

An Echinoderm Fauna from the Lower Miocene of Austria: Paleoecology and Implications for Central Paratethys Paleobiogeography

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(With 4 text-figures and 9 plates)

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Abstract

A Lower Miocene echinoid fauna from Lower Austria (Unternalb, Retz Formation) is reported. Ten taxa are described; among these, the genera *Arbacina*, *Astropecten* and *Luidia* are recorded for the first time from the Eggenburgian (corresponds to the Lower Burdigalian) of the Central Paratethys. An interpretation of the paleoecological requirements of the recorded taxa and of the paleo-environment of the investigation area is presented.

The first occurrence of *Arbacina* in the late Eggenburgian of the Austrian Molasse Basin is clear evidence to faunal migrations from the Rhône Basin into the Central Paratethys via the alpine foredeep.

Keywords: Echinodermata, Echinoidea, *Arbacina*-immigration, Paleobiogeography, Paleoecology, Austria, Unternalb, Lower Miocene, Eggenburgian, Retz Formation

Zusammenfassung

Eine untermiozäne Echinodermaten Fauna aus Österreich (Unternalb, Retz Formation) wird vorgestellt. Zehn Taxa werden beschrieben, darunter können die Gattungen *Arbacina*, *Astropecten* und *Luidia* erstmals aus dem Eggenburgium der Zentralen Paratethys nachgewiesen werden. Eine Interpretation der Palökologie der beschriebenen Taxa und des Ablagerungsraumes wird vorgestellt.

Das erste Erscheinen der Echinacea Gattung *Arbacina* im oberen Eggenburgium der Molasse wird als Hinweis für Migrationen aus dem Rhône Becken in die Zentrale Paratethys über die Alpenvertiefe gewertet.

Schlüsselwörter : Echinodermata, Echinoidea, *Arbacina*-Einwanderung, Paläobiogeographie, Palökologie, Österreich, Unternalb, Untermiozän, Eggenburgium, Retz Formation

Introduction (fig. 1)

In contrast to the marine fauna of the Horn Basin and Eggenburg Bay - the classical investigation areas of the Lower Miocene Eggenburgian stage - little attention has been focused on the usually poorly preserved fauna of the neighbouring Retz Formation of the Obermarkersdorf Basin and Nalb Bay.

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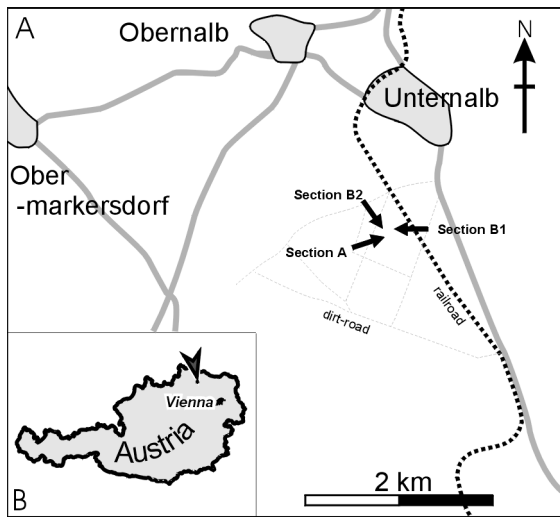


Fig. 1: Location of the logged sections near Unternalb, Lower Austria. Inset shows the position of the studied area within Austria.

Only scattered data on the flora and fauna of the siliciclastic, nearshore deposits have been reported during the past decades. The rather diverse bryozoan fauna was investigated by KÜHN (1955) and VAVRA (1979 & 1981). BERNHAUSER (1955) described some molluscs, and rare fragments of palms were documented by HOFMANN (1936). Over the last few years our knowledge on the Retz Formation has been improved during the mapping of sheet Hollabrunn and Retz (ÖK 50, nr. 22 and 9) by ROETZEL and through a workshop of the Geological Survey Vienna. This workshop resulted in a state-of-the-art summary of the lithostratigraphic and chronostratigraphic framework in the investigation area by ROETZEL, MANDIC & STEININGER (1999), a short comment on the nautilids of the Retz Formation by LUKENEDER & al. (1999), a palaeoecological analysis of the pectinid fauna of the region by MANDIC & HARZHAUSER (1999), and initial considerations on the echinoid fauna by HARZHAUSER & KROH (1999).

In the course of this study, the Retz Formation turned out to bear an extraordinarily rich echinoderm fauna consisting of at least ten taxa.

The associated echinoderm taxa derive mainly from micro-samples and are documented by single ossicles of astropectinids and unidentifiable remains of ophiuroids and comatulids.

In addition the first occurrence of the genera *Arbacina*, *Luidia*, *Astropecten* and of the families Diadematiidae and Cidaroidea in the Lower Miocene of the Austrian Molasse Basin is proved. The first occurrence of *Arbacina* in the Paratethys is of particular importance for the reconstruction of the Lower Miocene palaeobiogeography.

Finally, distinct associations can be recognised which - based on the sedimentology and ecology of recent echinoderms - allowed the interpretation of different palaeoecological environments.

Geological Setting (figs. 2-3)

The sediments of the Retz Formation are deposited in Nalb Bay, which was formed as a result of several NNW-SSE directed crystalline crests, projecting as numerous small

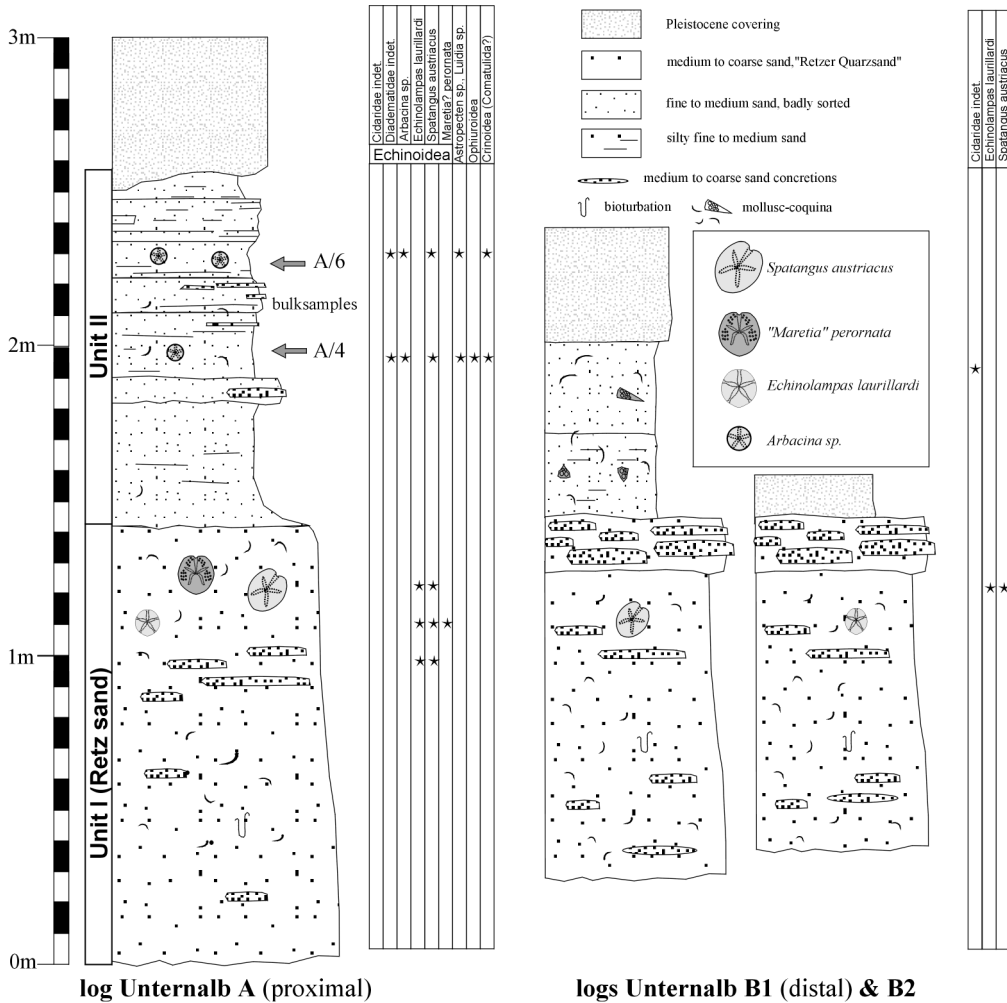


Fig. 2: Unterhalb, Lower Austria: Logged sections with distribution of the echinoderm taxa and position of the bulk samples within the sections.

offshore islands and submarine highs approximately 6 km into the Molasse Basin. The presented echinoderm fauna derives from shallow sublittoral coarse to fine quartzsands of the Retz Formation, which represents a siliciclastic equivalent to the limestones of the Zogelsdorf Formation. Its dating into the Eggenburgian is based on ostracods (ZORN, 1999); furthermore, the mollusc fauna allows an even more exact dating into the upper Eggenburgian (MANDIC & HARZHAUSER, 1999).

During the 19th century the coarse sands were exploited in two sand pits SSW of Unterhalb (Lower Austria). Today the pits are closed and overgrown by vegetation. Two sedimentary units can still be logged at the section; the underlying unit I consists of a few metres whitish to yellowish, poorly sorted and poorly rounded, immature, coarse quartzsands, deriving from the Thayabatholith-granite which formed the coast and ad-

jacent hinterland of Nalb Bay. This so-called "Retz sand" represents the earliest Cenozoic sediment in the investigation area and largely fills the crystalline relief. As hanging wall unit II, up to 3 m yellowish to greyish, immature fine to medium sand is developed, displaying a rapidly changing, patchy bio- and lithofacies. Three sections were logged within the pits (fig. 2); the log Unternalb A represents a proximal section, whereas Unternalb B1 is separated from the former by a small crystalline ridge and is in a more distal, basinward position. Unit I can be traced in all sections and displays similar lithological and biotic features. Besides large-sized echinoids, pectinids are the most important macrofossils in the coarse sands, whilst aragonitic shells are completely dissolved. In contrast, the sedimentology and bio-content of unit II are quite different in log B1 and A. Thus, unit II of log A bears accumulations of balanids, bryozoans, asteroids, regular echinoids, mytilids and glycymerids, but the distal log B1 comprises turritellids, scaphopods and several species of infaunal bivalves.

An idealised cross-section of the investigated area (fig. 3) explains the various facies represented here as result of a marine transgression onto the Bohemian Massif.

1. The first ingression of the Eggenburgian Sea invaded the granitic palaeorelief and resulted in rapid sedimentation of coarse, immature quartzsand, which largely filled the topography of the shallow sublittoral Nalb Bay; autochthonous deposition is also reflected by scattered granitic lithoclasts.

The most abundant macrofossils in these environments are pectinids such as *Pecten hornensis* and *Aquiptecten praescabriuscula*, which form vast but thin coquinas. Calcitic bivalves such as *Anomia ephippium* and various ostreids also appear in fair numbers. Venerids and lucinids may also occur, but due to the unfavourable preservation no specific identification is possible. Among the gastropods, *Turritella doublieri* and the medium-sized *Conus* cf. *mercati* prevail. Rare teredinid bivalves, casts of a large *Xenophora* and remains of the nautilid *Aturia aturi* complete the list of common molluscs. These mollusc associations are joined by a rich echinoderm fauna consisting of at least three irregular echinoids: *Spatangus austriacus*, *Maretia? perornata* and *Echinolampas laurillardii*. Large populations of *Spatangus austriacus* ploughed the coarse sand and developed nearly giant-sized shells. Due to heavy solution within unit I, the solid corona of the echinoids is often dissolved and therefore only internal casts are usually found on the fields close to the pits.

2. Rapid narrowing of the accommodation space and the northward shift of the coastline caused a change in sedimentation and resulted in the development of small-scale facies patterns. Littoral conditions became established at the topographic highs, which acted as islands or submarine ridges, such as at the small crystalline mound in the quarry close to log A. The coarse sands on these highs are typically dominated by balanid fragments and numerous shells of the archaeogastropod *Diloma (Paroxystele) amedei*, along with less abundant shells of *Patella* and *Ostrea*. All these animals prefer the well-agitated habitat in the rocky littoral.

