1982 *Actinastraea subdecaphylla* (Oppenheim) 1930 – Beauvais: (1), 13, figs 1, 2.

v2013 *Actinastrea regularis* (de Fromentel, 1887) – Löser, Werner and Darga: 43, pl. 1, figs 1, 2.

v2019 *Actinastrea* ? *subdecaphylla* Oppenheim, 1930 – Löser, Heinrich and Schuster: 48, figs 58a–d.

Material. BSPG 1947 XVI 60; one thin section.

Remarks. In Löser et al. (2013c) this specimen was assigned to *Actinastrea regularis* (de Fromentel, 1887). After examining the type material of *Actinastrea subdecaphylla* this assignation was corrected. Both species are similar but differ in the corallite dimensions (see Löser et al. 2019: 40 for comparison).

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria), upper Santonian of the Western Tethys (France), upper Campanian to lower Maastrichtian of the Arabian Peninsula (United Arab Emirates).

Superfamily Agaricioidea Gray, 1847

Description. In the Cretaceous only solitary corals. Septa compact, mostly in a subregular radial symmetry. Septa in places connected to each other. Lateral faces with thorns, upper margin smooth. Microstructure of septa of small trabeculae. Lonsdaleoid and main septa absent. Synapticulae present, mainly in the wall. Pali absent, columella by septal fusion. Endotheca generally made of thin tabulae. Wall compact, mainly septothecal with synapticulae. Marginarium absent. Coenosteum generally present, consists of costae. Budding intracalicinal.

Family Agariciidae Gray, 1847

Antilloseris **Vaughan, 1905**

Type species. *Turbinoseris eocaenica* Duncan, 1873.

Description. Solitary elliptical coral. Septa compact, in a regular radial symmetry. Septa of the first three cycles thicker in the corallite centre and free, septa of further cycles more regular in thickness and connected to each other. Septa lateral faces with thorns, directing to the corallite center. No pali. Columella styliform and small. Enthodeca absent. Wall perforated, with synapticulae.

Antilloseris **sp.**

Plate 1: figs 4–6

Material. LFU 8336SG015138#2; one thin section.

Dimensions. (LFU 8336SG015138#2).

c	16.8×23.8
septa	112

Remarks. The assignation of the present specimen to this genus is preliminary. It shares with *Antilloseris* the arrangement of septa, with the difference that the septa of the first three cycles are, in the present specimen, not thickened in the corallite centre. The columella is parietal and not styliform as in *Antilloseris*.

Trochoseropsis **Söhle, 1897**

Type species. *Trochoseropsis ettalensis* Söhle, 1897.

Description. Turbinate solitary coral with an elliptical or circular outline. The septa are in a regular radial symmetry, regularly connected to each other, and many of them are fused together in the centre of the corallite to form the columella.

Trochoseropsis ettalensis **Söhle, 1897**

*v1897 *Trochoseropsis Ettalensis* – Söhle: 45, pl. 7, figs 2, 2ab.

v1958 *Smilotrochus tarraconensis* nov. sp. – Alloiteau: 84, pl. 2, figs 7, 8.

v2013a *Trochoseropsis ettalensis* Söhle, 1897 – Löser: 16, figs 6b–i.

v2013 *Trochoseropsis ettalensis* Söhle, 1897 – Löser, Werner and Darga: 50, pl. 3, figs 7–9.

Material. BSPG 1947 XVI 15, 1947 XVI 16, 1947 XVI 24, 1947 XVI 28, 1947 XVI 29, 1947 XVI 73, 1947 XVI 74, 1991 X 63, LFU 8336SG015145, MB K2984#2, K2984#3; ten thin sections.

Other occurrences. Lower Albian of the Western Tethys (France), lower Cenomanian of the Central Tethys (Germany), Campanian of the Western Tethys (Spain).

Superfamily Caryophyllioidea Dana, 1846

Description. Mainly solitary, rarely colonial (phaceloid) corals. Septa compact, regular thickness, mostly in a regular radial symmetry. Septal upper margins smooth, lateral faces with few small thorns or granulae. Lonsdaleoid septa and main septum absent.

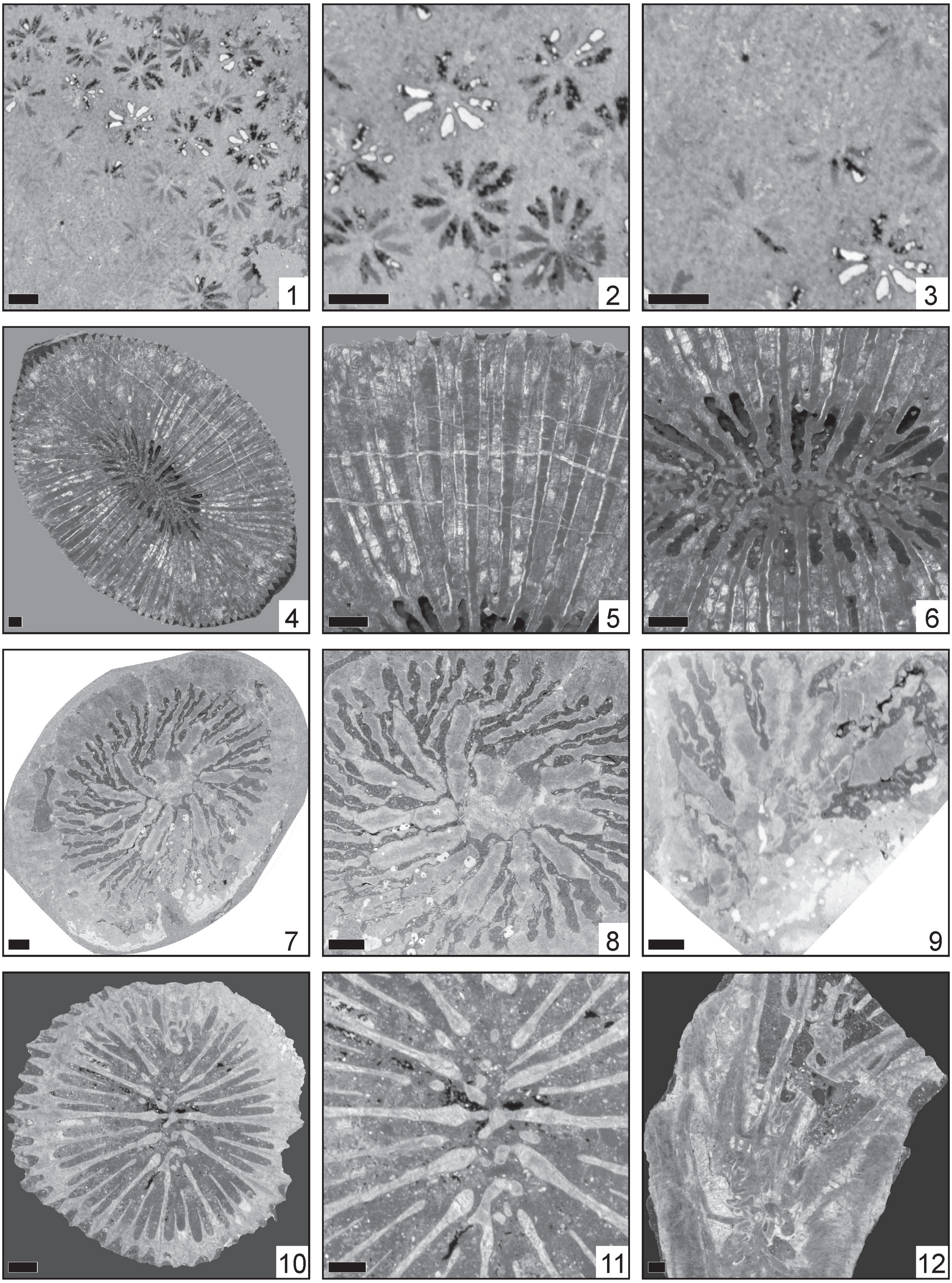

Plate 1. (1–3) *Actinastrea polygonata* Alloiteau, 1954. LFU 8336SG015004#1. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Transversal thin section, detail. **(4–6)** *Antilloseris* sp., LFU 8336SG015138#2. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Transversal thin section, detail. **(7–9)** Caryophylliidae indet. 1, LFU 8336SG015133#2. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. Longitudinal thin section. **(10–12)** Caryophylliidae indet. 2, LFU 8336SG015099#2. **10**. Transversal thin section. **11**. Transversal thin section, detail. **12**. Longitudinal thin section. Scale bars: 1 mm.

Microstructure of probably very small trabeculae that can only be traced by a dark line. Synapticulae absent. Pali and columella can be present. The endotheca is variable, but generally poorly developed in solitary forms. Marginarium absent. Wall septothecal. Coenosteum absent.

Family Caryophylliidae Dana, 1846

The classification of the family is difficult. Their fossil members are generally poorly known, and particularly this is the case for many type species. The reason is that solitary corals have been – in contrast to colonial corals – much less studied using thin sections. Whereas large coral colonies often provide pieces to prepare thin sections, the preparation of thin sections from a solitary coral generally results in its complete loss. The study of solitary corals always demands specimen-rich populations. These populations are not always available. Therefore, not all material shown here can be assigned to a genus.

Caryophylliidae indet. 1

Plate 1: figs 7–9

Material. LFU 8336SG015133#2; two thin sections.

Dimensions. (LFU 8336SG015133#2).

c	11×14.5
septa	48

Description. Coral with an elliptical outline. Septa free, in a regular hexameral symmetry. Twelve septa with very strongly inflated inner margins (that can be interpreted as pali). Columella very large, styliform. Endotheca poorly developed.

Caryophylliidae indet. 2

Plate 1: figs 10–12

Material. LFU 8336SG015099#2, 8336SG015132#1; four thin sections.

Dimensions. (LFU 8336SG015099#2).

c	14.1×14.6
septa	48

Description. The solitary coral has a regular septal symmetry with four septal cycles. Only the third cycle bears occasionally pali. The columella consists of some small elements.

Parasmilia Milne Edwards & Haime, 1848c

Type species. *Madrepora centralis* Mantell, 1822.

Description. Turbinate solitary coral with circular outline. A columella is present, but difficult to distinguish from the septa. No pali. The endotheca is poorly developed.

Parasmilia centralis (Mantell, 1822)

Plate 2: figs 1, 2

*v1822 *Madrepora centralis* – Mantell: 159, pl. 16, figs 2, 4.
v2016c *Madrepora centralis* Mantell, 1822 – Löser: 510, figs P30a, b.

Material. LFU 8336SG015132#2, 8336SG015132#3, 8336SG015132#4, 8336SG015133#1; seven thin sections.

Dimensions. (LFU 8336SG015132#2).

c	9.9×11.4
septa	48

Remarks. The coral *Parasmilia centralis* is far more than one hundred times cited in the literature. Since most of these citations are not accompanied by proper illustrations and/or corallite measurements and septal counts, a synonymy list cannot be compiled. The distribution data are based on material observed by the first author (H.L.).

Other occurrences. Cenomanian of the European Boreal (UK), Coniacian to lower Santonian of the Central Tethys (Austria), upper Coniacian to Maastrichtian of the European Boreal (UK, Germany).

Superfamily Cladocoroidea d’Orbigny, 1851

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

Family Cladocoridae d’Orbigny, 1851

Description. Phaceloid colonies. Septal symmetry sub-regularly radial. Pali present in some genera. Columella styliform, lamellar or parietal.

Procladocora Alloiteau, 1952

Type species. *Calamophyllia gracilis* d'Orbigny, 1850.

Description. Phaceloid colony. Corallites with a small diameter (< 6 mm). Septa in a sub-regular radial symmetry; but systems can be recognised. The number of septa increases with the corallite diameter. The septa of the first two cycles have pali. The columella is lamellar.

Procladocora simonyi (Reuss, 1854)

Plate 2: figs 4–6

*v1854 *Cladocora Simonyi* – Reuss: 112, pl. 12, figs 5–7.
v1930 *Cladocora libidinum* n. sp. – Oppenheim: 362, pl. 38, fig. 14.
v1936 *Cladocora jamaicaënsis* Vaughan 1899 – Hackemesser: 38, pl. 5, fig. 3.
v2000 *Procladocora jamaicaensis* (Vaughan 1899) – Löser: 52, pl. 3, figs 1–5.

Material. LFU 8336SG015082#3, 8336SG015162; three thin sections.

Dimensions. (LFU 8336SG015082#3).

c	4.1×5.7
septa	45

Other occurrences. Lower Albian of the Western Tethys (Spain), upper Cretaceous of the Central Tethys (Greece, Austria).

Procladocora sp.

Plate 2: fig. 3

v1997 *Pleurocora* cf. *alternans* Milne-Edwards and Haime, 1849 – Baron-Szabo: 77, pl. 10, figs 4, 6.

Material. LFU 8336SG015140#1; four thin sections.

Dimensions. (LFU 8336SG015140#1).

c	3.8×4.1
septa	28

Other occurrences. Upper Cenomanian of the Western Tethys (France), lower Coniacian of the Central Tethys (Austria).

Family Columastreidae Alloiteau, 1952

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

Eocolumastrea Löser & Zell, 2015

Type species. *Columnocoenia bucovinensis* Morycowa, 1971.

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

Eocolumastrea sp.

Plate 2: figs 7, 8

Material. LFU 8336SG015079#4; one thin section.

Dimensions. (LFU 8336SG015079#4).

	n	min–max	µ	s	cv	µ±s
clmin	10	1.55–2.03	1.76	0.16	9.0	1.60–1.92
clmax	10	1.87–2.30	2.10	0.16	7.6	1.94–2.26
ccd	13	2.22–3.72	2.91	0.36	12.5	2.55–3.27
septa	8	16–22	19.38	2.33	12.0	17–22

Remarks. The septal symmetry is particular in this specimen. Whereas in *Eocolumastrea* the septal symmetry is normally a multiple of six or ten, the present specimen shows varying systems such as eleven and ten.

Neocoenia Hackemesser, 1936

Type species. *Neocoenia renzi* Hackemesser, 1936.

Description. Plocoid colony with circular or elliptical corallites. Symmetry regular hexameral. The first two septal cycle bear pali; the columella is lamellar and small.

Neocoenia exsculpta (Reuss, 1854)

*v1854 *Astraea exsculpta* – Reuss: 114.
v1957 *Stephanaxophyllia Casterasi* nov. sp. – Alloiteau: 73, figs 20, 21, pl. 9, fig. 8, pl. 16, fig. 1.
vp2013 *Neocoenia* cf. *casterasi* (Alloiteau, 1957) – Löser, Werner and Darga: 44.
v2019 *Neocoenia exsculpta* (Reuss, 1854) – Löser, Heinrich and Schuster: 77, figs 107a, b.

Material. BSPG 1947 XVI 33, 1947 XVI 65, 1991 X 73, 1991 X 77, LFU 8336SG015079#1, 8336SG015079#3; nine thin sections.

Remarks. This material was formerly assigned to *Neocoenia* cf. *casterasi* (Alloiteau, 1957). After studying the type material of *Neocoenia exsculpta*, the determination could be improved.

Other occurrences. Upper Turonian to Santonian of the Central Tethys (Austria), Santonian of the Western Tethys (France).

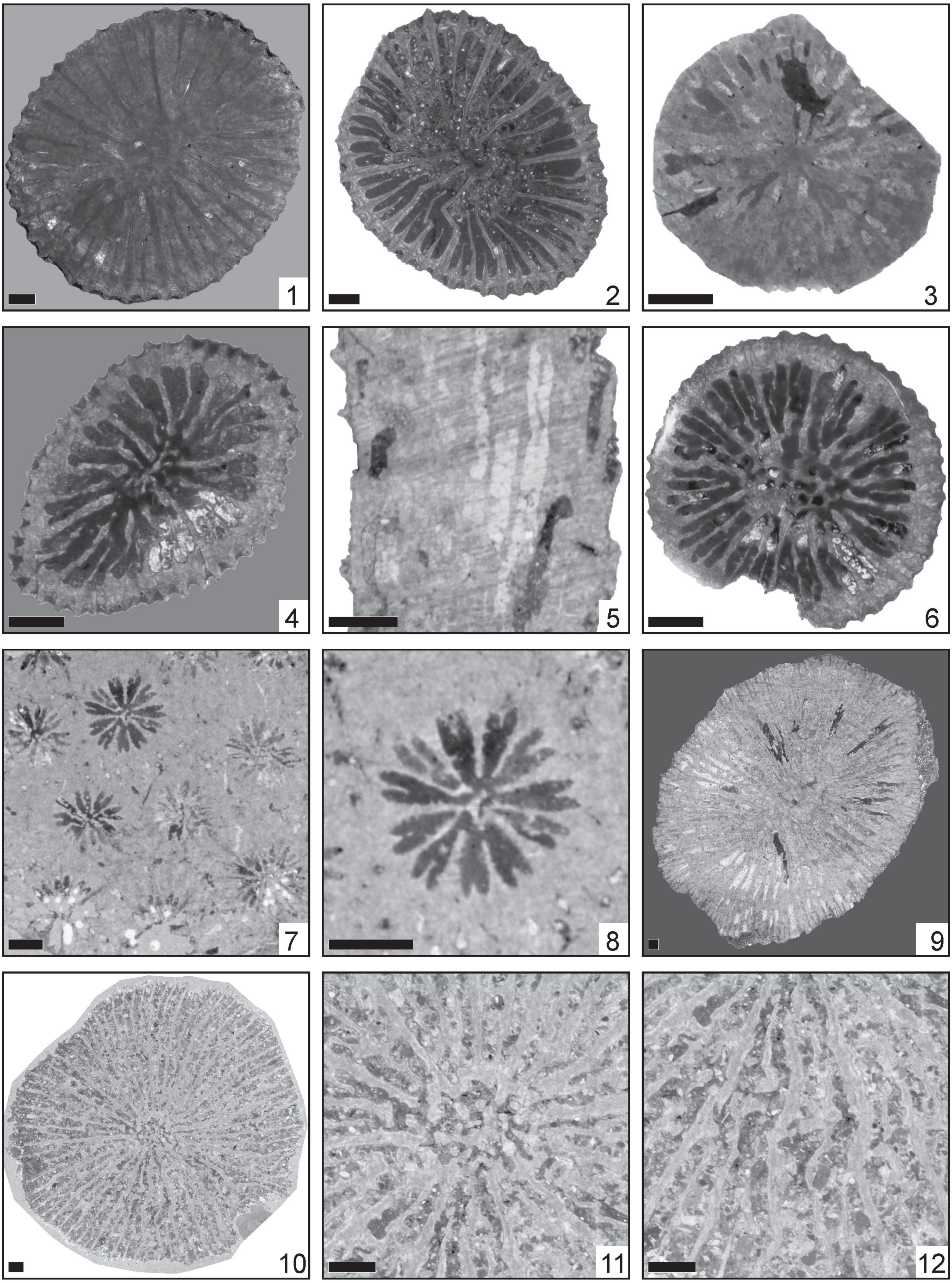

Plate 2. (1, 2) *Parasmilia centralis* (Mantell, 1822). **1**. LFU 8336SG015132#2, Transversal thin section. **2**. LFU 8336SG015132#4, Transversal thin section. **3**. *Procladocora* sp., LFU 8336SG015140#1. Transversal thin section. **(4–6)** *Procladocora simonyi* (Reuss, 1854). LFU 8336SG015082#3. **4**. Transversal thin section. **5**. Longitudinal thin section. **6**. LFU 8336SG015162, Transversal thin section. **(7, 8)** *Eocolumastrea* sp., LFU 8336SG015079#4. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. *Aulosmilia inflexa* (Reuss, 1854). BSPG 1947 XVI 72. Transversal thin section. **(10–12)** *Cyclastraea* sp., BSPG 1947 XVI 87. **10**. Transversal thin section. **11**. Transversal thin section, detail. **12**. Transversal thin section, detail. Scale bars: 1 mm.

Neocoenia kuehnii (Oppenheim, 1930)

v*1930 *Pleurocora kuehnii* n. sp. – Oppenheim: 371, pl. 38, fig. 13, pl. 40, fig. 9.
1982 *Barycora kuehnii* (Oppenheim) 1930 – Beauvais: (1), p. 99.
vp2013 *Neocoenia* cf. *casterasi* (Alloiteau, 1957) – Löser, Werner and Darga: 44, pl. 1, figs 7–9.

Material. BSPG 1991 X 48, 1991 X 74, 1991 X 75, 1991 X 76, 1991 X 78, 2012 X 4, LFU 8336SG015005#1; four thin sections.

Remarks. This material was assigned to *Neocoenia* cf. *casterasi* by Löser et al. (2013c). In 2016, it was possible to study the type material of Oppenheim (1930) and to clarify the taxonomy of the present material.

Other occurrences. Santonian of the Central Tethys (Austria).

Neocoenia renzi Hackemesser, 1936

v*1936 *Neocoenia renzi* n. g. n. sp. – Hackemesser: 24, pl. 3, figs 4–6.
v2013 *Neocoenia renzi* (Hackemesser, 1936) – Löser, Werner and Darga: 46, pl. 1, figs 10–12.
v2016c *Neocoenia renzi* Hackemesser, 1936 – Löser: 471, figs N4a, b.
v2019 *Neocoenia renzi* (Hackemesser, 1936) – Löser, Heinrich and Schuster: 77, fig. 105, figs 108a–c.

Material. BSPG 1947 XVI 10, 1947 XVI 46, 1947 XVI 8, LFU 8336SG015077, 8336SG015079#2; four thin sections.

Other occurrences. Middle Turonian to Santonian of the Central Tethys (Greece, Austria), upper Campanian of the Western Tethys (Spain), undefined Cretaceous of the Central Tethys (Greece).

Superfamily Cyclolitoidea Milne Edwards & Haime, 1849

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

Family Latomeandridae de Fromentel, 1861

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

Astraeofungia Alloiteau, 1952

Type species. *Astrea decipiens* Michelin, 1846.

Description. Thamnasterioid colony, with mostly only at the inner margin perforated septa, that barely differ in length and thickness. The corallites are regularly distributed, generally not in rows, or only when juvenile. Costae run between all corallites. There is no wall.

Astraeofungia decipiens (Michelin, 1846)

*1846 *Astrea decipiens* – Michelin: 200, pl. 50, fig. 13.
v1891 *Thamnastraea Crespoi* – Felix: 146, pl. 22, fig. 5.
v1951 *Thamnasteria jezoensis* Eguchi, n.sp. – Eguchi: 54, pl. 18, figs 5, 6.
v1957 *Astrea decipiens* Michelin – Alloiteau: 213, figs 153–155, pl. 3, fig. 3, pl. 14, fig. 5, pl. 18, fig. 6.
v1963 *Thamnasteria crespoi* (Felix) – Reyeros Navarro: 4, pl. 1, figs 1, 4.
v1994 *Thamnasteria cotteaui* Fromentel – Liao and Xia: 127, pl. 32, figs 6, 7.
v1996 *Synastrea* cf. *dubia* Fromentel, 1861 – Baron-Szabo and Steuber: 25, pl. 14, figs 1, 7.
v2013b *Astraeofungia tenochi* (Felix, 1891) – Löser: 20, fig. 3.2.
v2013 *Astraeofungia tenochi* (Felix, 1891) – Löser, Werner and Darga: 58, pl. 7, figs 4–6.
v2016c *Astrea decipiens* Michelin, 1841 – Löser: 181, figs A50a–c.
v2023 *Astraeofungia decipiens* (Michelin, 1841) – Samaniego-Pesqueira et al.: 123, fig. 5E.

Material. BSPG 1947 XVI 27; two thin sections.

Remarks. In Löser et al. (2013c) this specimen was assigned to *Astraeofungia tenochi* (Felix, 1891). Improved and more systematic measurements show that *Astraeofungia tenochi* has larger dimensions and higher septal counts than the present specimen.

Other occurrences. Valanginian to Aptian of the Western Atlantic (Mexico), lower Hauterivian of the European Boreal (Germany, France), Barremian of the Western Atlantic (Mexico), lower Aptian of the Western Tethys (France) and Central Tethys (Greece), upper Aptian of the Western Pacific (Japan), Aptian to lower Albian of the Central Tethys (Greece, Hungary), lower Albian of the Western Tethys (Spain) and Western Atlantic (Mexico), upper Aptian to Albian of the Eastern Tethys (Iran), middle Albian of the Western Atlantic (Mexico), middle Cenomanian of the European Boreal (France).

Astraeofungia schmidti (Koby, 1898)

*v1898 *Thamnastraea Schmidti* – Koby: 77, pl. 18, fig. 3.
v1935 *Synastrea Tombecki* d'Orb. – Cottreau: 39, pl. 75, fig. 4.
v2014b *Astraeofungia bellula* (Orbigny, 1850) – Löser: 35, fig. 5h.
v2015a *Astraeofungia bellula* – Löser: appendix.
v2015 *Astraeofungia* sp. – Löser, Arias and Vilas: 55, figs 6g–6i.
v2023 *Astraeofungia schmidti* (Koby, 1898) – Löser and Wilmsen: 283, figs 4.1, 4.2.

Material. BSPG 1991 X 79; one thin section.

Other occurrences. Valanginian to Aptian of the Western Atlantic (Mexico), lower Hauterivian of the European Boreal (France), and the Western Tethys (France), upper Barremian to lower Aptian of the Central Tethys (Switzerland), upper Aptian of North Africa (Algeria), and the Western Tethys (Spain), lower Albian of the Western Atlantic (USA, Mexico), Albian of the Western Tethys (Spain), lower Cenomanian of the Western Tethys (Spain), middle Cenomanian of the European Boreal (France), and upper Cenomanian of the European Boreal (Germany).

Dimorphastrea d'Orbigny, 1850

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

Description. Thamnasterioid colony with corallites arranged in concentric rows. The colony surface is plane, the corallite centres may be slightly depressed. Septa are more often connected between corallites of neighboured rows than with corallites of the same row. No wall. *Dimorphastrea* is similar to *Astraeofungia* and juvenile colonies of *Astraeofungia* and *Dimorphastrea* are difficult to distinguish.

Dimorphastrea cf. *hiraigaensis* (Eguchi, 1951)

cf1951 *Meandraraea hiraigaensis* Eguchi, n. sp. – Eguchi: 37, pl. 6, figs 5, 7, pl. 7, fig. 7.
v2013b *Dimorphastrea insignis* (Fromentel, 1887) – Löser: 20, fig. 3.3.
v2013 *Dimorphastrea regularis* (de Fromentel, 1857) – Löser, Werner and Darga: 60, pl. 6, figs 5–6.
v2015 *Dimorphastrea* sp. – Löser, Arias and Vilas: 56, figs 7a–c.

Material. BSPG 1947 XVI 11, 1947 XVI 9; two thin sections.

Remarks. The present material differs from *Dimorphastrea hiraigaensis* by a clearly higher number of septa.

Other occurrences. Lower Hauterivian of the European Boreal (France), Albian to lower Cenomanian of the Western Tethys (Spain), middle Cenomanian of the European Boreal (Germany).

Leptophyllaraea Alloiteau, 1952

Type species. *Leptophyllia granulata* de Fromentel, 1863b.

Description. Solitary cylindrical coral. Corallite outline elliptical, centre slightly depressed. Septa irregularly perforated, more common in the central part of the septal blade. Symmetry of septa irregular radial. Septa of younger generations are with their inner margins occasionally connected to septa of older generations. Synapticulae abundant. Columella absent or as some small elements, presumably trabecular extensions of septal inner margins.

Leptophyllaraea cf. *granulata* (de Fromentel, 1863b)

cf1863 *Leptophyllia granulata* – de Fromentel: 303, pl. 61, fig.1.
v2013 *Leptophyllaraea* cf. *granulata* (de Fromentel, 1863) – Löser, Werner and Darga: 60, pl. 7, figs 7–9.

Material. BSPG 1991 X 67, 1991 X 88; one thin section.

Microphyllia d'Orbigny, 1849

Type species. *Meandrina soemmeringi* Goldfuss, 1829.

Description. Meandroid colony with distinct corallites. Symmetry of septa irregular. Costae absent. Wall compact, synapticulothecal. Limits of rows tectiform.

