

# Silicified sea life – Macrofauna and palaeoecology of the Neuburg Kieselerde Member (Cenomanian to Lower Turonian Wellheim Formation, Bavaria, southern Germany)

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### ABSTRACT:

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With approximately 100 species, the invertebrate macrofauna of the Neuburg Kieselerde Member of the Wellheim Formation (Bavaria, southern Germany) is probably the most diverse fossil assemblage of the Danubian Cretaceous Group. Occurring as erosional relicts in post-depositional karst depressions, both the Cretaceous sediments and fossils have been silicified during diagenesis. The Neuburg Kieselerde Member, safely dated as Early Cenomanian to Early Turonian based on inoceramid bivalve biostratigraphy and sequence stratigraphy, preserves a predominantly soft-bottom community, which, however, is biased due to near-complete early diagenetic loss of aragonitic shells. The community is dominated by epifaunal and semi-infaunal bivalves as well as sponges that settled on various (bio-) clasts, and may widely be split into an early bivalve-echinoid assemblage and a succeeding sponge-brachiopod assemblage. In addition to these groups we document ichnofauna, polychaete tubes, nautilids and bryozoans. The fauna provides evidence of a shallow to moderately deep, calm, fully marine environment, which is interpreted as a large-scale embayment herein. The fauna of the Neuburg Kieselerde Member is regarded as an important archive of lower Upper Cretaceous sea-life in the surroundings of the Mid-European Island.

Key words: Late Cretaceous; Danubian Cretaceous Group; Macro-invertebrates; Facies; Silica diagenesis; Stratigraphy.

## INTRODUCTION

Although most people may never have heard about the Neuburg Kieselerde Member, which is mined as "siliceous earth" in the area of Neuburg an der Donau (Bavaria, southern Germany; Text-fig. 1), the eponymous sediment has entered a majority of our households straight through the front door, hidden in toys, jars and tubes. However, due to its unique composition of up to 99 weight percent of amorphous to nanocrystalline silica and variable quantities of kaolinite, the Neuburg Siliceous Earth is not only in great demand for industrial applications, but is also of particular scientific interest, especially with regard to its formation. As an additional peculiarity, the Neuburg Siliceous Earth today occurs only in the form of erosional relicts, infilling post-depositional karst depressions in the Upper Jurassic rocks of the southwestern Franconian Alb. The present study focuses on the macrofossil content of the Neuburg Siliceous Earth, trying to explain the genesis of the sediments from a palaeoecological point of view. Furthermore, we aim at providing a complete, taxonomically up-



Text-fig. 1. Geographical overview. Green colour indicates surface exposures and karst depressions filled with sediments of the Wellheim Formation. Red dots indicate localities mentioned in the text that yielded fossils or have been sampled for petrographic analysis

to-date inventory of the macrofauna, based on the entire material available from public collections, including a comprehensive photographic documentation.

## Nomenclature

During more than 130 years, a variety of formal and informal terms have been created for the Neuburg Siliceous Earth, its contents and its components. Many of these terms are outdated or have been misapplied in the literature. We therefore provide a short list of the most important terms. Only the synonyms that refer to the Neuburg Kieselerde Member in particular are considered in the following part and not those terms that are related to the Wellheim Formation in general (comp. Niebuhr *et al.* 2009).

Neuburg Kieselerde Member of the Wellheim Formation: Official lithostratigraphic term, introduced by Niebuhr (in Niebuhr *et al.* 2009), modified by Wilmsen and Niebuhr (2010) and approved by the Subkommission für Kreide-Stratigraphie (SKS) of the Deutsche Stratigraphische Kommission (DSK) (Text-fig. 2). With regard to lithostratigraphy, all other terms listed below are synonymous with or describe parts of the Neuburg Kieselerde Member (see stratigraphy section below for details).

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*Neuburger Kieselerde*; English: *Neuburg Siliceous Earth* (Göske and Kachler 2008): Informal term, currently applied for the unconsolidated, fine-grained, carbonate-free, predominantly siliceous sediment of the Neuburg Kieselerde Member, which is mined for industrial applications.

Neuburger Weiß (Gümbel 1889, 1891), Kieselsaure Tonerde (Hasselmann 1895a, b), Neuburger Kieselkreide (Kalkowsky 1902, cited in Schneider 1933), Kieselerde von Neuburg a.d.D. (Schneider 1933), globularer Tripel, Silikolith (Prokopowicz 1951), Neuburger Weißerde, Weißer Bollus, Kieselweiß, Kieselmulm: Outdated informal terms, being synonymous with Neuburg Siliceous Earth.



Text-fig. 2. Stratigraphic subdivision of the Wellheim Formation and corresponding lithostratigraphic units of the Regensburg–Kelheim area. Sequence boundaries (SB), sea level changes, lithofacies and inoceramid ranges are indicated. Absolute ages are obtained from Gradstein *et al.* (2012); the value in brackets is obtained from cyclostratigraphy by M.W. Abbreviations: *Cunningtoniceras*; *Ac. = Acanthoceras*; *In. = Inoceramus*; *Me. = Metoicoceras*; *Ne. = Neocardioceras*; *Wa. = Watinoceras*; *My. = Mytiloides*; *Co. = Collignoniceras*; *subherc. = subhercynicus*; herc. = hercynicus; Neu–Wel = Neuburg–Wellheim

*Opaline nodules*: Informal term currently applied for the silicified rock portions, which may occur scattered or enriched in layers in the Neuburg Siliceous Earth (Niebuhr *et al.* 2009; Wilmsen and Niebuhr 2010; see Text-figs 3–5). Locally, these nodules may enclose fossils, especially the inoceramid bivalve index taxon *Inoceramus crippsi crippsi*.

Kreidesteine (Kalkowsky 1902, cited in Schneider 1933; Prokopowicz 1951), Dichtquarzitbrocken (Schneid 1915): Wellheimer Inoceramenquarzit (Lehner 1933), Gaisit (Prokopowicz 1951; Kempcke 1958a; Doppler et al. 2002), Zementquarzit (Hoffmann et al. 1955): Informal, erroneous and/or outdated terms being synonymous with opaline nodules. Quartzites are metamorphic rocks, while the term Gaize (Germanised term: Gaisit) was established for fine-grained, calcareously cemented or porous glauconitic sandstones or calcarenites. Both rock types do not occur in the Neuburg Kieselerde Member.

#### Mining and applications

Presumably, Neuburg Siliceous Earth was already used by the Romans, in particular for the surfacing of kilns and as a basic material for pottery (Schneider 1933; Hoffmann Mineral 2003). Industrial application in the tempering of pottery clay and as a raw material for the production of melting pots for glass is documented for the 17th and 18th centuries (Schneider 1933). Since the 19th century, siliceous earth has been applied for polishing, and as an additive in the production of ultramarine pigment (Hasselmann 1894, 1895a, b). Originally a waste product of the conditioning of siliceous earth, the residual sand was utilised by the local glass and cement industry. With the rise of the industrial production of synthetic colours, rubber and plastic at the onset of the 20th century, siliceous earth became increasingly important as a filler. Today, the unique composition of crypto- to nano-crystalline silica and clay minerals (Göske and Kachler 2008), as well as its high degree of porosity still make the material an essential component of synthetic colours, rubber, plastic, varnish and (car) polish (Hoffmann Mineral 2008).

Of originally seven documented companies at Neuburg an der Donau that were mining and trading siliceous earth during the early 20<sup>th</sup> century, the Hoffmann Mineral GmbH & Co. KG is the sole mining company still extant (Dobner *et al.* 2002; Hoffmann Mineral 2003). Up to the 1970s, mining took place in underground mines. During the early days, the sediment was exploited with picks and shovels and transported to the processing plants by horse-drawn cart or tipper. Rising personnel expenses and technical difficulties finally led to the establishment of opencast mines, and today approximately 145,000 tons of siliceous earth per annum are exploited (Hoffmann Mineral 2003). After processing, 30–50 % of the raw material is utilisable, and sold and exported in variant qualities under the trade names Sillitin and Sillikolloid (Hoffmann Mineral 2003, 2008).

#### History of research

Going along with mining, research on the Neuburg Kieselerde Member also has an impressive tradition, starting with an initial documentation of the "Neuburger Weiß" by Gümbel (1889, 1891), characterized as a soft, powdery, white siliceous substance of unknown origin that consisted of 89.1 % insoluble silica, 0.6 % soluble silica, 6.5 % clay minerals and iron oxide, and 3.8 % water and organic material (Gümbel 1891, p. 296). Gümbel (1891) did not find any fossils and assumed that the Neuburg Siliceous Earth formed during the Cenozoic. A few years later, Hasselmann (1895a, b) published an additional geochemical analysis of the sediment, which he termed "Kieselsaure Tonerde" (= silicic alumina). After removing the sand content by a three-stage wet-sieving process, the residual product contained 86.38 % silica, 9.85 % clay minerals, 0.43 % iron oxide and 0.08 % magnesia.

Soon after, the term "Neuburger Kieselkreide" was established by Kalkowsky (1902, in Schneider 1933, p. 10). Slightly modified to "Neuburger Kieselerde" by Schneider (1933), this term is still in prevailing usage today, albeit numerous other terms were applied in the literature (Niebuhr *et al.* 2009). Kalkowsky (1902, in Schneider 1933) also studied thin-sections of opaline nodules from the Neuburg Kieselerde Member, and stated that these rocks consist of quartz grains that are bound by a dominant matrix of chalcedony. He assumed that the sediment had formed in freshwater.

Schneid (1915, p. 34) hypothesized that the Neuburg Siliceous Earth was an insoluble residual of eroded Jurassic chert rocks, considering that the opaline nodules were secondary concretions of identical petrographic composition, but of Cretaceous age. He was the first worker to correctly date these rocks as Cenomanian based on the occurrence of *Inoceramus crippsi* Mantell, 1822 (Schneid 1914, 1915, p. 38). He further stated that both rock types may have formed in shallow water, probably supplied from the same source.

Krumbeck (1917, p. 383) assumed a massive supply of quartz, which was partly solute in a shallow, warm marine basin. Deposited as "siliceous-clasticclayey" sediment at the sea-floor and transformed to sandy chert or silicified nodules during lithification, the rocks were subject to selective erosion in groundwater during subsequent regression. When finally raised above groundwater level, slow but steady subaerial erosion produced the Neuburg Siliceous Earth, according to Krumbeck's (1917) model.

A first systematic account of the fauna of the Neuburg Kieselerde Member was published by Leonhard Lehner, based on his own impressive collection of fossils, which he donated to the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG) in Munich. Lehner (1924) started his series of publications on the Cretaceous strata of the Franconian Alb with a brief, but comprehensive stratigraphic overview of the Cretaceous sediments. In 1928, Lehner passed away, leaving behind a number of manuscripts, which were edited by Richard Dehm (Munich) and published posthumously. In one of these papers, Lehner (1933) described a variety of relict rock types of Cenomanian age and listed all fossils discovered until then. The "Schwammsand von Wellheim" (= Wellheim sponge sands) and the "Wellheimer Inoceramenquarzit" (= Wellheim inoceramid quartzite) of his lithostratigraphic scheme largely correspond to the loose and lithified components respectively of the Neuburg Kieselerde Member. Lehner's work culminated in a two-volume monograph of the fauna (excluding the Inoceramidae) and flora from the Franconian Cretaceous strata (Lehner 1937a, b), which included descriptions and illustrations of several specimens from the Neuburg Kieselerde Member. Unfortunately, the entire Lehner collection was destroyed during World War 2. Parallel to Lehner's studies, Schneider (1933) conducted his (unpublished) PhD thesis on the Neuburg Siliceous Earth. He correctly identified the solid rock portions of the Neuburg Siliceous Earth as products of the local enrichment of silica, which formed concretions around grains of Cretaceous origin, usually around (bio-)clasts. Based on more than 200 specimens of Inoceramus crippsi Mantell, Schneider (1933) concluded a Cenomanian age for the stratum. Heavy mineral provenance analysis by Schnitzer (1953) revealed identical zircon-tourmalinerutile associations for the Neuburg Kieselerde Member, the contemporaneous Regensburg Formation of the Regensburg-Kelheim area and the Lower Cretaceous Schutzfels Formation, which indicate a Moldanubian origin for the siliciclastic components of the sediments

A few years later, the work of Oschmann (1958) marked a break and a major scientific step backwards in the stratigraphic interpretation of the Neuburg Kieselerde Member. Previous biostratigraphic results, inferred from the occurrence of Inoceramus crippsi Mantell (Cenomanian age; Schneid 1914, 1915; Lehner 1933; Schneider 1933) were simply regarded as resulting from misidentification (e.g., Wagner 1963, p. 170). Based on lithological similarities, the sediments of the Neuburg Kieselerde Member were correlated with the Lower Turonian "Reinhausener Schichten" of the Regensburg-Kelheim area (the present-day Reinhausen Member of the Winzerberg Formation; Niebuhr et al. 2009). As a result, the inoceramid bivalves were erroneously assigned to Mytiloides labiatus (Schlotheim, 1813) and an Early Turonian age was proposed for the Neuburg Kieselerde Member (Oschmann 1958, p. 96), which subsequently became deeply entrenched into the literature (e.g., Wagner 1963; Tillmann 1964; Gall et al. 1973; Meyer 1981, 1996, 2000).

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In the same year, Kempcke (1958a) published a brief account of the fauna of the Neuburg Kieselerde Member, based on fossils which he had collected during the late 1950s; part of the specimens figured by him are also depicted herein. Moreover, Kempcke (1958b) compiled a comprehensive unpublished list of fossils, named "Fossilium Catalogus Neuburgensis", which is supplemented with several photographs of fossils. Making use of Kempcke's extensive collection of fossil sponges (now housed in the BSPG), Wagner (1963) monographed the Porifera of the Neuburg Kieselerde Member. Additionally, Groiss (1964) studied the microfauna of three samples from different localities [Neuburg (= Kreuth), Gammersfeld and Biesenhard; see Text-fig. 1]. Groiss (1964) recorded more than 80 taxa of predominantly benthic Foraminifera, four of which were described as new species; a few planktic forms also occur. Additionally, he detailed three ostracod taxa, and reported sponge spicules, ophiuroidean skeletal elements, echinoid spines, bryozoan fragments, juvenile terebratulids, bivalve fragments and fish teeth from the microsamples of the Wellheim Formation. Interestingly, the foraminifer assemblages from the three samples have only up to three species in common. Although this highly significant difference may indicate deviant ecological conditions, this is neither particularly mentioned nor discussed by Groiss (1964). Furthermore, the narrow microbiostratigraphic assignment of the Neuburg Kieselerde Member into the Lower Turonian (Groiss 1964, p. 4, 5) is contradicted by the presented data. As stated by Groiss (1964, p. 4) himself, the benthic foraminifera rather indicate a broader stratigraphic interval ranging from the uppermost Lower into the lower Upper Cretaceous. However, the occurrence of the planktic foraminifer Rotalipora turonica Brotzen,

a subjective junior synonym of *R. cushmani* (Morrow), clearly indicates the presence of Middle to lower Upper Cenomanian sediments (Caron 1985).