Distally around the highs this facies passes into slightly less coarse sands with a rich mollusc fauna consisting of partly articulated shells of *Acanthocardium moeschanum*, *Pholadomya alpina* and *Glycymeris fichteli*, whereas *Babylonia eburnoides*, *Tudicla rusticula* and *Ficopsis burdigalensis* dominate the gastropod fauna, accompanied by two naticids and the very rare muricid *Typhis horridus*. Additionally, the diverse bryozoan fauna from the Retz Formation, described by KÜHN (1955) and VAVRA (1978 & 1981),

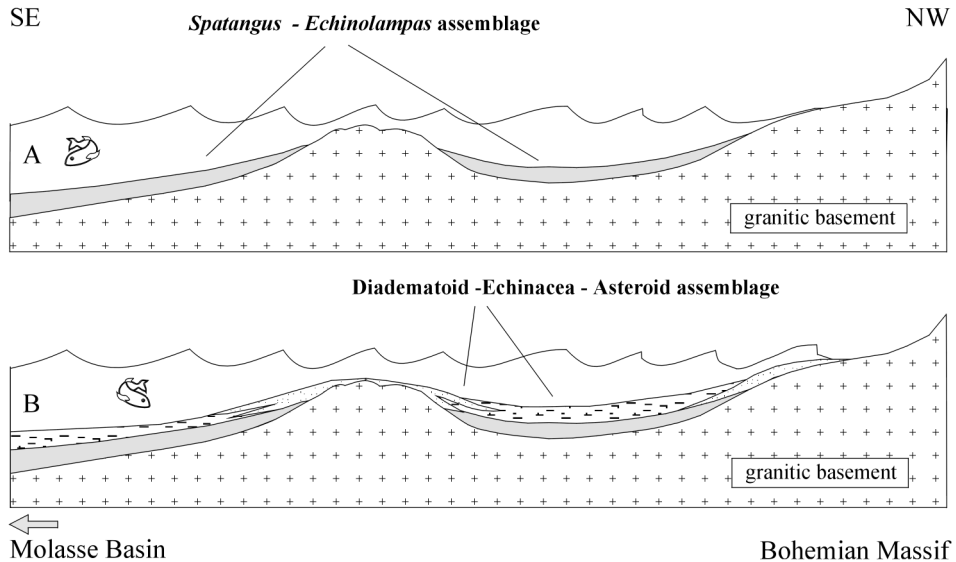


Fig. 3:

A: late Eggenburgian, marine transgression onto the Bohemian Massif (Unit I).

Coarse, immature quartz-sands largely fill the pre-existing relief. The typical "Retz sand" is deposited during this early stage. An assemblage of shallow-burrowing echinoids claims this environment (*Spatangus-Echinolampas* assemblage). Besides echinoids only pectinids and deep-burrowing glycymerids occur in fair numbers.

B: Small-scale facies pattern and diversification of echinoderms (Unit II).

Hardgrounds and coarse balanid sands characterize the topographic highs in the bay. Littoral conditions established themselves around these highs, being recorded by masses of balanids and archaeogastropods (*Diloma*). Laterally this facies passes into thin-bedded fine to coarse sands with bryozoans and a diverse echinoderm fauna. Bryozoa thickets and sandflats developed in the shallow marine bay, providing a habitat for asteroids, ophiuroids and the small echinoid *Arbacina*; shaded areas and cavities were probably settled by comatulids.

The echinoderm diversity distinctly declines in the outer bay. Silty sands with a rich mollusc infauna reflects a deepening towards the basin. Only epibenthic cidaroids were recorded, whereas infaunal echinoids seem to have been replaced by the predominant molluscs.

derives mainly from these sands. This agitated, shallow marine bay with its bryozoan thickets was settled by asteroids and ophiuroids as well as crinoids. Among the echinoids the small-sized *Arbacina* and diademmatids are recorded.

These nearshore, shallow sublittoral assemblages are restricted to the turbulent Nalb Bay but are replaced basinwards by a turrillid-aequipterinid assemblage in poorly sorted, muddy fine to coarse sands. A predominately infaunal mollusc fauna with masses of turrillids, venerids and scaphopods - in addition to *Panopea menardi* - characterises the biofacies.

Echinoderm remains are rare, although the well-preserved spines of cidaroids indicate that a small population of cidaroids inhabited the rather calm shallow sublittoral sand flats of the outer Nalb Bay.

A single layer of *Diloma amedei* apparently represents an allochthonous occurrence of shells; they were probably transported into the shallow basin from an adjoining littoral environment in the course of a storm.

Materials and methods

Apart from a few whole or at last partly preserved echinoid tests, all material was found in the form of isolated skeletal ossicles. Despite the problems when working with isolated skeletal elements of echinoderms, this approach was necessary because of the lack of whole specimens in this and adjacent outcrops for most of the echinoderm taxa. Additionally a few whole or at least partly preserved specimens have been collected in the field by the second author.

The isolated ossicles were obtained from two bulk samples (sample A/4 and A/6) taken from unit II of section Unternalb A. The bulk samples were splitted into grain-size fractions by wet sieving and the fractions larger than 0.5 mm and larger than 2.5 mm were scanned for echinoderm material under a dissecting microscope. All echinoderm material was removed from the samples. The material was cleaned subsequently by washing and using of an ultrasonic vibrator. After drying, the material was sorted and some apparently well-preserved specimens were taken for further analysis under the scanning electron microscope. These specimens were cleaned again by an ultrasonic vibrator, initially in a 10% solution of H₂O₂, then in a 50:50 solution of dishwashing detergent and water, and finally in clear water to remove traces of the detergent. After drying, the specimens were mounted on specimen stubs and gold-coated for the scanning electron microscope. All SEM-photos were taken by the first author on the SEM of the Institute for Palaeontology, University of Vienna; the macro-photos were taken by A. SCHUMACHER at the Natural History Museum of Vienna. All material used for this study is deposited at the Natural History Museum Vienna (the inventory numbers of the figured specimens are given in the plate descriptions, material not figured is stored under the number NHMW1999z0051/0028). All measurements were made with an electronic digital calliper (mean error: 0.03 mm) and are given in millimetres with one decimal.

Results

Systematic Part

Class Crinoidea MILLER, 1821

(pl. 4, figs. 1-4)

Subclass Articulata ZITTEL, 1879

Material: Ten brachials and six cirri were found in bulksample A/4 and five brachials in bulksample A/6, both from the section of Unternalb A. (figured specimens are stored under the number NHMW1999z0051/0001)

Description

Brachials (pl. 4, fig. 1-2): The brachials are rather large (width: 2,5 mm, height: 2 mm, thickness: 0,5 to 1 mm) and have a triangular to rectangular shape. The dorsal side is

rounded and bears small ridges in some specimens. The attachment area for the pinnulae, if present, lies ventrally and is as wide as the brachial is thick.

Cirri (pl. 4, fig. 3-4): The cirri are rather large, massive and of low cylindrical shape. The axial canal is relatively narrow and lies slightly ventrally of the centre. The distal and the proximal articulation surface are roughly parallel to each other and are inclined to the axis of the ossicle. The distal articulation surface bears a distinct articulation ridge, which is perforated by the axial canal. On the proximal articulation surface the axial canal lies in a shallow depression and the articulation ridge is not so prominent as the distal one.

Remarks: The ossicles found in the bulk samples are heavily abraded and overgrown by syntaxial rim cement in most cases. This and the fact, that only brachials and cirri were found, made a more accurate determination impossible. It seems likely, however, that these specimens are remains of comatulids and belong to the species *Discometra eggenburgensis* (SCHAFFER, 1912), which was originally attributed to the genus *Antedon* by SCHAFFER (1912a) but later revised by SIEVERTS-DORECK (1961), and of which centrodorsals and brachials are abundant in several localities near Eggenburg (Lower Austria). Up to now these were the only crinoid remains described from the Miocene of Austria, although in the Miocene of Hungary crinoids, especially comatulids, seem to be quite abundant at some localities (VADASZ, 1915).

Class Asteroidea DE BLAINVILLE, 1830

Numerous asteroid remains were found in the bulk samples from the profile Unternalb A, mainly marginal ossicles but also ambulacral ossicles and paxillae. In most cases they are abraded and overgrown by syntaxial rim cement. Only few could be cleaned sufficiently for detailed study and photography. The availability of isolated ossicles only and the bad state of preservation of most specimens, prevented specific determination. Generic determination was possible, but only by comparison with recent material (whole dried specimens as well as single skeletal ossicles from disarticulated specimens); additionally, the papers of BLAKE (1982) and SPENCER & WRIGHT (1966) were consulted. Asteroid remains, in most cases isolated ossicles, are common in many outcrops throughout the marine sediments of the Miocene in Austria, but were rarely described. To date only one taxonomic work on asteroids of the Vienna Basin has been published (HELLER, 1858), in which Lower Miocene material from Austria is not considered.

Order Paxillosida PERRIER, 1884

Family Luidiidae VERRILL, 1899

Luidia sp.
pl. 5, figs. 1-5

Material: About 16 inframarginalia and 4 ambulacralia of *Luidia* sp. were found in both bulk samples (A/4 and A/6) from unit II of section Unternalb A.

Description

Inframarginalia (pl. 5, fig. 1 and 2, NHMW1999z0051/0006, NHMW1999z0051/0007): The inframarginal ossicles are small (height: 2.5 mm, length: 3.8 mm, width: 2.2 mm) and crescent-shaped. The proximal articulation ridge is weakly developed, whereas the distal articulation ridge is large and trapezoid. The outer face is convex and bears three to four large spine bases. The inner face is concave and featureless.

Ambulacralia (pl. 5, fig. 4 and 5, NHMW1999z0051/0009, NHMW1999z0051/0010): The ambulacral ossicles are large (length: 5.7 mm, width: 1.9 mm) and relatively symmetrical. The ambulacral body is triangular, the dentition weakly developed with a medial gap. Lower insertion for transverse muscles small and triangular. Oral groove shallow, oral apophyse prominent and adambulacral notch deep and angular. The wing-like structures are almost symmetrical and articulation area with the neighbouring ambulacrum is elongated.

Paxillae (pl. 5, fig. 3, NHMW1999z0051/0008): Basal part of paxillae cross-shaped; the columella is broken.

Remarks: The distinct shape of the inframarginalia and ambulacralia allows (on the basis of comparison with disarticulated recent material) an assignment to the genus *Luidia*. A specific determination could not be made, due to the lack of articulated or at least partially articulated specimens.

Family Astropectinidae GRAY, 1840

Astropecten sp.

pl. 5, figs. 6-9

Material: More than one hundred marginals of *Astropecten* sp. were found in bulk samples A/4 and A/6 from unit II of section Unternalb A.

Description

Supramarginalia (pl. 5, fig. 6, NHMW1999z0051/0011): Massive, high (height: 4.6 mm, length: 3.5 mm, width: 2.6 mm) and in most cases narrower than inframarginals of similar size. The outer face is smooth and convex, whereas the inner face is almost flat. Both the distal and the proximal side bear a distinct articulation area which covers about the half of the surface of each side. The articulation area on the proximal side is slightly larger than on the distal side. The intermarginal face is concave.

Inframarginalia (pl. 5, fig. 7 and 8, NHMW1999z0051/0012, NHMW1999z0051/0013): Massive, slightly elongated (height: 3.2 mm, length: 4.9 mm, width: 2.9 mm) and roughly triangular in side view. The outer surface is covered by small tubercles and bears a row of larger spine bases along the proximal margin. The articulation area on both sides (proximal and distal) is large and distinct. On the proximal side it covers nearly the whole surface; on the distal side it is somewhat smaller. The intermarginal face is slightly convex.

Remarks: Their distinct shape makes marginals of the genus *Astropecten* well recognizable, especially when recent material is available for comparison. No specific determination could be made due to the lack of articulated or at least partially articulated specimens.

Distribution: In the section A at Unternalb marginalia of *Astropecten* are among the most common fossils. The authors observed similar ossicles in several localities in the region of Eggenburg (Lower Austria): Hengl Quarry at Limberg, Grübern and Zogelsdorf.

Undetermined Asteroid Ossicles

Material: Undetermined asteroid ossicles were found throughout unit II of section Unternalb A (including bulk samples A/4 and A/6). The figured specimen (pl. 5, fig. 9) stems from bulk sample A/4.

Description

Paxillae (pl. 5, fig. 9, NHMW1999z0051/0014): The figured specimens unfortunately lack the base and might belong to *Luidia* as well as to *Astropecten*. However, the paxillae of the recent specimens used for comparison were thicker and shorter in *Astropecten* than in *Luidia*; the figured ossicle therefore probably belongs to the genus *Astropecten*.

Class Ophiuroidea GRAY, 1840

Material: Three vertebrae and one lateral shield were found only in bulk sample A/4 from unit II of section Unternalb A.

Description

Lateral shields (pl. 4, figs. 10-13, NHMW1999z0051/0003) : According to HESS (1962) the lateral shields are best suited for a specific determination; unfortunately, only one has been found in the samples.

The single lateral shield is relatively small, slightly flexed and shows a distinct ridge running diagonally from the ventral to the dorsal margin, on its internal surface. On the outer surface the lateral shield shows fine wrinkles. The distal rim bears three spine bases.