Microphyllia cf. *oldhamiana* (Stoliczka, 1873)

cf1873 *Comoseris Oldhamiana*, Stoliczka – Stoliczka: 46, pl. 10, fig.3.
vp1935 *Meandraraea somalica* – Thomas: 34.
v1964 *Microphyllia acuta* (Solomko, 1888) – Morycowa: 90, pl. 27, fig. 2, pl. 29, fig. 3.
v2013 *Microphyllia* cf. *oldhamiana* (Stoliczka, 1873) – Löser, Werner and Darga: 62, pl. 7, figs 10–12.

Material. BSPG 1991 X 49, 1991 X 50, 1991 X 51; three thin sections.

Other occurrences. Bathonian of the Southern Tethys (Somalia), upper Kimmeridgian of the European Boreal (Germany), lower Aptian of the Central Tethys (Poland).

Placoseris de Fromentel, 1863b

Type species. *Placoseris patella* de Fromentel, 1863b.

Description. Solitary cylindric coral. Corallite outline circular or elliptical, centre slightly depressed. Symmetry of septa irregular radial. Synapticulae moderately common. Columella absent or developed as some small elements, presumably trabecular extensions of septal inner margins. Endotheca consists of numerous dissepiments. Wall absent or epithecal.

Remarks. As already explained in Löser et al. (2021b), in the historic literature the genus *Placoseris* was considered synonymous with *Acrosmilia* d'Orbigny, 1849.

Acrosmilia is a conceptual genus; the type specimen of the type species is available but so poorly preserved that important diagnostic features, such as the presence or absence of pennulae or the amount of septal perforation, cannot be observed. For this reason, the genus *Leptophyllia* Reuss, 1854 was applied (Löser et al. 2019) in place of *Acrosmilia*. *Leptophyllia* was for a long time considered to be a junior synonym of *Acrosmilia*. The study of type specimens and topotypical material has shown that *Leptophyllia* belongs to the mainly Late Cretaceous family Synastraeidae and is restricted to the Late Cretaceous, whereas *Placoseris* belongs to the Jurassic and mainly Lower Cretaceous family Latomeandridae. *Leptophyllia* has thicker and less perforate septa, whereas in *Placoseris* the septa are thinner and more perforate at the inner margin. Moreover, the septa are often connected to each other in the latter, a characteristic that is less common in *Leptophyllia* (see Löser et al. 2019 for details).

Placoseris eturbensis **(de Fromentel, 1857)**

Plate 3: figs 1, 2

*v1857 *Trochoseris Eturbensis* – de Fromentel: 19, pl. 1, fig. 8.
v1897 *Leptophyllia patellata* – Söhle: 44, pl. 6, fig. 5.
v1941 *Thecoseris cenomanensis* n.sp. – Alloiteau: 22, pl. 1, figs 18, 19.
v1989 *Acrosmilia patellata* (Michelin 1845) – Löser: 131, text-fig. 34, pl. 26, fig. 1.
v2015a *Acrosmilia* sp. – Löser: appendix.
v2018 *Placoseris eturbensis* (Fromentel, 1857) – Löser, Steuber and Löser: 42, pl. 4, figs 1–3.
v2023 *Placoseris eturbensis* (Fromentel, 1857) – Löser and Wilmsen: 293, figs 10.7–10.9.

Material. LFU 8336SG015085; six thin sections.

Dimensions. (LFU 8336SG015085).

c	26×31.8
septa	154

Other occurrences. Valanginian to Aptian of the Western Atlantic (Mexico), lower Hauterivian of the European Boreal (France), lower Albian of the Western Tethys (Spain), lower Cenomanian of the Central Tethys (Greece), the Western Tethys (Spain), and the European Boreal (Germany), middle Cenomanian of the European Boreal (France), upper Cenomanian of the European Boreal (Germany).

Placoseris **cf.** ***eturbensis*** **(de Fromentel, 1857)**

Plate 3: figs 3–5

cf1857 *Trochoseris Eturbensis* – de Fromentel: 19, pl. 1, fig. 8.
v2013 *Acrosmilia* sp. – Löser, Werner and Darga: 58, pl. 7, figs 1–3.
v2014b *Acrosmilia baumbergeri* (Koby, 1898) – Löser: 34, fig. 5d.

Material. BSPG 1947 XVI 4, 1947 XVI 5, 1991 X 64, 1991 X 65, 1991 X 66, 1991 X 68, 1991 X 69, LFU 8336SG015091; four thin sections.

Dimensions. (LFU 8336SG015091).

c	19.4×30.1
septa	202

Remarks. The present material differs from *Placoseris eturbensis* by a higher number of septa.

Other occurrences. Hauterivian to Cenomanian of the European Boreal (France, Germany), upper Cenomanian of the Western Tethys (France) and the European Boreal (Germany).

Polyastropsis **Alloiteau, 1957**

Type species. *Polyastropsis arnaudi* Alloiteau, 1957.

Description. Thamnasterioid-cerioid colony. Corallite outline irregular with corallite centres slightly depressed. Symmetry of septa irregular. Costae confluent or sub-confluent. Synapticulae occasional, mainly in the space between corallites. Columella consists of isolated trabeculae or one more solid element. Wall subcompact, made of synapticulae. *Polyastreopsis* differs from *Thalamocaeniopsis* by a poorly defined corallite outline, and a more incomplete wall.

Polyastropsis **cf.** ***fascigera*** **(Felix, 1909)**

cf1909 *Isastraea fascigera* – Felix: 172, pl. 7, fig. 2.
v2013 *Thalamocaeniopsis* sp. – Löser, Werner and Darga: 63, pl. 8, figs 7–9.

Material. BSPG 1947 XVI 56; two thin sections.

Remarks. In Löser et al. (2013c) this specimen was assigned to the genus *Thalamocaeniopsis*. This is changed here. *Thalamocaeniopsis* has polygonal corallites and a marked wall, even if thin and incomplete, whereas *Polyastreopsis* has no wall at all and the corallite outline is irregular. The specimen differs from *Polyastropsis fascigera* by having smaller distances of the corallites and a higher number of septa.

Other occurrences. Upper Aptian of the Western Tethys (Spain), lower Albian of the Western Atlantic (Mexico), lower Cenomanian of the European Boreal (Germany).

Thalamocaeniopsis **Alloiteau, 1954a**

Type species. *Thalamocaeniopsis ouenzensis* Alloiteau, 1954a.

Description. Cerioid colony. Corallite outline polygonal with centres slightly depressed. Symmetry of septa irregular. Synapticulae occasional, mainly in the space between corallites. No costae. Columella consists of isolated trabeculae or one more solid element. Wall subcompact, made of synapticulae. Budding extracalicinal.

Thalamocaeniopsis cf. *taramellii* (d'Achiardi, 1880)

Plate 3: figs 6–8

cf1880 *Latimeandra taramellii* – d'Achiardi: 249: pl. 17, fig. 7.
v2004 *Isastrea minima* Prever, 1909 – Löser and Mohanti: 583, fig. 2c.
v2018 *Thalamocaeniopsis* sp. – Löser, Steuber and Löser: 44, pl. 4, figs 10, 11.

Material. BSPG 1947 XVI 75; two thin sections.

Dimensions. (BSPG 1947 XVI 75).

	n	min–max	μ	s	cv	μ±s
clmin	10	1.55–2.03	5.71	1.17	20.5	4.54–6.88
clmax	10	5.65–10.3	8.00	1.69	21.1	6.31–9.69
ccd	10	3.84–8.71	5.82	1.58	27.2	4.24–7.40
septa	10	36–63	45.80	8.57	18.7	37–54

Remarks. The specimen differs from *Thalamocaeniopsis taramellii* by a lower number of septa.

Other occurrences. Lower Aptian of the Western Tethys (Spain), lower Cenomanian of the Central Tethys (Greece), Cenomanian of the Southern Tethys (India).

Thalamocaeniopsis sp. 1

Plate 3: figs 9–11

v1909 *Isastraea Hörnesi* – Prever: 95, pl. 7, fig. 7.
vp2015 *Thalamocaeniopsis* sp. – Bonilla González: 94, pl. 11, figs 4–6.

Material. BSPG 1948 III 2; two thin sections.

Dimensions. (BSPG 1948 III 2).

	n	min–max	μ	s	cv	μ±s
clmin	12	3.53–4.98	4.23	0.45	10.7	3.78–4.68
clmax	12	4.10–7.24	5.79	1.07	18.4	4.73–6.86
ccd	15	3.59–6.69	4.54	0.78	17.2	3.76–5.32
septa	8	45–57	49.13	3.68	7.5	45–53

Other occurrences. Lower Hauterivian of the European Boreal (France), lower Aptian of the Central Tethys (Italy), lower Albian of the Western Atlantic (Mexico).

Thalamocaeniopsis sp. 2

Plate 4: figs 1, 2

v1909 *Isastraea morchella* Reuss – Prever: 96, pl. 8, fig. 3.
v1996 *Latiastrea* cf. *kaufmanni* (Koby, 1897) – Baron-Szabo and Steuber: 25, pl. 15, figs 1, 2.
vp2008 *Microphyllia elevata* sp. n. – Roniewicz: 121.
vp2015 *Thalamocaeniopsis* sp. – Bonilla González: 94.
v2023 *Thalamocaeniopsis* sp. – Löser and Wilmsen: 299, figs 13.10–13.12.

Material. BSPG 1947 XVI 76; three thin sections.

Dimensions. (BSPG 1947 XVI 76).

	n	min–max	μ	s	cv	μ±s
clmin	7	4.71–6.21	5.58	0.46	8.3	5.12–6.04
clmax	8	5.80–8.44	6.86	0.89	12.9	5.97–7.75
ccd	8	5.46–8.35	6.40	20.90	14.1	5.49–7.30
septa	9	42–56	46.6	4.67	10.0	42–51

Other occurrences. Valanginian to lower Aptian of the Central Tethys (Bulgaria, Italy), lower Aptian of the European Boreal (UK) and the Central Tethys (Greece), lower Albian of the Western Tethys (Spain) and the Western Atlantic (Mexico), lower Cenomanian of the Western Tethys (Spain).

Family Microsolenidae Koby, 1889

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

Dimorpharaea de Fromentel, 1861

Type species. *Microsolena koechlini* Milne Edwards, 1860.

Description. Thamnasterioid colony with corallites arranged in rows. The corallites are well separated from each other. Septa run mostly between neighboured corallite rows, less between adjacent corallites. A central corallite may be present.

Dimorpharaea williamsonensis (Wells, 1944)

*v1944 *Microsolena williamsonensis* Wells, n.sp. – Wells: 100, pl. 20, figs 1–4.
v2013 *Dimorpharaea japonica* Eguchi, 1951 – Löser, Werner and Darga: 63, pl. 8, figs 10–12.
v2017 *Dimorpharaea japonica* Eguchi, 1951 – Löser and Bilotte: 9, figs 7g–i.

Material. BSPG 1991 X 80; two thin sections.

Remarks. In Löser et al. (2013c), this specimen was assigned to *Dimorpharaea japonica* Eguchi, 1951. *Dimorpharaea japonica* and *Dimorpharaea williamsonensis* have very similar dimensions but differ in the septal counts.

Other occurrences. Upper Aptian of the Western Tethys (Spain), Albian to lower Cenomanian of the Western Atlantic (Mexico, USA), lower Cenomanian of the European Boreal (Germany), upper Cenomanian of the Western Tethys (France).

Eocomoseris Melnikova et al., 1993

Type species. *Eocomoseris gurumdyensis* Roniewicz, 2011.

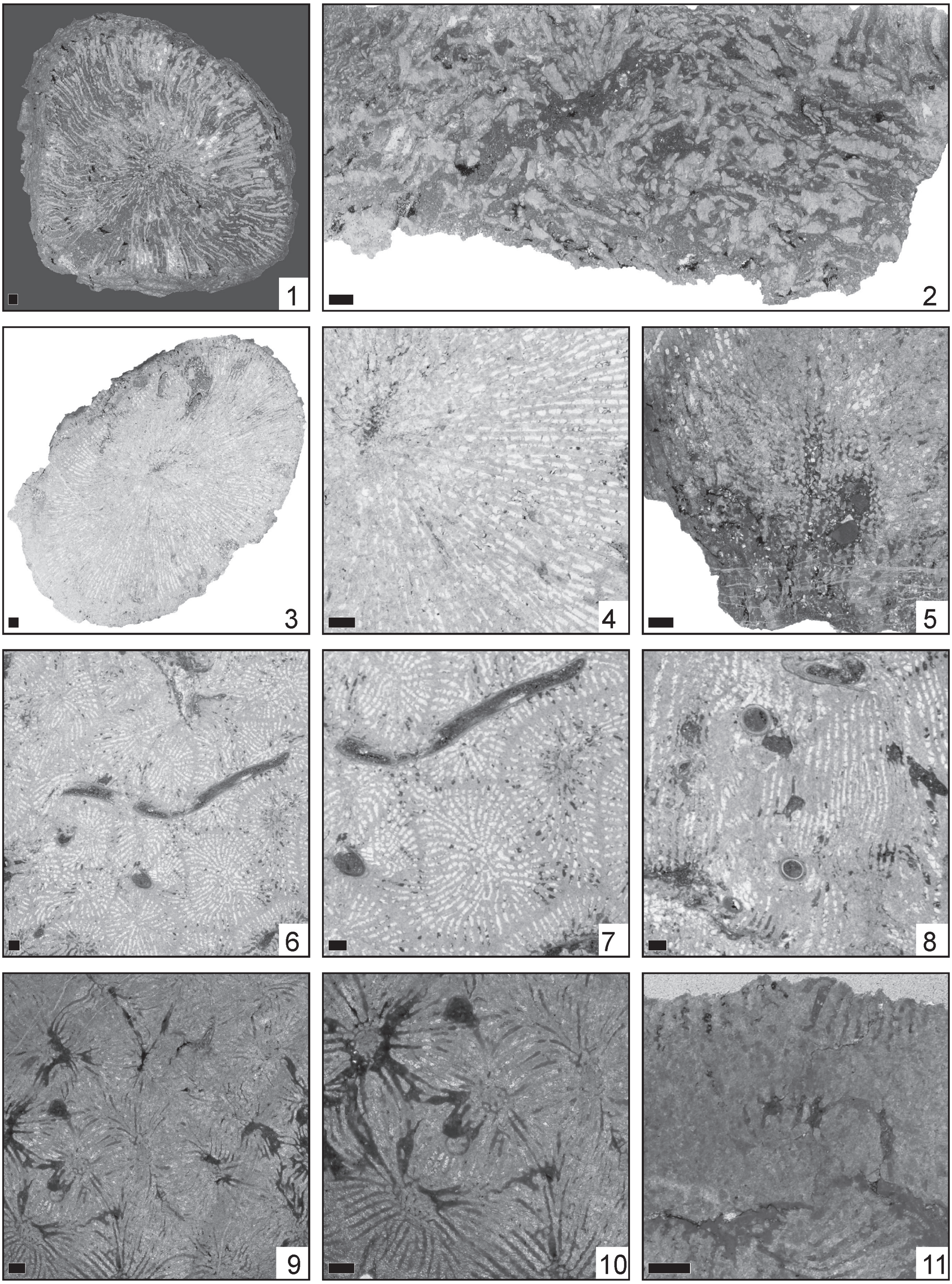

Plate 3. (1, 2) *Placoseris eturbensis* (de Fromentel, 1857). LFU 8336SG015085. **1**. Transversal thin section. **2**. Longitudinal thin section. **(3–5)** *Placoseris* cf. *eturbensis* (de Fromentel, 1857). LFU 8336SG015091. **3**. Transversal thin section. **4**. Transversal thin section, detail. **5**. Longitudinal thin section. **(6–8)** *Thalamocaeniopsis* cf. *taramellii* (d'Achiardi, 1880). BSPG 1947 XVI 75. **6**. Transversal thin section. **7**. Transversal thin section, detail. **8**. Longitudinal thin section. **(9–11)** *Thalamocaeniopsis* sp. 1, BSPG 1948 III 2. **9**. Transversal thin section. **10**. Transversal thin section, detail. **11**. Longitudinal thin section. Scale bars: 1 mm.

Description. Astreoid colony with small corallites. Symmetry of septa irregular, but two size orders can be distinguished. Number of septa up to 30. Septa occasionally connected to each other. Costae sub-confluent to non-confluent. Synapticulae fairly common. Columella styliform. Endotheca and wall absent. Coenosteum narrow.

Eocomoseris sp.

Plate 4: figs 3, 4

v2012 *Eocomoseris raueni* Melnikowa et al., 1993 – Bover Arnal, Löser and Moreno Bedmar: 58, figs 11I–K.

v2013 *Eocomoseris raueni* Melnikova et al. 1993 – Löser, Castro and Nieto: 25, pl. 8, figs 11, 12.

v2021 *Eocomoseris* sp. 1 – Löser, Nieto, Castro and Reolid: 25, figs 27.1–3.

Material. LFU 8336SG015094#3; one thin section.

Dimensions. (LFU 8336SG015094#3).

	n	min–max	μ	s	cv	μ±s
clmin	6	1.64–2.16	1.90	0.19	9.8	1.71–2.08
clmax	6	1.84–2.32	2.15	0.18	8.4	1.97–2.33
ccd	10	1.82–3.89	2.65	0.64	24.3	2.01–3.30
septa	7	19–28	23.9	3.63	15.2	20–27

Remarks. The difficulty of species separation was already discussed in Löser et al. (2021b).

Other occurrences. Lower Valanginian of the Western Tethys (Spain), Valanginian to Aptian of the Western Atlantic (Mexico), lower Aptian to middle Cenomanian of the Western Tethys (Spain, Portugal), Albian to lower Cenomanian of the European Boreal (UK).

Family Negoporitidae Eliášová, 1995

Description. Colonial (plocoid) corals. Septa with perforations. Septal symmetry bilateral. Septa connected to each other. Pali and columella present. Endotheca with tabulae. Wall incomplete, synapticulothecate. Coenosteum extended, with isolated trabeculae. Budding extracalicinal.

Negoporites Eliášová, 1989

Type species. *Porites michelini* Reuss, 1846.

Description. Plocoid colony. Corallite outline circular, corallites small (generally below 3 mm in diameter). Septa irregularly perforated. Symmetry of septa bilateral. Septal cycles differ in length, but hardly at all in thickness. Septa of younger cycles often and regularly connected to the septa of preceding cycles. Not well-separated pali irregularly present. Costae non-confluent. Synapticulae fairly common, mainly in the wall. Columella small, substyliform. Endotheca consists of numerous thin tabulae. Wall subcompact, synapticulothecal. Coenosteum moderately broad, consists of trabeculae and tabulae.

Negoporites cf. *quartus* Eliášová, 1995

cf1995 *Negoporites quartus* sp. n. – Eliášová: 28, pl. 2, fig. 2, pl. 3, figs 1, 2.

v2013 *Negoporites* cf. *quartus* Eliášová, 1995 – Löser, Werner and Darga: 62, pl. 8, figs 1–3.

Material. BSPG 1947 XVI 45; one thin section.

Other occurrences. Lower Cenomanian of the Western Tethys (Spain).

Negoporites sp.

v2013 *Negoporites* sp. – Löser, Werner and Darga: 62, pl. 8, figs 4–6.

Material. BSPG 1947 XVI 53; one thin section.

Paractinacis Löser & Heinrich, 2018

Type species. *Paractinacis uliae* Löser & Heinrich, 2018.

Description. Astreoid colony with strong, at the inner margin slightly perforated septa, that stand in a bilateral symmetry. The septal lateral faces are ornamented with pennulae. The columella is small and styliform. The wall is synapticulothecate, in places septothecal, subcompact. Endotheca with tabulae.

Paractinacis uliae Löser & Heinrich, 2018

Plate 4: figs 5–7

v2018 *Paractinacis uliae* spec. nov. – Löser and Heinrich: 131, fig. 4.

v2019 *Paractinacis uliae* Löser and Heinrich, 2018 – Löser, Heinrich and Schuster: 92, figs 126, 129a–c.

Material. BSPG 1947 XVI 69, LFU 8336SG015157; three thin sections.

Dimensions. (LFU 8336SG015157).

	n	min–max	μ	s	cv	μ±s
cmin	7	2.58–3.69	3.20	0.36	11.4	2.84–3.57
cmax	6	2.96–4.04	3.46	0.51	14.7	2.95–3.97
ccd	9	2.60–4.07	3.07	0.51	16.5	2.56–3.58
septa	24–32					

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria).

Family Synastreidae Alloiteau, 1952

Description. Solitary and (astreoid, meandroid, thamnasterioid) colonial corals. Septa almost compact with few perforations at the inner margins. Interseptal space smaller than septal thickness.

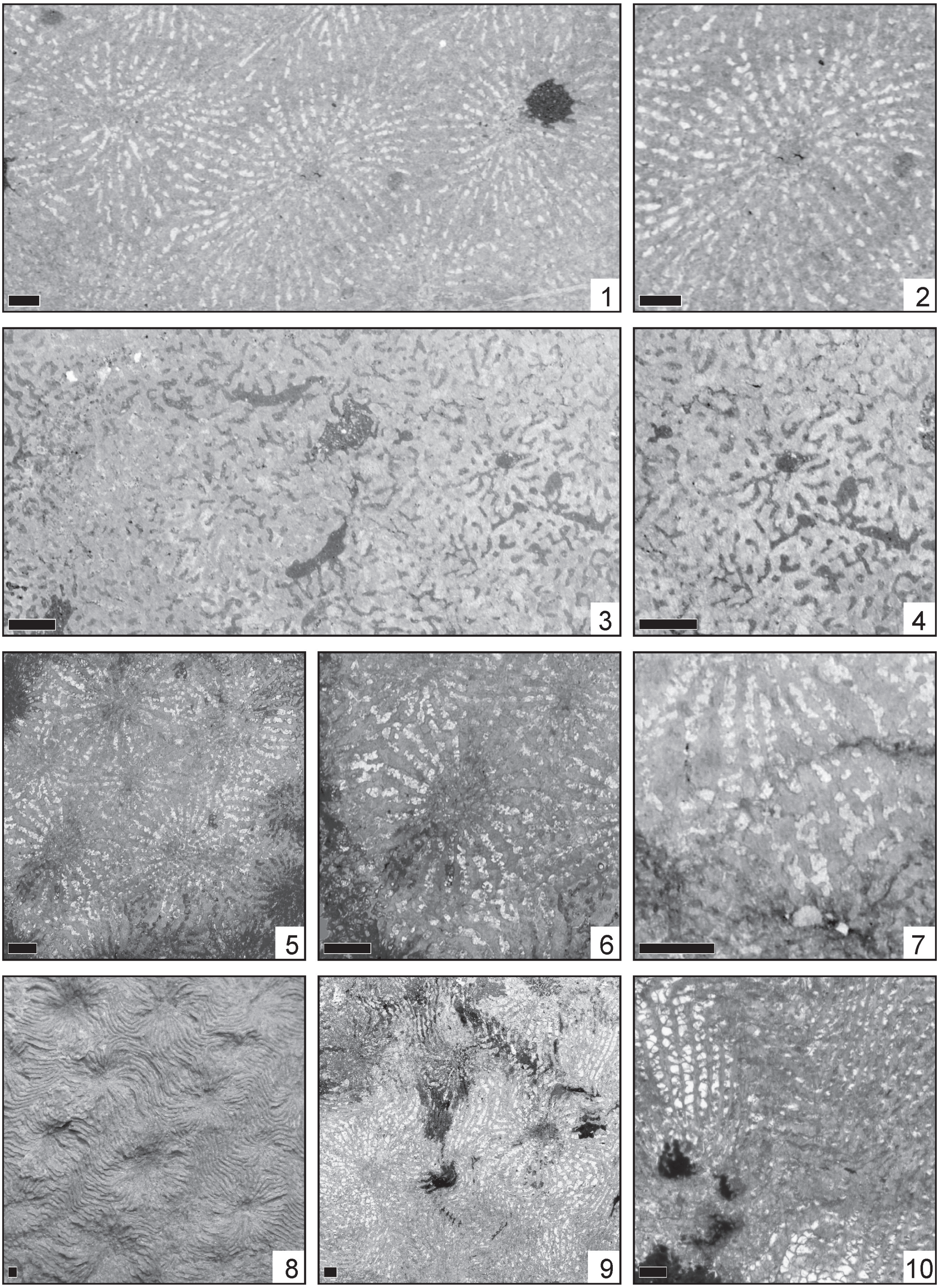

Plate 4. (1–2) *Thalamocaeniopsis* sp. 2, BSPG 1947 XVI 76. **1**. Transversal thin section. **2**. Transversal thin section, detail. **(3–4)** *Eocomoseris* sp., LFU 8336SG015094#3. **3**. Transversal thin section. **4**. Transversal thin section, detail. **(5–7)** *Paractinacis uliae* Löser & Heinrich, 2018. LFU 8336SG015157. **5**. Transversal thin section. **6**. Transversal thin section, detail. **7**. Longitudinal thin section. **(8–10)** *Brachycoenia* aff. *composita* (Sowerby, 1832). BSPG 1955 XIX 34. **8**. Colony surface. **9**. Transversal thin section. **10**. Longitudinal thin section. Scale bars: 1mm.

Brachycoenia Beauvais, 1982

Type species. *Adelastrea leptophylla* Reuss, 1854.

Description. Thamnasterioid colony, where – in contrast to *Synastrea* – the corallites are clearly marked and slightly elevated. The septa are bent outside the corallite.

Brachycoenia aff. *composita* (Sowerby, 1832)

Plate 4: figs 8–10

v2019 *Brachycoenia* aff. *composita* (Sowerby, 1832) – Löser, Heinrich and Schuster: 95, figs 135a–c.

Material. BSPG 1955 XIX 34; two thin sections.

Dimensions. (BSPG 1955 XIX 34).

	n	min–max	µ	s	cv	µ±s
cmin	10	6.50–8.36	7.26	0.62	8.5	6.64–7.87
cmax	10	6.32–8.58	7.24	0.80	11.1	6.43–8.04
ccd	10	8.33–10.1	9.11	0.65	7.1	8.46–9.76
septa	10	36–49	42.3	3.40	8.0	39–46

Remarks. The specimen has smaller corallite dimensions compared to *Brachycoenia composita*. Since the type material of *Brachycoenia composita* is not available and a correct comparison is not possible, a new species cannot be established for this specimen.

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria).

Leptophyllia Reuss, 1854

Type species. *Leptophyllia clavata* Reuss, 1854.

Description. Turbinate or trochoid solitary coral with circular, elliptical or irregular outline. The septa are numerous, thick, slightly perforated at the inner margin and rarely connected to each other. The endotheca is well developed.

Leptophyllia sp.

Plate 5: figs 1–3

vp1854 *Leptophyllia clavata* – Reuss: 101.

v2019 *Leptophyllia* sp. 2 – Löser, Heinrich and Schuster: 137, figs 203a–c.

Material. LFU 8336SG015155#1; two thin sections.

Dimensions. (LFU 8336SG015155#1).

c	10.6×12.9
septa	140

Remarks. This specimen marks the first stratigraphical occurrence of the genus.

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria).

Synastrea Milne Edwards & Haime, 1848b

Type species. *Astrea agaricites* Goldfuss, 1826.

Description. Thamnasterioid colony with strong, only at the inner margin perforated septa, that barely differ in length and thickness. The corallites are regularly distributed, often slightly depressed. Costae run between all corallites.

Synastrea agaricites (Goldfuss, 1826)

Plate 5: figs 4–6

*v1826 *Astraea Agaricites* – Goldfuss: 66, pl. 22, fig. 9.

v1854 *Thamnastraea procera* – Reuss: 120, pl. 5, figs 1, 2.

v2019 *Synastrea agaricites* (Goldfuss, 1826) – Löser, Heinrich and Schuster: 142, fig. 212, figs. 214a–c.

Material. LFU 8336SG015099#1; two thin sections.

Dimensions. (LFU 8336SG015099#1).

	n	min–max	µ	s	cv	µ±s
ccd	30	3.76–5.75	4.73	0.63	13.3	4.10–5.36
septa	10	49–61	53.9	3.81	7.1	50–58

Other occurrences. Upper Turonian to Santonian of the Central Tethys (Austria).