The peculiar composition of the sediment and its prevailing economic value lead to a continuous series of studies investigating the genesis and diagenesis of the sediments from various geological and mineralogical points of view (e.g., Mörtel and Paetsch 1975; Streit 1978, 1987; Kirchdörfer *et al.* 1983; Simonson 1991), including several unpublished diploma theses (Neubauer 1979; Grünberg 1987; Mitterer 2010). A brief overview of the Neuburg Kieselerde Member was presented by Mörs (1991), who figured a single, poorly preserved irregular echinoid.

In the course of the lithostratigraphic revision of the extra-alpine Cretaceous strata of Bavaria, the Neuburg Siliceous Earth was included in the Danubian Cretaceous Group, and the official lithostratigraphic term for the stratum, Neuburg Kieselerde Member of the Wellheim Formation, was established by Niebuhr *et al.* (2009) and modified by Wilmsen and Niebuhr (2010). Furthermore, Tröger *et al.* (2009) revised and extensively illustrated the Inoceramidae of the Neuburg Kieselerde Member. They re-established the correct determination of *Inoceramus crippsi* Mantell of earlier authors (Schneid 1914, 1915; Lehner 1933; Schneider 1933). Some of the specimens illustrated by Tröger *et al.* (2009) were refigured by Wilmsen and Niebuhr (2010) and/or are depicted herein.

#### GEOLOGY

#### **Geological overview**

During the Late Cretaceous, a stepwise transgression turned vast areas of the former northern Tethyan margin into peri-continental shelf seas (Ziegler 1990). In Bavaria, this process is recorded in the marine sediments of the Danubian Cretaceous Group, which document the onlap of the Upper Cretaceous sea onto the margins of the Mid-European Island that had formed around the Rhenish and Bohemian massifs (Trusheim 1935; Niebuhr et al. 2009; Wilmsen et al. 2010). With regard to lithostratigraphy, the Danubian Cretaceous Group comprises all extra-alpine, peri-continental Cretaceous strata in Bavaria, which crop out predominantly to the north of the North Alpine Foreland Basin and reach a thickness of 300-500 m. The individual formations represent non-marine to neritic environments and encompass various siliciclastics, calcarenites, siliceous opoka and limestones. Terrestrial deposits include the Lower Cretaceous Schutzfels Formation and the Turonian to ?Santonian Hessenreuth Formation, while marine units persist from the Lower Cenomanian to the Coniacian (Tröger *et al.* 2009; Wilmsen *et al.* 2009, 2010; Niebuhr 2011b; Niebuhr *et al.* 2011, 2012). The entire succession documents an almost symmetrical transgressive-regressive cycle with a maximum flooding interval during the upper Middle Turonian (Niebuhr *et al.* 2009).

Sedimentation started with the Lower Cretaceous Schutzfels Formation, which is restricted to palaeokarst depressions in the Upper Jurassic carbonates of the Franconian Alb. In the Regensburg–Kelheim area, the basal marine unit that unconformably overlies this palaeo-land surface is the up to 16 m thick Lower to lower Upper Cenomanian Regensburg Formation. It is followed by the uppermost Cenomanian–lowermost Turonian silty marls of the Eibrunn Formation and the spiculitic-calcareous siltstones (Reinhausen Member) and sandstones (Knollensand Member) of the Lower Turonian Winzerberg Formation.

In the Neuburg an der Donau and Wellheim regions, the Wellheim Formation replaces these strata (Niebuhr et al. 2009; Wilmsen and Niebuhr 2010). However, similarly to the underlying Schutzfels Formation, the Wellheim Formation is restricted to karst depressions in Upper Jurassic carbonates. The Neuburg Kieselerde Member of the Wellheim Formation occurs in numerous up to 130 m deep karst depressions, which are spread over an area of approximately 200 km<sup>2</sup> between Solnhofen and Neuburg an der Donau (Text-fig. 1). Karstification occurred gradually (collapse breccias are not documented) and often is associated with faults in the Jurassic rocks. Consequently, the Cretaceous sediments are sagged and form a "concentric" rather than horizontal succession (Text-fig. 4). More than 40 of these deposits have already been exploited (see Dobner et al. 2002) and the pits are now abandoned and restored. Another handful of pits are currently mined, and prospection for additional deposits is in progress.

#### Litho- and sequence stratigraphy

Although certain sediment types may occasionally be lacking, the succession of the infill of the individual karst depressions in the Neuburg–Wellheim area is basically identical (Text-figs 3, 4). The Upper Jurassic carbonates are overlain by a basal, several decimetres to a few metres thick residual clay layer (Neuburg Clay), varying in colour from white to brickred, violet, greenish or black. The sediment consists of clay with minor silty to sandy intercalations (Schneider 1933; Dobner *et al.* 2002); the clay fraction contains 55–65 weight % of kaolinite (Grünberg 1987). With a sharp contact, coarse-grained arkosic sands follow (Text-fig. 3A). Locally, nodular limonitic iron

ores (Amberg Member) occur scattered within this sandy unit. Both the Neuburg Clay and the overlying coarse-grained arkosic sands with the Amberg Mem-



Text-fig. 3. Schematic succession of the Schutzfels and Wellheim formations in the Upper Jurassic karst depressions of the Neuburg–Wellheim area. Approximate positions of thin-section samples (cf. Text-fig. 5) are indicated. Not to scale



Text-fig. 4. Schematic section of a typical deposit of a karst depression of the Neuburg-Wellheim area (modified from Doppler et al. 2002, p. 54). Not to scale

ber are part of the Lower Cretaceous terrigenous Schutzfels Formation of Niebuhr *et al.* (2009).

The onset of the Early Cenomanian Transgression is documented by shallow marine fine-grained sandy basis beds with foraminifers, sponge spiculae and bivalve shells (predominantly oysters), which belong to the basal Wellheim Formation. At the boundary to the overlying Neuburg Kieselerde Member, common opaline nodules (see Swineford and Franks 1959; Niebuhr 2011a) with the Lower Cenomanian inoceramid bivalve index fossil Inoceramus crippsi occur ("Inoceramenlage" = inoceramid layer of Schneider 1933), which represent the crippsi Event associated with the first intra-Cenomanian sequence boundary SB Ce 1 (see Wilmsen 2003 and Wilmsen and Niebuhr 2010 for details). Within the spiculitic silts of the Neuburg Siliceous Earth, nodules occur only loosely scattered and are often porous, and therefore not densely silicified.

The particle size of the unconsolidated Neuburg Siliceous Earth ranges from 1.6–400 µm (mean 20 µm) with a grain category distribution of c. 30 % clay, c. 40 % silt and c. 30 % fine-grained sands (Hoffmann et al. 1955; Doppler et al. 2002, fig. 41; Göske and Kachler 2008; Mitterer 2010). The aforementioned investigations revealed an average content of c. 80 % quartz, c. 15 % kaolinite, c. 5 % biogenic opal-CT, as well as traces of illite and manganese and iron oxides. In places, especially on fault planes, the latter may alter the usually whitish colour of the rocks to vellowish or reddish. Secondarily silicified spicules of siliceous sponges (see taphonomy section for details on diagenesis) are enriched in the silt fraction (see Textfig. 5B). The opaline and porous nodules within the unconsolidated Neuburg Siliceous Earth are of equivalent composition to the surrounding sediment.

Up-section, the input of detrital quartz sand increases, causing a gradual transition from the Neuburg Kieselerde Member to the overlying sandy beds. Bimodal size distribution in this unit, i.e. rounded coarsegrained quartz grains being embedded in a matrix of porous fine-grained quartz sand to silt (Text-fig. 5F), is related to a major sea-level fall in the latest Early Turonian (Niebuhr et al. 2011; Richardt et al. 2013), and the beds are capped by an unconformity surface (sequence boundary SB Tu 1). The lithic fragments of this so-called Hornsand facies (see Niebuhr et al. 2009 for description) comprise subrounded to rounded lydites, milky quartz, vari-coloured polycrystalline quartz ("q" in Text-fig. 5F) and opaline clasts ("o" in Text-fig. 5F). The youngest Cretaceous lithological unit that is preserved in the karst depressions is a silicified conglomerate containing opaline and porous clasts of the underlying sediments in a Hornsand matrix (Text-fig. 5G, H; "tertiärer Süßwasser-Konglomeratquarzit" = Tertiary freshwater conglomerate of Schneider 1933). It may be related to the pronounced early Middle Turonian transgression observed across the Danubian Cretaceous Group (Niebuhr et al. 2009, 2011; Richardt et al. 2013).

The four marine lithounits described above, i.e. sandy basis beds, Neuburg Kieselerde Member, overlying sandy beds and silicified conglomerate, form the typical succession of the Wellheim Formation of Niebuhr *et al.* (2009) and are early Early Cenomanian to earliest Middle Turonian in age. The Wellheim Formation is commonly overlain by Miocene clays and sands of the Upper Freshwater Molasse and/or Pleistocene loams (Text-fig. 4).

## **Biostratigraphy**

Inoceramid bivalves occur in all marine facies of the Danubian Cretaceous Group and are thus of prime importance for the biostratigraphic subdivision of these strata (Tröger *et al.* 2009; Niebuhr 2011b). The Neuburg Kieselerde Member of the Wellheim Formation yielded five inoceramid (sub-)species, which are assigned to two different genera (Text-fig. 2). The most common fossil of the Neuburg Kieselerde Member, *Inoceramus crippsi crippsi* Mantell, 1822, indicates an Early Cenomanian age, while *Inoceramus hoppenstedtensis* Tröger, 1967 persists into the early Middle Cenomanian. A mass occurrence of *I. crippsi crippsi* Mantell at the transition of the sandy basis beds to the Neuburg Siliceous Earth

Text-fig. 5. Microfacies of the Schutzfels Formation (A) and Wellheim Formation (B–H) in stratigraphic order. W = width of photomicrograph. A – Weakly cemented coarse-grained arkosic sandstone. Lower Cretaceous; Schaflache Pit, W = 15 mm. B – Opaline nodule of a spiculitic silt; sponge spicules filled with secondary silica. Sample with *Inoceranus crippsi crippsi* from the *crippsi* Event; lower Lower Cenomanian; near Wellheim; W = 5 mm. C – Opaline nodule of a spiculitic silt with silicified inoceramid (i) and non-inoceramid bivalves (b); inoceramid prisms are visible and still in contact. Upper Lower Cenomanian; near Neuburg an der Donau; W = 4 mm. D – Opaline nodule of a spiculitic silt with siliceous sponge *in situ*. Middle to Upper Cenomanian; Schaflache Pit; W = 15 mm. E – Strongly [opaline (o) = lower part] to weakly (dark = upper part) silicified spiculitic clay to silt; sample with *Inoceranus pictus pictus*. Upper Cenomanian; near Neuburg an der Donau; W = 4 mm. F – Porous nodule of a fine- to medium-grained sand with large isolated quartz grains (q) and opaline nodules (o). Hornsand facies of the uppermost Lower Turonian; Schaflache Pit; W = 8 mm. G – Lowermost Middle Turonian silicified conglomerate with reworked clasts from the underlying sands and spiculitic Neuburg Siliceous Earth (s) with diffuse transition to the Hornsand matrix; upper right corner: angular opaline nodule (o; similar to Text-fig. 5E) with sharp contact to the Hornsand matrix; lower right corner: angular glauconite grain (g), evidencing marine conditions during silicification of the conglomerate. W = 5 mm





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(Wilmsen and Niebuhr 2010, p. 275, fig. 5) characterizes the crippsi Event of the middle Mantelliceras mantelli Zone (see Text-figs 2, 3). Inoceramus pictus pictus J. de C. Sowerby, 1829 and I. p. cf. concentricoundulatus Tröger, 1967 indicate a Late, but not latest, Cenomanian age. Inoceramus pictus pictus J. de C. Sowerby was also found in the Eibrunn Formation of the Regensburg-Kelheim area, while I. p. ssp. aff. concentricoundulatus Tröger is known from the Regensburg Formation of the Bodenwöhrer Senke (Tröger et al. 2009). Mytiloides mytiloides (Mantell, 1822) occurs in the Lower Turonian of the Neuburg Kieselerde Member as well as in the Reinhausen and Knollensand members of the Winzerberg Formation of the Regensburg-Kelheim area (Tröger et al. 2009). Summarizing the data on inoceramid biostratigraphy, the Neuburg Kieselerde Member ranges from the lower Mantelliceras mantelli standard ammonite Zone (lower Lower Cenomanian, c. 100 Ma) to the Mammites nodosoides standard ammonite Zone (Lower Turonian, c. 93.5 Ma) (Text-fig. 2).

### MATERIAL AND METHODS

Almost the entire material from the Neuburg Siliceous Earth studied herein has been collected by the owners and employees of the Hoffmann Mineral Company (HMC) or other former mining companies at Neuburg. In the case of significant finds the mineworkers were granted beer or small amounts of money by the company (pers. comm. M. Hoffmann jun., 2012), which certainly would have motivated them to continue searching for fossils. As a result, the collections may represent a fairly comprehensive inventory of the fossilised fauna from the Neuburg Kieselerde Member. Usually, private collectors were not granted access to the pits, but would have been permitted to sample the dumps, which still yield fossils, in particular the abundant Inoceramus crippsi. Obviously, the unpublished "Fossilium Catalogus Neuburgensis" compiled by Kempcke (1958b) lists and figures most of the taxa and some of the specimens considered herein. As reported by Wagner (1963), most of the fossils collected by Kempcke were obtained during the late 1950s. Fossils were usually discovered within scattered rocks or among the residues of subsequent wet sieving (Kempcke 1958a).

With few exceptions, the content of fossils in the Neuburg Siliceous Earth is low, usually going along with poor preservation. Only a few out of 45 pits yielded fossils in significant quantities. The currently active pits have not yielded well-preserved fossils to date, which may also result from a lack of discovery due to industrial mining techniques with large excavators, where the rocks are no longer screened for fossils. Most of the fossils listed by Kempcke were collected from the Wellheim, Kreuzgründe and Gammersfeld pits (the latter include the "Konsteiner Sandgrube"), with minor additions from other localities. All of these pits (see Text-fig. 1) have been fully exploited (most of them by subsurface mining) and restored and are thus no longer accessible.