Vertebrae (pl. 4, figs. 5-9, NHMW1999z0051/0002; pl. 6, figs. 1-10, NHMW1999z0051/0004, NHMW1999z0051/0005): On their distal sides, all three vertebrae possess a set of medio-lateral projections in the form of three vertically elongated articulation ridges, of which the middle one lies about half of its length more ventrally. On the proximal side a depression is developed; it is surrounded by three articulation processes which form a hinge with their opposing counterparts of the distal side (zygospondylous articulation). The smallest of the three vertebrae shows a well-developed dorsal groove, which is only slightly visible in the second-largest specimen and missing in the largest.

Remarks: The ophiuroid ossicles found, are relatively well preserved, but the lack of complete or even partly preserved animals prevents a generic determination. If more isolated ossicles were available, then a determination based on comparison with recent material might be achieved. Nevertheless, the vertebrae found are all figured in five different views to provide easier comparison as suggested by HESS (1962).

All three vertebrae have a zygospondylous articulation and generally show similar morphologic features, indicating that they all belong to the same species. Vertebrae possessing this type of joint are often placed within a separate order, the Ophiurae (HYMAN, 1955).

It seems most likely that the described lateral shield represents the same species as the vertebrae, although this assumption cannot be proven.

Distribution: No ophiuroid remains were known from the Eggenburgian of Austria up until now. Only in the Karpatian (BINDER & STEININGER, 1967) and the Badenian (KÜPPER, 1954) have a few remains of ophiuroids been reported.

Class Echinoidea LESKE, 1778

The description of the coronal pores of the echinoids corresponds to the nomenclature of SMITH (1978, 1980b). The numbering of plate rows, where mentioned, follows the Lovénian system.

Subclass Cidaroidea CLAUS, 1880

Order Cidaroida CLAUS, 1880

Family Cidaridae GRAY, 1825

Cidaridae indet.

pl. 7, figs. 1-4

Material: Four fragments of spines belonging to the family Cidaridae were found in the upper part of the section Unternalb B1, which corresponds to unit II of the section Unternalb A. These spines are exceptionally well preserved, and no cement obscures the internal structures of the spines. Syntaxial rim cement overgrows the outer spine surface, cementing surrounding sediment particles to the spines and thereby obscuring surface details.

Description

Spines (pl. 7, fig. 4, NHMW1999z0051/0015): Primary spines slightly flattened, long and slender, tapering slightly from base towards the distal end. The surface of the spines is covered by small nodulae (see CUTRESS, 1980) arranged more or the less in vertical rows. Between these *nodulae*, even smaller, rounded protuberances, termed granulae here, are loosely spread. The collar as well as the milled ring are smooth, the acetabulum is not preserved in any specimen.

Cross section (pl. 7, figs. 1-3, NHMW1999z0051/0015): The medulla has a diameter of about 30 % of the corresponding spine diameter and consists of an irregular mesh. In the centre of the medulla, the holes of the mesh are larger than at the margin. The lamellae, which are connected to each other by trabeculae, radiate from this central part. The outermost layer of the spine is formed by moderately thick cortex. All three zones are clearly separated.

Dimensions: The largest spine fragment is 35.1 mm long and has a maximum diameter of 3.7-4.5 mm (spine flattened).

Remarks: Due to their characteristic external and internal features, this spines certainly belong to the family Cidaridae. No test fragments or even single plates were found,

making a more precise determination impossible. This is the first record of cidaroids from the Lower Miocene of Austria and also, to the authors' knowledge from the Central Paratethys.

Distribution: In the studied area, these spines were only found in the upper part (unit II) of section Unternalb B1. Similar spines were, however, observed by the authors in the following Eggenburgian localities: Hengl Quarry, Limberg (Lower Austria) and Grübern (Lower Austria).

Subclass Euechinoidea BRONN, 1860

Infraclass Acroechinoidea SMITH, 1981

Cohort Diadematacea DUNCAN, 1889

Order Diadematoidea DUNCAN, 1889

Family Diadematidae GRAY, 1855

Diadematidae indet.

pl. 8, figs. 1-7

Material: About one hundred spine fragments and 5 plates were obtained from the bulk samples A/4 and A/6 from Profile Unternalb A.

Description

Ambulacral plates (pl. 8, fig. 3, NHMW1999z0051/0021): Each plate bears one large perforate, crenulate marginal tubercle in the middle of the plate. The tubercles have a low arched mamelon, which has no undercut neck, with a large centrally perforation and a small platform with coarse crenulation. No inner tubercles are present. Each ambulacral plate bears three P2 isopore pairs. The pores in each pair are subcircular, of subequal size and nonconjugated. The perradial pores bear a small but distinct neural canal at their adoral margins. The ambulacral plates belong to the diadematoid compound type.

Interambulacral plates (pl. 8, figs. 1, 2, 4, NHMW1999z0051/0019, NHMW1999z0051/0020): Most of the plates found bear a single, large, perforate, crenulate primary tubercle, very similar to the marginal tubercles described above. Some plates show two primary tubercles. The remaining surface of the plates is smooth and lacks morphological details.

Spines (pl. 8, figs. 5, 6, 7, NHMW1999z0051/0022): The spines, respectively their fragments, are hollow, lacking any medullary structure. On the outside they show spinous processes arranged in spirals, producing a verticillate pattern. The bases of the spines are distinctly separated from the shaft by a prominent crenulated ring.

In cross section the spines show a central cavity, which is completely hollow. The spines are made up from wedge-shaped radial septa, which are rounded on their outer face and decrease in thickness inwards. At their bases these radial septa are fused together to form an axial pipe. This pipe is perforated by pores arranged in spirals. Trabeculae between the radial septa connect adjacent septa.

Dimensions: The spines have a diameter between 0.8 and 1.2 mm, the lengths of the fragments vary from one to several millimetres. A typical interambulacral plate is 3.3 mm long and 2.4 mm wide.

Remarks: The diadematoid compound plating, the large crenulate, perforate tubercles and the hollow, verticillate spines are typical for members of the family Diadematidae GRAY, 1855 (FELL, 1966; SMITH, 1980a).

Distribution: The family Diadematidae GRAY, 1855 is known from the lower Jurassic to recent (FELL, 1966b), but only few fossil diadematids have been described. This can probably be explained by the relatively fragile test and spines. Despite several studies on Lower Miocene echinoids from Austria (LAUBE, 1871; SCHAFFER, 1912b; STEININGER, 1971), diadematoids have not been recorded, nor have they been mentioned in other works. They are presented here for the first time for the Lower Miocene of Austria and probably for the entire Paratethys.

The studied material was found in the bulk samples (A/4 and A/6) from unit II of section Unternalb A.

Cohort Echinacea CLAUS, 1876

Superorder Camarodonta JACKSON, 1912

Order Temnopleuroida MORTENSEN, 1941

Family Temnopleuridae A. AGASSIZ, 1872

Genus *Arbacina* POMEL, 1869

Arbacina sp.

fig. 4; pl. 7, figs. 5-7

Material: Abundant material from bulk samples A/4 ad A/6 of section Unternalb A (unit II) was available for study; this included 22 whole coronas as well as about one hundred test fragments (NHMW1999z0051/0016, NHMW1999z0051/0017, NHMW1999z0051/0018). Most of the specimens were abraded or overgrown by syntaxial rim cement, and only a few could be cleaned sufficiently for detailed study and photography.

Description

Size and shape: The test is very small, hemispherical with circular outline. In profile the test is domed, with a tumid ambitus. The oral surface is flattened.

Apical system: The apical system is lacking in all specimens. The apical area is about one third as wide as the peristome.

Ambulacra: The ambulacra are about half as wide as the interambulacra. Each plate bears one large imperforate, noncrenulate marginal tubercle with a distinct boss and a globular mamelon with undercut neck. Along the adapical and perradial border of each ambulacral plate, several imperforate, noncrenulate inner tubercles are found. Two to three of these situated at the edges of the plates are distinctly enlarged, the remaining ones are small.

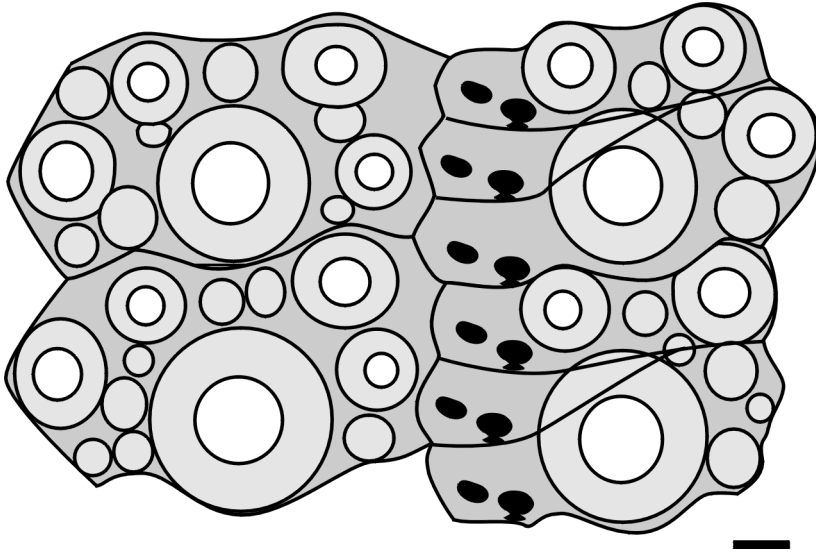


Fig. 4: Schematic drawing of two interambulacral and two ambulacral plates of the ambital region of *Arbacina* sp. (Redrawn from a SEM picture; scale bar equals 0.1 mm.)

Each ambulacral plate bears three partitioned isopores (type P2 of SMITH, 1978), which are distinctly oblique. The pores in each pair are subequal and subcircular; the perradial pores bear a distinct neural canal at their adoral margin. The interporal partition is a ridge with a knob-shaped central elevation. The plates belong to the echinoid compound type.

Interambulacra: Each interambulacral plate bears one large imperforate, noncrenulate primary tubercle with a distinct boss and a large globular mamelon with an undercut neck; this tubercle is situated slightly below the centre of each plate. The largest tubercles are found at the ambitus. Furthermore, each plate bears many imperforate, noncrenulate secondary tubercles covering nearly the entire plate surface. Four secondary tubercles are distinctly enlarged, two on each side of the primary tubercle.

Peristome: Situated centrally on the ventral surface; circular in outline, with shallow gill slits. The peristome is about half as wide as the test diameter.

Dimensions: Largest whole specimen: diameter: 6.5 mm; height: 3.7 mm; Typical specimen: diameter: 3.6 mm; height: 2.1 mm

Remarks: Although the depressions in the horizontal sutures, which MORTENSEN (1943) regards as critical feature for this genus, could not be observed, the specimens studied here are nevertheless placed within the genus *Arbacina*. These depressions can easily be obscured by growth of cement, which to various extent was observed on all specimens. All other features, such as the small hemispherical test, the dense secondary tuberculation and the lack of sculpture fit very well with the descriptions given for this genus by MORTENSEN (1943) and FELL & PAWSON (1966).

Distribution: The genus *Arbacina* occurs in the Lower to Middle Miocene of the Rhône Basin (LAMBERT, 1910-15), of Sardinia (COTTREAU, 1913) and Malta (CHALLIS, 1980),

as well as in the Miocene of Egypt (FORTEAU, 1920). Until now, in the Paratethys this genus was only known from the Middle Miocene of Poland (MACZYNSKA, 1966), the Ukraine (SZÖRÉNYI, 1950) and Hungary (VADASZ, 1915).

Cohort Irregularia LATREILLE, 1825

Superorder Microstomata, SMITH, 1984

Series Neognathostomata SMITH, 1981

Order Cassiduloida CLAUS, 1880

Family Echinolampadidae GRAY, 1851

Genus *Echinolampas* GRAY, 1825

***Echinolampas laurillardi* AGASSIZ & DESOR, 1847**

pl. 2, figs. 1-3

Synonymy

1869 *Echinolampas laurillardi* AGASSIZ et DESOR; DES MOULINS: 315; pl. 18, fig. 1-3

1871 *Echinolampas laurillardi* AGASSIZ; LAUBE: 66-67; pl. 18, fig. 1

1871 *Echinolampas angustistellatus* n. sp.; LAUBE: 67; pl. 18, fig. 4

1912 *Echinolampas laurillardi* AGASSIZ; SCHAFFER: 189; pl. 60, fig 4, 6

1912 *Echinolampas laurillardi* var. *acuminata* n. var.; SCHAFFER: 190; pl. 60, fig. 5

1955 *Echinolampas* sp.; BERNHAUSER: 182

1971 *Echinolampas laurillardi* AGASSIZ; STEININGER: 595, pl.3, fig. 3-4

Material: One slightly damaged specimen (NHMW1999z0049/0002) and several internal casts bearing only small fragments of the test.