Synastrea cf. *catadupensis* (Vaughan, 1899)

Plate 5: figs 7–9

cf1899 *Mesomorpha catadupensis*, n. sp. – Vaughan: 246, pl. 41, figs 1-3.

v2019 *Synastrea* cf. *catadupensis* Vaughan, 1899 – Löser, Heinrich and Schuster: 144, figs 216a–c.

Material. BSPG 1947 XVI 70, LFU 8336SG015088; six thin sections.

Dimensions. (BSPG 1947 XVI 70)

	n	min–max	µ	s	cv	µ±s
ccd	25	4.29–7.38	5.98	0.79	13.2	5.19–6.76
septa	12	38–56	45.25	5.51	12.2	40–51

Remarks. *Synastrea catadupensis* has higher septal counts compared to the present material.

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria).

Synastrea exaltata (Reuss, 1854)

Plate 5: figs 10–12

*1854 *Thamnastraea exaltata* – Reuss: 118, pl. 19, figs 5, 6.

v2019 *Synastrea* ? *exaltata* (Reuss, 1854) – Löser, Heinrich and Schuster: 146, figs 220a–c.

Material. LFU 8336SG015090#1; two thin sections.

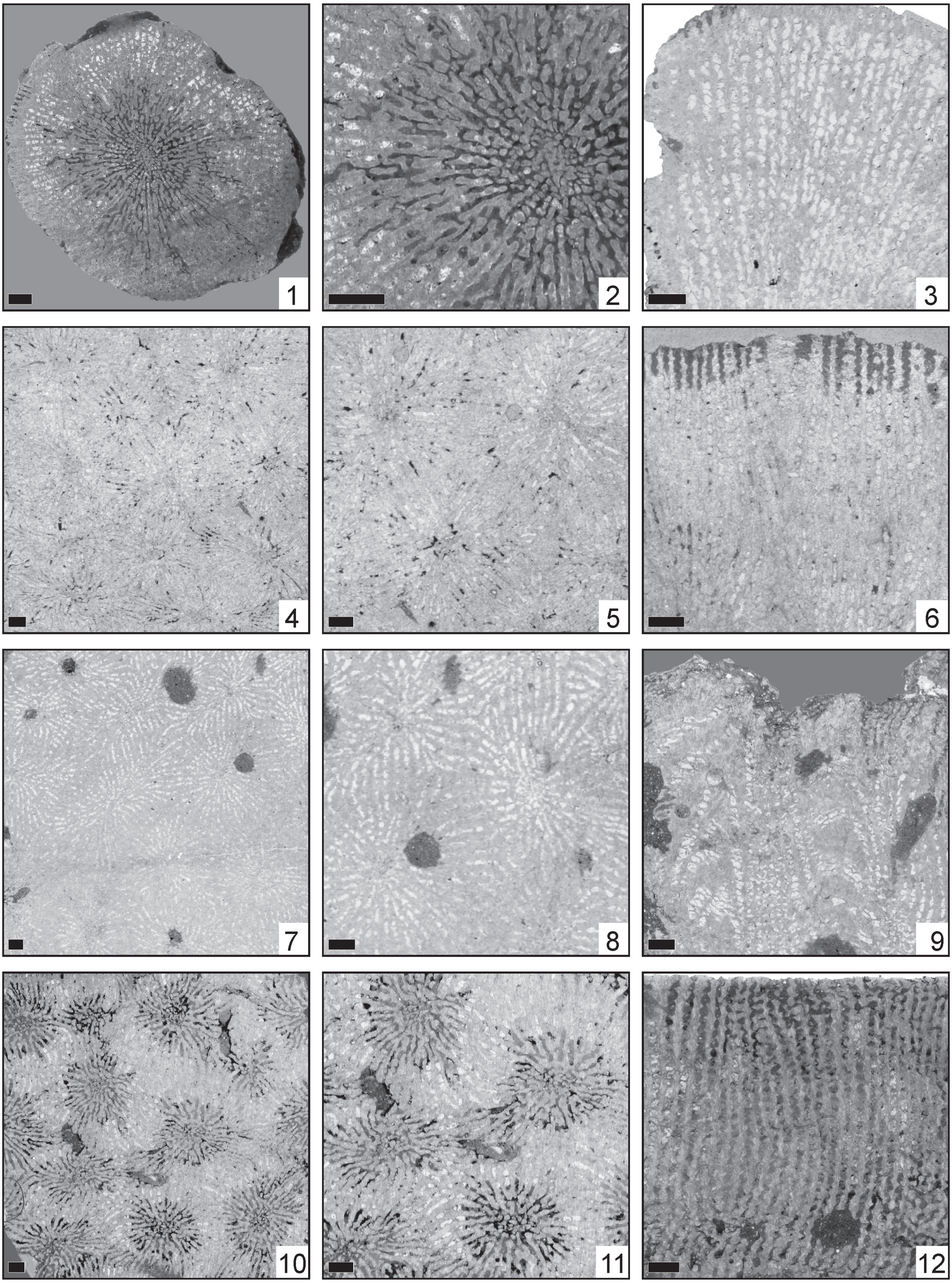

Plate 5. **(1–3)** *Leptophyllia* sp., LFU 8336SG015155#1. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–6)** *Synastrea agaricites* (Goldfuss, 1826). LFU 8336SG015099#1. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Longitudinal thin section. **(7–9)** *Synastrea* cf. *catadupensis* (Vaughan, 1899). BSPG 1947 XVI 70. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. Longitudinal thin section. **(10–12)** *Synastrea exaltata* (Reuss, 1854). LFU 8336SG015090#1. **10**. Transversal thin section. **11**. Transversal thin section, detail. **12**. Longitudinal thin section. Scale bars: 1 mm.

Dimensions. (LFU 8336SG015090#1).

	n	min–max	µ	s	cv	µ±s
ccd	15	4.16–6.39	5.35	0.77	14.3	4.59–6.12
septa	11	33–54	44.0	7.44	16.9	37–51

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria), Campanian to Maastrichtian of the Western Atlantic (Jamaica).

Synastrea heberti (Alloiteau, 1952)

Plate 6: figs 1–3

*v1952 *Uxacalcaraea Heberti* All. – Alloiteau: 665.

v1957 *Uxacalcaraea Heberti* nov. gen., nov. sp. – Alloiteau: 221, pl. 8, fig. 7, pl. 9, fig. 12.

v1997 *Thamnaraea cladophora* Felix, 1903 – Baron-Szabo: 80, pl. 13, fig. 1.

v2012a *Astraeofungia siva* (Stoliczka, 1873) – Löser: 28, figs 2.11–2.12.

v2016c *Uxacalcaraea heberti* Alloiteau, 1952 – Löser: p. 681, figs U1a–c.

v2019 *Synastrea heberti* Alloiteau, 1952 – Löser, Heinrich and Schuster: 147, figs 221a–c.

Material. BSPG 1947 XVI 67; two thin sections.

Dimensions. (BSPG 1947 XVI 67).

	n	min–max	µ	s	cv	µ±s
ccd	15	3.71–5.20	4.41	0.47	10.7	3.93–4.88
septa	8	31–46	38.6	5.18	13.4	33–44

Other occurrences. Upper Turonian of the Western Tethys (France), upper Turonian to Santonian of the Central Tethys (Austria), lower Coniacian of the Western Tethys (Spain), lower Campanian of the Central Tethys (Austria, Turkey).

Synastrea ?salisburgensis (Beauvais, 1982)

Plate 6: figs 4, 5

?*1982 *Fungiastraea salisburgensis* nov. sp. – Beauvais: (2), p. 75, pl. 27, fig. 5, pl. 28, fig. 1.

v2018 *Synastrea* sp. – Löser, Steuber and Löser: 46, pl. 6, figs 1–3.

v2019 *Synastrea salisburgensis* (Beauvais, 1982) – Löser, Heinrich and Schuster: 151, figs 226a–c.

Material. LFU 8336SG015227#2, 8336SG015228#3, 8336SG015228#5; three thin sections.

Dimensions. (LFU 8336SG015228#5).

	n	min–max	µ	s	cv	µ±s
ccd	20	4.33–6.90	5.69	0.85	14.9	4.85–6.54
septa	10	29–42	34.6	5.25	15.2	29–40

Remarks. As already mentioned in Löser et al. (2019), the type material of the species is not available and the morphometric data provided in the literature do not allow a clear separation from other species.

Other occurrences. Aptian to Santonian of the Central Tethys (Greece, Austria), Campanian to Maastrichtian of the Western Atlantic (Jamaica).

Synastrea sp.

v2013 *Synastrea* sp. – Löser, Werner and Darga: 63, pl. 9, fig. 1.

Material. BSPG 1991 X 95; one thin section.

Superfamily Dendrogyroidea Alloiteau, 1952

Description. Colonial corals. Septa strong, compact. Symmetry irregular. Septa often connected to each other. Septal distal margins smooth, lateral faces smooth or with thorns, inner margins slightly swollen. Lonsdaleoid septa absent. Main septum absent. Microstructure of very small trabeculae, only marked by a dark line. Synapticulae and pali absent. Columella by septal fusion. Endotheca mostly present, consisting of tabulae or dissepiments. Marginarium absent. Wall generally present, septothecal. Coenosteum present in some genera. Budding varies.

Family Dendrogyridae Alloiteau, 1952

Hydnophoraraea Oppenheim, 1930

Type species. *Monticularia styriaca* Michelin, 1847.

Description. Hydnophoroid colony. Corallite centres can be recognised in places. Septa straight, free, often alternating in length and thickness. Their lateral faces bear thorns or are smooth. The columella is rudimentarily developed; it is difficult to assign the elements between the crests to any morphological unit. Endotheca well developed.

Remarks. Formerly, this genus was assigned to the family Eugyridae (Löser 2016c, Löser et al. 2019). But it differs from this family by the less regular endotheca and thinner septa. Moreover, all other members of the Eugyridae became extinct before the Turonian. *Hydnophoraraea* shows certain similarities to the family Dendrogyridae, but there is also material that differs from this concept such as, for instance, by having a dissepimental instead of a tabular endotheca, or showing the lateral faces ornamented with thorns instead of being smooth. It is also possible that *Hydnophoraraea* encompasses heterogeneous material and it is also possible that further studies could reveal that the material assigned to *Hydnophoraraea* may belong to different genera. Further, it is also problematic that the type material of *Monticularia styriaca* Michelin, 1847, type species of *Hydnophoraraea*, is not available (despite being registered in the catalogue of the MNHN in Paris).

Hydnophoraraea aff. *digitata* (de Fromentel, 1877)

Plate 6: figs 6, 7

Material. LFU 8336SG015224; three thin sections.

Dimensions. (LFU 8336SG015224).

	n	min–max	µ	s	cv	µ±s
md	20	2.57–3.89	3.21	0.44	13.6	2.77–3.65
septa	15	17–22	19.73	1.75	8.9	18–21

Remarks. The present specimen differs from *H. digitata* by larger distances between the crests. Moreover, the crests are polygonal in *H. digitata*, but conical in the present specimen.

Hydnophoraraea obliqua (Reig Oriol, 1992)

v*1992 *Hydnophora obliqua* n. sp. – Reig Oriol: 26, pl. 1, fig. 6, pl. 5, figs 4, 5.
vp2012a *Hydnophora obliqua* Reig Oriol, 1992 – Löser: 26.
vp2013 *Hydnophora* cf. *obliqua* Reig Oriol, 1992 – Löser, Werner and Darga: 50, pl. 3, figs 4–6.

Material. BSPG 1947 XVI 21, 1947 XVI 22, 1963 VI 190, 1991 X 59, 1991 X 60; two thin sections.

Other occurrences. Middle Santonian of the Central Tethys (Austria), Early Campanian of the Central Tethys (Turkey), Campanian of the Western Tethys (Spain).

Hydnophoraraea parviconus Oppenheim, 1930

*v1930 *Hydnophoraraea parviconus* Oppenheim n. sp. – Oppenheim: 227, pl. 18, figs 3–5, 8.
v1930 *Hydnophoraraea aconus* n. sp. – Oppenheim: 232, pl. 18, fig. 2, pl. 19, fig. 4.
v1989 *Hydnophora minima* nov. sp. – Reig Oriol: 17, pl. 5, fig. 4.
vp2012a – *Hydnophora obliqua* Reig Oriol, 1992 – Löser: 26, figs 3.1–3.3.
vp2013 *Hydnophora* cf. *obliqua* Reig Oriol, 1992 – Löser, Werner and Darga: 50.
v2013 *Hydnophora* sp. – Löser, Werner and Darga: 48, pl. 4, figs 8, 9.
v2019 *Hydnophoraraea parviconus* Oppenheim, 1930 – Löser, Heinrich and Schuster: 159, figs 235, 236, 240a–c.

Material. BSPG 1963 VI 189, 1991 X 106; two thin sections.

Remarks. In Löser et al. (2013c) this material was assigned to *Hydnophora* cf. *obliqua* Reig Oriol, 1992 and, respectively, *Hydnophora* sp. After having been able to study the type material of Oppenheim (1930) in Jerusalem in 2016, it was possible to correct this assignation.

Other occurrences. Coniacian to Early Campanian of the Central Tethys (Austria, Turkey), Campanian of the Western Tethys (Spain).

Hydnophoraraea rapulum Oppenheim, 1930

Plate 6: figs 8, 9

v1877 *Hydnophora Styriaca* – de Fromentel: 468, pl. 120, fig. 2. [non *Monticularia styriaca* Michelin, 1847]
*v1930 *Hydnophoraraea rapulum* n. sp. – Oppenheim: 230, pl. 14, fig. 3, pl. 18, fig. 7.
1992 *Hydnophora dissimilis* n. sp. – Reig Oriol: 27, pl. 1, figs 4, 5, pl. 5, fig. 6.
v2019 *Hydnophoraraea rapulum* Oppenheim, 1930 – Löser, Heinrich and Schuster: 160, figs 242a, b.

Material. LFU 8336SG015087#1; two thin sections.

Dimensions. (LFU 8336SG015087#1).

	n	min–max	µ	s	cv	µ±s
md	15	1.97–2.55	2.31	0.20	8.5	2.11–2.51
septa	13	8–12	9.92	1.55	15.6	8–11

Other occurrences. Upper Cenomanian of the Western Tethys (France), Coniacian to Santonian of the Central Tethys (Austria), upper Santonian of the Western Tethys (France), Santonian to Campanian of the Western Tethys (Spain).

Hydnophoraraea aff. *rapulum* Oppenheim, 1930

Plate 7: figs 1–3

v2018 *Hydnophoraraea styriaca* (Michelin, 1847) – Löser, Steuber and Löser: 47, pl. 6, figs 4–6.

Material. LFU 8336SG015012#1; two thin sections.

Dimensions. (LFU 8336SG015012#1).

	n	min–max	µ	s	cv	µ±s
md	15	1.85–2.57	2.23	0.26	11.8	1.97–2.49
septa	20	10–14	12.20	1.47	12.1	11–14

Remarks. Compared to *Hydnophoraraea rapulum*, the distances between crests are lower but the septal counts are higher.

Other occurrences. Cenomanian of the Central Tethys (Greece).

Superfamily Eugyroidea d’Achiardi, 1875

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

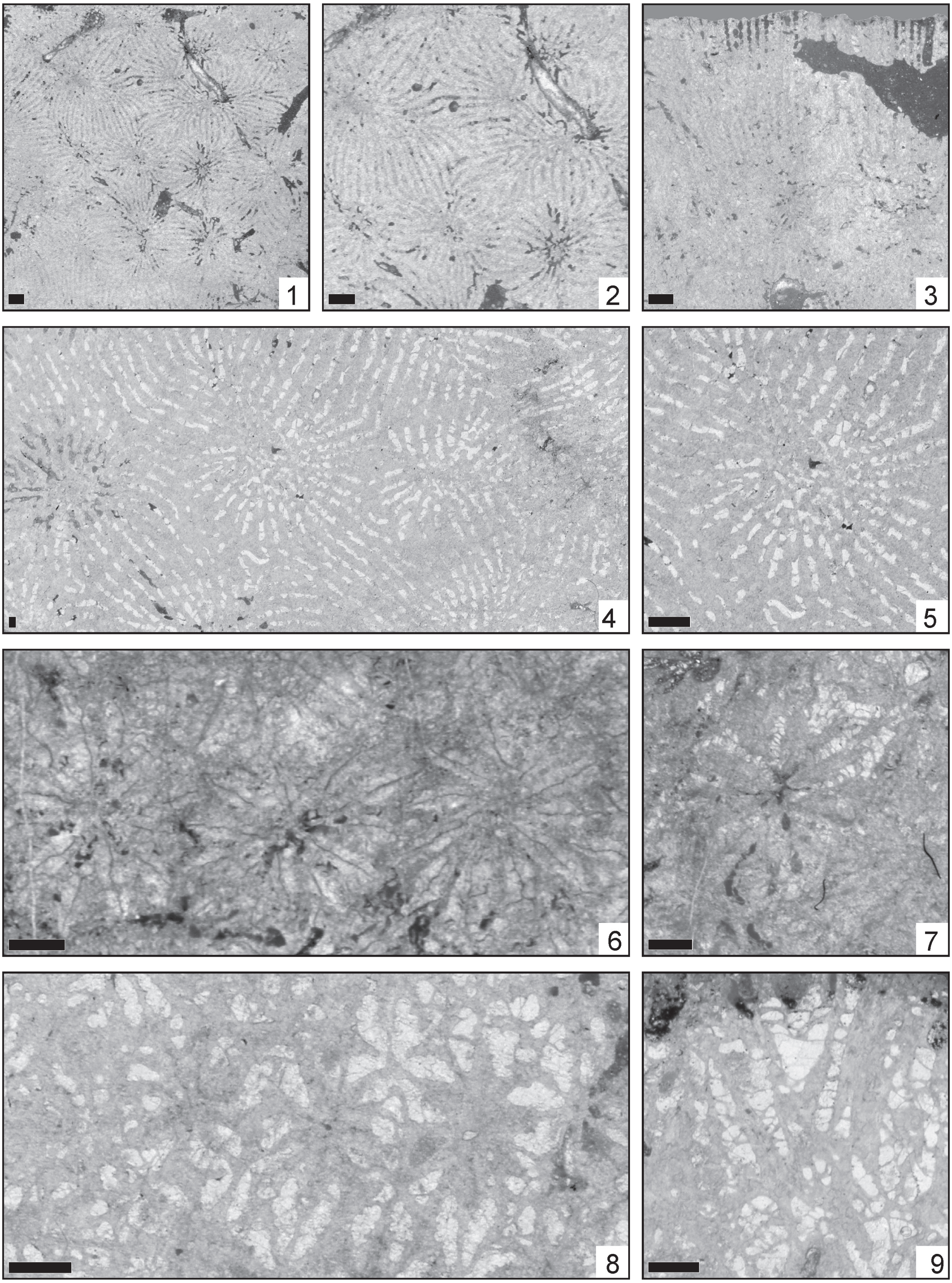

Plate 6. (1–3) *Synastrea heberti* (Alloiteau, 1952). BSPG 1947 XVI 67. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–5)** *Synastrea* ? *salisburgensis* (Beauvais, 1982). LFU 8336SG015228#5. **4**. Transversal thin section. **5**. Transversal thin section, detail. **(6–7)** *Hydnophoraraea* aff. *digitata* (de Fromentel, 1877). LFU 8336SG015224. **6**. Transversal thin section, detail. **7**. Transversal thin section. **(8–9)** *Hydnophoraraea rapulum* Oppenheim, 1930. LFU 8336SG015087#1. **8**. Transversal thin section. **9**. Longitudinal thin section. Scale bars: 1 mm.

Family Eugyridae d'Achiardi, 1875

Description. Colonial (cerioid, flabelloid, hydnophoroid, meandroid or hybrid) corals. Septa in size orders. Columella rare. Wall compact and septothecal by thickening of septa.

Columellophora Eliášová, 1989

Type species. *Columellophora velimensis* Eliášová, 1989.

Description. Hydnophoroid-cerioid colony with distinct corallites. Corallite outline irregular, centres depressed. Symmetry of septa radial and irregularly hexameral. Pali or paliform lobes absent. Costae absent. Columella styliform or by septal fusion in the centre of the corallite. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, septothecal. Coenosteum absent.

Columellophora velimensis Eliášová, 1989

*v1989 *Columellophora velimensis* n.sp. – Eliášová: 114, pl. 1, fig. 1, pl. 3, fig. 2.
v2013 *Columellophora* cf. *velimensis* Eliášová, 1989 – Löser, Werner and Darga: 48, pl. 2, figs 1–3.
v2016c *Columellophora velimensis* Eliášová, 1989 – Löser: 247, figs C38a–c.

Material. BSPG 1947 XVI 54, 1991 X 105; four thin sections.

Other occurrences. Upper Cenomanian of the Western Tethys (France), upper Cenomanian to lower Turonian of the European Boreal (Czech Republic).

Columellophora sp.

v2013 *Columellophora* sp. – Löser, Werner and Darga: 48, pl. 2, figs 4–6.

Material. BSPG 1947 XVI 51; two thin sections.

Other occurrences. Cenomanian of the European Boreal (Czech Republic).

Felixigyra group

Description. Colonial (hydnophoroid, meandroid) corals. Septal symmetry irregular. Septal inner margins swollen. Lonsdaleoid septa in *Rhipidomeandra*. Columella absent. Wall compact and septothecal.

Felixigyra Prever, 1909

Type species. *Felixigyra deangelisi* Prever, 1909.

Description. Hydnophoroid colony. Crests conical, thick, often connected to each other. Corallites distinct. No septal symmetry, but size orders can be distinguished. Pali or paliform lobes absent. Costae unknown. Columella absent. Endotheca consists of thin tabulae and dissepiments. Wall compact, septothecal. Coenosteum absent.

Felixigyra deangelisi Prever, 1909

*v1909 *Felixigyra Deangelisi* – Prever: 118, pl. 12, figs 7, 8.
v2013 *Felixigyra deangelisi* Prever, 1909 – Löser, Werner and Darga: 54, pl. 3, figs 1–3 [= with detailed synonymy].

Material. BSPG 1947 XVI 62, 1991 X 81, 1991 X 98, 1991 X 99; three thin sections.

Other occurrences. Lower Aptian of the Central Tethys (Italy).

Family Solenocoeniidae Roniewicz, 2008

Description. Cerioid and plocoid colonies. The septa are generally short. No columella. Wall compact and tabulothecal.

Confusaforma Löser, 1987

Type species. *Confusaforma weyeri* Löser, 1987

Description. Cerioid colony. Corallite outline irregular. Septa very short, with a triangular outline. Symmetry of septa irregular. Pali, costae, synapticulae, and columella absent. Endotheca consists of numerous and regular tabulae. Wall compact, probably tabulothecal.

Confusaforma weyeri Löser, 1987

Plate 7: figs 4–6

*v1987 *Confusaforma weyeri* n.sp. – Löser: 234, pl. 1, figs 1–3.
v2016c *Confusaforma weyeri* Löser, 1987 – Löser: 254, figs C49abc.
v2018 *Confusaforma weyeri* Löser, 1987 – Löser, Steuber and Löser: 48, pl. 6, figs 10–12. [here more detailed synonymy]

Material. BSPG 2016 XXII 1; two thin sections.

Dimensions. (BSPG 2016 XXII 1).

	n	min–max	µ	s	cv	µ±s
clmin	20	0.54–0.99	0.75	0.13	16.9	0.62–0.87
clmax	20	0.87–1.18	1.02	0.11	10.4	0.91–1.12

Remarks. The only specimen is poorly preserved and did not allow septal counts.

Other occurrences. Lower Aptian of the Central Tethys (Slovenia, Italy), lower Albian of the Western Atlantic (Mexico), lower Cenomanian of the Central Tethys (Greece) and the Western Tethys (Spain), upper Cenomanian of the European Boreal (Germany, Czech Republic).

Cryptocoenia d'Orbigny, 1849

Type species. *Astrea alveolata* Goldfuss, 1826

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

Cryptocoenia aguilerai (Reyeros Navarro, 1963)

*v1963 *Procyathophora aguilerai* n.sp. – Reyeros Navarro: 8, pl. 3, figs 3, 5.

v2013 *Cryptocoenia aguilerai* (Reyeros Navarro, 1963) – Löser, Werner and Darga: 64, pl. 9, figs 4–6 [with more detailed synonymy].

v2016 *Cryptocoenia aguilerai* (Reyeros Navarro, 1963) – Löser and Zell: 14, figs 5.1–3.

Material. BSPG 1991 X 70; two thin sections.

Other occurrences. Tithonian to lower Berriasian of the European Boreal (Czech Republic), Valanginian to Aptian of the Western Atlantic (Mexico), upper Barremian to lower Aptian of the Central Tethys (Germany, Greece), lower Aptian of the Western Tethys (Spain) and the Central Tethys (Greece), upper Aptian of the Western Tethys (Spain), upper Aptian to lower Albian of the Western Tethys (Spain, France), lower Albian of the Western Tethys (Spain, France), upper Albian of the European Boreal (UK).

Cryptocoenia antiqua d'Orbigny, 1850

*v1850 *Cryptocoenia antiqua* – d'Orbigny: (2), p. 92.

v1964 *Cyathophora steinmanni* Fritzsche 1924 – Morycowa: 24, pl. 3, fig. 2, pl. 5, figs 2, 3.

v1996 *Pentacoenia elegantula* d'Orbigny, 1850 – Baron-Szabo and Steuber: 8, pl. 3, fig. 3.

v1996 *Pseudocoenia annae* (Volz, 1903) – Baron-Szabo and Steuber: 8, pl. 2, fig. 1.

v2010 *Cryptocoenia atempa* (Felix, 1891) – Löser: 591, fig. 3.4.

v2013 *Cryptocoenia bulgarica* (Toula, 1884) – Löser, Werner and Darga: 64, pl. 9, figs 2–3.

v2016 *Cryptocoenia atempa* (Felix, 1891) – Löser and Zell: 15, figs 5.7–9.

Material. BSPG 1947 XVI 48, 1991 X 71; two thin sections.

Remarks. The material was in Löser et al. (2013c) identified as *Cryptocoenia bulgarica* (Toula, 1884). After this publication the type of *Cryptocoenia antiqua* became available and could be measured. The present material is much closer to *Cryptocoenia antiqua*; *Cryptocoenia bulgarica* has smaller dimensions.

Other occurrences. Lower Hauterivian of the European Boreal (France), upper Barremian of the Western Tethys (France), upper Barremian to lower Aptian of the Central Tethys (Poland, Greece), upper Aptian of the Western Tethys (Spain).

Cryptocoenia bernensis (Etallon, 1864)

Plate 7: figs 7–9

v*1864 *Stylina bernensis* – Etallon: 366, pl. 51, fig. 5.

1964 *Adelocoenia biedai* n.sp. – Morycowa: 26, text-fig. 2, pl. 4, fig. 2, pl. 5, fig. 5.

v1992 *Cyathophora regularis* Fromentel, 1875 – Eliášová: 402, pl. 2, figs 2, 3, pl. 8, fig. 8.

v2004 *Adelocoenia desori* (Koby, 1897) – Löser and Mohanti: 580, figs 2a, b.

v2008 *Solenocoenia sexradiata* (Goldfuss, 1826) – Roniewicz: 131, figs 16j–m.

v2010 *Cryptocoenia ramosa* Toula, 1889 – Löser: 595, fig. 3.9.

v2013a *Cryptocoenia bulgarica* (Toula, 1884) – Löser: 33, figs 11d, e.

v2015c *Cryptocoenia biedai* (Morycowa, 1964) – Löser: 19, figs 2D–F.

v2018 *Cryptocoenia* cf. *biedai* (Morycowa, 1964) – Löser, Steuber and Löser: 48, pl. 7, figs 1–3.

Material. LFU 8336SG015076#1; two thin sections.