Today, fossils from the Neuburg Kieselerde Member are housed in several institutions.

- (1) The Naturmuseum Augsburg (NMA) holds an impressive collection, including rich sedimentological reference material (Inventory number NMA–2013/687). The fossils have been donated by M. Hoffmann senior and obviously were collected by different persons. Many of the finds may have been made by Kempcke, since labels with his distinctive handwriting and several specimens figured by Kempcke (1958b) are present. Unfortunately, many labels are in disorder and specimens usually cannot confidently be assigned to specific localities.
- (2) A selection of well preserved specimens from Kempcke's collection is on display in the Archäologie-Museum Schloss Neuburg an der Donau (AMSN), which is a local branch of the Archäologische Staatssammlung (Inventory numbers AMSN H 21–32, H 67–97, H 100–119, E 42–52, E 261, E 281, and several unnumbered specimens). Additional material from the collection of the Historischer Verein Neuburg an der Donau e. V. is stored in the repository of the museum (unnumbered). Judging from the rather uniform labelling, most samples from the Neuburg Kieselerde Member seem to originate from collections of the HMC.
- (3) An important part of the Neuburg Kieselerde Member fossils is curated by the Hoffmann Mineral Company (HMC). Several outstanding specimens, including most of the originals of Kempcke (1958a, b) are on display in a showcase, while a small reference collection is stored in boxes, supplemented by typescript labels. Regular inventory numbers are lacking.
- (4) Another significant portion of the Kempcke Collection is present at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (BSPG; inventory numbers BSPG 1956 X 1–316, BSPG 1986 I 1). The material consists mainly of several hundred fossil sponges comprising the types and originals of Wagner (1963); several other fossils were donated by Kempcke's wife in 1965, after Kempcke had passed away. Furthermore, a few inoceramids collected by Franz Traub, a former freelance worker at the BSPG, are present.

Several other institutions in Bavaria including the Juramuseum Eichstätt, the Palaeontology Collection at the GeoZentrum Nordbayern (Friedrich-Alexander-University Erlangen-Nürnberg; labels with handwriting of Kempcke) and the geological collection of the Landesamt für Umwelt at Munich hold additional samples of minor importance.

All fossils from the Neuburg Kieselerde Member are silicified, rendering both chemical and mechanical preparation impossible. The specimens were documented by macro-, micro- and SEM-photography. For macro-photographs, most of the specimens were coated with ammonium chloride. The spiculation of sponges was studied using standard methods of scanning electron microscopy (Jeol JSM-6380) and optical microscopy (Nikon SMZ-645 using NIS-Elements software). For sedimentological analysis, a series of thin-sections was produced, which are housed in the Palaeozoology Collection of the Senckenberg Naturhistorische Sammlungen Dresden, Museum für Mineralogie und Geologie.

## SYSTEMATIC PALAEONTOLOGY

This section provides a comprehensive overview of the macrofauna from the Neuburg Kieselerde Member. Resulting from poor preservation, several taxa cannot be determined to species or even genus level and are thus kept in open nomenclature. Many of the specimens at NMA, AMSN and HMC repositories are not (correctly) labelled, and lack locality data and/or collection numbers. Only those data that confidently match the specimens in question are provided below. Both Lehner (1937a, b) and Kempcke (1958b), who obviously also included Lehner's data in his catalogue, listed several taxa (mainly bivalves and echinoids) which are neither represented in the studied collections, nor considered synonymous with any of the species treated herein. Since Lehner's collection has been lost, his determinations can no longer be reconsidered, but certainly the fauna of the Neuburg Kieselerde Member yielded additional rare elements not encountered herein.

The Porifera from the Neuburg Kieselerde Member have been monographed by Wagner (1963). A detailed taxonomic revision of this large group would be clearly beyond the scope (and limits) of the present paper. We thus provide only a general survey of the sponges and depict a selection of representative and well-preserved specimens. A list of all taxa described by Wagner (1963) is provided in the Appendix. The Inoceramidae have recently been detailed by Tröger *et al.* (2009). They are therefore only briefly considered and a selection of specimens is figured for completeness.

It should be mentioned that determinations of the nautilids, sabellids, serpulids and brachiopods are based on high-quality photographs only, while all other determinations are based on direct observation of the fossils. Synomymies are kept brief, and the authors of genus group and higher rank systematic categories are not included in the references. Open nomenclature follows Bengtson (1988).

The macroflora of the Neuburg Kieselerde Member only comprises a few pieces of fossil conifer driftwood (NMA–2013/687–0006, AMSN H 67), which are not completely silicified, do not preserve anatomic structures, and are thus indeterminable (Text-fig. 6B).

#### Ichnofossilia (Simon Schneider)

## Ichnogenus *Planolites* Nicholson, 1873 *Planolites* sp. (Text-fig. 6A)

1933. Cylindrites saxonicus Gein.; Lehner, p. 465.1937b. Cylindrites saxonicus (Geinitz 1842); Lehner, p. 188, pl. 17, figs 33–36.

MATERIAL: Three specimens on matrix (NMA–2013/687–0007, AMSN H 80).

REMARKS: The three specimens preserve 150 to 200 mm long, simple, almost cylindrical, slightly undulating burrows with a diameter of ca 10 mm. Since the infill of the burrows is unstructured, but more finegrained than the surrounding sediment, the burrows are assigned to *Planolites* (Bromley 1996: 203).

### Porifera (Radek Vodrážka)

Sponge spicules and skeletons are the most abundant and diverse macro-invertebrate remains occurring in the Neuburg Kieselerde Member. For his extensive monograph, Wagner (1963) had available more than 1600 sponges and sponge-skeleton fragments collected by E. Kempcke between 1956 and 1963. Most of the specimens come from the Kreuzgründe Pit (about 9 km NW of Neuburg; see Text-fig. 1), with a few additions from Ried Pit (near the village of Ried north of Neuburg).

Wagner (1963) listed 59 species of sponges belonging to 43 genera from the Neuburg Kieselerde Member. Out of these, 38 species represent lithistid



Text-fig. 6. A – *Planolites* sp.; burrow of an unidentified organism, associated with Lower Cenomanian *Inoceramus* ex gr. *crippsi*; NMA–2013/687–0007. B – Silicified conifer driftwood. NMA–2013/687–0006. Scale bar = 10 mm

demosponges, two species are choristid demosponges, 18 species belong to the hexactinellids and one species (*Elasmoierea* sp., a single poorly preserved specimen) possibly represents a calcareous pharetronid sponge (Appendix). The sponge classification follows the revised Porifera Treatise (Rigby *et al.* 2004).

Lithistid demosponges, which are thus the most common elements of the sponge assemblage (Wagner 1963) are represented mainly by the suborder Tetracladina Zittel (Text-figs 7A, H, J; 8G, H), but representatives of the suborders Megamorina Zittel, Dicranocladina Schrammen (Text-fig. 7I), Sphaerocladina Schrammen and Rhizomorina Zittel (Text-fig. 7F) also occur. A survey of the museum material from the Neuburg Kieselerde Member showed that hexactinellid sponges are as abundant as lithistid demosponges, but simply much less diverse at species level than the latter (see above). Hexactinellids are represented exclusively by hexactinosans (Text-figs 7B, C, E; 8A–D) and lychniscosans (Text-figs 7D, G; 8E, F).

Preliminary research has shown that Wagner's (1963) genus-level determinations are correct. There are, however, doubts about several determinations at species level, resulting from the fact that Wagner (1963) put a lot of emphasis on the significance of the outer shape of the sponges. This can be exemplified by the listing of five species of the genus *Guettardiscyphia* from the studied assemblage, which were distinguished mainly by the shape and position of wing-like outgrowths in the upper part of the skeletons (Wagner 1963). Preliminary stud-

Text-fig. 7. Porifera. A – Lithistid sponge Astrocladia subramosa (Roemer) (Demospongea, Tetracladina), with undetermined juvenile oyster (arrow) cemented onto its dermal surface. NMA-2013/687–0044. B – Laocoetis fittoni (Mantell) (Hexactinellida, Hexactinosa), with inhalant canal openings arranged in typical quadrangular pattern; AMSN. C – Guettardiscyphia stellata (Michelin) (Hexactinellida, Hexactinosa); NMA-2013/687–0043. D – Almost complete specimen of Exanthesis reticulatus (Hinde) (Hexactinellida, Lychniscosa). AMSN H94. E – Wall fragment of Laocoetis cf. tenuis (Roemer) (Hexactinellida, Hexactinosa); gastral surface. NMA–2013/687–0042. F. Cup-like lithistid sponge Laosciadia mantellii (Goldfuss) (Demospongea, Rhizomorina) overgrowing undetermined sponge skeleton; AMSN H87. G – Brachiolites fenestratus T. Smith (Hexactinellida, Lychniscosa) with partly silicified sediment between interconnecting tubes; AMSN H109. H – Jerea pyriformis Lamouroux (Demospongea, Tetracladina); AMSN H86. I – Phrissospongia hoffmanni Wagner (Demospongea, Dicranocladina) overgrowing fragment (below dashed line) of Pseudojerea excavata Moret (Demospongea, Tetracladina). NMA–2013/687–0041. J – Phyllodermia kempckei Wagner (Demospongea, Tetracladina). AMSN. Scale bars = 10 mm



ies show, however, that the actual number of *Guet-tardiscyphia* species from the Neuburg Kieselerde Member is lower. Nevertheless, the validity of the species of *Guettardiscyphia* listed by Wagner (1963) cannot be ascertained as (1) the original descriptions of these species are mostly vague and in urgent need of revision and (2) their morphological variability is poorly known.

The preservation of the majority of the sponge skeletons is rather poor due to intense and probably repeated calcification, silicification and desilicification. In most of the studied specimens it is impossible to recognize and/or identify the shape and size of the individual spicules forming the sponge skeleton. Generally, sponge spicules are better preserved close to the dermal and/or gastral surface of the skeletons. Interspicular areas are usually infilled with secondarily silicified sediment enabling studies of spiculation and canalization of the wall interior. In both hexactinellids and lithistids the most intensively silicified part of the skeleton is confined to the interior of the wall (Text-fig. 8B, F), whereas the uppermost layer of spicules on the dermal and/or gastral surface exhibits no secondary silica accumulation (Text-fig. 8A, E) but, in contrast, often silica dissolution (Text-fig. 8G, H).

Due to the fact that the hexactinellid skeleton is usually more massive and compact than the skeleton of lithistids, the hexactinellid sponges are generally better preserved than the lithistids. Their thick dictyonal strands are often formed by original siliceous material (Text-fig. 8F), but are also frequently partly (Text-fig. 8B, C) or completely (Text-fig. 8D) dissolved and replaced by secondary silica accumulations. The fact that the original siliceous skeleton is usually not preserved in tetractinellids is in accordance with observations on the taphonomy of most of the Upper Cretaceous sponge-bearing localities. Lithistid demosponges were usually secondarily calcified, while simultaneously losing the opaline silica that was the primary building material of their spicules (e.g., Žítt and Vodrážka 2013).

Desmas, especially tetraclones, are only rarely found in the intensively silicified specimens from

Neuburg Kieselerde Member. Their preservation is poor (Text-fig. 8G, H) and the surface of individual spicules is usually covered with small rounded concave depressions (3–10 mm in diameter), which result from silica dissolution. The same structures were observed on the surfaces of loose spicules within the sediment (monaxons, triaenes, dichotriaenes) as well as on the surface of hexactinellid sponges.

#### **Bivalvia (Simon Schneider)**

The bivalve assemblage from the Neuburg Siliceous Earth is undoubtedly biased due to the early diagenetic loss of aragonite, which surely also caused the absence of fossil gastropods. Furthermore, preservation of all taxa with considerable aragonitic shell portions is generally poor. In contrast, calcitic shells are often fully silicified, and may occasionally show delicate ornamentation details. In several cases, however, only internal moulds have been preserved. Despite of taphonomic loss, the bivalves still represent one of the most diverse groups in the Neuburg Kieselerde Member, comprising at least 29 species. Classification follows Carter *et al.* (2011).

Class Bivalvia Linnaeus, 1758 Subclass Autobranchia Grobben, 1894 Infraclass Pteriomorphia Beurlen, 1944 Order Mytilida Férussac, 1822 Family Mytilidae Rafinesque, 1815 Genus *Modiolus* Lamarck, 1799 *Modiolus reversus* (J. de C. Sowerby in Fitton, 1836) (Text-fig. 9D)

- \* 1836. *Modiola reversa*; J. de C. Sowerby in Fitton, p. 241, 342, pl. 17, fig. 13.
  - 1900. *Modiola reversa*, Sowerby, 1836; Woods, p. 94, pl. 15, figs 15–18, pl. 16, figs 1–3 [with extensive synonymy].

MATERIAL: Two left valves; one of them (NMA-2013/687-0008) severely distorted and thus of doubt-

Text-fig. 8. Porifera SEM micrographs. A–C – *Laocoetis* cf. *tenuis* (Roemer) (Hexactinellida, Hexactinosa). BSPG 1956 X 231. A – Gastral surface of the wall with well preserved cortex and quadrangularly organized exhalant canal openings. Note the intensively silicified skeleton within the wall just below the cortex (arrow) and numerous subangular quarz-grains trapped within the canals. B – Longitudinal section of the wall with heavily silicified interspicular areas in the wall interior and chalcedony accumulations within the canals (arrows). C – Original siliceous skeleton within the silicified sediment containing small ball-like voids of unknown origin; hollow voids within siliceous spicules result from the demineralization along axial canals (a) and within spicule centers (c). D – *Guettardiscyphia stellata* (Michelin) (Hexactinellida, Hexactinosa) with gastral surface formed by original siliceous skeleton; note the chalcedony in the central part of the wall. BSPG 1956 X 162. E. *Stauronema carteri* Sollas (Hexactinellida, Lychniscosa); transverse section through the wall; dermal surface at the top left; unusual appearance of the hexactinellid skeleton results from the presence of original siliceous skeleton (s) interlocking with intensively silicified sediment within interspicular area (i). BSPG 1956 X 189. G, H – *Prokaliapsis danubica* Wagner (Demospongea, Tetracladina). BSPG 1956 X 99. G – Poorly preserved but still recognizable tetraclones on the dermal surface; note numerous concave depressions resulting from silica dissolution. H – Transverse section of the skeleton with the dermal surface to the right; note strongly corroded silicified tetraclones (s) on the dermal surface contrasting empty voids of secondarily calcified and subsequently dissolved tetraclones (v)



ful assignment; the second one, from Wellheim, well preserved (HMC).