Description

Size and shape: The test is large with subpentagonal outline and is slightly elongated antero-posteriorly. The maximum width lies posterior of the apical system, about two-thirds of the test length away from the anterior margin. In profile the test is domed, the maximum height coinciding with the position of the apical system. The ambitus is rounded and tumid.

Apical system: Not preserved.

Ambulacra: Adapically the ambulacra are petaloid, moderately broad and straight. The petals extend about 75 % of the corresponding test radius from the apical system to the margin; distally they close somewhat. The ambulacral pores in the petals are conjugated anisopores, which are strongly conjugated and slightly oblique. The perradial pores in each pair are rounded, the adradial pores are elongated, up to twice as long as the per-radial pores and teardrop-shaped. The pores in each pair are connected by a narrow groove. Adjacent pore pairs are separated by a low, granulated ridge. Pores of the most distal pore pairs are subequal and rounded. Interporiferous zones within the petals inflated and up to five times as wide as a single poriferous zone. The poriferous zones are slightly depressed.

Adorally the ambulacra form moderately depressed phyllodes. They consist of four series of unipores in each ambulacrum. Two "outer" or adradial series with large, closely spaced unipores with rather large attachment area and two "inner" or perradial series with smaller, slightly vertically elongated unipores, which are more widely spaced. The two buccal pores are of similar size as the pores from the adradial series, but distinctly elongated vertically.

Interambulacral: Adapically the interambulacra are slightly inflated. Apically they are covered with small, crenulate, perforate tubercles which are deeply sunken and closely spaced. The areoles are inclined towards the margin of the test. The tubercle density on the apical surface ranges from 120 to 140 tubercles/cm², being highest near the apical system and decreasing gradually towards the margin. On the oral surface the tubercles are slightly larger and their density ranges from 80 to 100/cm²; the highest densities on the oral side are found near the margin. On the oral side the interambulacra are slightly inflated and form small, inflated bourrelets adorally.

Periproct: Situated inframarginally in interambulacrum 5; it is large, oval, transversely elongated and slightly rostrate.

Peristome: Situated slightly anterior of centre and lies in a shallow depression. It is sub-pentagonal and transversely elongated.

Dimensions: Figured specimen: length: 84.8 mm, width: 84.3 mm, height: 34.7 mm

Remarks: These specimens seem to be conspecific with specimens ascribed to *Echinolampas laurillardi* LAUBE, 1871, which is relatively abundant in the vicinity of Eggenburg. ROMAN (1965) regards *E. laurillardi* as synonymous to *E. richardi* (DESMAREST in BROGNIART, 1829), but gives no detailed description of figures. This question can only be resolved with many well-preserved specimens, which, unfortunately, were not available from the localities considered here. The name *E. laurillardi* is therefore retained until further examinations can be made.

LAUBE (1871) was the first to describe this species from localities in Austria; his description matches quite well with the specimens considered here, but his figures do not match with his own descriptions. Furthermore, he erected a new species of the genus *Echinolampas*: *E. angustistellatus*, based on a few fragmentary remains, in part from the same locality where he had found *E. laurillardi*. The figure he gave of his new species clearly is not very accurate because it lacks the periproct, but has instead a smooth area covered by tubercles. As SCHAFFER (1912b) suggested, it is likely that *E. angustistellatus*, LAUBE 1871 represents only a smaller morphotype of *E. laurillardi*.

Distribution: In Austria this species has been reported from various localities of Eggenburgian age by LAUBE (1871), SCHAFFER (1912b) and STEININGER (1971); all of them are situated in the region of Eggenburg, Lower Austria: Eggenburg (Kremserberg), Gauderndorf, Grübern and Zogelsdorf. In the studied area it was found in the lower part (unit I) of all three sections.

This species has also been reported from the Burdigalian of France (DES MOULINS, 1869).

Series Atelostomata ZITTEL, 1879**Order Spatangoida CLAUS, 1876****Suborder Micrasterina FISCHER, 1966****Family Spatangidae GRAY, 1825****Genus *Spatangus* GRAY, 1825*****Spatangus austriacus* LAUBE, 1871**

pl. 1, figs. 1-2 and pl. 3, fig. 2

Synonymy1871 *Spatangus austriacus* n. sp.; LAUBE: 73; pl. 19, fig. 2 and 2a1912 *Spatangus austriacus* LAUBE; SCHAFFER: 191-2; pl. 59, fig. 1-3; pl. 60, fig. 71971 *Spatangus austriacus* LAUBE; STEININGER: 595; pl. 2, fig. 3; pl. 3, fig. 5

Material: Fragments of this species were abundant in the sections Unternalb A and B1, but better preserved specimens could be obtained only from section A (NHMW1999z0049/0001). One specimen, although somewhat fragmentary, is rather well preserved (the figured specimen); two others are internal casts with fragments of the test adhering to them.

Description

Size and shape: Test large to very large, heart-shaped and slightly elongated anteroposteriorly, with distinct but shallow frontal sinus. The maximum width coincides with the position of the apical system and lies slightly anterior of the centre of the test. In profile the test is wedge-shaped with a strongly arched anterior slope and a gentle posterior slope. The anterior end is rounded, the posterior end pointed with a distinct rostrum, which overhangs the periproct. Slightly posterior of the apical system there is a distinct kink. The maximum height lies posterior of the apical system, about one-third of the distance apical system-posterior margin away from it. The ambitus is rounded and tumid. The oral side is flat; only the plastron is distinctly inflated.

Apical system: The apical system lies slightly anterior of the centre of the test. Although it is missing or damaged in all specimens available for this study, it is ethmolytic as observed on conspecific material from other localities.

Ambulacra: Ambulacrum III slightly depressed, increasingly so towards the anterior margin. The pore pairs are strongly oblique, widely spaced and arranged in straight rows. They are very small and lie in depressions. The pores in each pair are subequal in size and subcircular, with a small interporal partition in form of a low ridge between the two pores (partitioned isopores). The interporiferous zone is wide and bears only secondary and miliary tubercles.

Paired ambulacra petaloid, slightly depressed and moderately closed distally. The anterior paired petals form an obtuse angle of about 120° to 130°, the posterior paired petals an acute angle of about 60° with each other. The posterior paired petals are flexed slightly laterally at their distal tips.

The pore pairs are elongated isopores lying in shallow depressions. Adjacent pore pairs are separated by low ridges, which bear miliary tubercles only. The pores in each pair are rounded, slightly transversely elongated and subequal in size. The adradial pore in each pair tapers slightly on its perradial side. The interporal partition is 1 to 1.5 times as wide as the pores and has the form of a broad groove. The poriferous zones are slightly depressed, whereas the imporiferous zone, which is up to 2.5 times as wide as a single poriferous zone, is slightly inflated. Within the petals only loosely spread secondary tubercles and dense miliary tubercles are found. Only minute microunipores are present beyond the petals; they are situated at the adapical border of the plates, along the mid-line of each plate row.

Adorally, heavily cemented sediment and cement overgrowth prevent investigation.

Interambulacral: Adapically the interambulacra are slightly inflated between the petals. They bear a few crenulate, perforate primary tubercles with inclined areoles, which are arranged in chevron-shaped groups at the adapical border of each plate in interamb 1, 4 and 5. In interamb 2 and 3 the primary tubercles are situated along the borders of ambulacrum III, only a few being scattered along the adapical plate borders. Towards the margin of the test the primary tubercles are less numerous and smaller. The remaining surface of the interambulacra is covered by small, evenly distributed, crenulate perforate secondary tubercles with inclined areoles. Small miliary tubercles are densely scattered among them. On the oral surface heavily cemented sediment and cement overgrowth, as well as extensive testdamage, prevent investigation of many features. Nevertheless, the whole oral surface seems to be covered with crenulate, perforate primary tubercles with areoles, which are inclined towards the margin. Only few secondary and miliary tubercles are scattered among them. The largest tubercles are positioned between the peristome and the anterior margin. Towards the margin of the test the tubercles grow smaller. The plastron is large, inflated and is densely covered by crenulate, perforated primary tubercles, which are arranged in series radiating from a central elevation on the plastron.

Fascioles: No fascioles can be observed on the specimens from Unternalb, perhaps due to the rather poor surface preservation.

Peristome: The peristome is situated about 25 % of the test length away from the anterior margin. Although it is not well preserved in the specimens considered here, specimens from other localities show that it is crescentic with a small labrum (SCHAFER, 1912b).

Periproct: The periproct is situated inframarginally and overhung by a small rostrum. It is rather large and oval, transversely elongated. There is a distinct subanal depression, which is sparsely tuberculated.

Dimensions: Figured specimen: length: 126.2 mm, width: 117.9 mm, height: 52.8 mm

Discussion: The specimens clearly belong to the species *Spatangus austriacus* erected by LAUBE in 1871; no evidence suggests otherwise.

Distribution: *Spatangus austriacus* was found in unit I of section A and B1 at Unternalb, as well as in unit II of section A. This species has been recorded from Eggenburgian (Lower Miocene) and Badenian (Middle Miocene) sediments of Austria (LAUBE, 1871; SCHAFER, 1912b) and from the Middle Miocene of the Ukraine (SZÖRENYI, 1950).

Genus *Maretia* GRAY, 1855

Maretia? perornata (SCHAFFER, 1912) pl. 3, fig. 1

Synonymy

1912 *Spatangus* (*Maretia*) *perornatus* n.sp.; SCHAFFER: 190-1; pl. 59, fig. 4-6

1971 *Maretia perornata* (SCHAFFER, 1912); STEININGER: 596; pl. 1, fig. 5-6

Description

Size and shape: Test large, heart-shaped, slightly anteroposteriorly elongated, with a distinct frontal sinus. The maximum width lies slightly anterior of the apical system. In profile the test seems to be flat and wedge-shaped; the maximum height lies halfway between the apical system and posterior end. The ambitus is rounded and tumid. (Due to compaction of the sediment the examined specimen is crushed and very flat.)

Apical system: Not preserved.

Ambulacra: Ambulacrum III slightly depressed, narrow, straight and open. The pore pairs are very small, oblique and slightly depressed. The pores in each pair are subequal in size and subcircular, with a small interporal partition between the two pores (partitioned isopores). Only miliary tubercles are found in ambulacrum III.

The paired ambulacra are petaloid; the anterior paired ambulacra are straight and extend about two-thirds of the corresponding test radius from the apical system to the margin; the posterior paired ambulacra are flexed sharply posteriorly and their distal tips are flexed slightly laterally. The pore pairs lie in deep, steep-walled depressions. In the anterior poriferous zone of the anterior paired ambulacra, the uppermost ten pore pairs are very small, rudimentary conjugated isopores. The remaining pore pairs of the anterior poriferous zone and the pore pairs of the posterior poriferous zone, as well as the pore pairs of the posterior paired petals, are rather large, elongated isopores. The pores in each pair are subequal in size and rounded. The adradial pores taper slightly on their perradial side. The interporal area is about one-and-a-half times as wide as the pores and is crossed by a low transverse ridge, which links the two pores. Adjacent pore pairs are separated by high ridges lacking tuberculation. Only secondary and miliary tubercles are present in the ambulacra. Only very small microunipores are present beyond the petals. Adorally, heavily cemented sediment prevents investigation.

Interambulacra: Interambulacra not inflated, smooth. Interambulacra 1, 2, 3 and 4 bear very large, perforate, noncrenulate primary tubercles, which are recessed in camellae on the apical surface of the test. Interambulacra 1 and 4 each bear at least sixty, interambulacra 2 and 3 at least thirty-five such tubercles. These tubercles are not evenly distributed on the interambulacra; the plate rows adjacent to the anterior paired ambulacra bear distinctly more primary tubercles, and the primary tubercles on the plate rows, which do not border the anterior paired petals, are crowded near the interradian suture of the interambulacra. The surface between and around these enlarged primary tubercles is densely crowded with miliary tubercles. Secondary tubercles with distinct areoles are scattered among them, but are generally rather rare on the apical surface of the test; only

in interambulacrum 5 are there larger numbers of secondary tubercles, which are crowded along the interradial suture.

On the oral surface, densely crowded, perforate, crenulate secondary tubercles with a distinct steep boss, concave, asymmetrical parapet and inclined areoles are present. They decrease in size from the centre towards the margin; at the margin they are very small.

Periproct: Not preserved, but is situated inframarginally, oval-transversely elongated in specimens from other localities (see SCHAFFER, 1912b or STEININGER, 1971).

Dimension: Figured specimen: length: 97.6 mm, width: 89.0 mm, height: 22.9 mm (specimen is deformed!)