Dimensions. (LFU 8336SG015076#1).

	n	min–max	µ	s	cv	µ±s
clmin	15	1.38–1.87	1.64	0.14	8.6	1.50–1.78
clmax	15	1.52–2.09	1.79	0.15	8.5	1.64–1.94
septa	6+6					

Other occurrences. Lower Callovian of the Southern Tethys (Madagascar), Valanginian of the Central Tethys (Bulgaria), upper Barremian of the Western Tethys (France), upper Barremian to lower Aptian of the Central Tethys (Poland, Greece), Aptian to Lower Albian of the Western Atlantic (Mexico), lower Albian of the Western Tethys (France), Cenomanian of the Central Tethys (Greece) and the Southern Tethys (India), Middle Cenomanian of the European Boreal (Germany, Czech Republic).

Cryptocoenia waltoni (Milne Edwards & Haime, 1851)

v*1851 *Convexastrea waltoni* – Milne Edwards and Haime: 109, pl. 23, figs 5, 6.

v1873 *Astrocoenia Reussiana*, Stoliczka – Stoliczka: 27, pl. 5, figs 3, 4.

v1947 *Cyathophora Fontserei* Bataller 1944 – Bataller: 48, text-fig.

v1966 *Stylina elegans* Beauvais – Beauvais: 121, pl. 1, fig. 1.

v1974 *Cyathophora pygmaea* Volz – Turnšek and Buser: 12, 33, pl. 4, fig. 1.

v1981 *Cyathophora pygmaea* Volz 1903 – Turnšek and Mihajlovic: 18, pl. 13, figs 1, 2.

v1994 *Adelocoenia pygmaea* (Volz 1903) – Löser: 10, text-figs 4, 5, pl. 12, figs 1, 2.

v2013 *Cryptocoenia fontserei* (Bataller, 1947) – Löser, Werner and Darga: 66, pl. 9, figs 7–9.

v2015c *Cryptocoenia reussiana* (Stoliczka, 1873) – Löser: 21, figs 3D–F.

Material. BSPG 1947 XVI 12, 1947 XVI 20, 1947 XVI 23, 1947 XVI 49, 1947 XVI 6, 1947 XVI 77, 1991 X 43, LFU 8336SG015013#1, 8336SG015107, 8336SG015228#4; eight thin sections.

Remarks. In Löser et al. (2013c) this material was assigned to *Cryptocoenia fontserei* Bataller, 1947. Afterwards, it was possible to examine the types of *Cryptocoenia waltoni* and *Cryptocoenia fontserei*. It transpired that both species are synonymous.

Other occurrences. Aalenian to Callovian of the European Boreal (UK), Callovian of the Central Tethys (Tunisia), Kimmeridgian of the European Boreal (Germany), upper Barremian to lower Aptian of the Central Tethys (Bulgaria, Serbia, Slovenia), lower Aptian of the Western Tethys (Spain), lower Albian of the Western Atlantic (Mexico),

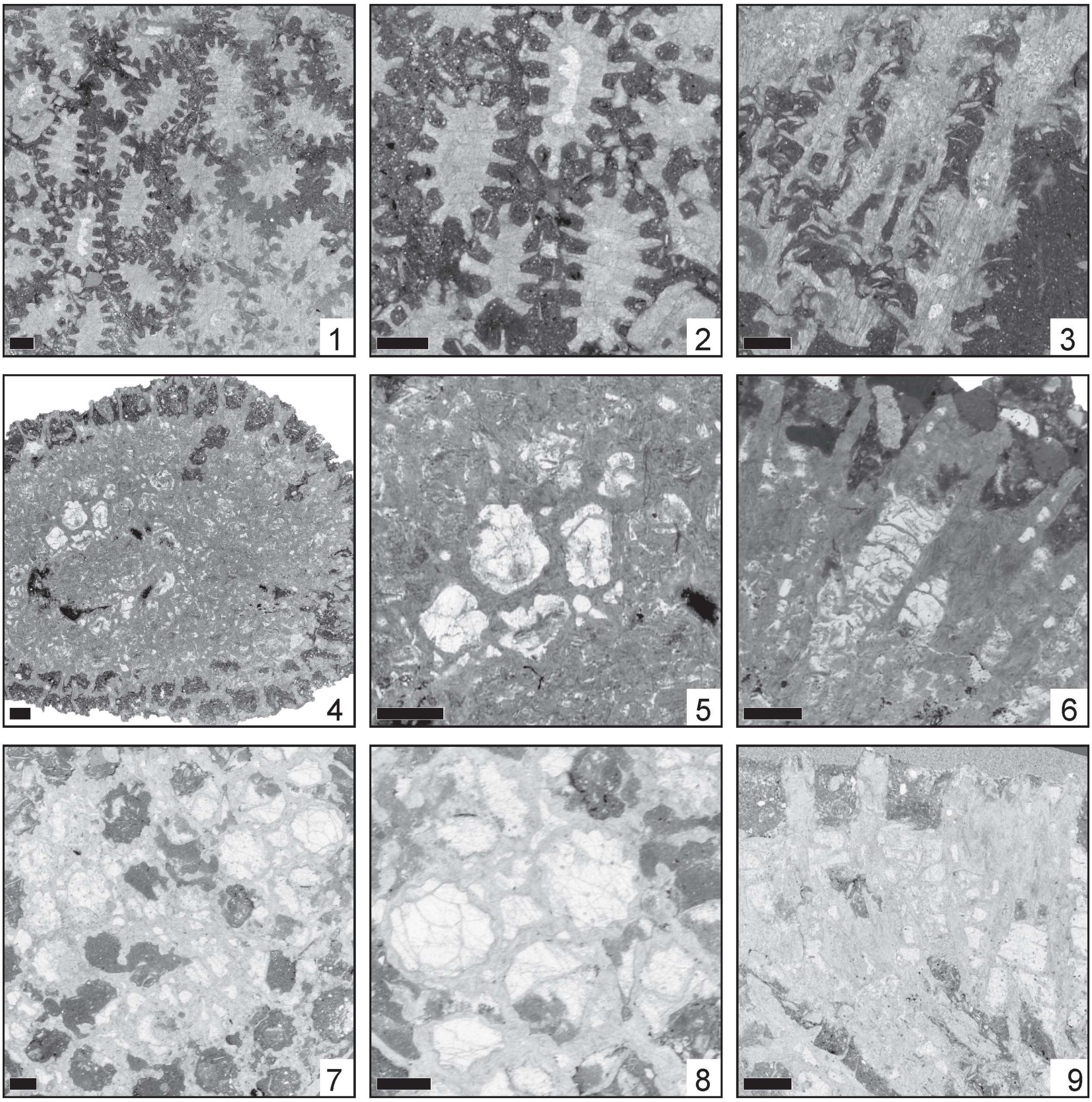

Plate 7. (1–3) *Hydnophoraraea* aff. *rapulum* Oppenheim, 1930. LFU 8336SG015012#1. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–6)** *Confusaforma weyeri* Löser, 1987. BSPG 2016 XXII 1. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Longitudinal thin section. **(7–9)** *Cryptocoenia bernensis* (Etallon, 1864). LFU 8336SG015076#1. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. Longitudinal thin section. Scale bars: 1 mm.

lower Albian to lower Cenomanian of the Western Tethys (Spain, France), upper Albian of the Southern Tethys (India) and the European Boreal (UK), lower Cenomanian of the Western Tethys (Spain), middle Cenomanian of the European Boreal (Belgium, Germany).

Cyathophoropsis Alloiteau, 1946

Type species. *Cyathophoropsis hupei* Alloiteau, 1946.

Description. Plocoid colony. Corallite outline circular. Symmetry of septa radial and regularly trimeral. Septa very short, free. Pali or paliform lobes absent. Costae present, sub-confluent to non-confluent. Columella absent. Endotheca consists of regular tabulae and occasional dissepiments. Wall compact, as tabulotheca. Coenosteum moderately broad, consists of costae and tabulae.

Cyathophoropsis sp.

Plate 14: figs 4, 5

Material. LFU 8336SG015227#1; one thin section.

Dimensions. (LFU 8336SG015227#1).

	n	min–max	µ	s	cv	µ±s
clmin	20	0.80–1.05	0.93	0.08	8.4	0.86–1.01
clmax	20	0.87–1.18	1.04	0.08	7.3	0.97–1.12
ccd	20	1.08–1.57	1.32	0.13	9.5	1.19–1.45
septa	3+3+6					

Remarks. This is so far the last occurrence of the genus.

Other occurrences. Lower Albian of the Western Tethys (Spain).

Superfamily Felixaraeoidea Beauvais, 1982

Description. Solitary and colonial (astreoid, meandroid, phaceloid) corals. Septa compact or perforated. Younger septal cycles have more perforations than older septal cycles. Septa very thick, those of the first cycles being the thickest. Septal symmetry regular or subregular radial. Septal upper margins with granulae, lateral faces with thorns. Lonsdaleoid septa and main septum absent. Microstructure of large trabeculae. Synapticulae common. Pali absent, columella parietal. Endotheca mostly absent. Marginarium and wall absent. Coenosteum in some genera. Budding extracalicinal.

Family Felixaraeidae Beauvais, 1982

Felixaraea Beauvais, 1982

Type species. *Felixaraea rennensis* Beauvais, 1982.

Description. Turbinate solitary coral with a circular outline. The septa are perforated, younger (thinner) septa more than older (thicker) septa.

Remarks. The present material of *Felixaraea* marks the first occurrence of the genus.

Felixaraea cf. *agassizi* (Vaughan, 1899)

Plate 8: figs 1–3

cf1899 *Leptophyllia agassizi* sp. nov. – Vaughan: 242, pl. 40, figs 1–4.
vp2013c *Felixaraea agassizi* (Vaughan, 1899) – Löser: 752.

Material. LFU 8336SG015135#1; two thin sections.

Dimensions. (LFU 8336SG015135#1).

c	29.2×38.1
septa	225

Remarks. The specimen is larger than *Felixaraea agassizi* and has a slightly higher septal count.

Other occurrences. Campanian to Maastrichtian of the Western Atlantic (Jamaica).

Felixaraea rennensis Beauvais, 1982

Plate 8: figs 4–6

vp1930 *Haplaraea reticularis* n. sp. – Oppenheim: 35, pl. 27, figs 11, 12. [non figs 8–10]
v1952 *Haplaraea rennensis* All. – Alloiteau: pl. 2, fig. 4, text-fig. 110. [without description]
v1957 *Haplaraea rennensis* n.sp. – Alloiteau: figs 278–280. [without description]
*1982 *Felixaraea rennensis* Alloiteau – Beauvais: (2), 25.
v2013c *Felixaraea rennensis* Beauvais, 1982 – Löser: 752, figs 1G–I.
v2016c *Felixaraea rennensis* Beauvais, 1982 – Löser: 339, figs F3a, b.
v2019 *Felixaraea rennensis* (Beauvais, 1982) – Löser, Heinrich and Schuster: 165, figs 247, 248, figs 253a, b.

Material. LFU 8336SG015135#2; one thin section.

Dimensions. (LFU 8336SG015135#2).

c	16.3×21.2
septa	100

Remarks. *Felixaraea rennensis* was only illustrated but not described by Alloiteau (1952, 1957). Illustrations alone do not constitute a valid first description of a species. Beauvais (1982) was the first to describe and illustrate the species.

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria), upper Santonian to middle Campanian of the Western Tethys (France, Spain).

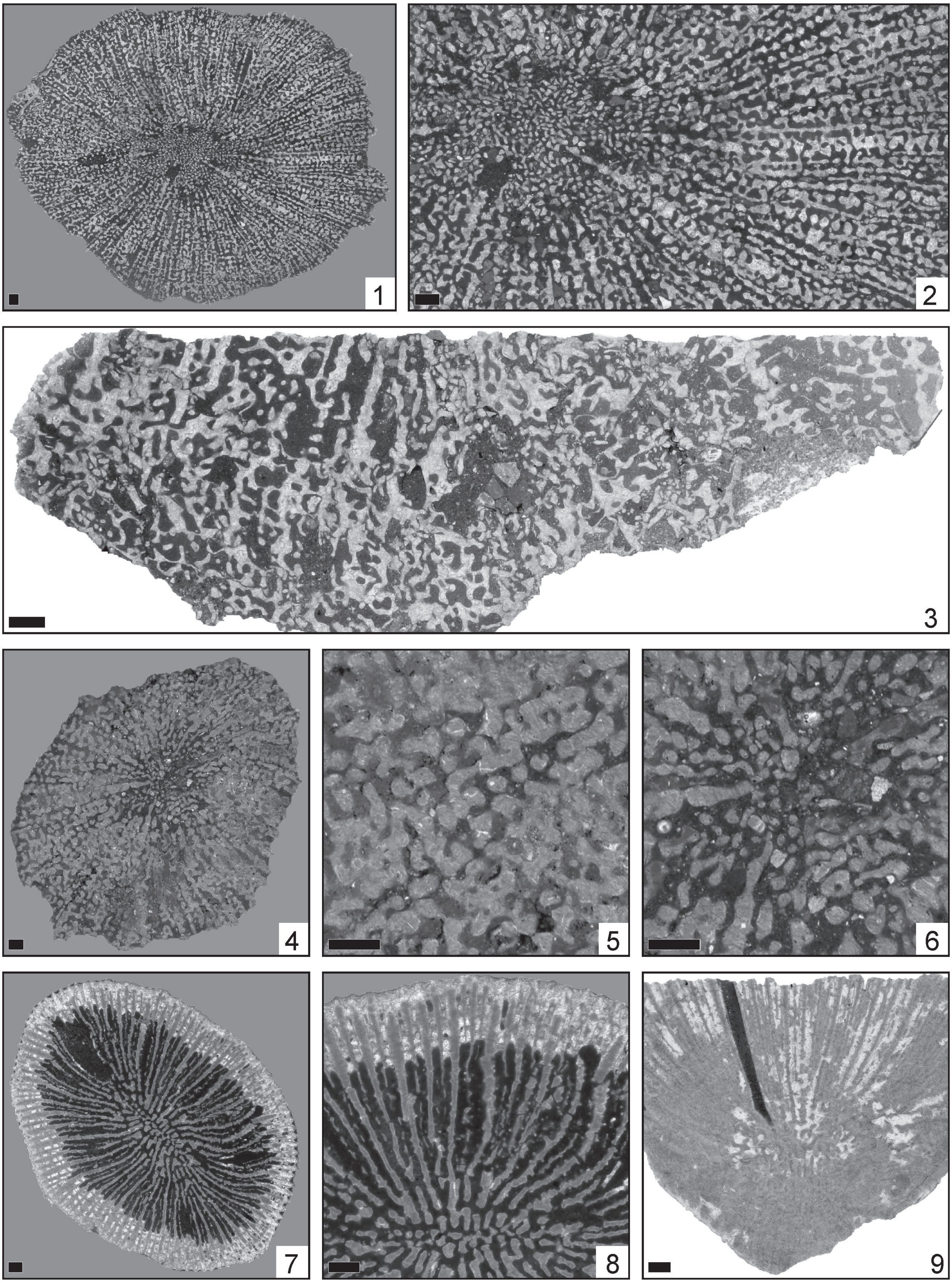

Plate 8. (1–3) *Felixaraea* cf. *agassizi* (Vaughan, 1899). LFU 8336SG015135#1. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–6)** *Felixaraea rennensis* Beauvais, 1982. LFU 8336SG015135#2. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Transversal thin section, detail. **(7–9)** Felixaraeidae indet., LFU 8336SG015138#1. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. Longitudinal thin section. Scale bars: 1 mm.

Felixaraeidae indet.

Plate 8: figs 7–9

Material. LFU 8336SG015138#1; two thin sections.

Dimensions. (LFU 8336SG015138#1).

c	16.4×22.1
septa	112

Description. Solitary turbinate coral with an elliptical outline. Septa made of large trabeculae. They are perforated, younger septa more than older septa. Septa rarely connected to each other. Symmetry irregular radial. Columella parietal. Wall with various rings of synapticulae. Endotheca absent.

Remarks. Even the position of the specimen within the family Felixaraeidae is uncertain. In the Felixaraeidae, the trabeculae are still larger, the septa are stronger and synapticulae are more frequent.

Superfamily Heterocoenioidea Oppenheim, 1930

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

Family Agatheliidae Beauvais & Beauvais, 1975

Description. Solitary corals or (phaceloid, plocoid) colonies. Septa in a higher number as in the other families, generally in a radial symmetry with septal cycles generally regular, except for large corallites. No costae. Lonsdaleoid and main septa absent. Columella weak. Marginarium absent.

Agasmilia Löser, 2014a

Type species. *Agasmilia cantabrica* Löser, 2014a.

Description. Solitary cylindrical coral. Corallite outline circular, corallite pit depressed. Septa in cross section centrally thicker. Symmetry of septa radial and regularly hexameral. Endotheca consists of central tabulae and numerous lateral dissepiments. Wall compact, consists of horizontal trabeculae. Epitheca present.

Agasmilia cantabrica Löser, 2014a

Plate 9: figs 1–3

*v2014a *Agasmilia cantabrica* n. sp. – Löser: 302, figs 3.1–3.3.

v2016c *Agasmilia cantabrica* Löser, 2014 – Löser: 153, figs A15a–d.

Material. BSPG 1948 III 3, MB K2983#4; five thin sections.

Dimensions. (BSPG 1948 III 3).

c	11.2×14.1
septa	24

(MB K2983#4)

c	12.5×14.2
septa	24

Other occurrences. Lower Cenomanian of the Western Tethys (Spain).

Eothelia Löser, Werner & Darga, 2013

Type species. *Eothelia hoelzli* Löser, Werner & Darga, 2013.

Description. Plocoid coral colony with circular corallites. Thick, compact septa in a regular septal symmetry. Septa in a regular hexameral symmetry. Septa of the first cycle attached to each other in the centre of the corallite forming the columella, septa of the second cycle shorter. Endotheca made of few tabulae, coenosteum consists of dissepiments and rare trabeculae.

Eothelia bavarica Löser, Werner & Darga, 2013

v2013 *Eothelia bavarica* n. gen., n. sp. – Löser, Werner and Darga: 52, pl. 5, figs 1–4.

Material. BSPG 1947 XVI 13, 1947 XVI 52, 1947 XVI 57, 1947 XVI 58, 1947 XVI 59, 1991 X 93; four thin sections.

Eothelia hoelzli Löser, Werner & Darga, 2013

v2013 *Eothelia hoelzli* n. gen., n. sp. – Löser, Werner and Darga: 52, pl. 4, figs 1–7.

Material. BSPG 1980 XIII 13, 1991 X 103, 1991 X 42; five thin sections.

Family Heterocoeniidae Oppenheim, 1930

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

Heterocoenia Milne Edwards & Haime, 1848c

Type species. *Lithodendron exigua* Michelin, 1847.

Description. Plocoid colony with circular corallites. Septal symmetry regular in varying systems. A main septum can be present. A trabecular wall always exists. The coenosteum is granulated at its surface.

?*Heterocoenia* sp.

Plate 9: figs 4–6

Material. LFU 8336SG015102; four thin sections.

Dimensions. (LFU 8336SG015102).

	n	min–max	µ	s	cv	µ±s
clmin	5	2.11–3.46	2.81	0.55	19.6	2.26–3.36
clmax	5	2.36–3.57	3.03	0.60	19.8	2.43–3.63
septa	4	11–13	12.50	1.0	8.0	11–13

Remarks. The present material shares most characteristics with *Heterocoenia* but differs in having a septothecal wall instead of a trabecular wall.

Styloheterocoenia Löser, Steuber & Löser, 2018

Type species. *Styloheterocoenia hellenensis* Löser, Steuber & Löser, 2018.

Description. Plocoid colony. Corallite outline irregular circular. Symmetry of septa radial and in various symmetries. Cycles of septa regular. Septa not connected to each other. Costae non-confluent, with pali-like outgrowths (costal pali). Endotheca consists of numerous and regular tabulae. Wall subcompact, septothecal. The Coenosteum is moderately broad and it consists of tabulae and costal pali.

Styloheterocoenia sp.

v2013 *Heterocoenia* sp. – Löser, Werner and Darga: 54, pl. 3, figs 10–12.

Material. BSPG 1991 X 101; three thin sections.

Remarks. The material was formerly assigned to the genus *Heterocoenia*. Löser et al. (2018) established for this coral type the new genus *Styloheterocoenia*.

Other occurrences. Lower Cenomanian of the Western Tethys (Spain).

Heterocoeniidae indet. 1

Plate 9: figs 7, 8

Material. BSPG 1947 XVI 82, LFU 8336SG015148, 8336SG015152#1, 8336SG015152#2; four thin sections.

Dimensions. (LFU 8336SG015152#2).

c	8.4×9.5
septa	28

Description. Plocoid to sub–phaceloid small colonies. Septa in a subregular hexameral symmetry. No wall.

Remarks. The small colonies very probably represent a new genus within the family Heterocoeniidae, but the low number of specimens and their small size do not allow to establish a new species and genus.

Heterocoeniidae indet. 2

Plate 9: figs 9–11

Material. BSPG 2012 X 2; two thin sections.

Dimensions. (2012 X 2).

	n	min–max	µ	s	cv	µ±s
cmax	7	1.35–2.24	1.77	0.29	16.2	1.48–2.05
cmin	7	1.11–1.75	1.37	0.22	16.0	1.15–1.58
septa	7	6–9	8.29	1.11	13.4	7–9

Description. (?) Phaceloid coral. Corallites densely packed, with a polygonal outline. The compact septa are low in number. A main septum can be present. No septal symmetry. Endotheca probably with dissepiments.

Remarks. The material is questionable and its systematic position uncertain.

Superfamily Misistelloidea Eliášová, 1976

Description. Solitary and colonial (phaceloid, plocoid) corals. Septa compact, with varying thickness, in a subregular radial symmetry. Septa not connected to each other (Rayasmiliidae) or connected only in the centre of the corallite (Misistellidae). Lateral faces with fine granulae or smooth, upper margin smooth. Lonsdaleoid and main septa absent. Microstructure of septa of small trabeculae. Synapticulae absent. Pali absent, columella present in most genera, lamellar or by septal fusion. Endotheca present. Marginarium absent. Wall absent, but an epitheca is often present (when preserved). Coenosteum varies. Budding intracalicinal.

Family Rayasmiliidae Löser, 2022

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

Ceratosmilia Alloiteau, 1957

Type species. *Ceratosmilia arnaudi* Alloiteau, 1957.

Description. Solitary turbinate coral. Corallite outline circular. Symmetry of septa radial and irregularly hexameral. Septa rarely connected to each other. Pali absent. Costae present. Columella absent.

Ceratosmilia arnaudi Alloiteau, 1957

*v1957 *Ceratosmilia Arnaudi* nov. sp. – Alloiteau: 116, 421, fig. 74, pl. 3, fig. 7.

v2013 *Ceratosmilia arnaudi* Alloiteau, 1957 – Löser, Werner and Darga: 56, pl. 5, figs 7–9.

Material. BSPG 1947 XVI 38, 1947 XVI 39, 1947 XVI 44, 1991 X 104, 1991 X 47, 1991 X 52, 1991 X 89, 1991

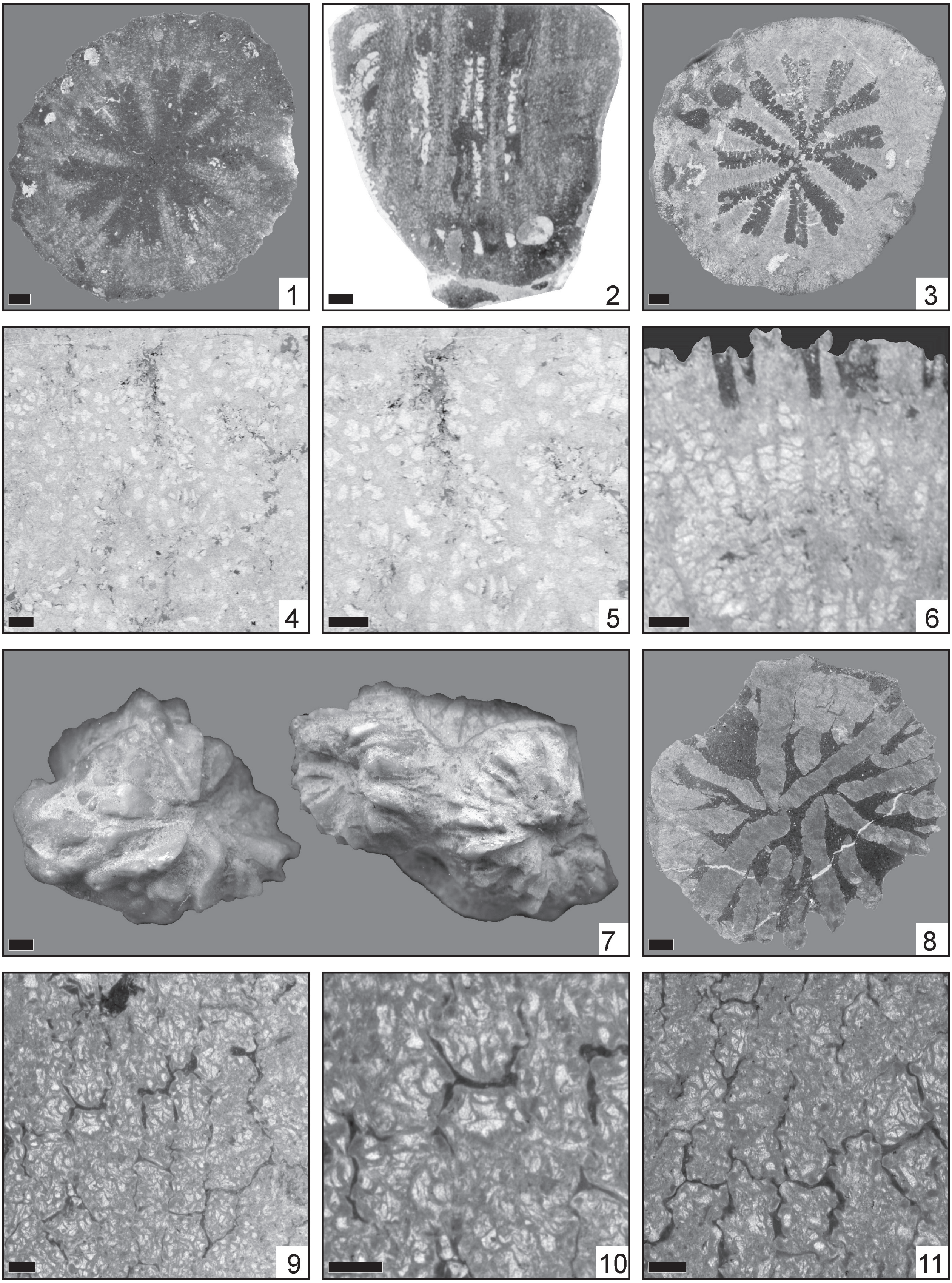

Plate 9. (1–3) *Agasmilia cantabrica* Löser, 2014. BSPG 1948 III 3. **1**. Transversal thin section. **2**. Longitudinal thin section. **3**. MB K2983#4, Transversal thin section. **(4–6)** ?*Heterocoenia* sp., LFU 8336SG015102. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Longitudinal thin section. **(7–8)** Heterocoeniidae indet. 1, LFU 8336SG015148. **7**. colony surface. **8**. LFU 8336SG015152#1; Transversal thin section. **(9–11)** Heterocoeniidae indet. 2, BSPG 2012 X 2. **9**. Transversal thin section. **10**. Transversal thin section, detail. **11**. Transversal thin section. Scale bars: 1 mm.

X 90, 1991 X 91, 2012 X 3, LFU 8336SG015082#1, 8336SG015137#2, 8336SG015153; two thin sections.

Other occurrences. Lower Cenomanian of the Western Tethys (France), upper Cenomanian of the European Boreal (Czech Republic), Turonian of the Central Tethys (Bulgaria).

Rayasmilia **Löser, 2022**

Type species. *Rayasmilia salvata* Löser, 2022.

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

?*Rayasmilia* sp.

Plate 10: figs 4–6

Material. LFU 8336SG015082#2; two thin sections.