DESCRIPTION: Shell of slender modioliform shape; anterior shell portion short, well-rounded; posterior shell portion much larger; strongly extended in posterior-ventral direction due to distinct allometric growth. Posterior-dorsal corner bluntly angled; posterior-ventral end well-rounded. Umbo prosogyrous, only slightly exposed, well-rounded and inflated, marking onset of broad, smoothly rounded, inflated radial bulge extending toward posterior-ventral end of shell. Shallow depression anterior to bulge causing slight incurvature at ventral margin. Commarginal growth lines regular; relatively distinct and prominent for genus; less pronounced on radial bulge.

REMARKS: The large, undistorted specimen from the Neuburg Kieselerde Member almost perfectly matches the drawings provided by Woods (1900) with regard to general shell shape and commarginal ornamentation. The specimen lacks the faint set of radial lines that is, according to Woods (1900), usually present in the shallow depression anterior to the bulge, which may, however, be a matter of preservation (see discussion on *Modiolus typicus* in Dhondt 1987). *Modiolus ligeriensis* (Orbigny, 1844) and *M. typicus* (Forbes, 1846) are apparently almost indistinguishable from *M. reversus*, and may well turn out to be conspecific when thoroughly revised. In England, *Modiolus reversus* mainly occurs in strata of Albian to Cenomanian age (Woods 1900).

> Order Arcida J. Gray, 1854 Family Cucullaeidae R. Stewart, 1930 Genus *Cucullaea* Lamarck, 1801 *Cucullaea*? sp. (Text-fig. 9B)

MATERIAL: A single internal mould of a double-valved specimen (NMA-2013/687-0009).

DESCRIPTION: Specimen strongly inflated, with markedly opisthogyrous, highly inequilateral valves. Umbo positioned in anterior third of shell; distinct, blunt ridge running from umbo towards posterior-ventral shell corner. Both posterior-dorsal and posteriorventral corners distinct; posterior shell margin slightly incurved. Anterior shell margin broken. Ill-defined imprint of anterior adductor muscle scar with straight inner margin visible in left valve.

REMARKS: The poorly preserved internal mould lacks traces of ornamentation, ligament, or dentition. Assignment to *Cucullaea* refers only to the general shape of the mould and the ill-defined anterior adductor muscle scar, and is thus tentative.

Order Myalinida H. Paul, 1939 Family Inoceramidae C. Giebel, 1852 Genus *Inoceramus* J. Sowerby, 1814 *Inoceramus crippsi crippsi* Mantell, 1822 (Text-fig. 10D)

- \* 1822. *Inoceramus crippsi* n. sp.; Mantell, p. 133, pl. 27, fig. 11.
   1911. *Inoceramus Crippsi*, Mantell, 1822; Woods, p. 273, pl. 48, figs 2, 3, text-figs 33–35.
  - 1914. Inoceramus Crippsi Mantell; Schneid, p. 39.
- 1915. Inoceramus Crippsi Mantell; Schneid, pl. 9, figs 4, 5.
- 1933. Inoceramus crippsi Mant.; Lehner, p. 465.
- 1958a. Inoceramus crippsi Mantell; Kempcke, p. 9, fig. 12.
- 1963. Inoceramus (Mytiloides) labiatus (Schlotheim); Wagner, p. 170.
- 1967. *Inoceramus crippsi crippsi* Mant., 1822; Tröger, p. 24, pl. 2, figs 4, 5. [with synonymy]
- 1982. *Inoceramus crippsi crippsi* Mantell, 1822; Keller, p. 44, pl. 1, fig. 5.
- 2001. *Inoceramus crippsi* Mantell, 1822; Wilmsen *et al.*, p. 129, pl. 1, fig. 1.
- 2009. *Inoceramus crippsi crippsi* Mantell, 1822; Tröger *et al.*, p. 62, figs 3A–C, 4A. [with additional synonymy]
- 2010. *Inoceramus crippsi crippsi* Mantell; Wilmsen and Niebuhr, p. 275, figs 4H, 5.

MATERIAL: Numerous specimens (NMA–2013/687–0001 and others, AMSN, HMC, BSPG 1956 X 304, 305).

DESCRIPTION: Shells equivalved, inequilateral, rounded-quadrate, sparsely inflated. Umbo not extending above hinge line. Ligament area wide, steeply sloping towards anterior shell margin; transition to posterior wing shallow. Onset of well-rounded undulations after few millimetres of growth; undula-

Text-fig. 9. Bivalvia: Mytilidae, Cucullaeidae, Pinnidae, Pteriidae, Bakevelliidae. A – Pteria? sp., preserved inside Cymatoceras cf. elegans. AMSN H 102. B – Cucullaea? sp. NMA–2013/687–0009. C, F – Pinna cretacea (Schlotheim, 1813). C – Slightly compressed individual in frontal view. NMA–2013/687–0010. F – Large, exceptionally well-preserved specimen with contiguous valves; right valve view. Gammersfeld Pit. HMC. D – Modiolus reversus (J. de C. Sowerby in Fitton, 1836); undistorted left valve. Wellheim. HMC. E – Gervillia? sp.; posterior shell fragment; right valve view. BSPG 1956 X 308. G – Gervillaria neptuni (Goldfuss, 1837); right valve. NMA–2013/687–0012. H – Pteria? sp.; right valve. NMA–2013/687–0011. Scale bars = 10 mm



tions slightly concave in juveniles, but moderately convex in adults. Hinge line long, with smooth transition to posterior margin. [adapted from Tröger *et al.* 2009]

REMARKS: Although usually compressed, the specimens are only moderately distorted and can thus be confidently determined. Contrary to the statement by Tröger *et al.* (2009), specimens from the Neuburg Kieselerde Member do preserve silicified shell; this, however, is rather fragile and brittle, and thus only remnants of it stick to the moulds (arrow in Text-fig. 10D). As outlined above, *Inoceramus crippsi crippsi* is an index fossil of the Lower Cenomanian *Mantelliceras mantelli* Zone and thus of the utmost biostratigraphic importance.

### Inoceramus hoppenstedtensis Tröger, 1967 (Text-fig. 10E)

- \* 1967. *Inoceramus crippsi hoppenstedtensis* n. ssp.; Tröger, p. 26, pl. 1, figs 9, 10.
  - 2001. "Inoceramus" hoppenstedtensis Tröger, 1967; Wilmsen et al., p. 130, pl. 1, figs 2–5.
- 2009. Inoceramus hoppenstedtensis Tröger, 1967; Tröger et al., p. 65, fig. 4B–D.
- 2010. *Inoceramus hoppenstedtensis* Tröger; Wilmsen and Niebuhr, p. 275, fig. 4F, I.

MATERIAL: Several specimens (NMA, HMC).

DESCRIPTION: Shell relatively small, equivalve, inequilateral, rounded-rectangular to oval, sparsely inflated. Umbo prosogyrous, inflated, but not extending above hinge line. Ligament area steeply sloping towards anterior shell margin; transition to posterior wing shallow. Anterior shell margin slightly concave. Onset of shallow undulations at a shell size of 10 to 20 mm. [adapted from Tröger *et al.* 2009]

REMARKS: *Inoceramus hoppenstedtensis* differs from *I. crippsi* in being smaller and less quadrate, having a slightly inflated umbo, and showing slightly less cycloidal undulations. Originally proposed as a subspecies of *I. crippsi*, *I. hoppenstedtensis* was raised to species rank by Wilmsen *et al.* (2001). Its first occurrence slightly post-dates that of *I. crippsi*; it typically marks the Lower to lowermost Middle Cenomanian.

# Inoceramus pictus pictus J. de C. Sowerby, 1829 (Text-fig. 10A)

- \* 1829. *Inoceramus pictus* n. sp.; J. de C. Sowerby, p. 215, pl. 601, fig. 1.
  - 1911. *Inoceramus pictus*, Sowerby, 1829; Woods, p. 279, pl. 49, figs, 5, 6, text-fig. 36.
  - 2009. *Inoceramus pictus pictus* Sowerby, 1829; Tröger *et al.*, p. 68, fig. 6A, D, F, H.
  - 2010. *Inoceramus pictus pictus* Sowerby; Wilmsen and Niebuhr, p. 275.

MATERIAL: Two specimens (NMA–2013/687–0003; BSPG 1956 X 306 from Kreuzgründe Pit).

DESCRIPTION: Shell distinctly inequivalve, inequilateral, slender-ovate. Umbo of right valve slightly inflated, slightly exposed above hinge line. Hinge line and posterior shell margin meeting at angles of 125– 140°. Posterior wing markedly detached from umbo. Transition from umbo to anterior shell margin bent steeply outward. Umbo of left valve distinctly exposed above hinge line. Transition from umbo to anterior shell margin bent steeply inward. Both valves ornamented with prominent commarginal growth lines in early shell portion. Onset of undulations at variable shell sizes. [adapted from Tröger *et al.* 2009]

REMARKS: All specimens are strongly compressed and markedly distorted, but still distinctly inequivalve. *Inoceramus pictus pictus* typically occurs in the Upper, but not uppermost Cenomanian, albeit the type specimen comes from the Plenus Marls (*Metoicoceras geslinianum* Zone of southern England).

## Inoceramus pictus cf. concentricoundulatus Tröger, 1967 (Text-fig. 10B)

cf. \* 1967. Inoceramus pictus concentricoundulatus n. sp.; Tröger, p. 46, pl. 3, fig. 7.

2009. Inoceramus pictus subsp. aff. concentricoundulatus Tröger, 1967; Tröger et al., p. 69, fig. 6G.

MATERIAL: A single double-valved specimen (HMC).

REMARKS: Inoceramus pictus concentricoundulatus closely resembles Inoceramus pictus pictus with regard to morphology, but clearly lacks undulations. Since the specimen is markedly compressed, assignment is still tentative (see Tröger *et al.* 2009). I. pictus concentricoundulatus has to date only been reported from the Upper Cenomanian of Saxony. A poorly preserved, doubtful specimen comes from

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Text-fig. 10. Bivalvia: Inoceramidae. A – Inoceramus pictus pictus J. de C. Sowerby, 1829; arrow indicates remnants of shell. NMA–2013/687–0003. B – Inoceramus pictus cf. concentricoundulatus Tröger, 1967. HMC. C – Mytiloides mytiloides (Mantell, 1822). NMA–2013/687–0004. D – Inoceramus crippsi crippsi Mantell, 1822; arrow indicates remnants of shell. NMA–2013/687–0001. E – Inoceramus hoppenstedtensis Tröger, 1967. HMC. Scale bars = 10 mm

the upper part (Cenomanian–Turonian boundary) of the Regensburg Formation (Tröger *et al.* 2009).

# Genus *Mytiloides* Brongniart, 1822 *Mytiloides mytiloides* (Mantell, 1822) (Text-fig. 10C)

- \* 1822. Inoceramus mytiloides n. sp.; Mantell, p. 251, pl. 28, fig. 2.
  - 1939. Inoceramus (Mytiloides) labiatus Schloth.; Dacqué, p. 103, pl. 5, figs 4, 5, pl. 6, fig. 13 [non figs 11, 12].
  - 2009. *Mytiloides mytiloides* (Mantell, 1822); Tröger *et al.*, p. 77, fig. 11A, B, fig. 15B, D, E, G. [with extensive synonymy]

MATERIAL: A single double-valved specimen (NMA-2013/687-0004).

DESCRIPTION: Shell equivalve, inequilateral, slender mytiliform. Umbo well-inflated, distinctly exposed above the hinge line, with a steep slope towards anterior shell margin. Posterior wing pointed, separated from umbo by marked sulcus. Hinge line long and straight. Main portion of shell ornamented with distinct commarginal growth lines, fading out on wing. [adapted from Tröger *et al.* 2009]

REMARKS: The specimen is obliquely compressed, but almost complete. *Mytiloides mytiloides* typically occurs in the Lower, but not lowermost, Turonian (*Mammites nodosoides* ammonite Zone). Within the Danubian Cretaceous Group, this species is also reported from the Winzerberg Formation (Dacqué 1939; Tröger *et al.* 2009).

Order Ostreida Férussac, 1822 Family Arctostreidae Vialov, 1983 Genus *Rastellum* Faujas de Saint-Fond, 1799 *Rastellum diluvianum* (Linnaeus, 1767) (Text-fig. 11A, B)

- \* 1767. Ostrea diluviana; Linnaeus, p. 1148.
  - 1913. *Ostrea diluviana* L.; Woods, p. 342, text-figs 98–138. [with extensive synonymy]
- ? non 1933. Ostrea diluviana L. var.; Lehner, p. 465.
- non 1937a. Ostrea diluviana Linn. 1767; Lehner, p. 198, pl. 26, fig. 24.
  - 1939. *Alectryonia diluviana* Lin.; Dacqué, p. 52, pl. 5, fig.7, p. 127, pl. 9, fig. 1. [with extensive synonymy]
  - 2011. Rastellum diluvianum (Linnaeus, 1767); Schneider et al., p. 799, fig. 8B.

MATERIAL: Two large specimens from Schensand Pit near Kreut, southwest of Neuburg (AMSN H 119).

DESCRIPTION: Both specimens relatively large and regularly grown; very slender. One specimen strongly incurved (Text-fig. 11A), the second one almost straight (Text-fig. 11B). Numerous regularly spaced, bluntly angled to well-rounded shell-folds extending from midline of shell; bending slightly outwards in both directions. Dorsal shell-portions poorly preserved.

REMARKS: The distinction of *Rastellum* and *Arctostrea* as suggested by Stenzel (1971) seems arbitrary and is not adopted herein. We follow Woods (1913), who has suggested that all Cretaceous *Rastellum* belong to a single, very variable species, i.e. *Rastellum diluvianum* (Linnaeus, 1767). In any case, the specimens from Sehensand Pit would have to be assigned to the *Arctostrea diluviana* group *sensu* Carter (1968). Although following a distinct bauplan, *Rastellum diluvianum* displays a wide range of morphologies resulting from strong substrate relationship. The two specimens from the Kieselerde are of rather typical shape and relatively well preserved, but visible only from the outside. Among the bivalves, *R. diluvianum* is probably the most reliable indicator of shallow water.

# Family Gryphaeidae Vialov, 1936 Genus *Rhynchostreon* Bayle, 1878 *Rhynchostreon suborbiculatum* (Lamarck, 1801) (Text-fig. 11C, D)

- \* 1801. Gryphaea suborbiculata. n.; Lamarck, p. 398.
- ? 1933. Exogyra conica Sow.; Lehner, p. 465.
- ? 1937a. Exogyra conica Sowerby 1813; Lehner, p. 203.
- ? 1937a. *Exogyra conica* Sow. var. *canaliculata* Sowerby 1813; Lehner, p. 204, pl. 24, fig. 16.
  - 1939. *Exogyra columba* Lam.; Dacqué, p. 53, p. 128, pl. 13, figs 1, 2. [with extensive synonymy]
  - 1982. *Rhynchostreon suborbiculatum* (Lamarck, 1801); Gründel, p. 155, pl. 2, figs 10, 11, pl. 3, figs 1–3. [with extensive synonymy]

MATERIAL: A small rock sample with juvenile specimens and several small and medium-sized specimens of more or less doubtful assignment (AMSN, NMA).