Material: One rather well-preserved specimen from section Unternalb A (NHMW 1999z0049/0003).

Remarks: Originally this species was attributed to the genus *Spatangus* (*Maretia*) by SCHAFFER (1912b) and given the name *S. perornatus*. STEININGER (1971) placed it within the genus *Maretia* and consequently corrected the name to *M. perornata*.

During this study, the generic assignment was re-evaluated because recent specimens of *Maretia* figured in various works (e. g. FISCHER 1966) seemed to be quite different from the species considered here. Therefore the attempt to achieve a better generic determination was made. The genus *Maretia* as described and figured in FISCHER (1966) fits well with the species considered here, except that the figured specimen has a shallow frontal sinus and, furthermore, no mention is made about rudimentary pores in the upper part of the anterior poriferous zone of the anterior paired petals.

In GRAY (1855) where, according to FISCHER (1966), the genus *Maretia* is erected, no figure and no detailed description is given; only a short statement can be found.

On the other hand, the subgenus *Phymapatagus* of the genus *Spatangus* as described and figured in FISCHER (1966) fits even better. Here, rudimentary pores in the uppermost plates of the anterior poriferous zone of the anterior, paired petals are mentioned as being characteristic for this subgenus. Unfortunately no comment on the plastron is made, which according to the figures and descriptions of SCHAFFER (1912b) is naked in *Maretia? perornata*. The type species of *Spatangus* (*Phymapatagus*) is *Spatangus britannus* TOURNOUER, 1869, but it is not figured in the original work and only a very brief description is given.

A third genus which is a potential candidate for *M.? perornata* is *Paramaretia*. This genus, too, has rudimentary pores in the uppermost plates of the anterior poriferous zone of the anterior, paired petals (FISCHER 1966).

Until a critical review, including a study of the type specimens, about the relationship and morphological differences of these three genera (*Maretia*, *Paramaretia* and *Spatangus* (*Phymapatagus*)) is made, the species considered here is placed within the genus *Maretia* with questionmark.

Distribution: The species *Maretia? perornata* was found only in a few localities, all of them near Eggenburg, Lower Austria: Eggenburg (Kremserberg) and Grübern.

In this study it is reported for the first time from Unternalb (section A, unit I).

Undetermined echinoid ossicles

Lantern elements (pl. 9, figs. 1-3, NHMW1999z0051/0023, NHMW1999z0051/0024, NHMW1999z0051/0025): Several lantern elements, namely rotulae and demipyramids, have been found in the bulk samples from Unternalb section A (unit II). They could not be determined accurately, but most probably belong to *Echinacea*.

Spines (pl. 9, figs. 4-7, NHMW1999z0051/0026, NHMW1999z0051/0027): Many small spine fragments were isolated from the bulk samples A/4 and A/6 from unit II of Unternalb section A. Most of these spine fragments belong to spatangoids (pl. 9, fig. 4-6), probably to *Spatangus austriacus*, which is the most common spatangoid in the samples. Only a few spine fragments of regular echinoids (pl. 9, fig. 7) were found.

Palaeoecology

Unit I

The coarse quartzsands of the Retz Formation, as exposed in Unternalb, Lower Austria, yielded a relatively diverse echinoid fauna. *Spatangus austriacus* LAUBE, 1871 and *Echinolampas laurillardii* AGASSIZ & DESOR, 1847 are the dominating elements; furthermore, *Maretia? perornata* (SCHAFFER, 1912) is rarely found. When compared with their living relatives and judged by their morphological features, it seems likely that all three forms were shallow-burrowing endobionts which fed on fine organic detritus within the sediment and occasionally on its surface. All of them are typical faunal elements of the Eggenburgian stage, and occur in various localities around Eggenburg, Lower Austria (e. g. Eggenburg, Zogelsdorf, Grübern).

The specimens of *Spatangus austriacus* LAUBE, 1871 from Unternalb as well as from other localities are often of remarkable size. Most specimens in public and private collections easily reach a test length of 10 to 13 centimetres. This is quite large compared with other fossil and recent species of *Spatangus*. Specimens of the modern species *Spatangus purpureus* LESKE, 1778, which lives in the Mediterranean and the Atlantic, frequently reach similar sizes (pers. observation on museum material; RIEDL, 1983). The frequent occurrence of such large-sized echinoids in the studied area leads to the assumption that these animals were well adapted and lived here in nearly optimal conditions. Extant forms of the cosmopolitan genus *Spatangus* were found at depths between 10 and 50 m in coarse-grained sediment, whereas in fine sediments they were reported from depths below 180 m (CHALLIS, 1980).

Similarly, specimens of *Maretia? perornata* (SCHAFFER, 1912) attain a rather large size compared with recent species of the genus *Maretia*. Recent *Maretia* species were found in coarse sand, an environment which very likely was that of *M.? perornata* as well. *Maretia planulata* (LAMARCK, 1816) was found in intertidal to shallow subtidal sands of the Red Sea by DOLLFUS & ROMAN (1981). Today, this genus is restricted to the Indopacific realm, whereas in former times it was cosmopolitan (FISCHER, 1966).

Echinolampas laurillardii AGASSIZ & DESOR, 1847 is, as both forms mentioned above, interpreted as an inhabitant of coarse sands. MORTENSEN (1948) reported *E. ovata* (LESKE, 1778) in a depth of 9 m to 75 m; *E. crassa* (BELL, 1880) was found on coarse sandy sub-

strates between 18 m and 24 m in False Bay, South Africa (THUM & ALLEN, 1975). The cosmopolitan genus *Echinolampas* appears in the Eocene (KIER, 1966) and is a typical element of many Oligo-Miocene echinoid faunas in the Mediterranean and the Central Paratethys (COTTREAU, 1913; LAMBERT, 1910-15; ROMAN, 1965; VADASZ, 1915).

The palaeoenvironment of unit I, the typical "Retz sand", is consequently interpreted as being shallow sublittoral under fully marine conditions, close to the coast. Here, shallow-burrowing echinoids, being relatively tolerant to stronger water currents, found optimal living conditions and little competition for food or living space from other organisms. Typical for such an unstable, coarse sediment is the apparent lack of epibenthic regular echinoids and deep-burrowing spatangoids.

This hypothesis is supported by data provided by mollusc palaeoecology (LUKENEDER & al., 1999; MANDIC & HARZHAUSER, 1999). Only epifaunal bivalves, namely pectinids and deep-burrowing, thick-shelled glycymerids, occur.

Unit II

The upper part of Unternalb section A consists of fine, poorly sorted sands containing abundant bryozoans and numerous fragments of balanids. A rich echinoderm fauna, preserved mostly as disarticulated ossicles, was obtained from bulk samples of these sediments. Within the Eggenburgian of Austria the richness and diversity of this echinoderm fauna, is only comparable to the echinoderm fauna of the Zogelsdorf Formation at Limberg (Lower Austria), which is of the same age (ROETZEL, MANDIC & STEININGER, 1999). Except for the holothuroids all modern echinoderm classes are represented in the samples.

The most common elements found were isolated ossicles of asteroids, which were often not determinable, due to the abrasion and cement overgrowth. However, the genera *Astropecten* and *Luidia* could be identified. Recent species of both genera are common elements in many modern seas. They are typically inhabitants of sandy bottoms and are sometimes associated with seagrass patches (RIEDL, 1983; ZAVODNIK, 1988). Both *Astropecten* and *Luidia* are reported to prey on molluscs, other echinoderms and arthropods (BLAKE, 1982; RIEDL, 1983; ZAVODNIK, 1988).

KACZMARSKA (1987) found a similar asteroid assemblage (four different *Astropecten* species, two species of *Luidia* and indeterminable goniasterids), in the form of isolated ossicles, in the Middle Miocene of the Korytnica Basin in Poland. The generic composition of the fauna leads her to conclude, that the fauna "shows certain affinities to the recent asteroid fauna of the tropical Indo-Pacific" (KACZMARSKA, 1987, p. 142). Although it is true that the genera *Astropecten* and *Luidia* are common elements in the Indopacific, note that both genera, along with goniasterids, are also very common elements of the warm-temperate Mediterranean Sea (RIEDL, 1983).

While asteroid ossicles are abundant in the bulk samples, ophiuroid remains are very rare: only three vertebrae and a single lateral shield were found. Either they were not abundant or a taphonomic bias prevents their preservation. The difficulties mentioned above precluded determination and no clues can be drawn from these fossils.

Very common are spines and frequently single plates belonging to the family Diadematae. The distinct morphology of the spines allows an assignment even if only

small fragments are available. Living *Diadema* specimens bear spines of up to thirty to forty centimetres (MORTENSEN, 1940). Their morphology causes them to fragment very easily, explaining the high number of spine versus test fragments. Recent forms of the Diadematidae are often associated with coral reefs in tropical waters (FELL, 1966b; e.g. *Diadema antillarum* (PHILIPPI) HENDLER et al., 1995), although some forms of this group are adapted to the rocky sublittoral, like *Centrostephanus longispinus* (PHILIPPI, 1845), which is found on hard substrate and sandy bottoms in the Mediterranean Sea (RIEDL, 1983), or *Centrostephanus coronatus* (VERRILL, 1867) and *Diadema mexicanum* AGASSIZ, 1863, which inhabit the low intertidal and subtidal on rocky substrates at Galápagos (HICKMAN, 1998).

Another common element in the bulk samples are small coronas and fragments of tests of the genus *Arbacina*. This extinct genus (Fell & PAWSON, 1966) is mainly found in sandy sediments. CHALLIS (1980) interpreted *Arbacina piae* LOVISATO, 1895 as an epibiont on coarse sandy sediments of the shallow sublittoral. Today, morphologically similar forms are found as epibionts in sheltered sublittoral environments, for example beneath rocks, in small crevices, in bryozoan thickets, seagrass beds or reefs.

Additionally, fragments of spatangoids were found in the bulk samples, they were identified as *Spatangus austriacus* fragments.

A few remains of crinoids, namely brachial and cirral ossicles, were also encountered in the bulk samples. Because of their bad preservation a determination was not possible. Nevertheless, these ossicles are most likely remains of comatulids, which were described by SIEVERTS-DORECK (1961) from the nearby localities of Zogelsdorf and Eggenburg (both in Lower Austria), where they are rather common. These animals are suspension feeders, which are in many cases nocturnal and retreat in small crevices during daytime (MESSING, 1997). This is evidence, that the surroundings of the sections at Unternalb were a highly structured habitat. A further indication to that effect is the common occurrence of the bryozoan *Myriapora truncata* (PALLAS) (KÜHN, 1955; VAVRÁ, 1979). This species which lives in the Mediterranean today, according to RIEDL (1983) it is typically found in the shallow, shaded areas of the rocky shore and on the bottom of marine caves, as well as on secondary hardgrounds and stone ridges below 20 m.

The palaeoenvironment for unit II of section A at Unternalb is therefore interpreted as shallow sublittoral with full marine conditions, where sandy bottoms and hardgrounds as well as sheltered habitats (e.g. bryozoan thickets, seagrass beds) were available. The presence of such different conditions can be explained by the small-scale facies patterns encountered near rocky shores.

Unit II of section B1, which is separated from section A by a small crystalline ridge, is characterised by poorly sorted fine to middle sands. These sands are rich in molluscs and can be correlated with unit II of section A; the different lithologies can be explained by the more basinward position of section B1.

Here, cidaroid spines - but unfortunately no coronal plates - have been found. Extant cidaroids occur in a great depth range; most of them prefer hard bottoms, and only few forms with long slender spines, corresponding to the described type, live on muddy or sandy bottoms (FELL, 1966a).

Discussion

Two distinct echinoderm assemblages have been found in the studied sections:

1. *Spatangus-Echinolampas* assemblage

This assemblage, which is reported from the lower part of section A (unit I), consists of shallow-burrowing echinoids; the dominating genera are *Spatangus* and *Echinolampas*. It is associated with coarse-grained sediments of the shallow sublittoral.

2. *Diadematoid-Echinacea-Asteroid* assemblage

This assemblage, which is reported from the upper part of section A (unit II), consists of diadematoids, small *Echinacea* (in this case *Arbacina* sp.) and asteroids (here *Astropecten* sp. and *Luidia* sp.); furthermore, comatulids and ophiuroids can occur. This assemblage is associated with a fine- to medium-grained bryozoan sand of a highly structured shallow sublittoral environment with sandy bottoms and rocky hard substrates.

None of the reported Lower Miocene echinoid associations from the Central Paratethys achieves a similarly high diversity as the one from Unternalb. Nonetheless, unpublished data on a synchronous and partly synfacial echinoderm fauna from the Hengl quarry at Limberg in the adjacent Eggenburg Bay hint to an even better-preserved and very rich echinoderm fauna with complete ophiuroids and asteroids.