Dimensions. (LFU 8336SG015082#2).

c	11.7×16.2
septa	82

Description. Solitary turbinate coral with an elliptical outline. Septa made of small trabeculae, in a regular hexameral symmetry, not connected to each other. Septal lateral faces strongly dentated. Columella parietal. Wall septothecal. Endotheca unknown.

Remarks. The assignation of this specimen to the Rayasmiliidae is preliminar. It differs from this family by strongly ornamented lateral septal faces and the septothecal wall, but coincides in the septal outline, septal microstructure, and regular symmetry.

Trochophyllia **Alloiteau, 1952**

Type species. *Montlivaltia melania* de Fromentel, 1861.

Description. Cylindric or turbinate solitary coral with circular or slightly elliptical outline. No columella, no pali. Endotheca made of large dissepiments. No wall, just a thin epitheca that is often not present.

Trochophyllia aprutina **(Prever, 1909)**

v*1909 *Coelosmilia aprutina* – Prever: 109, text-fig. 14, pl. 10, fig. 25.
v2013 *Paramontlivaltia ruvida* (Prever, 1909) – Löser, Werner and Darga: 56, pl. 6, figs 10–12.

Material. BSPG 1947 XVI 30, 1947 XVI 31, 1947 XVI 32; two thin sections.

Remarks. This material was described as *Paramontlivaltia ruvida* (Prever, 1909) by Löser et al. (2013c). This species is very similar to *Trochophyllia aprutina* and differs only by smaller corallite dimensions. It is possible that the species are synonyms.

Other occurrences. Lower Aptian of the Central Tethys (Italy), lower Cenomanian of the Western Tethys (Spain, France).

Trochophyllia melania **(de Fromentel, 1861)**

Plate 10: figs 1–3

*v1861 *Montlivaltia melania* – de Fromentel: 116.
v2016c *Montlivaltia melania* Fromentel, 1861 – Löser: 672, fig. T25.

Material. BSPG 2016 XXII 4, LFU 8336SG015109; three thin sections.

Dimensions. (LFU 8336SG015109).

c	36.9×42.15
septa	92

Other occurrences. Middle Oxfordian of the Western Tethys (France).

Trochophyllia ruvida **(Prever, 1909)**

*v1909 *Epismilia ruvida* – Prever: 113, text-fig. 19.
v1909 *Trochosmilia polymorpha* – Prever: 108, text-figs 12, 13, pl. 10, figs 5–23.
vnon2013 *Paramontlivaltia ruvida* (Prever, 1909) – Löser, Werner and Darga: 56, pl. 6, figs 10–12.

Material. LFU 8336SG015137#3; one thin section.

Remarks. The specimens assigned in Löser et al. (2013c) to *Paramontlivaltia ruvida* belong to *Trochophyllia aprutina*. Both species are similar in their number of septal cycles but *T. aprutina* has a larger corallite diameter (13–15 mm) compared to *T. ruvida* (8–11 mm).

Other occurrences. Aptian to Santonian of the Central Tethys (Italy, Greece, Austria).

Superfamily Montlivaltioidea Felix, 1900

Description. Solitary and (astreoid, cerioid, flabelloid, meandroid, phaceloid, thamnasterioid) colonial corals. Septa compact. Septal thickness regular, septa in an irregular radial symmetry, but septal generations can be distinguished. Septa not connected to each other. Septal lateral faces with vertical keels, upper margins with granulae. Lonsdaleoid septa and main septum absent. Microstructure of large trabeculae. Synapticulae absent. Pali rarely present. Columella in some genera, generally lamellar. Endotheca well-developed. Marginarium absent. Wall poorly defined, generally only with an epitheca. Coenosteum present, depending on the organisation form. Budding generally extracalicinal.

Family Montlivaltiidae Felix, 1900

Description. The ornamentation of septal lateral faces is more pronounced in this family. Generally no columella.

Kobyphyllia Baron-Szabo & Fernández Mendiola, 1997

Type species. *Kobyphyllia recta* (Koby, 1884).

Description. Solitary turbinate coral. Corallite outline elliptical. Symmetry of septa irregular radial. Septa free. Pali absent. Columella lamellar, short. Endotheca not well observable but marginal dissepiments exist. Wall absent but epitheca present.

Kobyphyllia sp.

Plate 10: figs 7–9

Material. LFU 8336SG015137#1; two thin sections.

Dimensions. (LFU 8336SG015137#1).

c	14.2×17.5
septa	98

Superfamily Phyllosmilioidea Felix, 1903b

Description. Solitary and (astreoid, flabelloid, meandroid, phaceloid, plocoid) colonial corals. Septa compact. First septal generation thicker than all others. Symmetry irregular or subregular radial. Septa in some genera connected to each other. Septal distal margins smooth, lateral faces with fine thorns, inner margins often swollen or T-shaped. Lonsdaleoid septa very rare. Main septum absent. Microstructure of very small trabeculae, only marked by a dark line. The costae are made by medium-sized trabeculae that result in granulated costal surfaces. Synapticulae and pali absent. Columella present or absent. Endotheca mostly present. Marginarium absent. Wall generally present, septothecal. Coenosteum present in some genera. Budding varies.

Family Phyllosmiliidae Felix, 1903b

Aulosmilia Alloiteau, 1952

Type species. *Trochosmilia archiaci* de Fromentel, 1863b.

Description. Solitary coral with an elliptical outline. Costae are not pronounced. The septal symmetry is quite regular, but not all septa reach the upper margin. The columella is lamellar, but generally deep in the corallite. The endotheca is poorly developed.

Aulosmilia cristata Beauvais, 1982

Plate 10: figs 10, 11

vp1921 *Placosmilia bofilli*, n. sp. – Vidal: 4, pl. 4, figs 6, 7.
*1982 *Aulosmilia cristata* nov. sp. – Beauvais: (1), 224, pl. 19, fig. 9.
v1997 *Peplosmilia fromenteli* Angelis d'Ossat, 1905 – Baron-Szabo: 72, pl. 8, fig. 1.
v2019 *Aulosmilia cristata* Beauvais, 1982 – Löser, Heinrich and Schuster: 239, figs 378a, b.

Material. LFU 8336SG015006#1; two thin sections.

Dimensions. (LFU 8336SG015006#1).

c	20.4×28
septa	133
sd	9/5mm

Remarks. *Placosmilia bofilli* Vidal, 1921 is based on two syntypes that belong to different species: *Aulosmilia inconstans* and *Aulosmilia cristata*. Only one specimen was illustrated. A lectotype has so far not been selected.

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria), Santonian of the Western Tethys (Spain).

Aulosmilia inconstans (de Fromentel, 1862b)

v*1862b *Trochosmilia inconstans* – de Fromentel: 266, pl. 30, fig. 1, pl. 33, fig. 1.
v1862b *Trochosmilia heterophyllia* – de Fromentel: 272, pl. 35, fig. 1.
vp1921 *Placosmilia bofilli*, n. sp. – Vidal: 4.
v1952 *Aulosmilia archiaci* de From. 1862 – Alloiteau: 636, fig. 92, pl. 7, fig. 2.
v1952 *Strotogyra* (*Rhipidogyra*) *granulata* All. – Alloiteau: pl. 3, fig. 3.
v1957 *Phragmosmilia crassa* nov. sp. – Alloiteau: 86, figs 35, 36, pl. 2, fig. 1, pl. 19, fig. 9.
v2013 *Aulosmilia ? inconstans* (de Fromentel, 1862) – Löser, Werner and Darga: 55, pl. 6, figs 7–9.
v2016c *Trochosmilia inconstans* Fromentel, 1862 – Löser: 522, figs P45a, b.
v2019 *Aulosmilia inconstans* Fromentel, 1862 – Löser, Heinrich and Schuster: 240, figs 373–375, figs 379a–c.

Material. BSPG 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; four thin sections.

Remarks. During the systematic revision of the Coniacian and Santonian corals of the Gosau Group, the genus *Aulosmilia* was profoundly investigated (Löser et al. 2019) and much Upper Cretaceous coral type material was studied. The present material can now clearly be assigned to *Aulosmilia inconstans*.

Other occurrences. Upper Cenomanian to Santonian of the Western Tethys (France), Coniacian to Santonian of the Central Tethys (Austria), Santonian to middle Campanian of the Western Tethys (Spain, France).

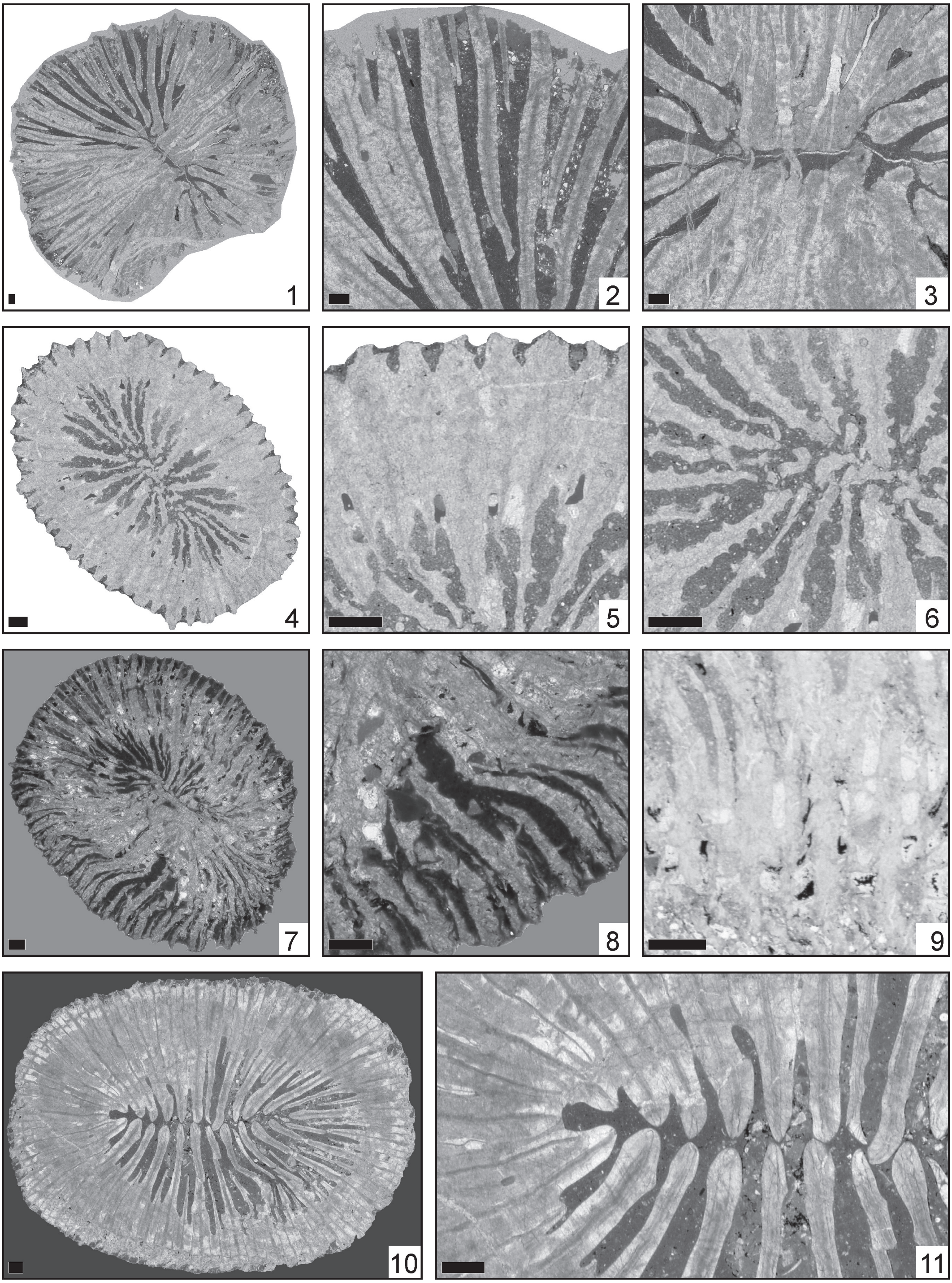

Plate 10. (1–3) *Trochophyllia melania* (de Fromentel, 1861). LFU 8336SG015109. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Transversal thin section, detail. **(4–6)** ?*Rayasmilia* sp., LFU 8336SG015082#2. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Transversal thin section, detail. **(7–9)** *Kobyphyllia* sp., LFU 8336SG015137#1. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. Longitudinal thin section. **(10–11)** *Aulosmilia cristata* Beauvais, 1982. LFU 8336SG015006#1. **10**. Transversal thin section. **11**. Transversal thin section, detail. Scale bars: 1 mm.

Aulosmilia inflexa (Reuss, 1854)

Plate 2: fig. 9

*v1854 *Trochosmilia inflexa* – Reuss: 86, pl. 5, figs 3–5.
v2019 *Aulosmilia inflexa* (Reuss, 1854) – Löser, Heinrich and Schuster: 240, figs 380a, b

Material. BSPG 1947 XVI 72; one thin section.

Dimensions. (BSPG 1947 XVI 72).

c	21.6×27.3
septa	156

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria), middle Eocene of the Eastern Pacific (Mexico).

Aulosmilia aff. *magnifica* (Duncan, 1870)

Plate 11: figs 1, 2

Material. LFU 8336SG015003; two thin sections.

Dimensions. (LFU 8336SG015003).

c	51.8×75.4
septa	160

Remarks. The specimen differs from *Aulosmilia magnifica* by much higher septal counts.

Other occurrences. Lower Cenomanian of the Western Tethys (Spain, France).

Aulosmilia parkinsoni (Milne Edwards & Haime, 1848c)

*v1848c *Placosmilia Parkinsonii* – Milne Edwards and Haime: 235.
v1854 *Placosmilia consobrina* – Reuss: 84, pl. 5, figs 17–19.
v1862a *Placosmilia angulata* – de Fromentel: 225, pl. 18, fig. 3.
v1903b *Platysmilia multicincta* Felix (Reuss sp.) – Felix: 285, pl. 20, figs 2–5.
v1903b *Trochosmilia chondrophora* nov. sp. – Felix: 327, pl. 24, fig. 12.
v1921 *Trochosmilia osensis*, n. sp. – Vidal: 4, pl. 3, figs 4–6.
v1930 *Trochosmilia chondrophora* Felix – Oppenheim: 483, pl. 31, fig. 8.
v2006 *Aulosmilia cuneiformis* (Milne-Edwards and Haime, 1848) – Baron-Szabo: 69, pl. 14, figs 2, 4.
v2013 *Aulosmilia* ? *bipartita* (Reuss, 1854) – Löser, Werner and Darga: 54, pl. 6, figs 1, 2.
vp2013 *Aulosmilia* ? *consobrina* (Reuss, 1854) – Löser, Werner and Darga: 55.
v2019 *Aulosmilia parkinsoni* (Milne Edwards and Haime, 1848) – Löser, Heinrich and Schuster: 241, figs 381a, b.

Material. BSPG 1947 XVI 18, 1947 XVI 19, 1991 X 82, 1991 X 83, 1991 X 84; three thin sections.

Remarks. In Löser et al. (2013c) this material was assigned to *Aulosmilia* ? *bipartita* and *Aulosmilia* ? *consobrina*. More recent research on the very variable genus (e.g. Löser et al. 2019) has shown that species must be understood in a much wider concept. Hence, the material is now nearly entirely assigned to *Aulosmilia parkinsoni*.

Other occurrences. Lower Coniacian of the Western Tethys (France), upper Turonian to Santonian of the Central Tethys (Austria), Coniacian to Santonian of the Western Tethys (France), Santonian of the Western Tethys (Spain, France), Maastrichtian of the Western Atlantic (Jamaica), Paleocene to Eocene base of the Central Tethys (Austria).

Aulosmilia sp.

vp2013 *Aulosmilia* ? *consobrina* (Reuss, 1854) – Löser, Werner and Darga: 55.
v2019 *Aulosmilia* sp. – Löser, Heinrich and Schuster: 241, figs 383a, b.

Material. BSPG 1947 XVI 17; two thin sections.

Other occurrences. Upper Turonian to Santonian of the Central Tethys (Austria), middle Campanian of the Western Tethys (Spain).

Pachygyra Milne Edwards & Haime, 1848a

Type species. *Lobophyllia labyrinthica* Michelin, 1847.

Description. Meandroid colony with long, straight or sinuous corallite rows, that are separated by a mostly wide coenosteum. Individual corallites cannot be distinguished. The corallite rows can be in the same level as the coenosteum, or can be elevated. In the latter case, the coral appears flabelloid. Columella lamellar.

Pachygyra cucullata (Zuffardi-Comerci, 1930)

v*1930 *Eugyra cucullata* n. sp. – Zuffardi-Comerci: 15, pl. 3, figs 3, 8.
v2013 *Pachygyra krameri* Oppenheim, 1930 – Löser, Werner and Darga: 55, pl. 5, figs 5, 6.
v2019 *Pachygyra cucullata* (Zuffardi-Comerci, 1930) – Löser, Heinrich and Schuster: 274, figs 442a, b.

Material. BSPG 2012 X 1; five thin sections.

Remarks. In Löser et al. (2013c) this specimen was assigned to *Pachygyra krameri* Oppenheim, 1930. In 2016 it was possible to study the type specimen of this species and it transpired that it has much smaller dimensions as discernable from the publication of Oppenheim (1930).

Other occurrences. Turonian to Santonian of the Central Tethys (Italy, Austria), upper Santonian of the Western Tethys (France).

Superfamily Poritoidea Gray, 1842

Description. Colonial (astreoid, plocoid) corals. Septa irregularly perforated. Symmetry of septa irregular radial or bilateral. Septa connected to each other. Septal distal margin coarsely dentated, lateral face with rare granulae, inner margin slightly swollen in places. Lonsdaleoid septa and main septum absent. Microstructure of medium-sized trabeculae. Synapticulae abundant. Pali present in some genera. Columella and endotheca present. Marginarium absent. Wall varies. Coenosteum generally present. Budding extracalicinal.

Family Actinacididae Vaughan & Wells, 1943

Description. Astreoid colonies. Septa in a regular radial or bilateral symmetry.

Actinacis d'Orbigny, 1849

Type species. *Actinacis martiniana* d'Orbigny, 1849.

Description. Astreoid colony. The corallites are small, elliptical, well marked, and with large distances to each other. Septal symmetry is between radial and bilateral. Septa often and regularly connected to each other. Pali present but because of the septal perforations not well visible.

Actinacis ? *remesi* Felix, 1903a

Plate 11: figs 3–5

?*1903a *Actinacis Remesi* – Felix: 567, text-figs 1, 2.
v1911 *Actinacis Remesi* – Trauth: 75, text-fig. 4, pl. 4, fig. 1.
v1921 *Actinacis Remesi* Felix – Zuffardi-Comerci: 11, pl. 2, figs 1, 2.
v1957 *Actinacis vignyensis* n.sp. – Alloiteau: pl. 18, fig. 9 [= nom. nud.].
v2000 *Actinacis remesi* Felix, 1903 – Baron-Szabo: 119, pl. 10, figs 3, 6.
v2013 *Actinacis magna* Alloiteau 1958 – Löser, Castro and Nieto: 27, pl. 9, figs 5, 6.
v2019 *Actinacis* sp. 2 – Löser, Heinrich and Schuster: 306, figs 499a, b.
v2022 *Actinacis* ? *remesi* Felix, 1903 – Löser and Callapez: 157, figs 7.j–l.

Material. LFU 8336SG015228#2; one thin section.

Dimensions. (LFU 8336SG015228#2).

	n	min–max	μ	s	cv	μ±s
clmin	5	1.53–2.05	1.76	0.21	12.1	1.55–1.98
clmax	5	1.78–2.54	2.16	0.29	13.5	1.86–2.45
septa	5	24–31	28.2	2.77	9.8	25–31

Remarks. The material can clearly be assigned to the genus *Actinacis*, but could not be assigned to an existing species with certainty. Closely related is material labelled as "Actinacis vignyensis Alloiteau, 1957" (MNHN; but never formally described) and material labelled as *Actinacis remesi* Felix, 1903 (NHMW, coll. Trauth; PU, coll. Zuffardi-Comerci) from the Eocene of Klokocov (Moravia, Czech Republic) and the Turonian of Libya, but the type of *Actinacis remesi* itself is unknown.

Other occurrences. Upper Albian of the Western Tethys (Spain), Turonian of North Africa (Libya), Turonian to lower Coniacian of the Western Tethys (Portugal, Spain), middle Santonian of the Central Tethys (Austria), upper Campanian to Maastrichtian of the Arabian Peninsula (United Arab Emirates), Palaeocene to Eocene of the European Boreal (France, Czech Republic).

Actinacis sp.

Plate 11: figs 6, 7

v1997 *Actinacis martiniana* d'Orbigny, 1849 – Baron-Szabo: 79, pl. 11, figs 2, 5, 6.

Material. BSPG 1947 XVI 78; one thin section.

Dimensions. (BSPG 1947 XVI 78).

	n	min–max	μ	s	cv	μ±s
clmin	5	1.44–1.76	1.60	0.14	8.8	1.46–1.74
clmax	5	1.78–2.22	1.96	0.19	9.6	1.77–2.15
septa	8+8+16					

Other occurrences. Lower Cenomanian of the Western Tethys (Spain), upper Turonian to lower Coniacian of the Central Tethys (Austria).

Superfamily Rhizangioidea d'Orbigny, 1851

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

Family Cyclastraeidae Alloiteau, 1952

Description. Only cyclolitid forms. Septa (younger more than older) at the inner margins perforated. Symmetry radial and irregular hexameral, often connected to each other. Synapticulae not common.

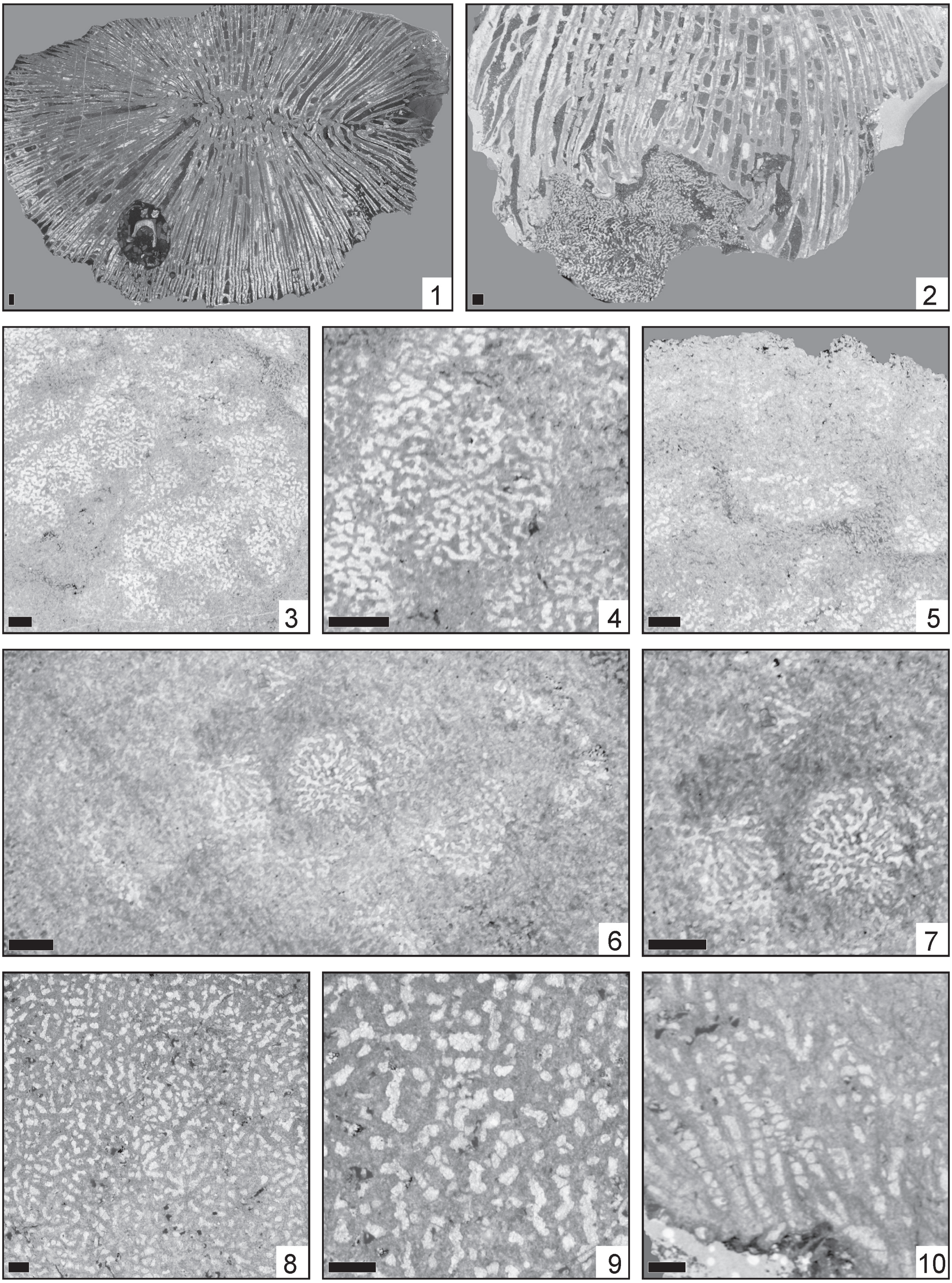

Plate 11. (1–2) *Aulosmilia* aff. *magnifica* (Duncan, 1870). LFU 8336SG015003. **1**. Transversal thin section. **2**. Longitudinal thin section. **(3–5)** *Actinacis* ? *remesi* Felix, 1903. LFU 8336SG015228#2. **3**. Transversal thin section. **4**. Transversal thin section, detail. **5**. Longitudinal thin section. **(6–7)** *Actinacis* sp., BSPG 1947 XVI 78. **6**. Transversal thin section. **7**. Transversal thin section, detail. **(8–10)** Aulastraeoporidae indet. 1, BSPG 1947 XVI 66. **8**. Transversal thin section. **9**. Transversal thin section, detail. **10**. Longitudinal thin section. Scale bars: 1 mm.

Cyclastraea Alloiteau, 1952

Type species. *Cyclolites spinosa* de Fromentel, 1863a.

Description. Solitary patellate coral with a circular outline. Septa in a regular radial symmetry, regularly connected to each other.

Cyclastraea sp.

Plate 2: figs 10–12

Material. BSPG 1947 XVI 87; one thin section.

Dimensions. (BSPG 1947 XVI 87)

c	17×19
septa	91

Family Rhizangiidae d'Orbigny, 1851

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

Eosiderastrea Löser, 2016a

Type species. *Siderastrea cuyleri* Wells, 1932.

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

Eosiderastrea cf. *glomerata* (Reuss, 1854)

cf1854 *Brachyphyllia glomerata* – Reuss: 104, pl. 2, figs 11, 12.
v2013 ?*Diploastrea* sp. – Löser, Werner and Darga: 48, pl. 1, figs 5, 6.
v2016b *Eosiderastrea* sp. 5 – Löser: 397, pl. 7, figs 1–3.

Material. BSPG 1991 X 97; two thin sections.

Remarks. This specimen is very closely related to *Eosiderastrea glomerata* in showing a decameral septal symmetry and four septal cycles, but differs from this species clearly in smaller corallites.

Other occurrences. Lower Cenomanian of the Central Tethys (Greece).

Eosiderastrea stefani Löser, 2016b

v2013 ?*Diploastrea tanohataensis* (Eguchi, 1951) – Löser, Werner and Darga: 46, pl. 2, figs 7–9.
2014 *Diploastrea crassa* Kuzmicheva, 1980 – Baron-Szabo: pl. 69, figs 2, 3.
v2015a "*Diploastrea*" *tanohataensis* (Eguchi, 1951) – Löser: 281, fig. B.
v*2016b *Eosiderastrea stefani* n. sp. – Löser: 394, pl. 2, figs 7–9.
v2018 *Eosiderastrea stefani* Löser, 2016 – Löser, Steuber and Löser: 69, pl. 19, figs 10, 11.
v2023 *Eosiderastrea* cf. *stefani* Löser, 2016c – Samaniego-Pesqueira et al.: 142, figs 14H, I.