DESCRIPTION: Left valve strongly opisthogyrous, coiled, inflated, increasing rapidly in diameter. Early shell portion ornamented in places with sub-radial wrinkles. Hinge and ligament not visible.

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Text-fig. 11. Bivalvia: Ostreidae, Gryphaeidae. A, B – Rastellum diluvianum (Schlotheim, 1813), Sehensand Pit, AMSN H 119. C, D – Rhynchostreon suborbiculatum (Lamarck, 1801). C – Rock sample with juveniles. AMSN. D – Young specimen with remnants of shell, showing radial striation. AMSN. E – Gryphaeidae indet.; small specimen exemplifying the usual preservation of oysters from the Neuburg Kieselerde Member. NMA–2013/687–0040. Scale bars = 10 mm

REMARKS: *Rhynchostreon suborbiculatum* is probably the most common bivalve of the Danubian Cretaceous Group and can, e.g., be regarded as the characteristic fossil of the Lower Cenomanian Saal Member of the Regensburg-Kelheim area (Dacqué 1939). Since it preferred siliciclastic sediments rather than carbonates for settlement, it is much less abundant, and specimens are particularly small in the partly contemporaneous Neuburg Kieselerde Member. Gründel (1982) expands on the similarity of juvenile *R. suborbiculatum* and the Albian– Cenomanian *Amphidonte conica* (J. Sowerby, 1813), and states that juvenile shells are hardly confidently determinable. The specimens described herein are evenly inflated and lack a posterior ridge, which is usually present in *A. conica*. Moreover, they increase more rapidly in diameter than *A. conica* during growth, and some of the specimens preserve sub-radial ornament in early shell portions (compare Gründel 1982, pl. 3, fig. 1). Based on these characters, the specimens are confidently assigned to *R. suborbiculatum*.

# Gryphaeidae indet. (Text-fig. 11E)

REMARKS: Several indeterminable specimens of gryphaeid oysters are present in the collections. All of these specimens are poorly preserved and lack details

of the ligament area, rendering more detailed assignment impossible.

# Family Pinnidae Leach, 1819 Genus *Pinna* Linnaeus, 1758 *Pinna cretacea* (Schlotheim, 1813) (Text-fig. 9C, F)

- \* 1813. *Pinnites cretaceus* Fauj.; Schlotheim, p. 113. 1933. *Pinna cretacea* Schloth.; Lehner, p. 465.
- 1937. Pinna cretacea Schlotheim, 1813; Lehner, p. 169.
- 1958a. Pinna cretacea Schlotheim; Kempcke, p. 9, fig. 14.
- 1963. Pinna cretacea; Wagner, p. 227.
- 2003. *Pinna cretacea* (Schlotheim, 1813); Seeling and Bengtson, p. 477, fig. 4A–D. [with extensive synonymy]

MATERIAL: A single large almost complete double-valved individual from Gammersfeld (HMC) and numerous fragments of usually double-valved specimens (NMA–2013/687–0010, HMC, AMSN H 115, BSPG 1956 X 312).

DESCRIPTION: Shell of typical *Pinna* shape, relatively slender; moderately inflated. Dorsal part of shell ornamented with 12 to more than 20 pronounced radial ribs. Delicate growth lines in dorsal shell portion only faintly visible in moulds, but distinct on remnants of shell; crossing ribs almost at right angles. Growth lines in ventral shell portion distinct, also in moulds, meeting lowermost radial rib at acute angles.

REMARKS: We follow Dhondt (1987) and Seeling and Bengtson (2003) in considering *Pinna decussata* Goldfuss, 1837 as a junior synonym of *P. cretacea* (Schlotheim, 1813). Seeling and Bengtson (2003) have documented considerable variability with regard to general shell shape and ornamentation for this species. The specimens from the Neuburg Kieselerde Member clearly and almost invariably range among the most slender variants, while the number of radial ribs is rather variable. *Pinna cretacea* is one of the most abundant and characteristic bivalve species of the Neuburg Kieselerde Member.

> Family Pteriidae J. Gray, 1847 Genus *Pteria* Scopoli, 1777 *Pteria*? sp. (Text-fig. 9A, H)

1933. [Gervillia] rostrata Sow.; Lehner, p. 465.
1937a. Gervillia rostrata (Sowerby 1836); Lehner, p. 171, pl. 22, figs 12, 13, pl. 26, fig. 22.

MATERIAL: One small double-valved specimen with remnants of shell, preserved on the interior mould of a nautilid, *Cymatoceras* cf. *elegans* (AMSN H 102), and one severely distorted right valve (NMA–2013/687–0011).

REMARKS: Both specimens are poorly preserved and not confidently determinable at genus or species level, since the ligament and hinge are unknown. Based on the presence of a distinct but relatively small anterior wing and a relatively large, extended posterior wing, the specimens most likely belong to *Pteria* although an affiliation with the Bakevelliidae cannot be fully excluded.

> Family Bakevelliidae W. King, 1850 Genus *Gervillia* Defrance, 1820 *Gervillia*? sp. (Text-fig. 9E)

? 1933. Gervillia solenoides Defr.; Lehner, p. 465.
? 1937a. Gervillia solenoides Defrance 1820; Lehner, p. 171, pl. 22, fig. 11.

MATERIAL: Posterior fragment of a single specimen with contiguous valves, preserved on matrix, visible only from right valve view (BSPG 1956 X 308).

REMARKS: The small shell fragment preserves the posterior ends of both valves of a very slender bivalve. Several closely related genera among the Bakevelliidea, e.g., *Gervillia, Gervillella, Cultriopsis* or *Virgellia*, have similar posterior shell portions, and a confident determination is thus impossible. Presumably, the poorly preserved specimen described and figured as *Gervillia solenoides* [sic] by Lehner (1937a) is conspecific with the fragmentary individual reported herein. *Gervillia solenoidea* Defrance, 1820 is the type species of the genus.

# Genus Gervillaria Cox, 1951 Gervillaria neptuni (Goldfuss, 1837) (Text-fig. 9G)

- \* 1837. *Cardium Neptuni* nobis; Goldfuss, p. 221, pl. 144, fig. 9a, b.
- ? 1933. Oxytoma pectinata Sow.; Lehner, p. 465.
- ? 1937a. Oxytoma pectinata (Sowerby 1836); Lehner, p. 168, pl. 22, fig. 10.

MATERIAL: A single mould of a fragmentary doublevalved specimen with large parts of the right valve preserved (NMA–2013/687–0012).

DESCRIPTION: Shell strongly inequilateral-triangular, with straight dorsal margin, high wing-like posterior part and low and narrow anterior shell portion (missing). Central part of shell ornamented with > 15 relatively sharp, irregularly spaced radial ribs. Posterior shell portion smooth, with faint commarginal growth lines.



Text-fig. 12. Bivalvia: Pectinidae, Spondylidae, Neitheidae, Anomiidae, Limidae. A, E – Spondylus sp. A. Attached valve cemented onto gastral surface of a hexactinellid sponge, Stauronema carteri Sollas. NMA–2013/687–0019. E – External mould of free valve. NMA–2013/687–0020. B, C – Camptonectes virgatus (Nilsson, 1827). B – External mould of left valve, with partial internal mould of slightly dislocated right valve, forming smooth, inclined rim along anterior margin. NMA–2013/687–0014. C – External mould of right valve. NMA–2013/687–0015. D – Lima parallela (J. Sowerby, 1812). NMA–2013/687–0024. F – Merklinia aspera (Lamarck, 1819); small fragment showing typical ornamentation. NMA–2013/687–0013. G – Neithea cf. regularis (Schlotheim, 1813). NMA–2013/687–0021. H. Neithea coquandi (Peron, 1877). HMC. I – Pseudolimea cf. composita (J. de C. Sowerby in Fitton, 1836). NMA–2013/687–0025. J, K – Neithea quinquecostata (J. Sowerby, 1814). J – Juvenile left valve. NMA–2013/687–0023. K – External (K1) and internal (K2) mould of a juvenile right valve. AMSN E 281. L – Anomia papyracea Orbigny, 1847. NMA–2013/687–0022. M. Plagiostoma sp. NMA–2013/687–0026. Scale bars = 10 mm



Text-fig. 13. Bivalvia: Entoliidae, Pectinidae. A, D – Entolium orbiculare (J. de C. Sowerby, 1817). NMA–2013/687–0027, 0028. B, C, F – Mimachlamys robinaldina (Orbigny, 1847). B – Exterior mould showing imprints of spines. BSPG 1956 X 309. C – Shell fragment showing details of ornamentation in rib interspaces. NMA–2013/687–0017. F – Left valve with delicate spines. AMSN. E – Chlamys elongata (Lamarck, 1819). NMA–2013/687–0016. G – Pectinidae indet. NMA–2013/687–0018. H. Syncyclonema haggi Dhondt, 1971. AMSN. Scale bar = 10 mm

REMARKS: Although the preservation of the specimen is poor, part of the distinguishing characters reported by Dhondt (1987), i.e. the irregular radial ribs and the smooth posterior wing, are clearly visible. From Lehner's figure and description it is unclear if the specimen reported as *Oxytoma pectinata* (Sowerby 1836) actually belongs to *G. neptuni*. According to Dhondt (1987), the species ranges from the Turonian to the Campanian and occurs in central Europe and France. Order Pectinida J. Gray, 1854 Family Pectinidae Rafinesque, 1815 Genus *Merklinia* Sobetski, 1960 *Merklinia aspera* (Lamarck, 1819) (Text-fig. 12F)

\* 1819. Pecten asper; Lamarck, p. 180, no. 8.
1939. Pecten (Aequipecten) asper Lam.; Dacqué, p. 45, pl. 2, fig. 4, pl. 3, fig. 1.

1976. *Merklinia aspera* (J.B. Lamarck, 1819); Dhondt, p. 6, pl. 1, fig. 1. [with extensive synonymy]

MATERIAL: A single small shell fragment (NMA-2013/687-0013).

DESCRIPTION: Shell fragment ornamented with seven primary ribs. Each primary rib subdivided into one strong central rib and two less prominent side riblets, all of them triangular in cross-section.

REMARKS: The overall preservation of the specimen is rather poor, and spines, if present at all, may have become eroded. In any case, the shell fragment shows the characteristic rib shape and arrangement of *Merklinia aspera* that allows for a confident determination. In the Danubian Cretaceous group, *Merklinia aspera* is relatively abundant in the Saal Member of the Regensburg Formation (Niebuhr *et al.* 2009).

Genus Camptonectes Agassiz in Meek, 1864 Camptonectes virgatus (Nilsson, 1827) (Text-fig. 12B, C)

- \* 1827. Pecten virgatus n.; Nilsson, p. 22, pl. 9, fig. 15.
  - 1972. Camptonectes (Camptonectes) virgatus (S. Nilsson, 1827); Dhondt, p. 18, pl. 2, fig. 1a–c. [with extensive synonymy]
  - 2011. Camptonectes (Camptonectes) virgatus (S. Nilsson, 1827); Schneider et al., p. 800, fig. 8F, H.

MATERIAL: An external mould of a small left and a small right valve respectively (NMA–2013/687–0014, NMA–2013/687–0015).

DESCRIPTION: Shell sub-circular, with small, almost rectangular posterior and large, well-rounded anterior auricles. Disc ornamented with *Camptonectes*-type narrow, dichotomous, sub-radially diverging striae, crossed by irregular, widely-spaced, relatively weak commarginal growth lines. Auricles ornamented with reticulate pattern of radial striae (diverging in anterior auricle) and distinct growth lines.

REMARKS: The two specimens from the Neuburg Kieselerde Member are preserved as external moulds, showing the delicate ornamentation of disc and auricles in great detail as negative structures. All characters match the description of the species given by Dhondt (1972). At first sight, the left valve seems to have a peculiar, smooth rim, which actually represents a partial internal mould of the corresponding, obvi-

ously slightly detached right valve. From the Danubian Cretaceous Group, *Camptonectes virgatus* has previously been reported from the Turonian to Coniacian Sandbach Formation (Schneider *et al.* 2011).

> Genus *Chlamys* Röding, 1798 *Chlamys elongata* (Lamarck, 1819) (Text-fig. 13E)

\* 1819. Pecten elongatus; Lamarck, p. 181, no. 10.
1973a. Chlamys ? elongata (J.-B. Lamarck, 1819); Dhondt, p. 19, pl. 2, fig. 1. [with extensive synonymy]

MATERIAL: A single fragmentary valve with remnants of shell (NMA-2013/687-0016).

DESCRIPTION: Shell fragment ornamented with several slightly irregularly tripartite ribs; partitions wellrounded in cross-section, densely covered with distinct plicate spines.

REMARKS: Although only remnants of the shell are preserved, the single valve from the Neuburg Kieselerde Member can be relatively confidently assigned to *Chlamys elongata*, based on the characteristic ornamentation described by Dhondt (1973a).

# Genus *Mimachlamys* Iredale, 1929 *Mimachlamys robinaldina* (Orbigny, 1847) (Text-fig. 13B, C, F)

- \* 1847. Pecten robinaldinus d'Orbigny; Orbigny, p. 587, pl. 431, figs 1–4.
- 1933. Pecten hispidus Gf.; Lehner, p. 465.
- ? 1933. Pekten rhotomagensis d'Orbigny [sic]; Schneider, p. 19.
- 1937. *Pecten (Chlamys) hispidus* Goldfuss 1833; Lehner, p. 186, pl. 23, fig. 4, 10.
- 1937. Pecten (Chlamys) hispidus Goldf. var. stutchburiana Sowerby 1836; Lehner, p. 187, pl. 23, fig. 5, pl. 26, fig. 7.
- 1973a. *Minachlamys robinaldina* (A. d'Orbigny, 1847) [sic]; Dhondt, p. 56, pl. 7, fig. 2. [with extensive synonymy]

MATERIAL: A single well-preserved left valve (AMSN), an additional shell fragment (NMA–2013/687–0017) and a fragmentary external mould (BSPG 1956 X 309).