The unusually high echinoderm diversity and density is explained on the one hand by the complex topography of the investigation area, resulting in small-scale facies patterns in the littoral to shallow sublittoral. On the other hand the high-energy conditions in the rather unprotected Nalb Bay allowed the establishment of large populations of well-adapted echinoids like *Spatangus austriacus* LAUBE, 1871, while the competition from infaunal molluscs typical in the more calm Eggenburg Bay was reduced.

This hypothesis seems to be valid at least for the assemblages of the coarse sandy unit I, where the shallow-burrowing spatangoids suffered little competition: infaunal bivalves were rare or mainly represented by deep-burrowing taxa as *Glycymeris*, and the frequent, epifaunal pectinids were neither spatial nor feeding rivals. The mobile, coarse sands were thus settled by shallow-burrowing or semiinfaunal echinoids which tolerate even strongly turbulent water but hindered the spread of echinaceans or deep-burrowing spatangoids.

Unit II reflects littoral to shallow sublittoral environments which provided hardgrounds, sand flats and bryozoan thickets as documented in section A. The latter were settled by numerous, small-sized, epifaunal echinoids such as *Arbacina*, whereas diadematoids occupied the hardgrounds of the topographic highs. Astropectinids and Luidiids hunted in these environments but might have favoured sandy areas of the bay, where their ossicles contribute in fair numbers to the sediment. Competition by epifaunal molluscs was very low; most of the recorded gastropods were carnivorous but did not prey on echinoids, and the scattered herbivorous taxa such as *Diloma* derive rather from the adjoining rocky littoral.

In contrast the outer bay lacks a diverse echinoderm fauna but contains a large number of molluscs. Among these, infaunal taxa prevail; they covered the whole tiering in the

sediment from rather shallow- to deep-burrowing forms, thus leaving few niches for echinoids. Hence, echinoids from the outer bay are only recorded in the form of epifaunal, long-spined cidaroids; they settled the sandy-muddy bottom and were associated with few epifaunal molluscs such as *Aequipecten* and dwarfed oysters.

The sand pits at Unternalb represent one of the most impressive Lower Miocene Echinodermata faunas in the entire Central Paratethys, along with the unpublished fauna of Limberg in Lower Austria. Their richness and diversity, as well as the opportunity to study three distinct, geographically closely related, synchronous echinoid facies, emphasise the importance of the described fauna.

Palaeobiogeographic Implications

The echinoderm fauna reported here is, despite its richness, rather typical in its composition for the Central Paratethys. Affinities of the benthic fauna from the Eggenburgian with the tropical Indopacific region have been frequently proposed by various authors, and similar (tropical) conditions have been interpreted for the region of Eggenburg. The echinoderm fauna as preserved in the studied sections, however, does not afford tropical conditions. Forms similar to those reported here inhabit also in the warm temperate Mediterranean today (*Astropecten*, *Luidia*, *Centrostephanus* [Diadematidae], *Cidaris* [Cidaridae], *Spatangus*, comatulids, ophiuroids).

Most of the recorded echinoids such as *Spatangus austriacus* LAUBE, 1871, *Echinolampas laurillardii* AGASSIZ & DESOR, 1847 and *Maretia? perornata* (SCHAFFER, 1912) appear in the Paratethys during the Lower Eggenburgian and are generally missing in Egerian deposits. *Spatangus austriacus* is documented from the early Eggenburgian Fels Formation whereas the latter two taxa appear in the Gauderndorf Formation (*E. laurillardii*) and in the Zogelsdorf Formation (*M.? perornata*).

In contrast to these species the genus *Arbacina* enters the Central Paratethys in the late Eggenburgian and is unknown in this bioprovince from deposits older than the Retz Formation. During the Middle Miocene Badenian stage the small echinoids settled the entire Central Paratethys and spread as far east as Poland (MACZYNSKA, 1996).

Outside the Central Paratethys, *Arbacina* has its first occurrence in the Aquitanian of the Western Mediterranean: CHALLIS (1980) found *Arbacina piae* LOVISATO, 1895 in the Aquitanian to Langhian of Malta; LAMBERT (1907-9) reports the same species from the Aquitanian to Langhian of Sardinia. Furthermore, the genus is reported from the Burdigalian of the Rhône Basin (LAMBERT, 1910-15; ROMAN, 1974). During the Middle Miocene, *Arbacina* became a common, widespread animal in the Lusitanian bioprovince; it is described from various localities throughout the Mediterranean (COTTREAU, 1913).

Thus, the arrival of *Arbacina* in the Central Paratethys in the late Eggenburgian Retz Formation has palaeobiogeographic implications, since the migration coincides well with the immigration of several bryozoan taxa into the Molasse Basin during the late Lower Miocene as described by VAVRÁ (1981). The bryozoan, which are also recorded from Unternalb, are interpreted by RÖGL (1998) to have migrated from the Rhône Basin into the Central Paratethys via the alpine foredeep. In the same way, the echinoid *Arbacina* seems to have taken the western route from the Western Mediterranean, through the Rhône Basin via the re-opened seaway (fig. 5).



Fig. 5: Suggested migration pathway of *Arbacina* from the Rhône Basin to the Central Paratethys via the alpine foredeep. (Palaeogeography after RÖGL).

No occurrences of *Arbacina* from the Ottnangian and Karpatian stages are reported; this indicates a retreat of the genus from the Paratethys during the latest Lower Miocene. Nevertheless, as mentioned above, it appears again in the Middle Miocene, but then seems to have entered the Paratethys during the Badenian transgression via a southern or eastern route.

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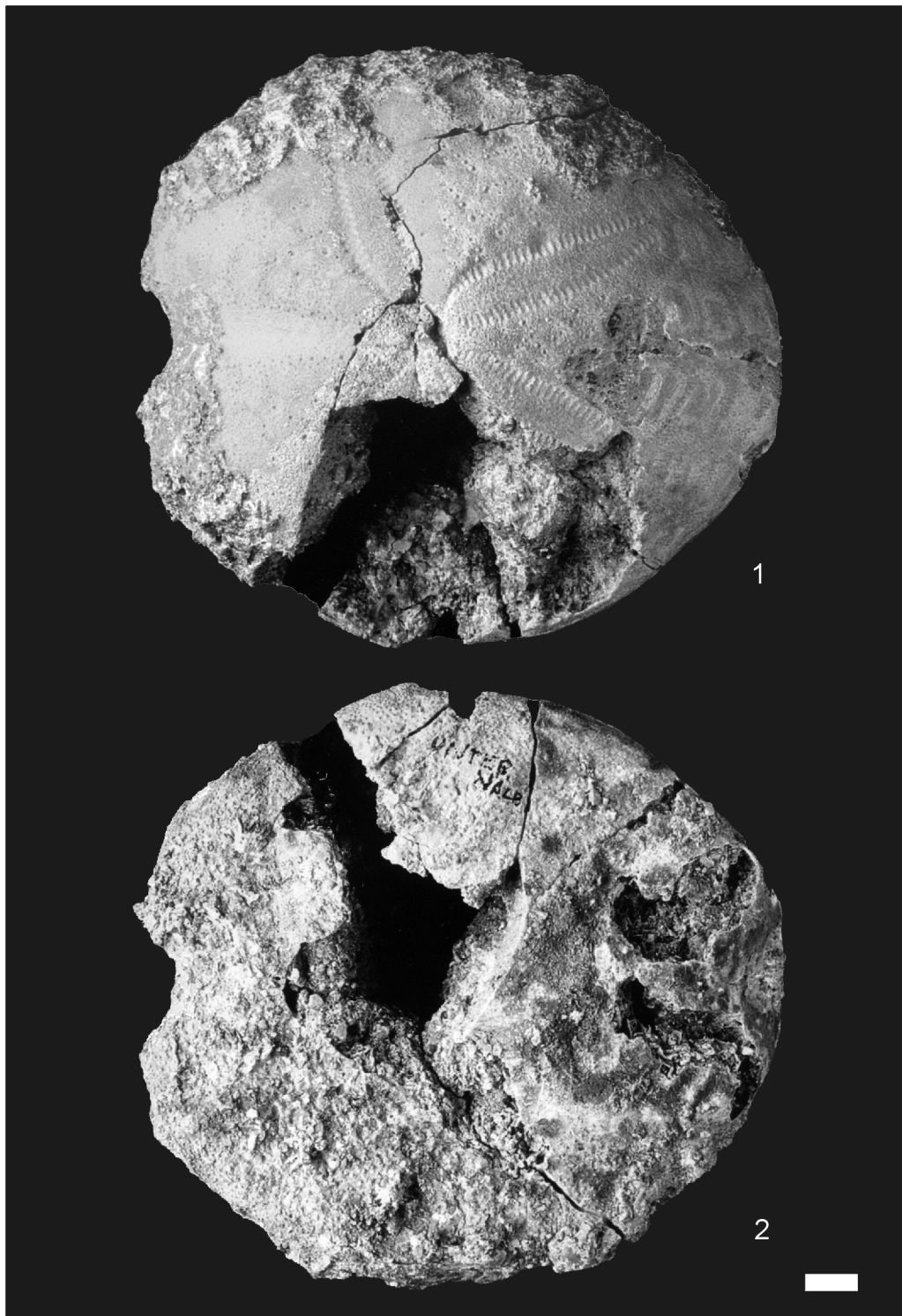
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Plate 1

- 1 *Spatangus austriacus* LAUBE, 1871, apical view
(NHMW1999z0049/0001)
- 2 *Spatangus austriacus* LAUBE, 1871, oral view
(NHMW1999z0049/0001)

scale bar equals 1 cm



1

2

Plate 2

- 1 *Echinolampas laurillardi* AGASSIZ & DESOR, 1847, apical view
(NHMW1999z0049/0002)
- 2 *Echinolampas laurillardi* AGASSIZ & DESOR, 1847, oral view
(NHMW1999z0049/0002)
- 3 *Echinolampas laurillardi* AGASSIZ & DESOR, 1847, side view (anterior is left)
(NHMW1999z0049/0002)

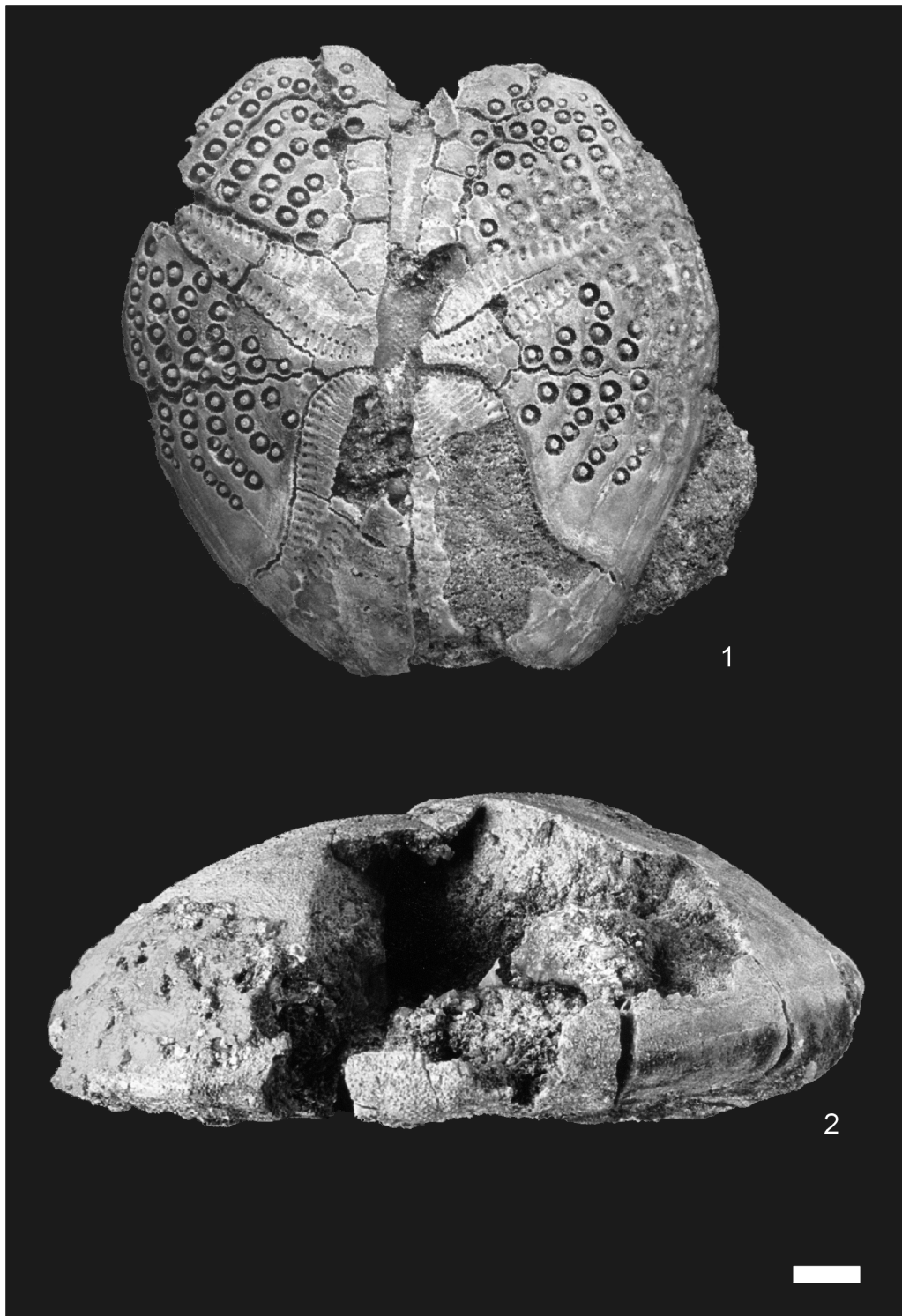
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Plate 3