Material. BSPG 1947 XVI 47; two thin sections.

Remarks. In Löser et al. (2013c), this specimen was assigned to ?*Diploastrea tanohataensis*. In Löser (2016a) the new genus *Eosiderastrea* was established and in Löser (2016b) systematically revised.

Other occurrences. Upper Barremian to lower Aptian of the Central Tethys (Germany), upper Aptian to lower Albian of the Western Tethys (Spain), middle Albian of the Western Atlantic (Mexico), lower Cenomanian of the Western Tethys (France, Spain) and the Central Tethys (Greece), middle Cenomanian of the European Boreal (France). Lower Cretaceous without specification of the Central Tethys (Israel).

Eosiderastrea sp.

Plate 13: figs 7–9

Material. LFU 8336SG015227#3; two thin sections.

Dimensions. (LFU 8336SG015227#3).

	n	min–max	μ	s	cv	μ±s
cmin	5	8.10–9.99	8.84	0.84	9.5	8.00–9.67
cmax	5	9.91–10.8	10.5	0.44	4.2	10.0–10.9
ccd	8	5.99–11.7	8.73	1.71	19.6	7.02–10.4
septa	4	36–45	42.5	4.36	10.3	38–47

Remarks. The present specimen has a decameral septal symmetry with three septal cycles. All other *Eosiderastrea* with such a symmetry and large corallite dimensions (as the present specimen) have four septal cycles. Hence, the present specimen is very probably a new species.

Siderohelia Löser et al., 2021a

Type species. *Siderohelia aquilai* Löser et al., 2021a.

Description. Phaceloid. Corallite circular to elliptical. Septa in a regular radial symmetry and varying systems. Younger septa attached to older septa in a regular plan. Costae short. Columella by septal fusion. Synapticulae rare, only close to the wall. Wall compact, septothecal. Endotheca absent.

Siderohelia sp.

Plate 14: figs 1–3

Material. LFU 8336SG015150; two thin sections.

Dimensions. (LFU 8336SG015150).

c	10.3×11.3
septa	67

Remarks. The septal symmetry is difficult to decipher and is probably hexameral.

Superfamily Stylinoidea d'Orbigny, 1851

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

Family Aulastraeoporidae Alloiteau, 1957

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

Aulastraeoporidae indet. 1

Plate 11: figs 8–10

Material. BSPG 1947 XVI 66; two thin sections.

Dimensions. (BSPG 1947 XVI 66).

	n	min–max	µ	s	cv	µ±s
ccd	25	2.62–3.71	3.15	0.31	10.1	2.83–3.47
septa	15	10–18	14.9	2.03	13.6	13–17

Description. Astreoid colony with small corallites. No septal symmetry. The wall is incomplete, septothecal. Endotheca well developed with numerous small dissepiments.

Remarks. The assignation of the unique specimen to a genus is difficult. It can be compared to *Preverastraea* Beauvais, 1976. Although *Preverastraea* varies in its corallite arrangement, it has always a wall that is incomplete in the present material.

Aulastraeoporidae indet. 2

Plate 12: figs 1–3

Material. LFU 8336SG015115#1; two thin sections.

Dimensions. (LFU 8336SG015115#1).

	n	min–max	µ	s	cv	µ±s
crw	15	0.35–0.46	0.41	0.03	8.1	0.38–0.44
crd	10	1.66–3.13	2.22	0.49	22.1	1.73–2.72

Description. Meandrinoid colony with straight and parallel rows. Rows very narrow, coenosteum wide. In places large isolated corallites are present. Septa in rows short and irregular, in isolated corallites well developed, in a hexameral symmetry. Endotheca well developed.

Remarks. The single specimen does not allow to establish a new genus and species.

Kozaniastrea Löser, Steuber & Löser, 2018

Type species. *Kozaniastrea pachysepta* Löser, Steuber & Löser, 2018.

Description. Cerioid colony. Corallite outline irregularly polygonal, with a small diameter. Symmetry of septa radial and irregularly hexameral. Septa not connected to each other. Pali absent. Costae hardly present, confluent. Endotheca consists of numerous tabulae. Wall subcompact, septothecal. Coenosteum absent.

Kozaniastrea sp.

Plate 12: figs 4–6

Material. BSPG 2016 XXII 2; two thin sections.

Dimensions. (BSPG 2016 XXII 2).

	n	min–max	µ	s	cv	µ±s
ccd	7	2.15–3.48	3.03	0.46	15.0	2.57–3.48
septa	4	9–18	15.0	4.08	27.2	11–19

Family Stylinidae d'Orbigny, 1851

Description. Colonial (phaceloid, plocoid) corals. Septal symmetry radial, in varying systems, bilateral in one genus. Lonsdaleoid septa absent. Columella well-developed, styliform or lamellar. Wall septothecal.

Enallhelia Milne Edwards & Haime, 1849

Type species. *Lithodendron compressa* Goldfuss, 1829.

Description. Plocoid colony growing in the form of branches which show corallites only on one face. Corallite outline circular. Symmetry of septa radial and regularly hexameral, rarely octameral. Pali absent. Costae present, non-confluent. Columella styliform. Endotheca consists of thin tabulae. Coenosteum broad.

Enallhelia octasepta sp. nov.

https://zoobank.org/6D68644E-A87C-43A7-9995-91D5DB8D8284
Plate 12: figs 7, 8

Derivatio nominis. The new species has a remarkable octameral symmetry of septa.

Holotype. LFU 8336SG015215#1 with one thin section.

Locus typicus. Germany, Bavaria, community of Lenggries, Roßsteinalmen.

Stratum typicum. Cretaceous, middle Cenomanian, Branderfleck Fm.

Paratype. LFU 8336SG015215#2 with one thin section.

Material. Holotype and paratype.

Diagnosis. *Enallhelia* with an octameral septal symmetry, two septal cycles, a small corallite diameter of 1.1–1.2 mm and a larger corallite diameter of 1.4 -1.7 mm.

Description. Plocoid colony growing in the form of branches which show corallites only on one face. Corallite outline slightly elliptical. Symmetry of septa radial and regularly octameral, two septal cycles. Septa of the first cycle are thicker and longer than septa of the second cycle. Septa compact, with occasional auriculae at their inner margins. Pali absent. Costae present, non-confluent. Columella styliform. Endotheca consists of thin tabulae. Wall compact, probably septothecal. Coenosteum broad.

Remarks. The genus has, to date, a stratigraphical range from the Oxfordian to the lower Albian. It is more common in the Upper Jurassic than the Lower Cretaceous. The present two specimens constitute the youngest occurrence of the genus.

Relationship. *Enallhelia* has generally a hexameral septal symmetry. There are no formally established species with an octameral septal symmetry as in the present material.

Dimensions. (LFU 8336SG015215#1).

	n	min–max	μ	s	cv	μ±s
clmin	13	1.05–1.23	1.13	0.07	6.0	1.07–1.20
clmax	13	1.32–1.87	1.57	0.16	10.5	1.40–1.73
ccd	15	1.28–2.25	1.97	0.24	12.0	1.73–2.21
septa	8+8					

Stylina de Lamarck, 1816

Type species. *Stylina insignis* de Fromentel, 1861.

Description. Plocoid colony. Corallite outline circular. Symmetry of septa regular radial. Costae non-confluent. Columella styliform. Endotheca consists of thin tabulae. Wall compact, septothecal. Coenosteum broad, consisting of costae and exothecal dissepiments.

Stylina arborea d'Achiardi, 1880

Plate 13: figs 1–3

*v1880 *Stylina arborea* – d'Achiardi: 290, pl. 19, fig. 8.
vnon1897 *Stylina arborea* d'Achiardi – Ogilvie: 169, pl. 17, fig. 1.
v2009 *Stylina* cf. *parviramosa* Beauvais, 1964 – Reolid, Molina and Löser: 581, fig. 5b.
v2021 *Stylina arborea* Achiardi, 1880 – Löser, Nieto, Castro and Reolid: 39, figs 49.1–3

Material. BSPG 1991 X 44, LFU 8336SG015223; three thin sections.

Dimensions. (LFU 8336SG015223).

	n	min–max	μ	s	cv	μ±s
clmin	15	0.92–1.28	1.10	0.13	11.7	0.97–1.23
clmax	15	1.10–1.48	1.24	0.09	7.4	1.14–1.33
ccd	20	2.09–3.32	2.68	0.33	12.3	2.35–3.01
septa	10	14–17	15.70	0.82	5.2	15–17

Remarks. The septal symmetry is octameral with two septal cycles. The species is, to date, only known from the middle Jurassic to the Valanginian.

Other occurrences. Bathonian of the Southern Tethys (Madagascar), Aalenian to lower Valanginian of the Western Tethys (Spain), Kimmeridgian of the European Boreal (Germany), lower Tithonian of the Central Tethys (Italy).

Stylina inwaldensis (Ogilvie, 1897)

v1880 *Stylina bernardana* ? – d'Achiardi: 288. [non *Stylina bernardana* Etallon, 1859]
v*1897 *Diplocoenia inwaldensis* – Ogilvie: 165, pl. 18, figs 7, 8.
v2013 *Stylina inwaldensis* (Ogilvie, 1897) – Löser, García-Barrera et al.: 396, figs 4g–i . [here more detailed synonymy]
v2015 *Stylina inwaldensis* (Ogilvie, 1897) – Löser, Arias and Vilas: 59, figs 3h, i.
v2019 *Stylina inwaldensis* (Ogilvie, 1897) – Löser, Arias and Vilas: 281, figs 11.1–3.

Material. BSPG 1947 XVI 42, 1991 X 45, 1991 X 46, 2010 VI 1; three thin sections.

Other occurrences. Lower Tithonian of the Central Tethys (Italy), Tithonian to lower Berriasian of the European Boreal (Czech Republic), Berriasian of the Central Tethys (Ukraine), upper Valanginian of the Western Tethys (Spain), lower Hauterivian of the Central Tethys (Ukraine) and the European Boreal (France), upper Barremian to lower Aptian of the Western Atlantic (Mexico, Venezuela), Aptian of the Central Tethys (Greece), upper Albian to lower Cenomanian of the Western Tethys (Spain).

Stylina sp.

Plate 13: figs 4–6

Material. BSPG 1947 XVI 35; three thin sections.

Dimensions. (BSPG 1947 XVI 35).

	n	min–max	μ	s	cv	μ±s
clmin	15	0.73–1.08	0.88	0.11	12.2	0.77–0.99
clmax	10	0.91–1.19	1.07	0.10	9.5	0.97–1.17
ccd	20	1.60–2.72	2.19	0.37	17.1	1.82–2.56
septa	8					

Other occurrences. Lower Hauterivian of the European Boreal (France).

Subclass Octocorallia Haeckel, 1866

The classification of the octocorals follows McFadden et al. (2022).

Order Malacalcyonacea McFadden et al., 2022
Family Isididae Lamouroux, 1812

Moltkia Steenstrup, 1847

Type species. *Moltkia isis* Steinmann & Döderlein, 1890.

Remarks. The genus was revised by Löser (2015b).

Moltkia sp.

Plate 13: figs 10, 11

Material. MB K2983#1.

Remarks. The specimen represents a holdfast of an octocoral with an approximate diametre of 15 mm.

Order Scleralcyonacea McFadden et al., 2022

Family Helioporidae Moseley, 1876

Description. The family encompasses genera that form small plocoid colonies. The corallites are small (generally below 2 mm in diameter). The structure is simple because it is only made up of trabeculae and tabulae. The so-called septa are just short wing-like extensions of the trabeculae that reach into the corallites. Pali, a columella or synapticulae do not exist. The tabulae cross corallites and coenosteum in the same level. The coenosteum is formed by trabeculae and is granulated on its surface.

Heliopora de Blainville, 1830

Type species. *Millepora coerulea* Pallas, 1766

Description. The genus forms small spheric, fingerlike or incrusting colonies. The corallites are circular and very regular. The septa are short. The coenosteum appears cellular with very fine pores and tiny spines, or is rarely vermiculate.

Remarks. As explained in Hernández Morales and Löser (2018), the genus *Polytremacis* is a junior synonym of the extant genus *Heliopora*. The corallite dimensions of the species of the study area are compared in Table 1.

Heliopora lindstroemi (Remeš, 1898)

Plate 14: figs 6, 7

1862 *Chaetetes radians* – Roemer: 617.
*1898 *Polytremacis Lindströmi* n. sp. – Remeљ: 7, pl. 1, figs 1a–c.

Material. LFU 8336SG015125#1; one thin section.

Dimensions. (LFU 8336SG015125#1).

	n	min–max	μ	s	cv	μ±s
clmin	13	0.99–1.43	1.20	0.11	8.9	1.09–1.31
clmax	13	1.16–1.56	1.40	0.12	8.8	1.28–1.52
septa	4	18–20	19.0	0.82	4.3	18–20

Remarks. The type material of this species is very probably based on specimens that were first reported by Roemer (1862) as ”Chaetetes radians” from Carboniferous glacial drift material. The name ”Chaetetes radians” was solely mentioned, without giving a description or illustration. Remeš (1898) has, therefore, the priority.

Other occurrences. Upper Albian of the European Boreal (UK), Turonian of the European Boreal (Poland), Coniacian of the Central Tethys (Austria), Danian of the European Boreal (France).

Table 1. Measurements of the *Heliopora* species in the studied fauna.

Clmax (mm)	Clmin (mm)	Septa	species
0.38–0.5	0.33–0.45	12–16	sp. 1
0.56–0.65	0.52–0.62	13–16	*ramosa*
0.68–0.81	0.6–0.74	13–16	*urgonensis*
0.86–0.95	0.75–0.89	14–16	*somaliensis*
1.11–1.34	1.02–1.2	18–22	*radiata*
1.27–1.48	1.18–1.35	19–23	sp. 2
1.28–1.52	1.09–1.31	18–20	*lindstroemi*
1.47–1.74	1.32–1.56	24–26	sp. 3

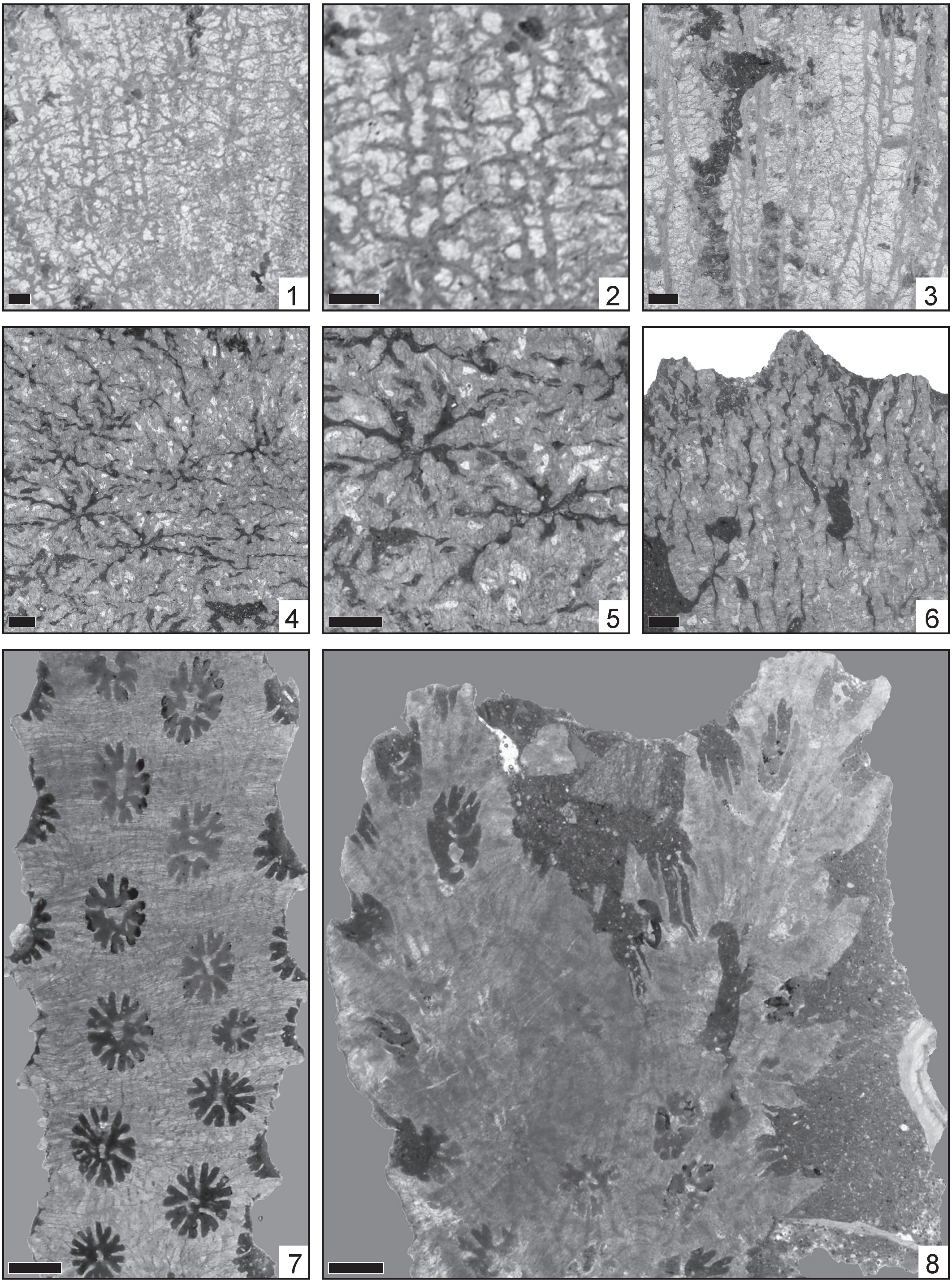

Plate 12. (1–3) Aulastraeoporidae indet. 2, LFU 8336SG015115#1. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–6)** *Kozaniastrea* sp., BSPG 2016 XXII 2. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Longitudinal thin section. **(7–8)** *Enallhelia octasepta* sp. nov. **7**. Holotype LFU 8336SG015215#1, Transversal thin section. **8**. Paratype LFU 8336SG015215#2, Longitudinal thin section. Scale bars: 1 mm.

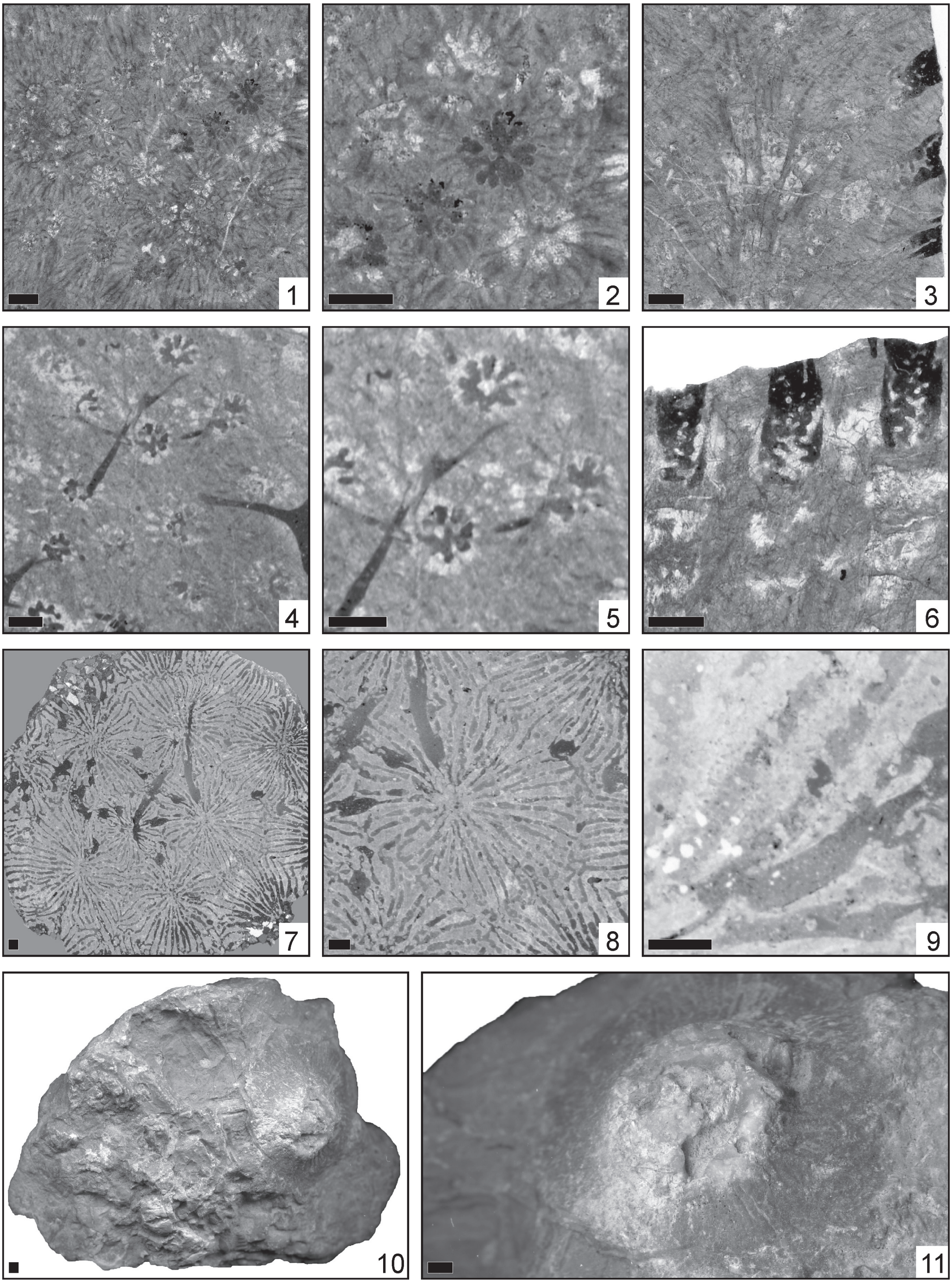

Plate 13. **(1–3)** *Stylina arborea* d'Achiardi, 1880. BSPG 1991 X 44. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–6)** *Stylina* sp., BSPG 1947 XVI 35. **4**. Transversal thin section. **5**. Transversal thin section, detail. **6**. Longitudinal thin section. **(7–9)** *Eosiderastrea* sp., LFU 8336SG015227#3. **7**. Transversal thin section. **8**. Transversal thin section, detail. **9**. Oblique thin section. **(10–11)** *Moltkia* sp., MB K2983#1. **10**. surface. **11**. surface, detail. Scale bars: 1 mm.

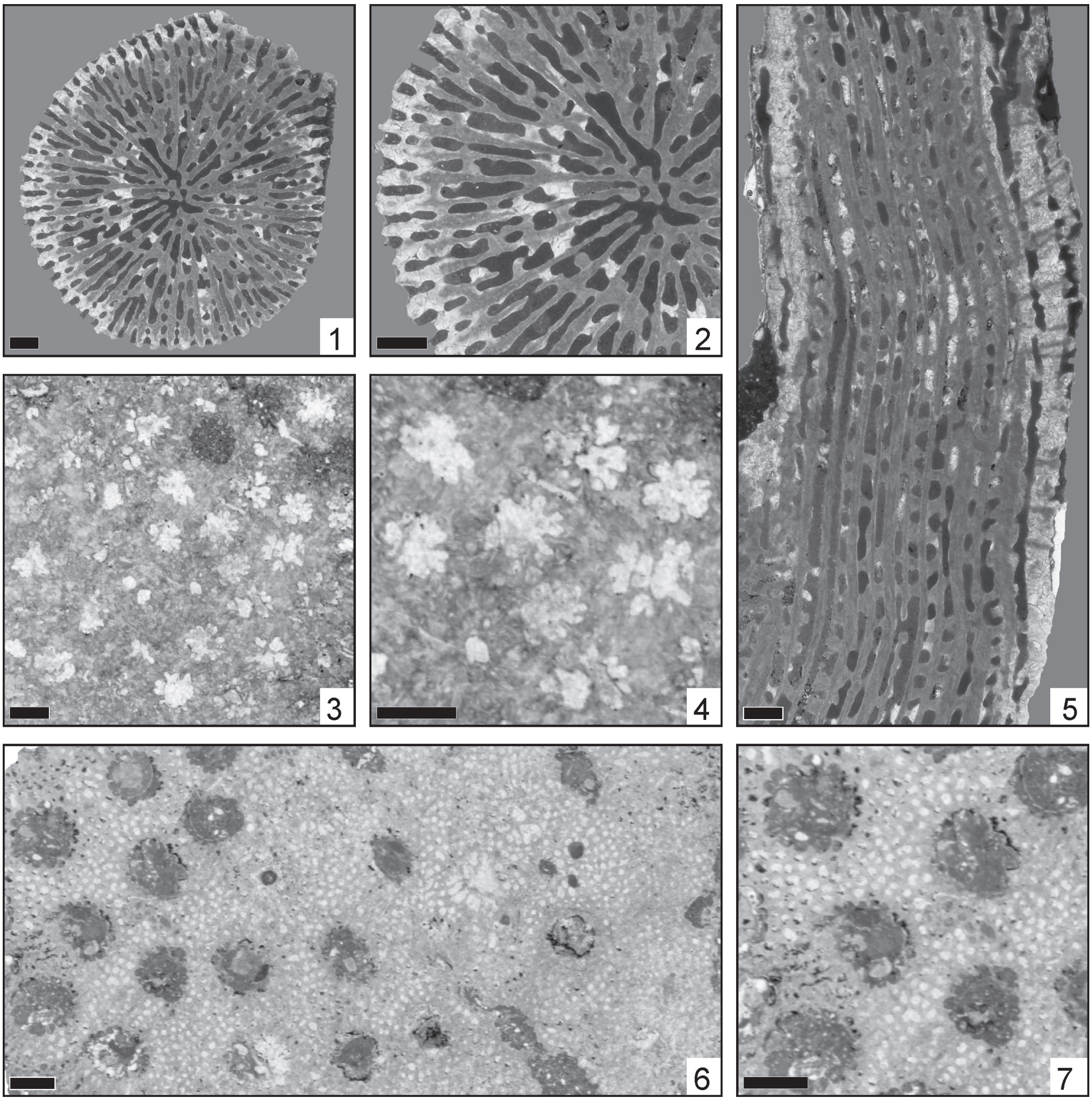

Plate 14. (1–3) *Siderohelia* sp., LFU 8336SG015150. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–5)** *Cyathophoropsis* sp., LFU 8336SG015227#1. **4**. Transversal thin section. **5**. Transversal thin section, detail. **(6–7)** *Heliopora lindstroemi* (Remeš, 1898). LFU 8336SG015125#1. **6**. Transversal thin section. **7**. Transversal thin section, detail. Scale bars: 1 mm.

Heliopora radiata (d'Orbigny, 1850)

v1850 *Centrastrea radiata* – d'Orbigny: (2), p. 207.
v2013 *Polytremacis vermiculata* (Felix, 1903) – Löser, Werner and Darga: 67, pl. 10, figs 7–9.
v2018 *Heliopora radiata* (Orbigny, 1850) – Löser, Steuber and Löser: 69, pl. 20, figs 7–9.
v2019 *Heliopora radiata* Orbigny, 1850 – Löser, Heinrich and Schuster: 324, figs 529a–c.

Material. BSPG 1947 XVI 43, 1947 XVI 55; two thin sections.

Remarks. In Löser et al. (2013c), these specimens were assigned to *Polytremacis vermiculata* (Felix, 1903b), but afterwards it was possible to examine the type material of *Heliopora radiata* (d'Orbigny, 1850) and to take more detailed measurements in the (only) syntype of *Heliopora vermiculata* that show that both species differ in their dimensions.

Other occurrences. Upper Aptian to lower Cenomanian of the Western Tethys (Spain, France), lower Cenomanian of the Central Tethys (Greece) and the Western Tethys (Spain, France), Coniacian to Santonian of the Central Tethys (Austria), upper Santonian of the Western Tethys (France), Maastrichtian of the Arabian Peninsula (United Arab Emirates).