DESCRIPTION: Fully grown, well-preserved left valve (Text-fig. 13F) ornamented with more than 60

densely spaced ribs. Approximately 45 primary ribs relatively variable in width, bearing numerous prominent spiny plicae at very regular distances. Approximately 15 narrower secondary, intercalated ribs in central part of the disc and ornamented, if at all, with very tiny spines. External mould fragment (Text-fig. 13B) with relatively similar arrangement of ribs, covered with numerous prominent spiny plicae. Primary ribs more variable with regard to width and rib interspaces much wider than in large shell described above. Shell fragment ornamented with more than 30 relatively regular, more or less smooth primary ribs with wide interspaces, which are covered with distinct, densely-spaced commarginal striae (Text-fig. 13C). In anterior and posterior parts of disc, striae cross radial ribs at sharp angles, thus appearing oblique.

REMARKS: *Mimachlamys robinaldina* is among the most variable pectinids of the European Cretaceous (Woods 1902; Dhondt 1973a), and even the three specimens depicted herein display considerable variability with regard to number, arrangement, width and ornamentation of ribs, as well as rib interspaces. Nevertheless, the ornament including the spiny plicae and quasi-oblique commarginal striae clearly distinguishes this species.

# Pectinidae indet. (Text-fig. 13G)

REMARKS: Pectinids are obviously relatively abundant in the Neuburg Kieselerde Member, but often, like the figured fragment (Text-fig. 13G; NMA–2013/687–0018) too poorly preserved to allow for determination. Presumably, most fragments belong to the three species described above, but additional taxa may also be present.

# Family Spondylidae J. Gray, 1826 Genus *Spondylus* Linnaeus, 1758 *Spondylus* sp. (Text-fig. 12A, E)

MATERIAL: A single external mould of a free (left) valve, and a single partly preserved attached (right) valve on a sponge (NMA–2013/687–0019, NMA–2013/687–0020).

DESCRIPTION: External mould of more or less equal-sided free valve ornamented with six pronounced principal ribs, each pair intercalated with five to six less prominent but distinct intercalary ribs. All ribs slightly undulating. Partly preserved slightly irregularly shaped right valve cemented onto a sponge. Early growth stages ornamented with pronounced commarginal rugae, as can be seen from imprint of disc. Ornament of numerous distinct, equal-sized, narrow radial ribs persisting during adulthood.

REMARKS: For both specimens the combination of all characters strongly suggests assignment to *Spondylus*, which has a number of similarly ornamented species occurring in the Upper Cretaceous. Basically, the deviant ornamentation of the two valves might indicate assignment to different species. However, spondylids may display considerable variation with regard to ornamentation (e.g., Woods 1901, pls 10, 12) and, in any case, specific assignment of both specimens is hampered by poor preservation.

Family Neitheidae Sobetski, 1960 Genus *Neithea* Drouet, 1825 *Neithea quinquecostata* (J. Sowerby, 1814) (Text-fig. 12J, K)

- \* 1814. Pecten quinquecostata; J. Sowerby, p. 122, pl. 56, figs 4–8.
- p.p. 1937a. *Neithea regularis* Schlotheim 1813; Lehner, p. 191, pl. 26, figs 2, 3. [non pl. 26, fig. 1]
  - 1973b. *Neithea (Neithea) quinquecostata* (J. Sowerby, 1814); Dhondt, p. 29, pl. 2, fig. 2a–c. [including extensive synonymy]
  - 2011. *Neithea (Neithea) quinquecostata* (J. Sowerby, 1814); Schneider *et al.*, p. 800, fig. 8M.

MATERIAL: External and internal mould of a single small right valve (AMSN E 281), and a single small left valve (NMA–2013/687–0023).

DESCRIPTION: Shell ornamented with six salient primary ribs in both left and right valve. Each pair of primary ribs intercalated with four much less prominent, but distinct intercalary ribs. Both areas and auricles densely covered with filae.

REMARKS: Although fairly small, the two specimens show the characteristics of *Neithea quinquecostata* as described by Dhondt (1973b). The species has previously been reported from the middle to upper Turonian Kagerhöh Formation of the Regensburg area (Lehner 1937a; Dhondt 1973b) and the Turonian to Coniacian Sandbach Formation of the Passau region (Schneider *et al.* 2011). Furthermore, it has been recorded from Cenomanian and Turonian strata in the adjacent Czech Republic (Dhondt 1973b).

## Neithea cf. regularis (Schlotheim, 1813) (Text-fig. 12G)

cf. \* 1813. Pectinites regularis; Schlotheim, p. 112.
cf. 1973b. Neithea (Neithea) regularis (E.F. von Schlotheim, 1813); Dhondt, p. 20, pl. 1, fig. 3, pl. 2, fig. 1a–d. [including extensive synonymy]

MATERIAL: Two large fragmentary right valves (NMA-2013/687-0021, HMC).

DESCRIPTION: Shell strongly inflated; umbo broad and blunt. Shell ornamented with six primary ribs, with three intercalary ribs between each pair. Ribs broad, near-equal in strength, with relatively narrow interspaces. Primary ribs only slightly more pronounced than intercalary ribs.

REMARKS: Both specimens from the Neuburg Siliceous Earth lack the auricles almost entirely. Due to poor preservation of the shell surface, the presence of filae on the areas and auricles can neither be proven nor excluded, and specific assignment remains somewhat tentative. The two specimens from the Neuburg Siliceous Earth seem to match best with *Neithea regularis*, according to the descriptions provided by Dhondt (1973b). Although *N. regularis* has previously not been recorded from Bavaria, it has been documented from Cenomanian to Turonian strata of adjacent regions, i.e. Saxony and the Czech Republic (Dhondt 1973b).

## Neithea coquandi (Peron, 1877) (Text-fig. 12H)

- \* 1877. *Janira coquandi* Peron; Peron, p. 501, pl. 7, fig. 2.
- ? p.p. 1937a. Neithea regularis Schlotheim 1813; Lehner, p. 191, pl. 26, fig. 1. [non pl. 26, figs 2, 3]
  - 1973b. *Neithea (Neithea) coquandi* (Peron, 1877); Dhondt, p. 26, pl. 3, fig. 1a–c. [including extensive synonymy]

MATERIAL: A single, relatively well-preserved right valve, lacking large parts of the outermost shell layer (HMC).

REMARKS: Like N. cf. regularis, the specimen is characterized by six primary ribs, with three inter-

calary ribs between each pair. However, the primary ribs are much more pronounced than the intercalary ribs and the umbo is relatively pointed and narrow. Moreover, the areas, in which at least part of the outer shell layer is preserved, as well as the posterior auricle, appear entirely smooth. To date, *Neithea coquandi* has not yet been confidently recorded from the areas surrounding the Upper Cretaceous Mid-European Island. However, a specimen from the middle to upper Turonian Kagerhöh Formation of the Regensburg– Kelheim area, figured by Lehner (1937a) under the name *N. regularis*, is tentatively assigned to *N. coquandi* by Dhondt (1973b).

> Family Anomiidae Rafinesque, 1815 Genus Anomia Linnaeus, 1758 Anomia papyracea Orbigny, 1847 (Text-fig. 12L)

- \* 1847. *Anomia papyracea*, d'Orbigny, 1847; Orbigny, p. 755, pl. 489, figs 7–10.
- 1899. *Anomia papyracea*, d'Orbigny, 1847; Woods, p. 31, pl. 5, figs 13–16.

MATERIAL: A single internal mould of a left valve (= free valve) with remnants of shell (NMA-2013/687-0022).

DESCRIPTION: Shell poorly inflated, very thin and fragile, lacking distinct hinge. Shell outline slightly irregular, with extended posterior-ventral end; posterior-dorsal margin slightly incurved. Umbo markedly shifted in anterior direction. Small remnants of shell in the centre and parts of internal mould ornamented with very faint, obtuse commarginal riblets.

REMARKS: The above-described characters perfectly match the description and figures of A. papyracea provided by Woods (1899). This species has been recorded from Upper Cenomanian strata in Great Britain, which correspond well to the Neuburg Kieselerde Member both with regard to age and environment. Accordingly, the irregular shells with an almost smooth surface may either represent an ecophenotype of A. laevigata J. de C. Sowerby, 1836, as suggested by Lehner (1937a), or a distinct species. We favour the interpretation of Woods (1899) since the morphology of the specimens is simple but striking. Moreover, transitional specimens between A. papyracea and typical A. laevigata, which usually has an almost central umbo and non-incurved dorsal margin, seem to be lacking.

Family Limidae Rafinesque, 1815 Genus *Lima* Bruguière, 1797 *Lima parallela* (J. Sowerby, 1812) (Text-fig. 12D)

- \* 1812. *Modiola parallela*; J. Sowerby, p. 31, pl. 9, righthand top figure.
- 1904. *Lima (Mantellum) parallela* (Sowerby), 1812; Woods, p. 28, pl. 5, figs 14, 15.

1933. Lima parallela Sow.; Lehner, p. 465.

1937a. *Lima (Mantellum) parallela* Sowerby 1812; Lehner, p. 179, pl. 22, fig. 22.

# MATERIAL: A single right valve (NMA-2013/687-0024).

REMARKS: The well-preserved specimen conforms closely to the description given by Woods (1904). It is distinctly higher than long, has a slightly concave upper anterior margin, and is ornamented with approximately 20 prominent, relatively sharp-crested but smooth primary radial ribs with well-rounded interspaces. In places, even the faint intercalated secondary ribs described by Woods (1904) are visible.

Genus *Pseudolimea* Arkell in Douglas and Arkell, 1932 *Pseudolimea* cf. *composita* (J. de C. Sowerby in Fitton, 1836) (Text-fig. 12I)

- cf. \* 1836. *Pecten compositus* M.; J. de C. Sowerby in Fitton, p. 241, p. 342, pl. 17, fig. 20.
- ? 1937a. *Lima aspera* Mantell 1822; Lehner, p. 175, pl. 22, fig. 21.
- cf. 1989. *Limea (Pseudolimea) composita* (Sowerby in Fitton, 1836); Dhondt, p. 108, pl. 1, figs 13–15. [including extensive synonymy]

MATERIAL: A single external mould of a double-valved specimen in butterfly position (NMA-2013/687-0025).

DESCRIPTION: Fragmentary mould with imprints of markedly inflated, slightly unequal-sided valves, ornamented with 25 distinct radial ribs. Each rib internally subdivided into three cords, ornamented with numerous granulae. Towards shell margin, in particular on anterior part, granulae becoming more prominent, forming spiny scales, causing almost reticulate appearance of ornament.

REMARKS: As pointed out by Dhondt (1989), Pecten

*compositus* J. de C. Sowerby in Fitton, 1836 is a junior primary homonym of *Pecten compositus* Goldfuss, 1836. Since *Pecten compositus* J. de C. Sowerby in Fitton, 1836 is now referred to *Pseudolimea*, however, the junior primary homonym becomes available (ICZN 1999: Article 59.2).

*Pseudolimea composita* (J. de C. Sowerby in Fitton, 1836) and *P. granulata* (Nilsson, 1827) are obviously closely related and difficult to distinguish. However, the specimen from the Neuburg Siliceous Earth appears to be rather coarsely ornamented, which suggests assignment to *P. composita*. Moreover, the determination is corroborated by the stratigraphic range of the species, since *P. composita* is a typical Cenomanian species, while its supposed successor *P. granulata* appears in the Turonian.

## Genus *Plagiostoma* J. Sowerby, 1814 *Plagiostoma* sp. (Text-fig. 12M)

? 1933. Lima hoperi Mant.; Lehner, p. 465.

? 1937a. *Lima (Plagiostoma) hoperi* Mantell 1822; Lehner, p. 176, pl. 22, fig. 18.

MATERIAL: A single internal mould of a left valve with remnants of shell (NMA-2013/687-0026).

REMARKS: The poor preservation of the specimen prevents specific assignment. The slightly inflated left valve with an opisthogyrous umbo, as well as the radially-structured remnants of shell preserved in the central part of the mould, strongly suggest assignment to *Plagiostoma*, although the presence of an auricle cannot be proven. The drawings of *Lima (Plagiostoma) hoperi* provided by Lehner (1937a) show a slightly shorter and less opisthogyrous specimen, which, however, relatively closely resembles the individual described herein.

> Family Entoliidae Teppner, 1922 Genus *Entolium* Meek, 1865 *Entolium orbiculare* (J. Sowerby, 1817) (Text-fig. 13A, D)

- \* 1817. *Pecten orbicularis*; J. Sowerby, p. 193; pl. 186. 1933. *Pecten orbicularis* Sow.; Lehner, p. 465.
- 1937a. Pecten (Syncyclonema) orbicularis Sowerby 1817; Lehner, p. 181, pl. 26, fig. 5.
- 1939. Pecten (Syncyclonema) orbicularis Sow.; Dacqué, p. 51, pl. 1, fig. 4, pl. 4, fig. 1.
- 1971. *Entolium orbiculare* (Sowerby, 1817); Dhondt, p. 8, pl. 1, fig. 1a, b.

MATERIAL: Several specimens (NMA–2013/687–0027, NMA–2013/687–0028, AMSN, BSPG 1956 X 310).

REMARKS: A detailed description and extensive synonymy of this common, long-ranging species (Berriasian to Turonian) has been provided by Dhondt (1971). The specific characteristics of *Entolium orbiculare*, i.e. dorsally projecting triangular auricles and commarginal ridges, separated by narrow, shallow furrows, are obvious in one of the figured specimens (Text-fig. 13A). The second specimen (Text-fig. 13D) shows imprints of the typical auricular crurae of *Entolium* (Dhondt 1971).

> Genus Syncyclonema Meek, 1864 Syncyclonema haggi Dhondt, 1971 (Text-fig. 13H)

1827. Pecten laevis; Nilsson, p. 24; pl. 9, fig. 17.

- 1837a. Pecten (Syncyclonema) laevis Nilsson 1827; Lehner, p. 184, pl. 23, fig. 1.
- \* 1971. *Syncyclonema haggi* nom. nov.; Dhondt, p. 48; pl. 2. [including extensive synonymy]

MATERIAL: A single, well-preserved external mould of a left valve (AMSN).

REMARKS: The specific epithet *haggi* was introduced by Dhondt (1971) as a replacement name for the preoccupied *Pecten laevis* Nilsson, 1827. *Syncyclonema haggi* is characterized by a smooth outer shell surface, long apical margins, attaining approximately two-thirds of the total shell height, relatively large auricles, and small size (Dhondt 1971). These features are all clearly visible in the figured specimen (Text-fig. 13H).