- 1 *Maretia? perornata* (SCHAFFER, 1912), apical view
(NHMW1999z0049/0003)
- 2 *Spatangus austriacus* LAUBE, 1871, side view (anterior is left)
(NHMW1999z0049/0001)

scale bar equals 1 cm



1

2

Plate 4

- 1 Crinoidea indet., brachial; x 20
(NHMW1999z0051/0001)
- 2 Crinoidea indet., brachial with articulation area for a pinnulae; x20
(NHMW1999z0051/0001)
- 3 Crinoidea indet., cirral; x20
(NHMW1999z0051/0001)
- 4 Crinoidea indet., cirral, side view; x20
(NHMW1999z0051/0001)
- 5 Ophiuroidea indet., vertebra, distal view; x20
(NHMW1999z0051/0002)
- 6 Ophiuroidea indet., vertebra, proximal view; x20
(NHMW1999z0051/0002)
- 7 Ophiuroidea indet., vertebra, lateral view; x20
(NHMW1999z0051/0002)
- 8 Ophiuroidea indet., vertebra, dorsal view; x20
(NHMW1999z0051/0002)
- 9 Ophiuroidea indet., vertebra, ventral view; x20
(NHMW1999z0051/0002)
- 10 Ophiuroidea indet., lateral shield, lateral view; x20
(NHMW1999z0051/0003)
- 11 Ophiuroidea indet., lateral shield, inside view; x20
(NHMW1999z0051/0003)
- 12 Ophiuroidea indet., lateral shield, distal view; x20
(NHMW1999z0051/0003)
- 13 Ophiuroidea indet., lateral shield, detail of outer surface; small scale bar equals 10 μ m
(NHMW1999z0051/0003)

scale bar equals 1 mm

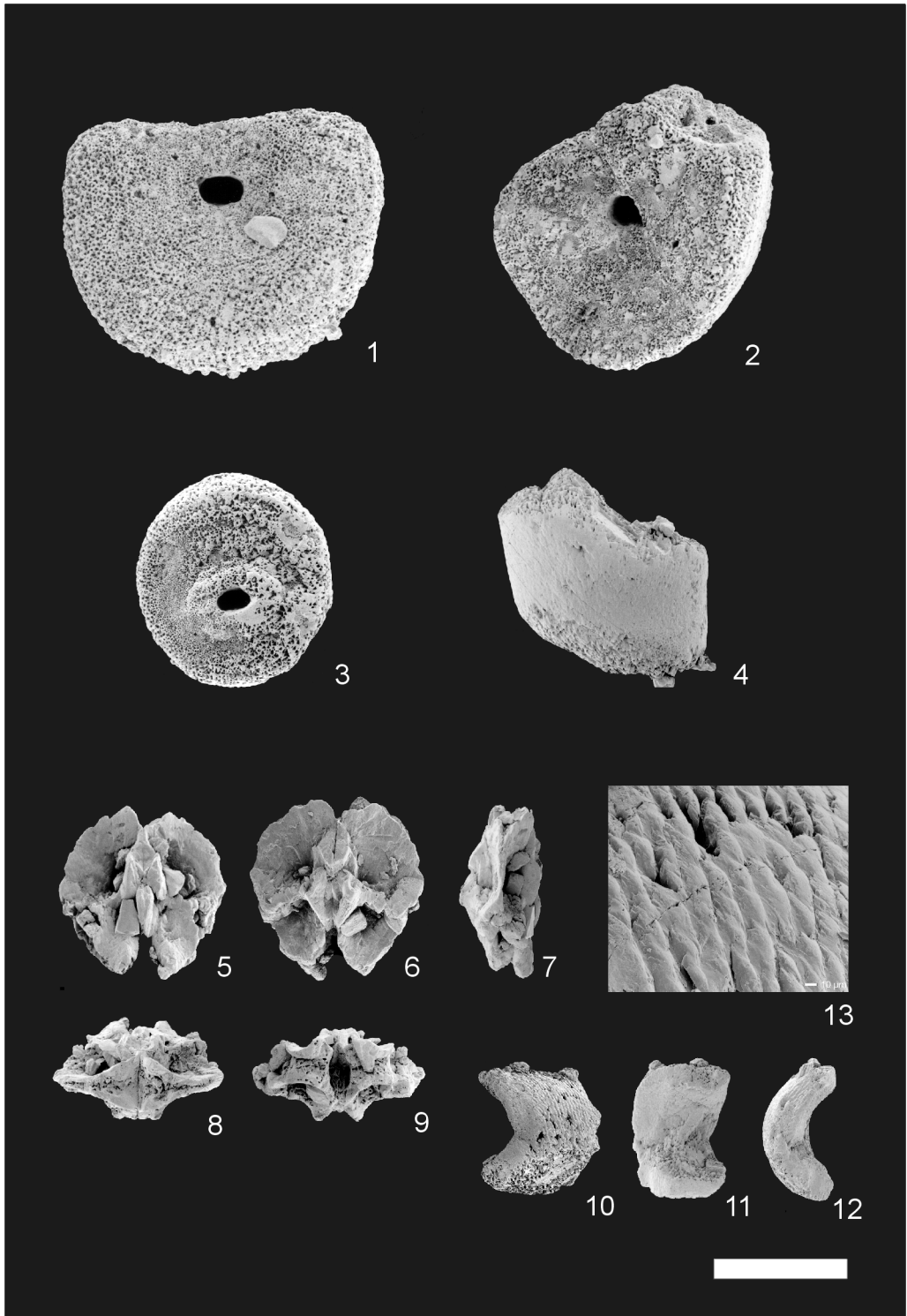


Plate 5

- 1 *Luidia* sp., inframarginal, lateral view; x10
(NHMW1999z0051/0006)
- 2 *Luidia* sp., inframarginal, distal view; x10
(NHMW1999z0051/0007)
- 3 *Luidia* sp., paxilla, dorsal view; x10
(NHMW1999z0051/0008)
- 4 *Luidia* sp., ambulacral, ventral view; x10
(NHMW1999z0051/0009)
- 5 *Luidia* sp., ambulacral, dorsal view; x10
(NHMW1999z0051/0010)
- 6 *Astropecten* sp., supramarginal, distal view; x10
(NHMW1999z0051/0011)
- 7 *Astropecten* sp., inframarginal, distal view; x10
(NHMW1999z0051/0012)
- 8 *Astropecten* sp., inframarginal, proximal view; x10
(NHMW1999z0051/0013)
- 9 Indetermined asteroid, possibly *Astropecten*, paxilla, side view; x10
(NHMW1999z0051/0014)

scale bar equals 1 mm

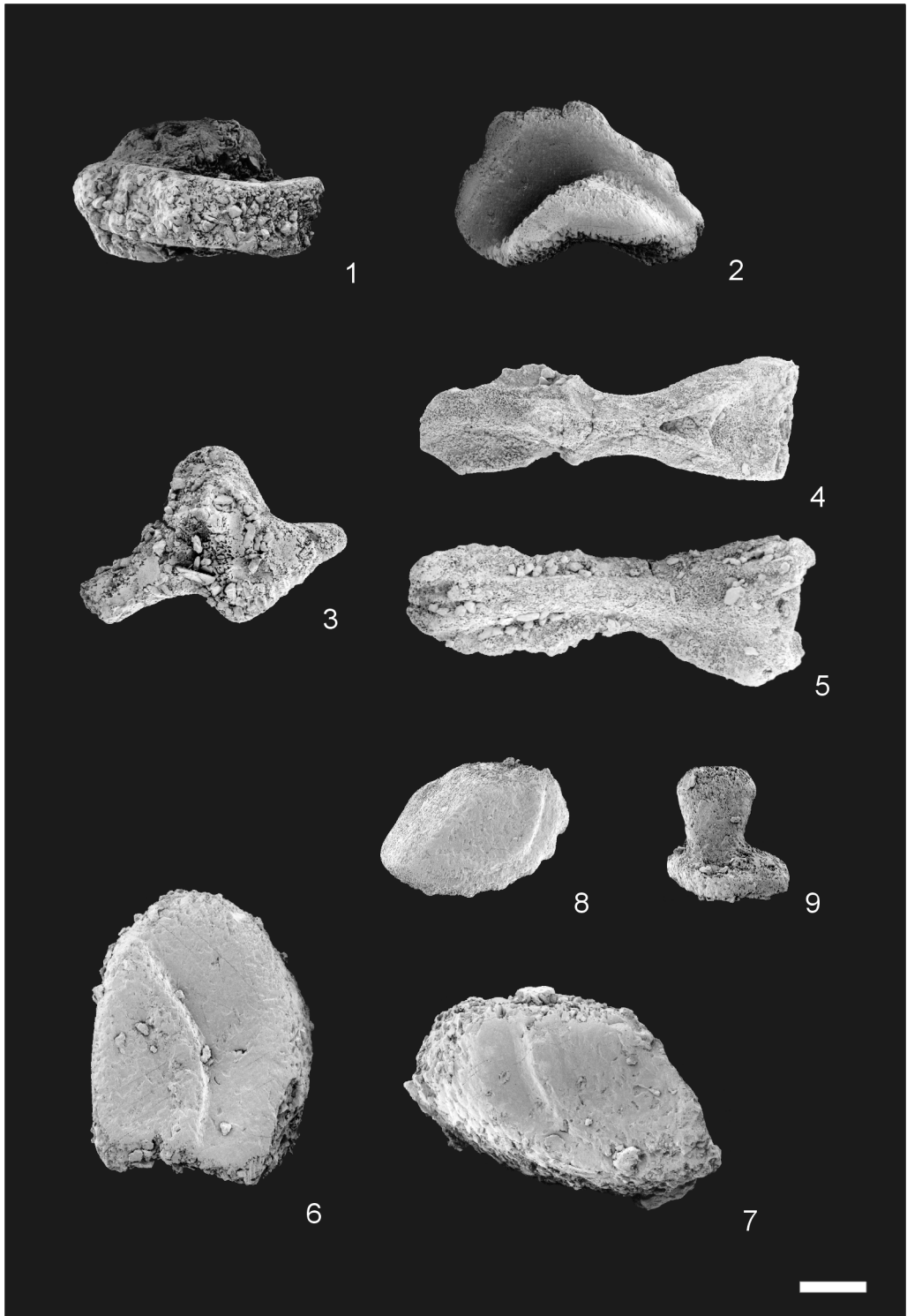


Plate 6

- 1 Ophiuroidea indet., vertebra, distal view; x10
(NHMW1999z0051/0004)
- 2 Ophiuroidea indet., vertebra, proximal view; x10
(NHMW1999z0051/0004)
- 3 Ophiuroidea indet., vertebra, lateral view; x10
(NHMW1999z0051/0004)
- 4 Ophiuroidea indet., vertebra, dorsal view; x10
(NHMW1999z0051/0004)
- 5 Ophiuroidea indet., vertebra, ventral view; x10
(NHMW1999z0051/0004)
- 6 Ophiuroidea indet., vertebra, distal view; x20
(NHMW1999z0051/0005)
- 7 Ophiuroidea indet., vertebra, proximal view; x20
(NHMW1999z0051/0005)
- 8 Ophiuroidea indet., vertebra, dorsal view; x20
(NHMW1999z0051/0005)
- 9 Ophiuroidea indet., vertebra, ventral view; x20
(NHMW1999z0051/0005)
- 10 Ophiuroidea indet., vertebra, lateral view; x20
(NHMW1999z0051/0005)