Heliopora ramosa (d'Orbigny, 1849)

Plate 15: figs 1–3

*v1849 *Dactylacis ramosa* – d'Orbigny: p. 11.
v1850 *Dactylacis ramosa* – d'Orbigny: (2), p. 183.

v2016c *Dactylacis ramosa* Orbigny, 1849 – Löser: 276, fig. D1.
v2018 *Heliopora ramosa* (Orbigny, 1849) – Hernández Morales and Löser: 357, fig. 2.6.
v2019 *Heliopora ramosa* (Orbigny, 1849) – Löser, Heinrich and Schuster: 325, figs 530a–c.

Material. LFU 8336SG015104; two thin sections.

Dimensions. (LFU 8336SG015104).

	n	min–max	µ	s	cv	µ±s
clmin	30	0.48–0.67	0.57	0.05	8.8	0.52–0.62
clmax	30	0.55–0.72	0.61	0.05	7.4	0.56–0.65
septa	20	12–16	14.4	1.10	7.6	13–16

Other occurrences. Lower Albian of the Western Atlantic (Mexico), Cenomanian to lower Coniacian of the Western Tethys (France, Spain), Coniacian to Santonian of the Central Tethys (Austria).

Heliopora somaliensis Gregory, 1900

Plate 15: figs 4, 5

v1882 *Polytremacis* cf. *blainvilleana* d'Orb. – Toula: 35, pl. 4, fig. 14.
*v1900 *Heliopora somaliensis*, n.sp. – Gregory: 298, pl. 2, figs 8 a–c.
v1911 *Heliopora tenera* – Trauth: 89, pl. 4, fig. 3, text-fig. 6.
v1932 *Eomontipora harrisoni*, sp.n. – Gregory: 93, pl. 3, figs 1–3.
v1948 *Heliopora japonica* n.sp. – Eguchi: 363, pl. 60, figs 1, 2, 5, 7.
v1981 *Polytremacis edwardsana* (Stoliczka 1873) – Turnšek and Mihajlovic: 39, pl. 48, figs 1–8.
v1997 *Polytremacis edwardsana* (Stoliczka, 1873) – Eliášová: 69, pl. 8, figs 1, 2.
v2006 *Pseudopolytremacis japonica* (Eguchi, 1948) – Löser and Ferry: 485, fig. 6.9.
v2013b *Polytremacis* ? *tenera* (Trauth, 1911) – Löser: 22, fig. 3.12.
v2019 *Heliopora tenera* Trauth, 1911 – Löser, Heinrich and Schuster: 326, figs 532a–c.
v2020 *Heliopora somaliensis* Gregory, 1900 – Löser, Mendicoa and Fernández Mendiola: 232, figs 8a–c.

Material. LFU 8336SG015228#1; one thin section.

Dimensions. (LFU 8336SG015228#1).

	n	min–max	µ	s	cv	µ±s
clmin	12	0.72–0.92	0.82	0.07	8.4	0.75–0.89
clmax	12	0.83–0.98	0.90	0.04	4.8	0.86–0.95
septa	5	13–16	14.8	1.30	8.8	14–16

Other occurrences. Lower Hauterivian of the European Boreal (France), upper Barremian of the Western Tethys (France), upper Barremian to lower Aptian of the Central Tethys (Bulgaria, Serbia), lower Aptian of the Central Tethys (Greece, Serbia) and the Western Tethys (Spain), upper Aptian of the Western Pacific (Japan), lower Albian of the Western Atlantic (Mexico), upper Cenomanian of the European Boreal (Czech Republic), Turonian of the Central Tethys (Somalia), Coniacian to Santonian of the Central Tethys (Austria), lower Eocene of the Central Tethys (Somalia) and the European Boreal (Czech Republic).

Heliopora urgonensis (Koby, 1898)

v*1898 *Polytremacis urgonensis* – Koby: 87, pl. 21, fig. 5.
v1936 *Heliopora edwardsana* Stoliczka 1873 – Hackemesser: 76, pl. 6, fig. 11.

Material. BSPG 1947 XVI 40, 1947 XVI 41, 1947 XVI 7, 1991 X 62; two thin sections.

Dimensions. (BSPG 1947 XVI 7).

	n	min–max	µ	s	cv	µ±s
clmin	25	0.56–0.78	0.67	0.07	9.9	0.60–0.74
clmax	25	0.63–0.86	0.74	0.07	8.9	0.68–0.81
septa	22	11–17	14.86	1.58	10.6	13–16

Other occurrences. Barremian of the Central Tethys (France), lower Albian of the Western Atlantic (Mexico), Coniacian to Santonian of the Central Tethys (Austria), Cretaceous without specification of the Central Tethys (Greece).

Heliopora sp. 1

v2013 *Polytremacis* sp. – Löser, Werner and Darga: 68, pl. 10, figs 10–12.

Material. BSPG 1947 XVI 63; one thin section.

Other occurrences. Coniacian of the Central Tethys (Austria), upper Eocene of the Western Atlantic (Panama).

Heliopora sp. 2

Plate 15: figs 6–8

v1997 *Pseudopolytremacis* cf. *spinoseptata* Morycowa, 1971 – Baron-Szabo: 89, pl. 15, fig. 6.

Material. LFU 8336SG015021#1, 8336SG015021#2; three thin sections.

Dimensions. (LFU 8336SG015021#2).

	n	min–max	µ	s	cv	µ±s
clmin	9	1.11–1.36	1.27	0.09	6.9	1.18–1.35
clmax	9	1.22–1.52	1.38	0.11	7.6	1.27–1.48
septa	3	19–23	21.33	2.08	9.8	19–23

Other occurrences. Lower Aptian of the Central Tethys (Italy), upper Cenomanian of the Western Tethys (France), upper Turonian to Santonian of the Central Tethys (Austria), Palaeocene of the European Boreal (Germany).

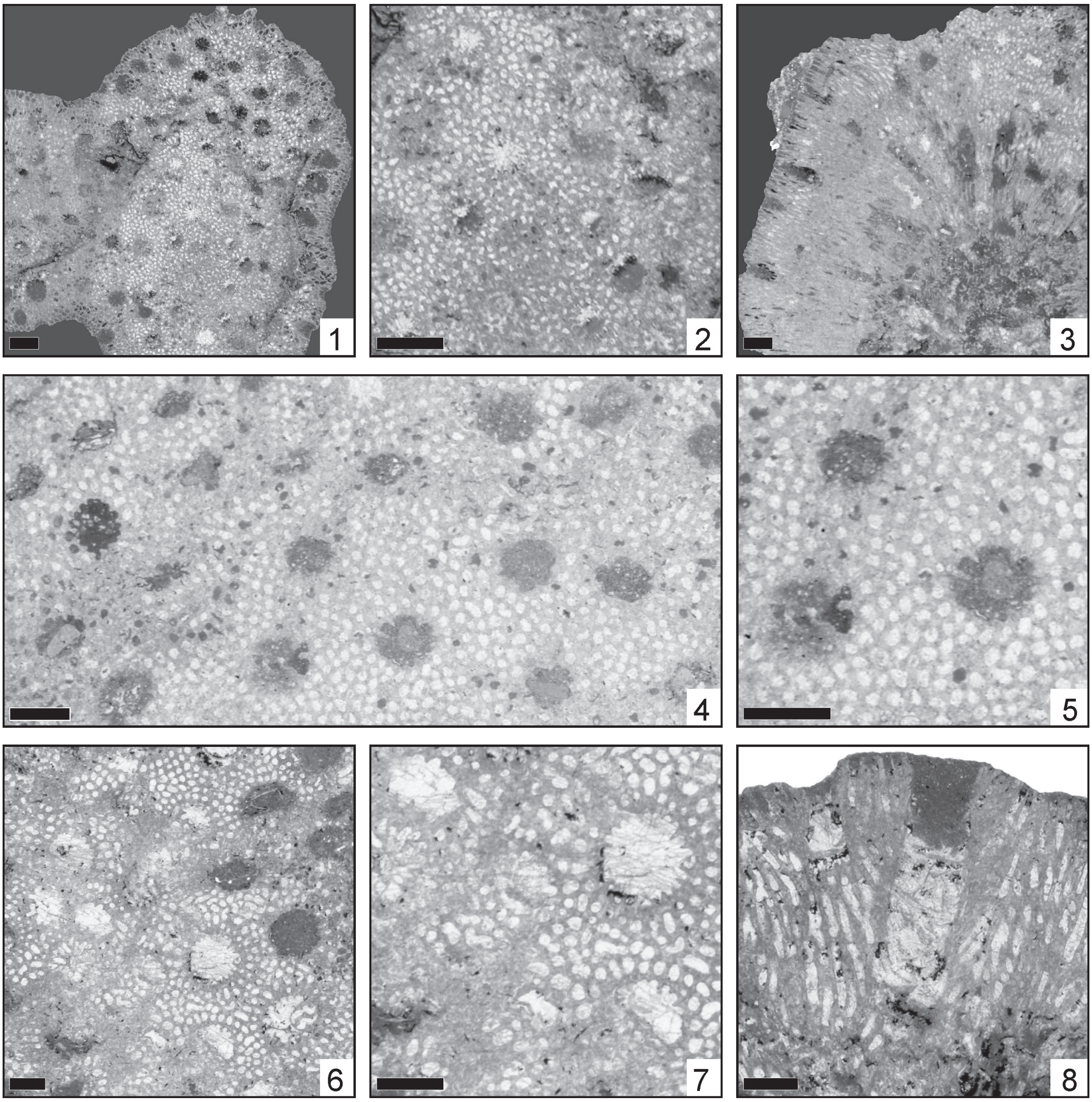

Plate 15. (1–3) *Heliopora ramosa* (d'Orbigny, 1849). LFU 8336SG015104. **1**. Transversal thin section. **2**. Transversal thin section, detail. **3**. Longitudinal thin section. **(4–5)** *Heliopora somaliensis* Gregory, 1900. LFU 8336SG015228#1. **4**. Transversal thin section. **5**. Transversal thin section, detail. **(6–8)** *Heliopora* sp. 2, LFU 8336SG015021#2. **6**. Transversal thin section. **7**. Transversal thin section, detail. **8**. Longitudinal thin section. Scale bars: 1 mm.

Heliopora sp. 3

v2013 *Polytremacis bofilli* (Bataller, 1936) – Löser, Werner and Darga: 67, pl. 10, figs 1–3.

vp2019 *Heliopora partschi* Reuss, 1854 – Löser, Heinrich and Schuster: 324.

Material. BSPG 1947 XVI 14, 1947 XVI 25, 1947 XVI 50, 1991 X 40, 1991 X 61, LFU 8336SG015015#1, 8336SG015015#2, 8336SG015096; seven thin sections.

Remarks. In Löser et al. (2013c), the material was assigned to *Polytremacis bofilli*. After more detailed measuring it transpires that the dimensions are larger than in *Heliopora bofilli*. *Heliopora bofilli* itself is probably a junior synonym of *Heliopora blainvilleana* Michelin, 1841. This is difficult to decide; the type material of *Heliopora blainvilleana* comes from Uchaux (Vaucluse, France) and is very poorly preserved. Therefore, *Heliopora blainvilleana* probably should be discarded. The type material of *Heliopora partschi* is available but did not deliver well-constrained morphometric data.

Other occurrences. Coniacian to Santonian of the Central Tethys (Austria), lower Santonian of the Western Tethys (France), Campanian to Maastrichtian of the Western Atlantic (Jamaica), Maastrichtian of the Western Tethys (France).

Discussion

In the first description of the coral fauna from the Roßsteinalm area, 39 species in 25 genera were described. This amount has more than doubled, now reaching 98 species in 46 genera. The new material from the Bayerisches Landesamt für Umwelt - Geologie/Paläontologie (Hof) and the Museum für Naturkunde der Humboldt-Universität (Berlin) is taxonomically very different from the formerly studied material kept at the Bayerische Staatssammlung für Paläontologie und Geologie (Munich). We can only speculate about the reasons. Most material (Hof and Munich) was sold or donated by the private collector Otto Hölzl, as aforementioned. It is possible that the Bayerisches Landesamt für Umwelt - Geologie/Paläontologie first picked out attractive material from his collection and the remaining material went to the Bayerische Staatssammlung für Paläontologie und Geologie. Another possibility is that the material was collected at different times and at slightly different places or horizons at the Roßsteinalmen, or that the attractive specimens were the first to be collected and later all of the rest were collected. For example, all of the material of the genus *Eothelia* (that is unattractive for collectors) is housed at the Bayerische Staatssammlung für Paläontologie und Geologie (Munich). No specimen was found in the other two collections. On the other hand, the (attractive) specimens of the genus *Felixarea* are all from the Bayerisches Landesamt für Umwelt - Geologie/Paläontologie (Hof).

The new material has enriched the fauna considerably but various taxonomic assignments – genera and species – of the first revision have changed (Table 2). This has different reasons:

1. After the publication, numerous collections in Europe and the USA were visited by the first author (H.L.) and much type material was studied. Of importance for the present revision was the study of the collections of Johannes Felix (Leipzig), Paul Oppenheim (Jerusalem), and August Emanuel Reuss (Vienna).
2. With the publication of the systematic revision of the Cretaceous corals on the genus level (Löser 2016c) an improved classification system was proposed. Therefore, the systematic position of many genera was modified, and many genera became synonyms.
3. The revision of the corals of the Conacian and Santonian corals of the area of Rußbach and Gosau (Austria) by Löser et al. (2019) has improved the knowledge on Late Cretaceous corals that also had influence on the taxonomy of Cenomanian corals.
4. Finally, the improved methods of recording and analysing morphometric data in Scleractinian corals changed the viewpoint at the species concept level and the way in which species are distinguished. Many type specimens were measured with more details and much more morphometric data became available overall.

Faunal composition

The present middle Cenomanian coral fauna encompasses 98 coral species, with 88 species belonging to the subclass Hexacorallia, and ten species belonging to the subclass Octocorallia. Compared to other Cretaceous coral faunas, this is a comparably high value which is so far only nearly reached or even exceeded by two Cenomanian coral faunas: Kozani (Greece; Löser et al. 2018) and Cantabria (Spain; Löser and Wilmsen 2022). There are two further upper Cretaceous species-rich faunas: the Turonian to Santonian coral faunas from Austria (Löser et al. 2019), and a Campanian fauna from Spain (e.g. Bataller 1937). Both coral faunas are allochthonous, in that the material was brought together from different areas and may also differ slightly in age. This is not the case for the present coral fauna.

With the exception of one specimen originating from the upper part of the Roßsteinalmen section, all other specimens certainly come from the marly facies of the lower part of this section. However, an attribution to single horizons and thus a separation of different palaeocommunities is not possible.

In our first compilation, published in 2013, we stated that solitary corals dominate the collection in number of specimens (80%), whereas colonial forms dominate in number of genera. The new material includes coral genera of various growth forms and although colonial coral genera still dominate the association, the number of solitary coral genera increased (Fig. 3). The new specimens - solitary and colonial corals - are also small, rarely exceeding 5 cm in their largest dimension. This may suggest - as already discussed in Löser et al. (2013c) - unfavourable

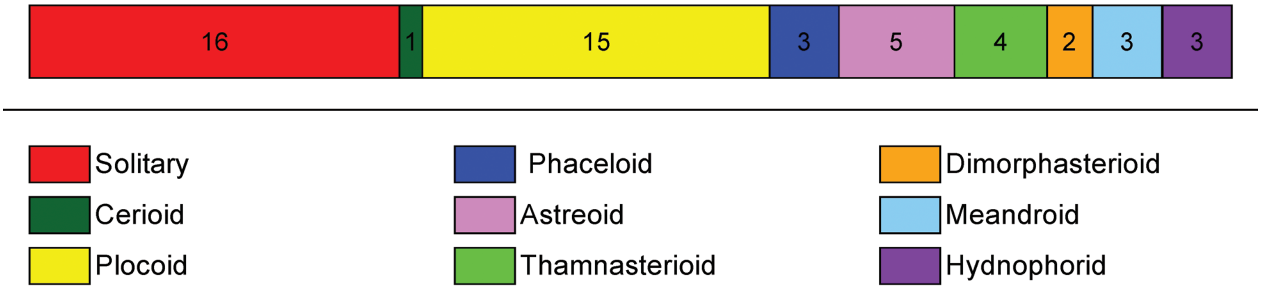

Figure 3. Distribution of the corallite integration types in the studied fauna. The total number of genera (50) is larger because all corals where included, also those not assigned to any genus.

Table 2. Changes in the taxonomy for the Roßsteinalmen coral fauna published in 2013.

Löser, Werner and Darga (2013)	**This paper**
Acrosmilia sp.	*Placoseris* cf. *eturbensis* (de Fromentel, 1857)
Actinastrea regularis (de Fromentel, 1887)	*Actinastrea subdecaphylla* (Oppenheim, 1930)
Astraeofungia tenochi (Felix, 1891)	*Astraeofungia schmidti* (Koby, 1898)
Aulosmilia ? bipartita (Reuss, 1854)	*Aulosmilia parkinsoni* (Milne Edwards & Haime, 1848)
Aulosmilia ? consobrina (Reuss, 1854)	*Aulosmilia parkinsoni* (Milne Edwards & Haime, 1848)
Aulosmilia ? consobrina (Reuss, 1854)	*Aulosmilia* sp.
Aulosmilia ? inconstans (de Fromentel, 1862)	*Aulosmilia inconstans* (de Fromentel, 1862)
Ceratosmilia arnaudi Alloiteau, 1957	*Ceratosmilia arnaudi* Alloiteau, 1957
Columellophora cf. *velimensis* Eliášová, 1989	*Columellophora velimensis* Eliášová, 1989
Columellophora sp.	*Columellophora* sp.
Cryptocoenia aguilerai (Reyeros Navarro, 1963)	*Cryptocoenia aguilerai* (Reyeros Navarro, 1963)
Cryptocoenia bulgarica (Toula, 1884)	*Cryptocoenia antiqua* d'Orbigny, 1850
Cryptocoenia fontserei (Bataller, 1947)	*Cryptocoenia waltoni* (Milne Edwards & Haime, 1851)
Dimorpharaea japonica Eguchi, 1951	*Dimorpharaea williamsonensis* (Wells, 1944)
Dimorphastrea regularis (de Fromentel, 1857)	*Dimorphastrea* cf. *hiraigensis* (Eguchi, 1951)
?*Diploastrea* sp.	*Eosiderastrea* cf. *glomerata* (Reuss, 1854)
?*Diploastrea tanohataensis* (Eguchi, 1951)	*Eosiderastrea stefani* Löser, 2016
Eothelia bavarica gen. nov. et sp. nov.	*Eothelia bavarica* (Löser et al., 2013)
Eothelia hoelzli gen. nov. et sp. nov.	*Eothelia hoelzli* (Löser et al., 2013)
Felixigyra deangelisi Prever, 1909	*Felixigyra deangelisi* Prever, 1909
Heterocoenia sp.	*Styloheterocoenia* sp.
Hydnophora cf. *obliqua* Reig Oriol, 1992	Hydnophoraraea obliqua Reig Oriol, 1992
Hydnophora cf. *obliqua* Reig Oriol, 1992	Hydnophoraraea parviconus Oppenheim, 1930
Hydnophora sp.	*Hydnophoraraea parviconus* Oppenheim, 1930
Leptophyllaraea cf. *granulata* (de Fromentel, 1863)	*Leptophyllaraea* cf. *granulata* (de Fromentel, 1863)
Microphyllia cf. *oldhamiana* (Stoliczka, 1873)	*Microphyllia* cf. *oldhamiana* (Stoliczka, 1873)
Negoporites cf. *quartus* Eliášová, 1995	*Negoporites* cf. *quartus* Eliášová, 1995
Negoporites sp.	*Negoporites* sp.
Neocoenia cf. *casterasi* (Alloiteau, 1957)	*Neocoenia exsculpta* (Reuss, 1854)
Neocoenia cf. *casterasi* (Alloiteau, 1957)	*Neocoenia kuehnii* (Oppenheim, 1930)
Neocoenia renzi (Hackemesser, 1936)	*Neocoenia renzi* (Hackemesser, 1936)
Pachygyra krameri Oppenheim, 1930	*Pachygyra cucullata* (Zuffardi-Comerci, 1930)
Paramontlivaltia ruvida (Prever, 1909)	*Trochophyllia aprutina* (Prever, 1909)
Paramontlivaltia ruvida (Prever, 1909)	*Trochophyllia ruvida* (Prever, 1909)
Polytremacis bofilli (Bataller, 1936)	*Heliopora* sp. 3
Polytremacis sp.	*Heliopora* sp. 1
Polytremacis vermiculata (Felix, 1903)	*Heliopora radiata* (d'Orbigny, 1850)
Stelidioseris minima (de Fromentel, 1857)	*Actinastrea limbata* Alloiteau, 1954
Synastrea sp.	*Synastrea* sp.
Thalamocaeniopsis sp.	*Polyastropsis* cf. *fascigera* (Felix, 1909)
Trochoseropsis ettalensis Söhle, 1897	*Trochoseropsis ettalensis* Söhle, 1897

substrate conditions and limited light. All of those limiting factors had no influence on the species richness.

Twenty-seven superfamilies of the order Scleractinia were distinguished in Löser (2016c) for the Cretaceous. Another superfamily is introduced here (Dendrogyroidea) and one superfamily (Ficariastraeoidea) is put into synonymy with the Phyllosmilioidea. Of the resulting 27 superfamilies, 22 occur in the Middle Cenomanian. In the studied fauna, 15 of those superfamilies are present. For the remaining seven superfamilies Dendrophyllioidea, Fungioidea, Haplaraeoidea, Madreporoidea, Micrabacioidea, Orbicelloidea, and Stylophoroidea an occurrence in the Middle Cenomanian is confirmed, but they were not found in the study area.

Fig. 4 shows the comparison of the number of genera per superfamily for the Albian to Turonian on a global scale to the number of genera per superfamily in the study area (only order Scleractinia). Both global and local data are very similar, with the difference that in the present fauna the Caryophyllioidea, Eugyroidea, Montlivaltioidea and Phyllosmilioidea have less genera compared to the global data, whereas the Cyclolitoidea and Stylinoidea are represented by slightly more genera. The lower number of Caryophyllioidea genera in the present shallow water fauna can be explained by the preference of this superfamily for deeper marine environments. On the whole the faunal composition is comparable to other coral faunas of Cenomanian age.

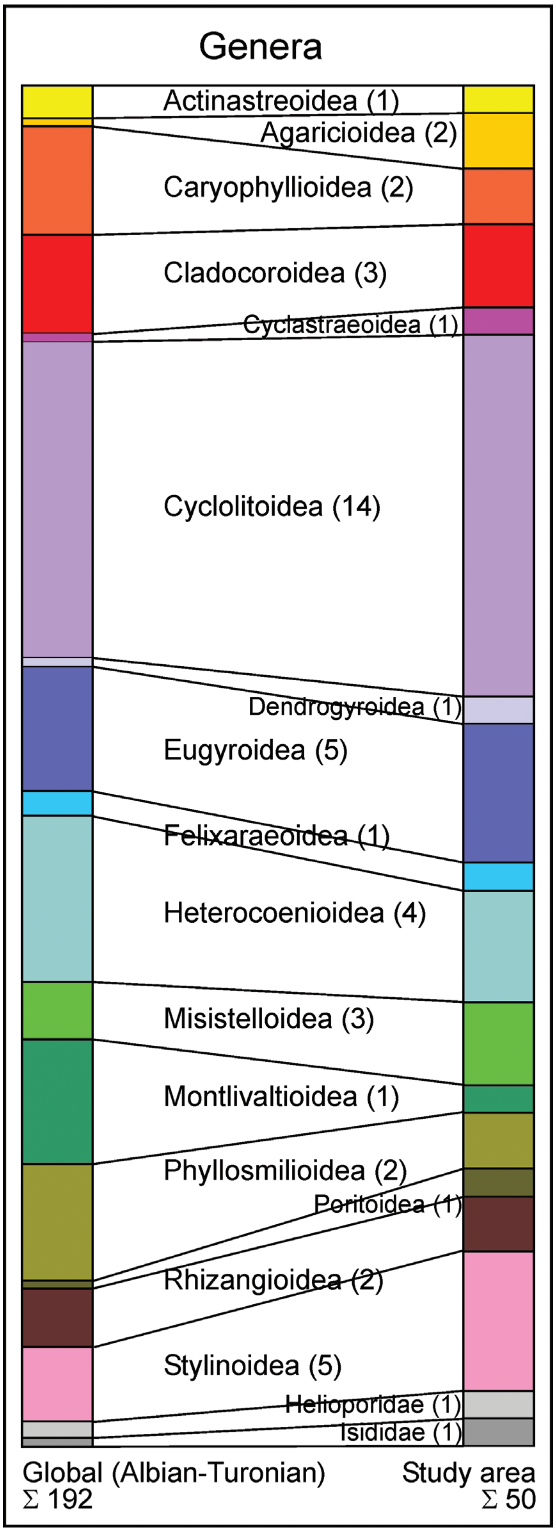

Figure 4. Distribution of genera of the studied fauna among superfamilies (order Scleractinia) based on verified stratigraphical ranges. These ranges were obtained through the observation of material and do not come from the literature. A comprehensive compilation of the ranges were published in Löser (2016c). The left bar shows the distribution of (192) genera worldwide that have an occurrence (at least partly) in the Cenomanian. Only those superfamilies are shown that occur also in the study area, resulting in 124 genera. The right bar shows the distribution of (50) genera of the studied fauna.

Stratigraphic distribution

Fig. 5 is an alphabetical chart that shows the stratigraphical distribution of the species of the study area in other areas. It can be observed that the species of the same genus have a comparable stratigraphical distribution. Some genera have their principal distribution in the Lower Cretaceous and others in the Upper Cretaceous. This is obvious for the lower Cretaceous genera *Astraeofungia*, *Cryptocoenia*, *Stylina* and the upper Cretaceous genera *Actinastrea*, *Aulosmilia*, *Hydnophoraraea*, *Synastrea*. Only a few genera are occurring throughout the whole Cretaceous, such as the octocoral *Heliopora*.

When looking directly at the stratigraphical distribution of the genera (Fig. 6), this polarisation is even more obvious: 15 genera occur in the Lower Cretaceous but have their last occurrence in the Cenomanian; 14 genera occur before and continue after the Cenomanian; eight genera occur only in the Cenomanian; nine genera originate in the Cenomanian and continue into the Upper Cretaceous.

The summarised data in Fig. 7 for both species and genera show that more taxa of this study have their stratigraphic distribution in the Lower Cretaceous than in the Upper Cretaceous. There are many genera that had their last occurrence in the Cenomanian, some were present in the whole Cretaceous and many others had their first occurrence in the Cenomanian. Some genera experienced a range extension with the present fauna; the most striking are *Cyathophoropsis*, *Enallhelia* and *Felixaraea*.

Palaeobiographic relationships

Fig. 8 shows the correlation of palaeo-provinces (faunules) based on (76) species of the study area that have a distribution in other areas. The number of joint species is generally low and, therefore, no clear pattern can be observed. The highest number of species (16 out of 76) shares the present fauna with the coral fauna from Córbeces (Cantabria, Spain; Löser and Wilmsen 2022). Generally, the present fauna tends to correlate more with Tethyan faunas; Boreal faunas are in a separate cluster. Even if not shown in Fig. 8, the present fauna shares many species with the well-studied Coniacian to Santonian coral fauna of the area of Rußbach and Gosau (Austria); out of the 76 species that were indicated at other places, 27 occur also in the Rußbach/Gosau area. When comparing only coral faunas with a range in the Cenomanian (Fig. 9), the fauna from Córbeces again shows the highest number of joint species. The correlation with other areas does not allow a clear conclusion; very probably because the number of joint species is too low.