### Nautilida (Markus Wilmsen)

Systematic, taxonomic and stratigraphic studies on Cretaceous nautiloids are comparatively rare, possibly related to their morphological conservativeness and long species ranges, rendering them less attractive for detailed research. However, Kummel (1956, 1964), Wiedmann (1960), and Dzik (1984) presented significant contributions to the taxonomy and systematics of post-Triassic nautiloids while Shimansky (1975) and Matsumoto *et al.* (1984) focused mainly on Cretaceous taxa and their phylogeny. Nevertheless, familyand genus-level classifications are still controversial, especially with respect to the family Cymatoceratidae Spath, 1927 (see discussion in Wilmsen 2000; Wilmsen and Yazykova 2003; Wilmsen and Esser 2004; Frank 2010; and Frank *et al.* 2013). Here, the classification of Shimansky (1975) is followed (grouping of most 'cymatoceratid' genera with the family Nautilidae Blainville, 1825). Morphological features and terms follow Teichert (1964). The few specimens are all preserved as (composite) internal moulds.

Order Nautilida Agassiz, 1847 Family Nautilidae Blainville, 1825 Genus *Cymatoceras* Hyatt, 1884 *Cymatoceras* cf. *elegans* (J. Sowerby, 1816) (Text-fig. 14B)

cf. \* 1816. Nautilus elegans n. sp. J. Sowerby, p. 33, pl. 116.

cf. 2002. *Cymatoceras elegans* (J. Sowerby); Kennedy, p. 226, pl. 43, figs 3, 7, text-fig. 10.2c.

MATERIAL: One specimen from the Neuburg Museum (AMSN H102), a flattened fragmentary body chamber.

DESCRIPTION: The large fragment is characterized by a conspicuous dense ribbing on the flanks. Ribs arise at the umbilical margin and are weakly concave on the innermost flank where numerous bifurcations can be observed. They are broadly convex on the midand outer flanks, crossing the venter in concavity. All ribs are low in height and separated by narrow interspaces of approximately one-third of the rib width. Due to continuing bifurcations, the width of the ribs only slightly increases towards the venter.

REMARKS: *Cymatoceras elegans* and *C. columbinum* (Fritsch, 1872) are difficult to distinguish, the former having a slightly broader umbilicus, a less depressed whorl section, slightly closer-spaced septa and a more dorso-central position of the siphuncle. None of these characters are visible in the present specimen, but the conspicuous fine, dense ribbing (which is much coarser in *C. columbinum*) allows an identification of the species. However, due to the fragmentary preservation, we keep the specimen in open nomenclature. The serpulid-encrusted specimen illustrated in Text-fig. 15G may also belong here.

OCCURRENCE: Cenomanian of Europe (England, France and Germany).

Cymatoceras columbinum (Fritsch, 1872) (Text-fig. 14A, C, D)

- \* 1872. *Nautilus Columbinus* Fr. n. sp. Fritsch and Schlönbach, p. 20, pl. 11, fig. 3, pl. 15, fig. 1.
  - 1960. *Eutrephoceras columbinum* (Fritsch) 1872; Wiedmann, p. 154, pl. 22, figs A, C.
  - 2008. *Eutrephoceras columbinum* (Fritsch, 1872); Frank, p. 25.
  - 2010. Cymatoceras columbinum (Fritsch, 1872); Košťák et al., p. 426.

MATERIAL: Three specimens, i.e. two fragments of body chambers (BSPG 1956 X 315, NMA–2013/687–0029) as well as a complete internal mould from Pfaffengrund Pit (HMC; plaster cast: BSPG 1986 I 1).

DESCRIPTION: Very involute nautilid with depressed whorl section. The flanks and venter are regularly rounded. The greatest whorl breadth is on the lower flanks, close to the umbilicus, and the whorl section can be weakly trapezoidal in adults. Flanks and ven-



Text-fig. 14. Nautilida. A, C, D – Cymatoceras columbinum (Fritsch, 1872). A – Fragmentary body chamber. NMA–2013/687–0029. C – Internal mould of an almost complete specimen. HMC. D – Fragmentary external mould of body chamber. BSPG 1956 X 315. B – Cymatoceras cf. elegans (J. Sowerby, 1816). AMSN H 102. Scale bars = 10 mm

ter are characterized by conspicuous sigmoid, broadly rounded ribs, separated by narrow interspaces. Ribs originate at the umbilicus and are very thin and slightly prorsiradiate, crossing the flanks in broad convexity. At the ventrolateral shoulders, they curve backwards, traversing the venter in concavity and forming obtuse chevrons. Ribs widen considerably from the umbilicus towards the venter and only a few bifurcated or intercalated ribs are present, mainly on the inner and middle part of the flanks. The ribbing is most conspicuous on the body chamber. The septa are rather distant and only moderately folded. The suture shows a shallow, narrow saddle on the lower flanks, a broad lobe on the middle and outer flank and a rounded saddle at the venter. The position of the siphuncle is not visible.

REMARKS: *Nautilus columbinus* Fritsch, 1872 has been placed in the genus *Cimomia* Conrad by Kummel (1956) and in *Eutrephoceras* Hyatt by Wiedmann (1960). However, the species has recently been discussed by Frank (2008) who suggested that ribs are only missing due to taphonomic reasons, and that *C. atlas* (Whiteaves, 1876) is a subjective junior synonym of *C. columbinum* (Fritsch, 1872). Košťák *et al.* (2010) placed Fritsch's species in *Cymatoceras* and stated that the holotype of Fritsch (1872) is from the Korycany Beds, lower Upper Cenomanian Peruc-Korycany Formation, at Holubice (Czech Republic). The species is differentiated from the co-occurring *C. elegans* by means of its different ribbing pattern, closed umbilicus and inflated shell.

OCCURRENCE: Cenomanian of Czech Republic, England and Germany. Wiedmann (1960) reports the species also from South America.

#### Polychaeta (Manfred Jäger)

Class Polychaeta Grube, 1850 Subclass Canalipalpata Rouse and Fauchald, 1997 Order Sabellida Fauchald, 1977 Family Sabellidae Latreille, 1825 Subfamily Sabellinae Chamberlin, 1919 Genus *Glomerula* Brünnich Nielsen, 1931

REMARKS: Since the early 19<sup>th</sup> century (e.g., Schlotheim 1820; Münster in Goldfuss 1831), several types of fossil calcareous tubes of polychaetes have been documented, which closely resemble those seen in fossil and living Serpulidae. Much later, the genus name *Glomerula* was introduced for some of these forms (Brünnich Nielsen 1931; Regenhardt 1961). Un-

til the publication of Perkins (1991), not a single fossil or extant representative of the Sabellidae, which are closely related to the Serpulidae, had been described to possess a calcareous tube, and it therefore seemed logical to affiliate Glomerula with the Serpulidae. Perkins (1991) newly described and illustrated the tubes and soft part anatomy of an extant species, Calcisabella piloseta, which unambiguously has to be assigned to the Sabellidae, even though its calcareous tube is unusual for this family. Jäger (2005) and Ippolitov (2007) independently recognised the close similarity of the extant Calcisabella and fossil Glomerula tubes and considered Calcisabella as a subjective synonym of Glomerula (or, respectively, of its junior synonym Cycloserpula Parsch, 1956). As a result, Glomerula is now confidently assigned to the Sabellidae also by neontologists (Read and Fauchald 2013).

*Glomerula* tubes are easily recognized by their simple tube structure and strong tendency to form narrow curves and chaotic knots, thigmotaxically adnating closely but not too firmly to either a foreign solid substrate, earlier-constructed portions of its own tube, or to tubes of other individuals. The enormous intraspecific variability and the limited set of diagnostic morphological features render discrimination of species in *Glomerula* a highly difficult task. A simple, albeit at least partly artificial scheme was introduced by Jäger (2005), who distinguished three morphospecies of Cretaceous *Glomerula*, (1) the small-sized *Glomerula lombricus* (Defrance, 1827), (2) the large but more or less solitary *G. serpentina* (Goldfuss, 1831) and (3) the large, social *G. plexus* (J. de C. Sowerby, 1829).

In specimens from fine-grained offshore facies, discrimination of G. lombricus from the two larger species is unambiguous. In specimens from coarsegrained nearshore facies, however, the size spectrum is continuous, and discrimination between large and small species impossible. The smallest specimen from the Neuburg Siliceous Earth attains a maximum tube diameter of approximately 0.8 mm, which is just intermediate between the typical size classes of G. lombricus versus G. serpentina/plexus. All other specimens are larger. As a result, typical specimens of G. lombricus may be considered to be absent. With the exception of a few very large clusters consisting of dozens to hundreds of tubes, collected from the chalk of southern England, the chalk-like calcareous marlstone of Misburg (northern Germany) and the rocky shore facies at Ivø Klack (southern Sweden), discrimination between the solitary Glomerula serpentina and the social G. plexus is very artificial. In large, denselyspaced populations, small clusters consisting of two to approximately five tubes were commonly formed by



Text-fig. 15. Sabellidae and Serpulidae. A, D, E – Glomerula serpentina? (Goldfuss, 1831). A. BSPG 1956 X 316. D, E – NMA–2013/687–0034, 0035. B, C – Glomerula plexus (J. de C. Sowerby, 1829). BSPG 1956 X 316. F–H – Serpulidae indet. F, H. NMA–2013/687–0036, 0037. G. AMSN. Scale bars = 10 mm

chance, instead of following the social bauplan of *G. plexus*. However, several large *Glomerula* clusters from the Neuburg Siliceous Earth consist of a large number of tubes and can therefore be confidently assigned to *G. plexus* (Text-fig. 15B, C).

Glomerula plexus (J. de C. Sowerby, 1829) (Text-fig. 15B, C)

\* 1829. Serpula Plexus; J. de C. Sowerby, p. 201, pl. 598, fig. 1.
 2005. Glomerula plexus (J. de C. Sowerby, 1829); Jäger, p. 131.

MATERIAL: Four specimens (AMSN, BSPG 1956 X 316).

REMARKS: See remarks for genus.

*Glomerula serpentina*? (Goldfuss, 1831) Text-fig. 15A, D, E

- \* 1831. Serpula gordialis Schloth. Varietas serpentina; Goldfuss, p. 240, pl. 71, fig. 4.
- 2005. *Glomerula serpentina* (Goldfuss, 1831); Jäger, p. 130, pl. 1, fig. 1.

MATERIAL: Three specimens (NMA-2013/687-0034, NMA-2013/687-0035, BSPG 1956 X 316).

REMARKS: See remarks for genus.

Family Serpulidae Rafinesque, 1815 Serpulidae indet. (Text-fig. 15F–H)

MATERIAL: Several specimens of poorly preserved tubes, attached to a nautilid shell (AMSN) and to different Porifera (NMA–2013/687–0036, 0037).

REMARKS: True serpulids seem to be less common than *Glomerula* in the Neuburg Siliceous Earth. Remnants of several tubes are attached to a nautilid shell (Text-fig. 15G). Due to poor preservation, confident determination of these specimens is impossible. One of the two tubes at the right side of the image may belong to *Filogranula cincta* (Goldfuss, 1831), since it presumably possessed three keels. The three subcircular to spiral fragments in the centre and at the left side of the image may probably be assigned to the subgenus *Serpula* (*Cementula*) Regenhardt, 1961. Both taxa are common in Upper Cretaceous deposits. Additional specimens, mostly attached to sponges, are poorly preserved and hardly determinable.

#### Bryozoa (Kamil Zágoršek)

Bryozoans were found only sporadically within the studied material. The general diversity is low, but at least six different taxa can be recognised. The poor preservation limits taxonomy. In all specimens, the surface of the colonies is severely abraded and taxonomically important features like heterozooecia, gonozooecia, the shape and size of apertures etc. cannot be observed. In absence of these features, most taxa can only be placed in open nomenclature. Classification follows Bassler (1953), with modifications by P.D. Taylor and D. Gordon, available from Bock (2013).

> Phylum Bryozoa Ehrenberg, 1831 Class Stenolaemata Borg, 1926 Order Cyclostomatida Busk, 1852

REMARKS: Almost all bryozoan colonies from the Neuburg Kieselerde Member belong to the Cyclostomatida. Generally, two types of erect ramified colonies can be distinguished. Additionally, multilamellar globular or irregular forms are relatively abundant. Most common are colonies that probably belong to the Cerioporidae. Encrusting colonies are very rare but also occur with several types.

> Suborder Cerioporina Hagenow, 1851 Family Cerioporidae Reuss, 1866 Cerioporidae indet. 1 (Text-fig. 16A–D)

1933. *Heteropora coalescens* Reuss; Lehner, p. 465.
1958a. *Heteropora coalescens* Reuss; Kempcke, p. 5, fig. 5, p. 9, fig. 11.

MATERIAL: Three large colonies (HMC, AMSN H 75) and a few small fragments (BSBG 1956 X 303), all from the Kreuzgründe Pit.

REMARKS: These colonies are characterized by thick, massive stems, and slightly diversified pores on their surface (Text-fig. 16C). However, the pores lack fascicles, or any other arrangement. The individual branches are approximately 3 mm thick. The diameter of large pores (apertures) is approximately 150 µm, while the diameter of small pores (heterozooecia) is about 70 µm. The largest colony (Text-fig. 16B) has a hollow, tubeshaped basis, indicating that it has been growing around a stalk or branch. The colonies generally resemble those seen in the genera Ceriopora, Ditaxia and Heteropora as described by Nye (1976). Moreover, Leiosoecia is similar with regard to its ramification, but this genus has to date only been reported from the Cenozoic of the USA. Likewise, Ceriocava sarthacensis (Orbigny, 1850) grows in similar colonies, but has to date only been recorded from Jurassic strata.

This type of colony has previously been reported from the Neuburg Kieselerde Member as *Heteropora coalescens* Reuss (Lehner 1933; Kempcke 1958a). Actually, the dimensions of *Heteropora coalescens* Reuss coincide with the features observable on the studied specimens (with of branches ca 4–5 mm, diameter of apertures ca 0.13–0.6 mm). However, without observing gonozooecia and a well-preserved colony surface a definitive assignment to this species is impossible.

> ? Cerioporidae indet. 2 (Text-fig. 17A, B, D)

MATERIAL: Several colonies (NMA, AMSN H 109, AMSN H 111, BSPG 1956 X 302).