scale bar equals 1 mm

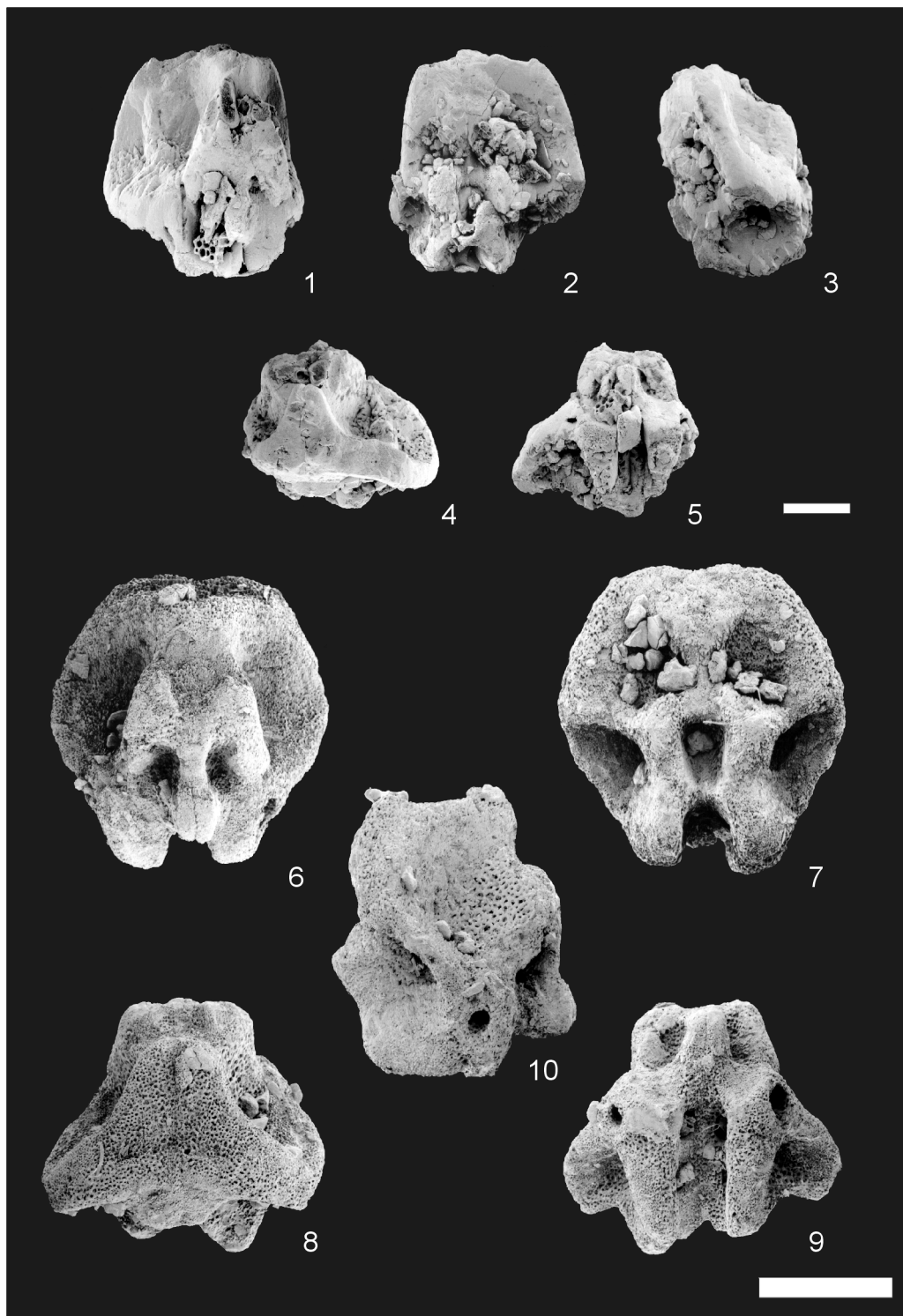
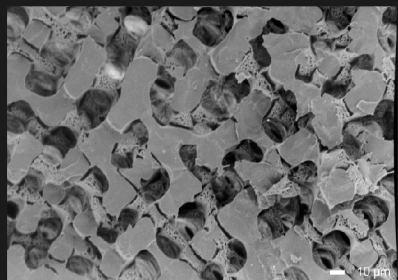


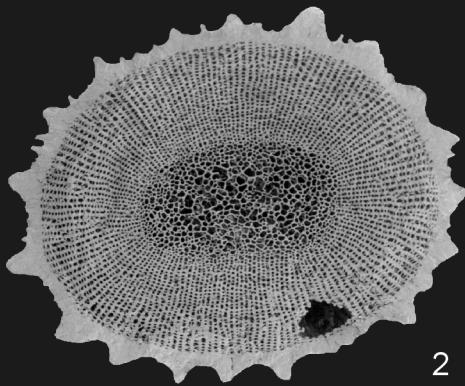
Plate 7

- 1 Cidaridae indet., detail of cross section, lamellae
(NHMW1999z0051/0015)
- 2 Cidaridae indet., cross section; x20
(NHMW1999z0051/0015)
- 3 Cidaridae indet., detail of cross section, medulla
(NHMW1999z0051/0015)
- 4 Cidaridae indet., Spine, lateral view
(NHMW1999z0051/0015)
- 5 *Arbacina* sp., apical view; x20
(NHMW1999z0051/0016)
- 6 *Arbacina* sp., lateral view; x20
(NHMW1999z0051/0017)
- 7 *Arbacina* sp., detail
(NHMW1999z0051/0018)

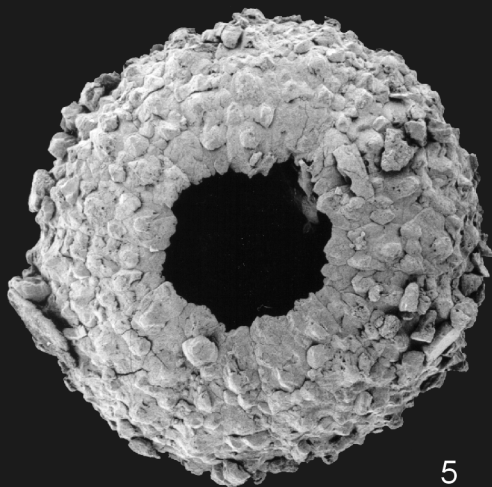
scale bars equal 1 cm, except when otherwise indicated



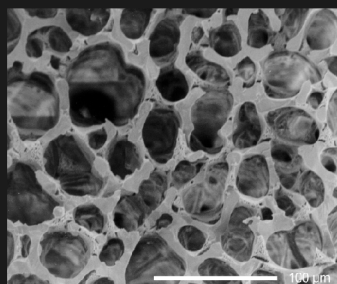
1



2

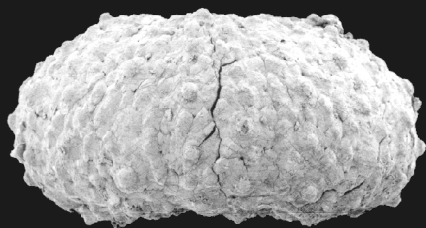


5

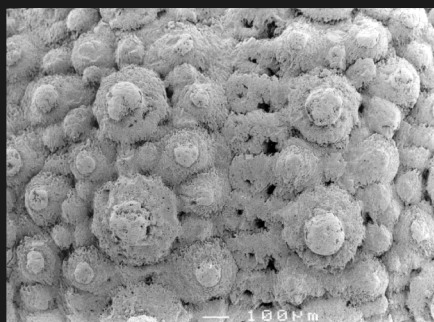


3

4



6



7

Plate 8

- 1 Diadematidae indet., interambulacral plate; x20
(NHMW1999z0051/0019)
- 2 Diadematidae indet., interambulacral plate; x20
(NHMW1999z0051/0020)
- 3 Diadematidae indet., ambulacral plate; x20
(NHMW1999z0051/0021)
- 4 Diadematidae indet., side view of a crenulate, perforate primary tubercle
of an interambulacral plate; x40
(NHMW1999z0051/0020)
- 5 Diadematidae indet., primary spine, cross section; x40
(NHMW1999z0051/0022)
- 6 Diadematidae indet., primary spine, side view; x30
(NHMW1999z0051/0022)
- 7 Diadematidae indet., base of primary spine, side view; x20
(NHMW1999z0051/0022)

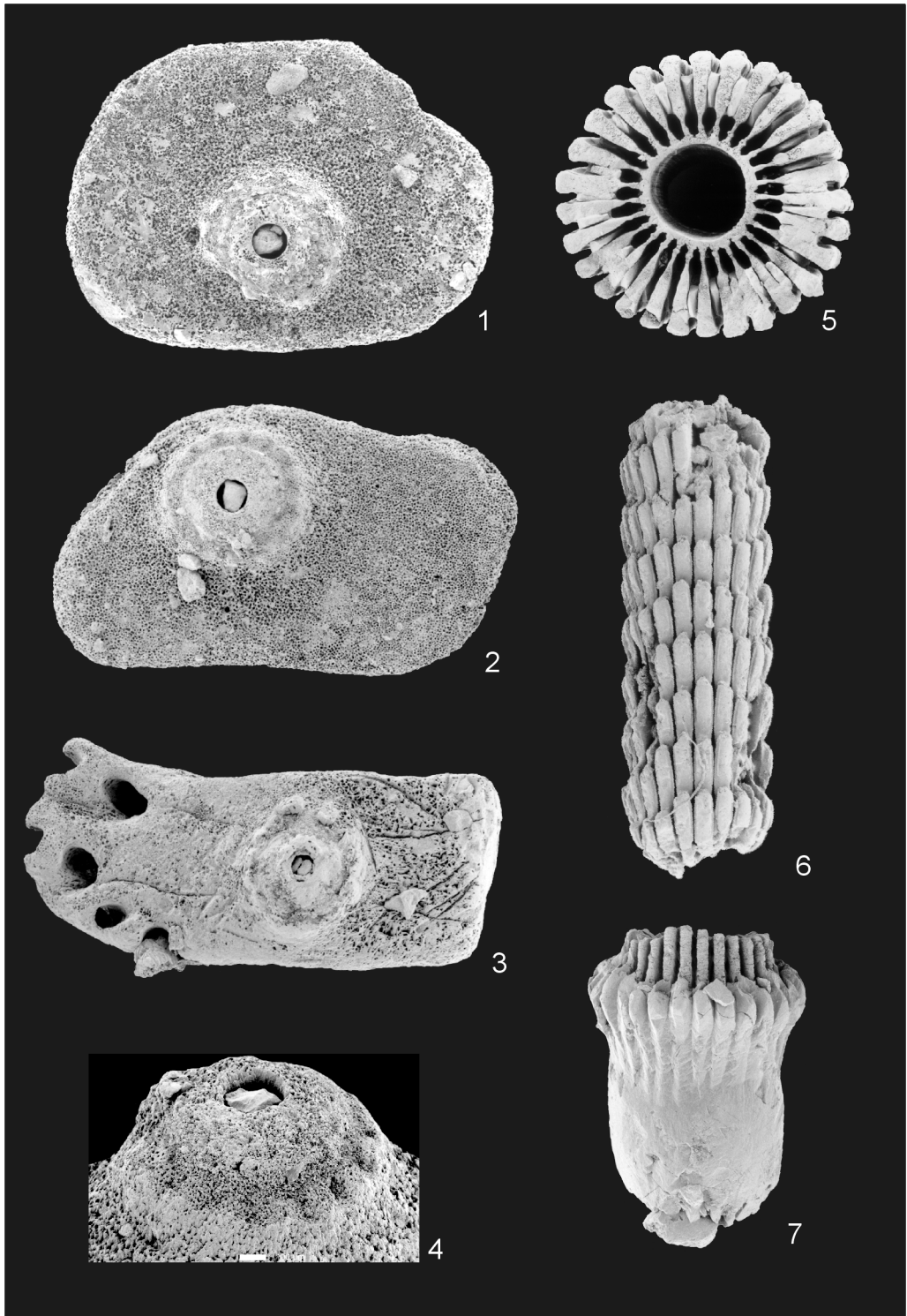


Plate 9

- 1 Echinacea indet., rotula; x15
(NHMW1999z0051/0023)
- 2 Echinacea indet., demipyramid; x15
(NHMW1999z0051/0024)
- 3 Echinacea indet., demipyramid; x15
(NHMW1999z0051/0025)
- 4 Spatangoida indet., primary spine, side view; x30
(NHMW1999z0051/0026)
- 5 Spatangoida indet., base of primary spine, side view; x30
(NHMW1999z0051/0026)
- 6 Spatangoida indet., primary spine, cross section; x150
(NHMW1999z0051/0026)
- 7 Echinacea indet., base of spine; x30
(NHMW1999z0051/0027)