Evolutionary aspects

Almost ten years have passed since the publication of the first part of the coral fauna from the Northern Calcar-

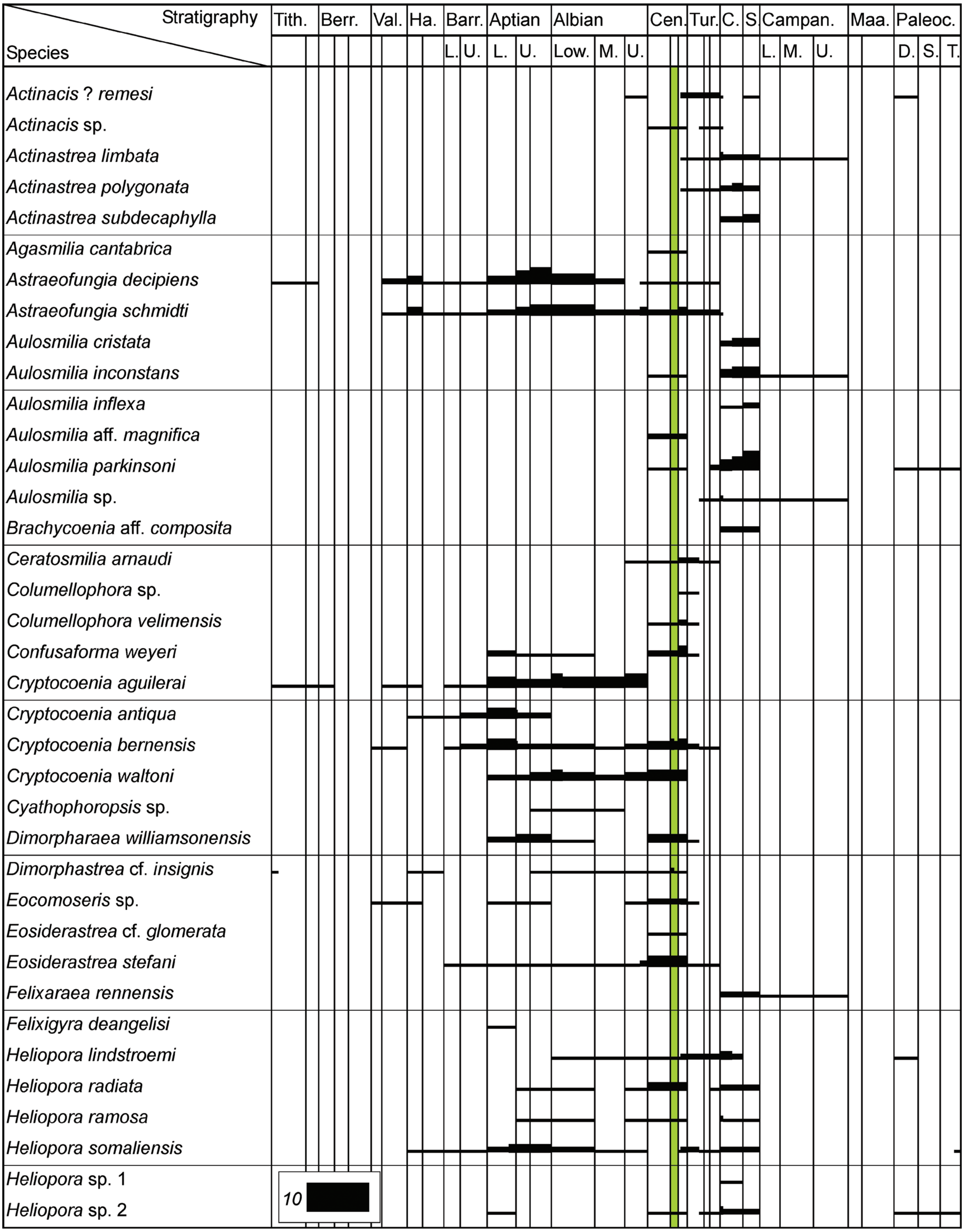

Figure 5. Distribution of species of the studied fauna in localities outside of the study area. The thickness of the horizontal bars corresponds to the number of localities where the species was found. The vertical green bar marks the age of the investigated coral fauna. Only Tithonian to Palaeocene is shown.

eous Alps . At the same time or afterwards, more large Albian to Cenomanian coral faunas were published (e.g. Löser 2013a, 2014b, 2015a; Löser et al. 2015; Löser et al. 2013a; Löser and Bilotte 2017; Löser et al. 2018; Löser and Wilmsen 2022, 2023). The Coniacian to Santonian coral fauna of the Gosau area was revised (Löser et al. 2019). All of these revisions have extended or limited the stratigraphical ranges of the coral genera. When correlat-

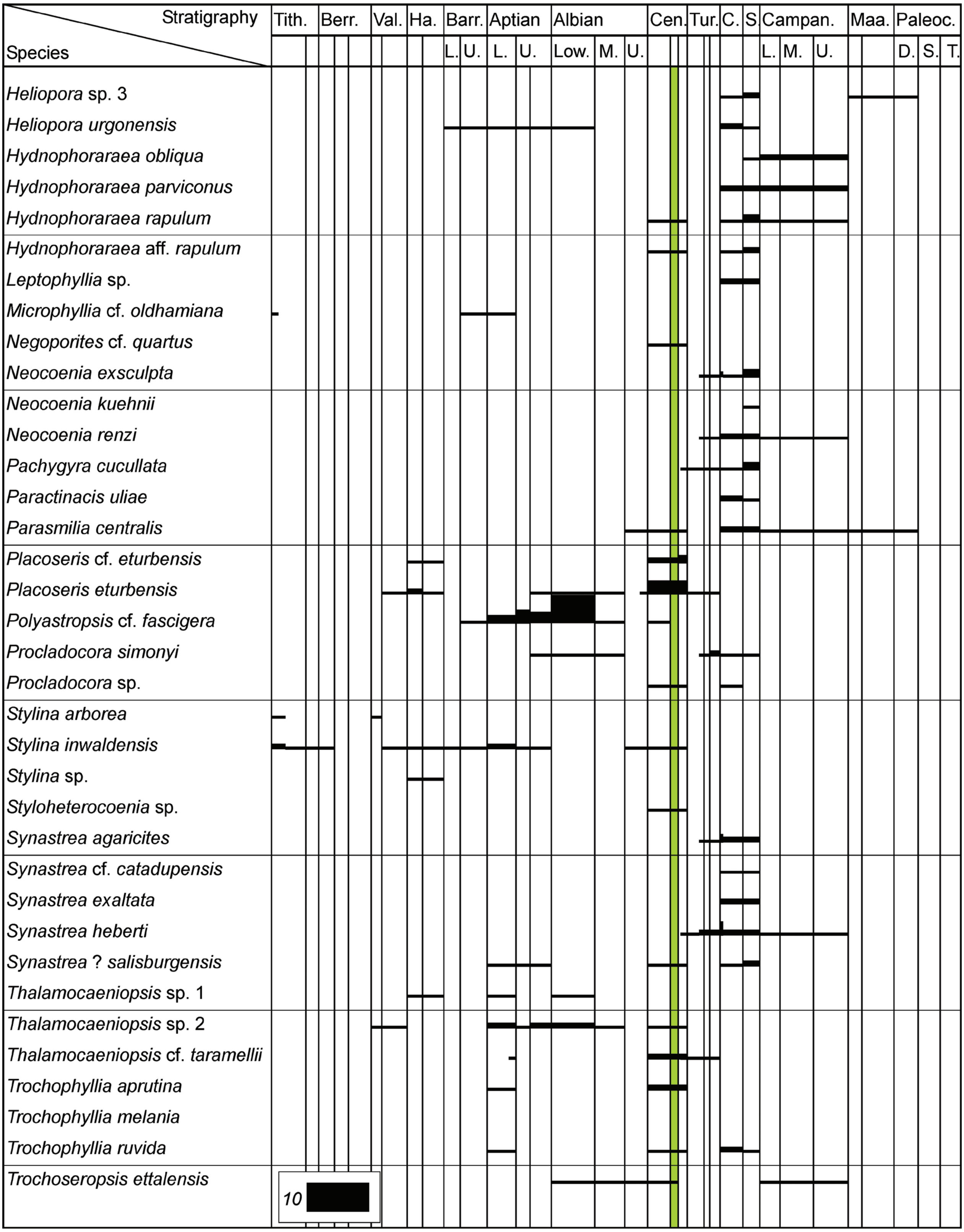

Figure 5. Continued.

ing the palaeo-provinces based on genera (Fig. 10), two major groups can be observed, the Lower Cretaceous plus Cenomanian and the Turonian to Santonian. There is one exception; the Quillan Basin of Cenomanian age is grouped together with the Turonian to Santonian provinces. The Quillan Basin province encompasses, principally, the locality of Prat-Périe (Sougraigne, Les Corbières, Aude, France) with an Uppermost Cenomanian age (*juddii*-zone; Bilotte 1985; Michel Bilotte personal communication). It is shown again that the faunal turnover (see

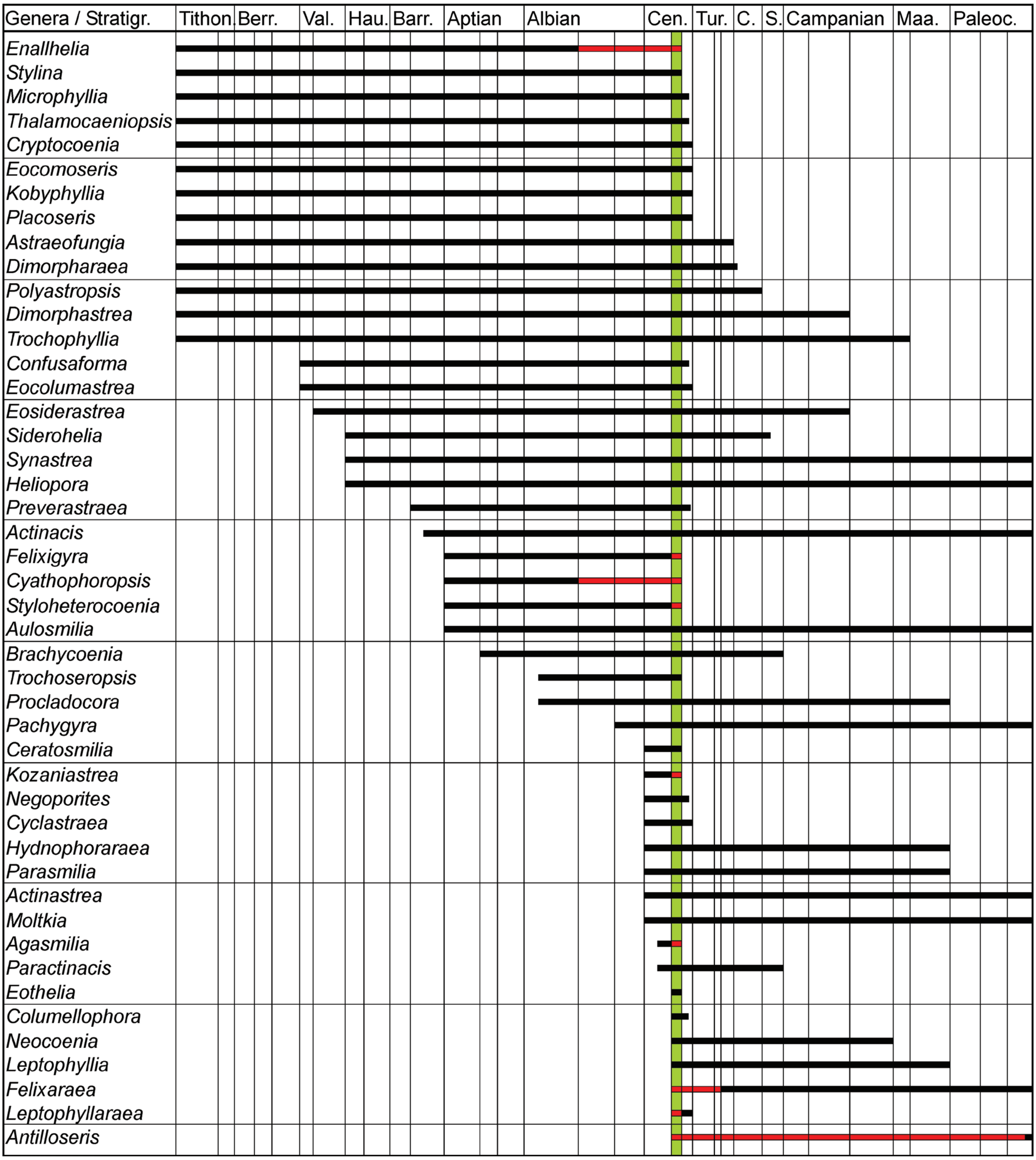

Figure 6. Verified stratigraphic ranges of the coral genera in the study area, sorted according to their occurrence. Ranges as above after Löser (2016c), but improved by newer data. Red lines mark range extensions as a result of this study. The vertical green bar indicates the age of the studied fauna. Only Tithonian to Palaeocene is shown; some genera may have longer ranges.

also Löser and Callapez 2022, fig. 9) from the Lower Cretaceous plus Cenomanian to the Turonian and younger strata was transitional and can only be partly connected to the sea level highstand and Ocean Anoxic Event 2 at the Cenomanian/Turonian boundary. When looking at the stratigraphic distribution of the superfamilies (that may represent monophyletic groups), the faunal turnover is less obvious (Fig. 11). Only three superfamilies became extinct during the Cenomanian, and three superfamilies originated.

Concluding remarks

During the Cenomanian, the general trend of a rising sea level continued (Haq et al. 2014). Whereas the lower Cenomanian is characterised by a sea level increase, the middle Cenomanian experienced a slight decrease. During the upper Cenomanian, the sea level increased again, reaching a high stand at the Cenomanian/Turonian boundary. Globally, nearly all precisely dated large Cenomanian coral faunas can be assigned either to the

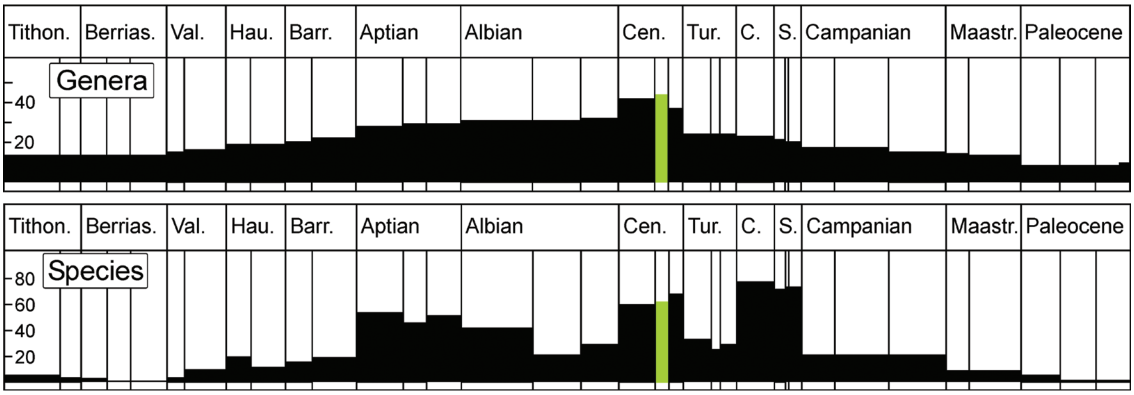

Figure 7. Summarised ranges of genera and species. The chart of genera shows the verified distribution of the genera of the study area (based on Löser 2016c with later precision). The chart of species shows the number of faunules where the species from the study area occurred (not localities). The new data obtained in the present study are not shown in both charts. The vertical green bar marks the time interval of the study area.

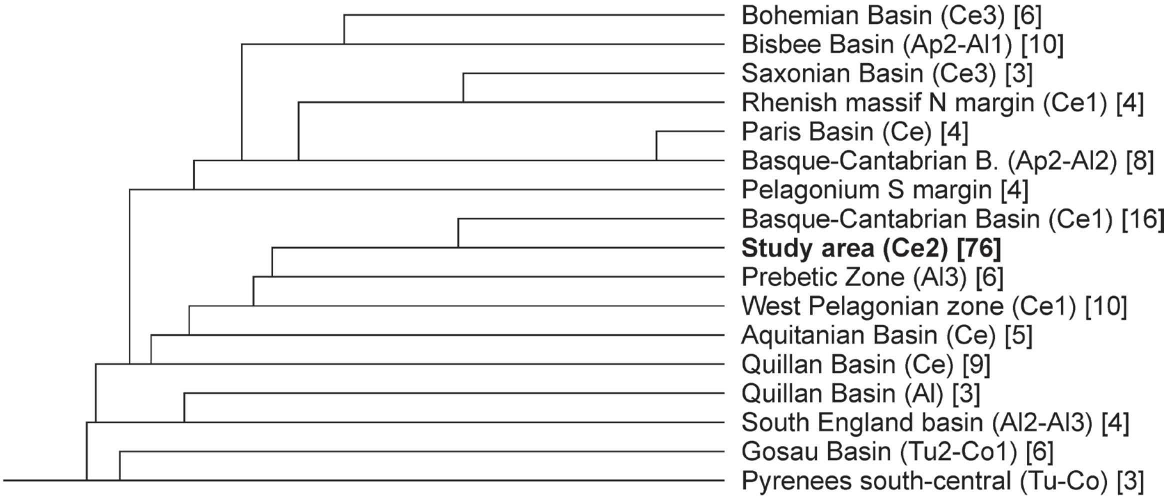

Figure 8. Correlation of the palaeo-provinces where species of the studied fauna occur. Only provinces with more than two species were included, and only the time period Albian to Turonian is considered. The Correlation Ratio coefficient was applied. Abbreviations: Ap, Aptian; Al, Albian; Ce, Cenomanian, Tu, Turonian, Co, Coniacian. The number 1. indicate lower, the number 2. middle, and the number 3. upper. The numbers in brackets are the numbers of joint species. The stratigraphy of the area Pelagonium S margin is uncertain. The study area is marked in bold letters.

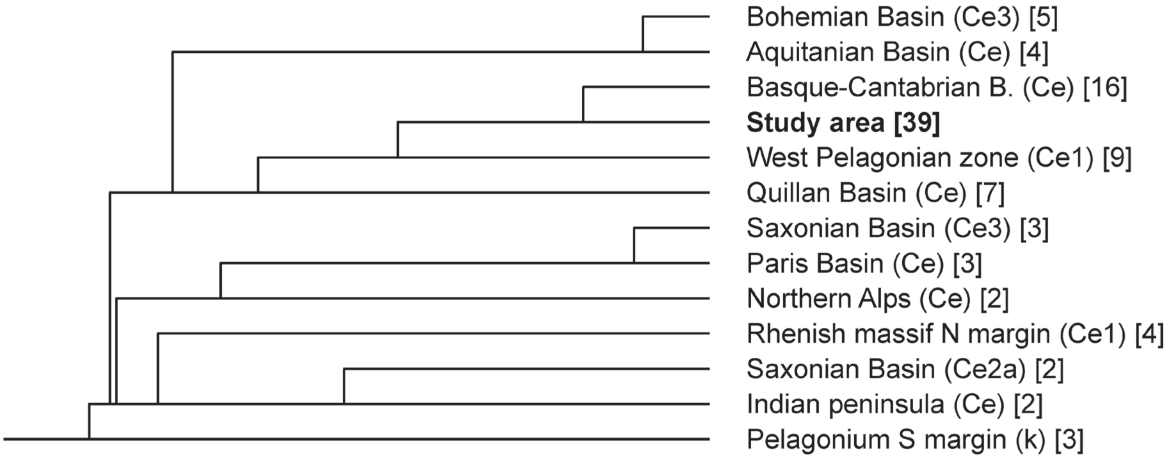

Figure 9. Correlation of the palaeo-provinces with a range in the Cenomanian where species of the studied fauna occur. Only provinces with more than one species were included. The Correlation Ratio coefficient was applied. Abbreviations: Ap, Aptian; Al, Albian; Ce, Cenomanian, Tu, Turonian, Co, Coniacian. Number 1. indicates lower, number 2. indicates middle and number 3. indicates upper. The numbers in brackets are the numbers of joint species. The stratigraphy of the area Pelagonium S margin is uncertain, but also clearly includes Cenomanian corals. The study area is marked in bold letters.

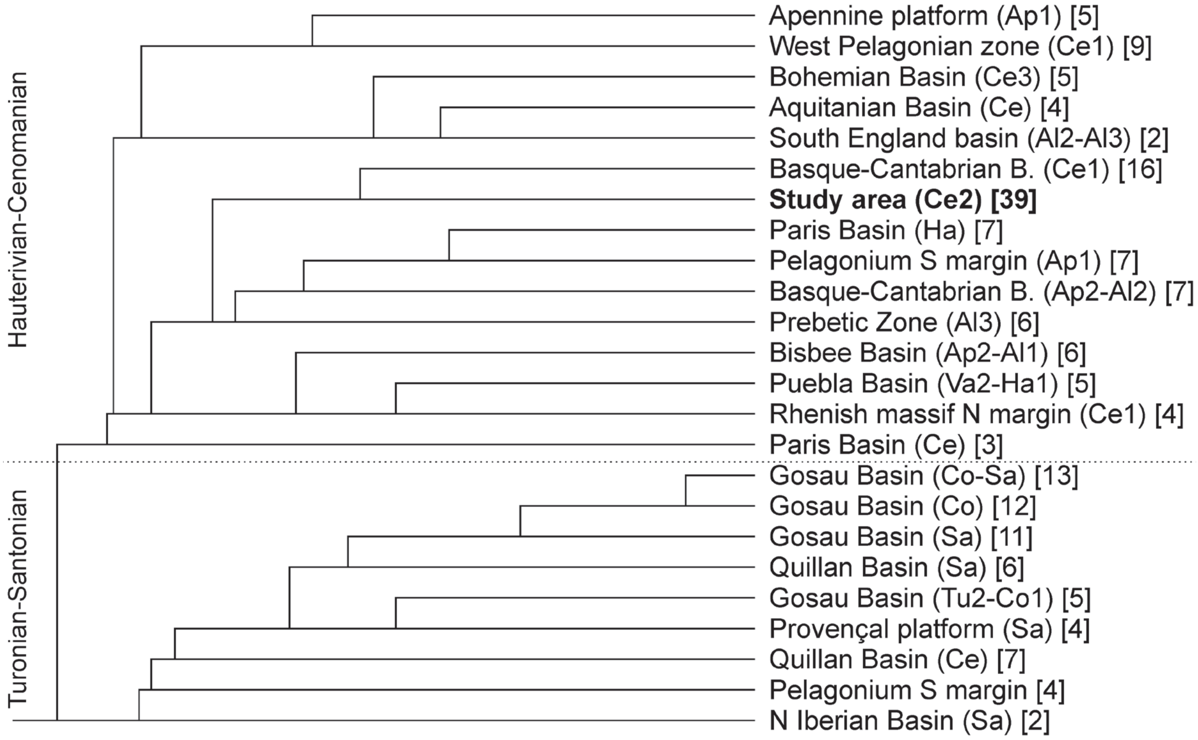

Figure 10. Correlation of the palaeo-provinces where genera of the studied fauna occur. Only provinces with more than two genera were included, and only the time period Hauterivian to Santonian was considered. The Correlation Ratio coefficient was applied. Abbreviations: Va, Valanginian; Ha, Hauterivian; Ap, Aptian; Al, Albian; Ce, Cenomanian, Tu, Turonian, Co, Coniacian; Sa, Santonian. Number 1. indicates lower, number 2. indicates middle and number 3. indicates upper. The numbers in brackets are the numbers of joint genera. The stratigraphy of the area Pelagonium S margin is uncertain. The study area is marked in bold letters. The dotted line separates Hauterivian to Cenomanian and Turonian to Santonian palaeo-provinces (with one exception).

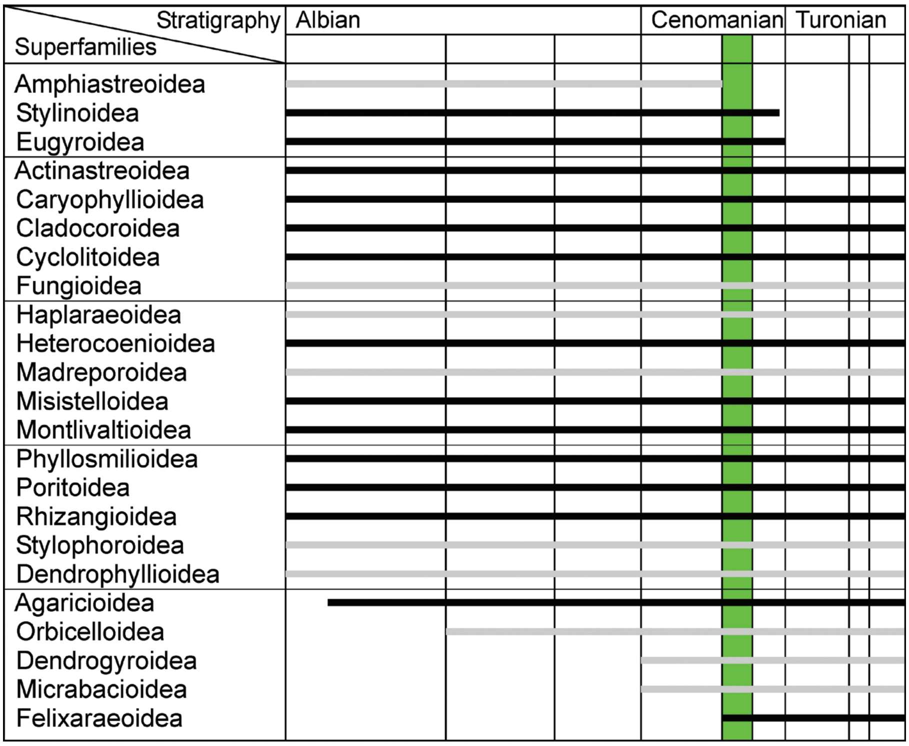

Figure 11. Verified stratigraphic distribution of the superfamilies. The ranges are based on the verified distribution data for the genera, as explained above. Only Albian to Turonian is shown. The vertical green bar marks the age of the studied fauna. All superfamilies are shown, as well as those superfamilies that do not occur in the studied fauna. Superfamilies that do not occur in the study area are shown as light grey bars.

lower or the upper Cenomanian (for example, for the Boreal regions see Löser 1994, for the Western Tethys Löser and Wilmsen 2022, for the Central Tethys Löser and Bilotte 2017, for the Eastern Tethys Löser et al. 2018, and literature cited therein). Shallow marine middle Cenomanian coral faunas are poorly reported. The classical Cenomanian outcrop area near Le Mans (Sarthe, France) can only be assigned to the middle to upper Cenomanian (Morel ed. 2015). Middle to Upper Cenomanian corals are mentioned from the Batna area in Algeria (Vila 1977). Some of these outcrops could be restricted to the middle Cenomanian. Unrevised coral faunas of a lower to middle Cenomanian age are reported from Tournai beds in Hainaut (Belgium; d'Archiac 1847) The Boreal coral fauna of the Meißen Fm (Saxon, Germany) has a lower middle Cenomanian age (Löser 2014b).

The present large coral fauna that can clearly be restricted to the middle Cenomanian is, therefore, an exceptional record. The duration of the lower, middle and upper Cenomanian is too short to allow the recognition of evolutionary changes, but the present fauna links together, even more solidly, the typical upper Lower Cretaceous coral faunas (Barremian to Albian) and the lower Upper Cretaceous (Turonian to Santonian). One reason may be the marly facies; other Cenomanian coral faunas are found in coastal transgressive areas with a considerable siliciclastic input, or in deposits of carbonate ramps. Other Cenomanian coral faunas in a marly facies such as from the study area are hardly known.

With the present study it can be confirmed that the shallow marine coral faunas experienced a transition that already started in the Lower Cretaceous and continued during the Cenomanian. The gap in the fossil coral record during the Turonian is just the lack of shallow marine sediments (and therefore outcrop areas; Löser 2016c, Fig. 6.3.5.3) due to the regression during the Turonian and the subsequent erosion. Coniacian coral faunas differ from Cenomanian faunas which concerns particularly the genus richness of vicariant families. As, for instance, Latomeandridae became reduced in the number of genera, Synastraeidae increased, or Montlivaltiidae were reduced in genera but Phyllosmiliidae were increased (cf. Löser 2016c, Fig. 6.2.2).

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