REMARKS: Another common type of colonies is multilamellar, often globular but occasionally also flat or irregular in shape. Characteristic features are the presence of protuberances on the colony surface, the almost uniform diameter of the apertures and the presence of regularly dispersed caverns. These caverns usually occur between entire layers and are semilunar in shape (Text-fig. 17D). These colonies resemble Ceriopora tuberosa (Roemer, 1839) as described by Hillmer (1971) from the early Hauterivian of northern Germany, as well as Ceriopora cavernosa von Hagenow, 1851 from the Maastrichtian of the type region in The Netherlands. Furthermore, Heteropora cryptopora (Goldfuss, 1826) as described by Nye (1976) from the Maastrichtian of St. Petersberg near Maastricht may produce similar colonies. Moreover, certain tubuliporids (e.g., Tholopora) or lichenoporids (see Voigt 1953), as well as Reptomulticava Orbigny, 1854 and Semimulticavea Orbigny, 1853

(see Pitt and Taylor 1990) may grow in colonies which are similar in shape. Due to the poor preservation a confident assignment to any of these taxa is impossible. Suborder Tubuliporina ? Tubuliporina indet. (Text-fig. 16E–G)



Text-fig. 16. Bryozoa. A-D – Cerioporidae indet. 1. A, C, D – AMSN H 75. B – Large colony with tube-shaped basis. HMC. E-G – ? Tubuliporina indet. AMSN H 76. Scale bars: A, B = 10 mm; C = 1 mm; D, E = 5 mm; F, G = 2 mm



Text-fig. 17. Bryozoa. A, B, D -? Cerioporidae indet. 2. A – BSPG 1956 X 302. B, D – AMSN H 111. C – '*Berenicea*' sp. NMA–2013/687–0038. E, G -? Caloporidae indet. AMSN H 110. F – *Reptomultelea* cf. sarthacensis (Orbigny, 1853). NMA–2013/687–0039. Scale bars: A, B = 5 mm; C–F = 1 mm

MATERIAL: A single large colony from the Kreuzgründe Pit (AMSN H 76).

REMARKS: A second type of erect bryozoan colonies from the Neuburg Kieselerde Member is characterized by relatively thin branches with almost uniform pores on the surface (Text-fig. 16F). The branches are approximately 2.5 mm thick, and the surface pores reach approximately 300  $\mu$ m in diameter. These colonies are generally similar to those seen in *Meliceritites* or in several genera traditionally assigned to the Semiceidae Buge, 1952. However, the density of the apertures on the surface may also indicate an affiliation with the Tubuliporidae or Cerioporidae.

# Family 'Bereniceidae' Buge, 1957 Genus '*Berenicea*' Lamouroux, 1821 '*Berenicea*' sp. (Text-fig. 17C)

MATERIAL: A single encrusting colony (NMA-2013/687-0038).

REMARKS: Circular encrusting bryozoans like the single specimen from the Neuburg Kieselerde Member, forming a discoidal, unilamellar colony with radially arranged tubes, cannot be safely identified when characteristic gonozooids are lacking. Therefore, the specimen is assigned to the informal genus '*Berenicea*' herein, following the suggestions made by Taylor and Sequeiros (1982).

Family Eleidae Orbigny, 1852 Genus *Reptomultelea* Orbigny, 1853 *Reptomultelea* cf. *sarthacensis* (Orbigny, 1853) (Text-fig. 17F)

- cf. \* 1853. *Reptelea sarthacensis* d'Orbigny; p. 640, pl. 604, figs 9, 10, pl. 738, fig. 15.
  - cf. 2011. *Reptelea sarthacensis* d'Orbigny; Taylor and Zágoršek, p. 412, fig. 3. [see Taylor 1994: 49 for comprehensive synonymy]

MATERIAL: A single small colony (NMA–2013/687–0039).

DESCRIPTION: Colony encrusting, unilamellar. Autozooids moderately small, about twice as long as wide; frontal wall occupying approximately half of frontal surface. Aperture longitudinally elongate, gothic arch-shaped, pointed distally. Eleozooids longer than autozooids, with elongate aperture prolonged distally, with narrow, rounded tip. Operculum and gonozooids not observed.

REMARKS: The colony is relatively small, but the elongated aperture of the avicularia and the gothic arch-shaped apertures closely resemble *Reptomultelea sarthacensis* (Orbigny, 1853). *Reptomultelea sarthacensis* is among the most common bryozoans in the Late Cretaceous of Europe, and has been reported from the Cenomanian and Turonian of England (Pitt and Taylor 1990), France and Germany (Taylor 1994), and the Czech Republic (Taylor and Zágoršek 2011). As a result, it is highly probable that the studied specimen belongs to this species.

Class Gymnolaemata Allman, 1856 Order Cheilostomata Busk, 1852 Suborder Flustrina Smitt, 1868 Family Caloporidae Norman, 1903 ? Caloporidae indet. (Text-fig. 17E, G)

MATERIAL: A single small colony (AMSN H 110).

REMARKS: Only a single potential cheilostome bryozoan colony was found. It is a very small colony with severely abraded surface. Nevertheless, the radially dispersed arrangement of the autozooecia, the bifurcated budding pattern and the oval shape of the autozooecia with massive mural rims indicate affiliation with the Cheilostomata, and allow for a tentative assignment to the Caloporidae.

## Brachiopoda (Christopher J. Wood)

The silicification of the Neuburg brachiopods has obscured finer details of the shell such as growth lines and microstructure. Because only limited museum material is available, there has been no opportunity to investigate the internal features, and the suggested determinations are based entirely on inspection of the external gross morphology and on comparison with taxonomically well described taxa of a similar age range. The material shows extremely low diversity. With the exception of a single, probably generically indeterminate terebratulid (Text-fig. 18L), and two brachiopods (Text-fig. 18B, C) that cannot be safely identified at the generic level, the fauna comprises only rhynchonellids. These can be safely assigned to the morphologically distinctive genus Cyclothyris, which typically characterizes shallow water settings. A single specimen is

assigned to the unrelated long-ranging Lower–Middle Cenomanian rhynchonellid *Grasirhynchia grasiana*, which is well represented in both arenacous and marly limestone facies. Lehner (1937b) described some brachiopods from broadly contemporaneous sediments of the adjacent Franconian Alb but this fauna (judging from the illustrations because the material was lost during World War 2) is rather different.

Phylum Brachiopoda Duméril, 1806 Order Rhynchonellida Kuhn, 1949 Family Rhynchonellidae Gray, 1848 Subfamily Cyclothyridinae Makridin, 1955 emended Owen, 1962 Genus *Cyclothyris* M'Coy, 1844 *Cyclothyris* sp. (Text-fig. 18A, E–K)

MATERIAL: More than 20 specimens (NMA–2013/687–0030, 0031, AMSN H 113, HMC, BSPG 1956 X 299, 300).

REMARKS: Cyclothyris is a long-ranging (Aptian-Turonian?), morphologically distinctive, medium to large-sized rhynchonellid genus that typically characterizes shallow water lithofacies and is absent from contemporaneous deeper water marls and argillaceous limestones. It is particularly well represented in marginal coarse-grained arenaceous Cenomanian deposits throughout Europe and can commonly dominate the brachiopod faunas to the virtual exclusion of other taxa. In the initial study of the genus by Owen (1962), he described in detail the following Cenomanian taxa, C. scaldisensis (d'Archiac, 1843), C. schloenbachi (Davidson, 1852), the long-ranging C. difformis (Valenciennes in Lamarck, 1819) and C. compressa (Valenciennes in Lamarck, 1819). In his later paper on British and European Cenomanian brachiopods, Owen (1988) again discussed and illustrated C. difformis and C. compressa, and introduced three new species, namely C. punfieldensis, C. formosa and C. juigneti. He also described and illustrated C. lamarckiana (Orbigny, 1849), which was not included in his earlier paper. In the discussion of the Neuburg material, C. scaldisensis, C. schloenbachi and the three new Cenomanian species can probably be excluded from consideration and attention can be concentrated on C. difformis, C. compressa and C. lamarckiana, which characterize different shallow water lithofacies units in the complex transgressive/regressive interdigitating successions in northern France (for stratigraphy see Juignet et al. 1973).

Silicified specimens of C. difformis are a common and dominant element in the brachiopod fauna of the the calcarenitic Lower Cenomanian (Mantelliceras dixoni ammonite Zone) Wilmington Sands in Devon, southwest England, listed by Mortimore et al. (2001). Owen (1988) notes that the species is common in the Lower Cenomanian deposits in northern France and that it ranges up into the Middle Cenomanian. In Germany, he recorded it from the Lower Cenomanian Essen Greensand (Westphalia) and from the Lower Cenomanian part of the Danubian Cretaceous succession in the area around Regensburg (Bavaria) (Owen 1978, 1988). In both papers, Owen emphasized the extreme morphological variability of this species, illustrating this by line-drawings of thirteen different variants in a single figure (Owen 1962; fig. 7) and he also commented on the tendency for the anterior commissure to show asymmetry.

*C. compressa* is one of the most distinctive species of *Cyclothyris* (see Owen 1962), being characterized by its acutely subtriangular outline, strong angular costae, flattened shape in anterior view, short beak and small foramen (cf. Owen 1962; pl 5, fig. 8a–c). It is particularly common in the upper Middle Cenomanian (*Acanthoceras jukesbrownei* ammonite Zone) Sables de Perche in Sarthe, in which it is the only rhynchonellid present, but it ranges down into the underlying sandy beds and up into the overlying Upper Cenomanian (*Calycoceras guerangeri* ammonite Zone) Marnes à Ostracés, a unit characterized by the large, strongly biconvex and coarsely costate *C. lamarckiana*. (cf. Owen 1988; pl. 3, figs 7–15).

It is unclear whether the Neuburg Cyclothyris material represents largely a single, morphologically extremely variable taxon, showing a variability analagous to that described in C. difformis, or whether several taxa are present. In view of the unusual, siliceous and relatively shallow-water lithofacies (see palaeoecology section below), it is equally possible that at least some of the Cyclothyris represent an undescribed taxon. According to Owen (1962, 1988), the three species of Cyclothyris discussed above differ in respect of the number of costae in each valve. C. difformis and C. compressa show forty to forty-five and forty costae respectively, and only C. lamarckiana, with thirty costae in each valve, shows a significantly smaller number. Although it is difficult to count the costae accurately, the Neuburg Cyclothyris can be sorted into three groups:

(1) Specimens A and K, with circa thirty-three to thirty-five costae. These could be tentatively assigned to *C. difformis*, albeit the number of costae is lower than in the English and French material.

- (2) Specimens E, G, H, I and J, with twenty-six to thirty costae. On the basis of the low number of costae and, particularly, the small number of costae in the anterior commissure, these specimens show some affinity to C. lamarckiana, but differ in lacking the inflated biconvex profile in lateral view shown by the specimens illustrated by Owen (1988; figs 7-15). Specimens H and I are notable for their compressed profile in anterior view and, in this respect alone, show some similarity to C. compressa. However they clearly differ from this species in the large prominent beak and large foramen, as well as in the very much smaller number of costae. In costal number and beak size, they are closer to the specimen from the Marnes à Ostrea biauriculata illustrated by Owen (1988; pl. 3, figs 22-27) than to the more typical specimen from an unknown horizon in Sarthe figured by Owen (1962; pl. 5, fig. 8a-c). Specimen E, differently preserved from the other members of this group, is characterized by the very small number of costae in the fold and sulcus.
- (3) Specimen F, with well over forty-five costae, shows some similarity to *C. zahalkai* Nekvasilová from the Upper Cenomanian of the Czech Republic (cf. Zitt *et al.* 2006; fig. 12h–k).

To summarize, it is probable that the majority of the Neuburg Cyclothyris are closest to the two French shallow water forms from the upper Middle Cenomanian Acanthoceras jukesbrownei and lower Upper Cenomanian Calycoceras (Proeucalycoceras) guerangeri ammonite zones respectively, but probably cannot be safely assigned to either species. It is therefore likely that one or more undescribed taxa or ecomorphic variants of existing taxa are represented. Specimens H and I are morphologically quite distinctive and could easily represent an undescribed species of Cyclothyris. Specimens G and J, with their low costal number and markedly arcuate anterior commissure could likewise possibly represent another undescribed species. Some consideration also needs to be given to the species Cretirhynchia bohemica (Schloenbach, 1868) described and illustrated by Nekvasilová (1974) on the basis of silicified material from the Lower Turonian of the Czech Republic, which, from the nature of its costation, probably belongs to Cyclothyris or a closely related genus. However, this is a relatively small species, with a width of less than 20 mm, and the specimens illustrated (Nekvasilová 1974; p. 1, figs 1-4) do not compare particularly well with any of the Neuburg Cyclothyris.

Genus Grasirhynchia Owen, 1968 Grasirhynchia grasiana (Orbigny, 1848) (Text-fig. 18D)

- \* 1848. *Rhynchonella grasiana* d'Orbigny p. 38, pl. 497, figs 7–10.
- 1968. *Grasirhynchia grasiana* (d'Orbigny, 1848); Owen, p. 20, pl. 2, figs 7a–c.
- 1988. *Grasirhynchia grasiana* (d'Orbigny, 1848); Owen, p. 90, pl. 5, figs 20–23. [with full synonymy]

MATERIAL: A single specimen (BSPG 1956 X 301).

REMARKS: From external morphology, the single specimen is referred to *G. grasiana* on the basis of its relatively inflated biconvex shape, simple costation and the markedly arcuate anterior commissure. The brachial valve of the studied specimen shows greater convexity than the pedicle valve, a feature that Owen (1968) considered to characterize this species.

The species was originally described from Cenomanian deposits near Le Havre on the coast of Normandy in northern France. According to Owen (1968), the typical form occurs in Middle Cenomanian argillaceous chalk or limestone facies. In England, northern France and northern Germany, it forms part of the diverse small brachiopod assemblage in this facies in the Middle Cenomanian Acanthoceras rhotomagense ammonite Zone, Turrilites acutus Subzone. However, it is also common in arenaceous, more marginal lithofacies, notably in the basal Lower Cenomanian Rye Hill Sands (Mantelliceras mantelli Zone, Neostlingoceras carcitanense Subzone) in Wiltshire and the Wilmington Sands (Mantelliceras dixoni Zone) of Devon in southern England (see Mortimore et al. 2001), as well as in the Essen Greensand in northern Germany. Owen (1968) considers that the taxon is represented by smaller, more coarsely ribbed forms in marginal facies.

OCCURRENCE: Lower and Middle Cenomanian, England, northern France and northern Germany

Order Terebratulida Waagen, 1883 Family Terebratulidae Gray, 1840 Genus *Concinnithyris* Sahni, 1929 *Concinnithyris*? sp. (Text-fig. 18L)

Text-fig. 18. Brachiopoda. A, E–K – *Cyclothyris* sp. A, G, I – AMSN H 113. E, F – NMA–2013/687–0030, 0031. H, J, K – HMC. B – Brachiopoda indet. NMA–2013/687–0032. C – Brachiopoda indet. NMA–2013/687–0033. D – *Grasirhynchia grasiana* (Orbigny, 1848). BSPG 1956 X 301 L – *Concinnithyris*? sp. AMSN. Scale bars = 10 mm



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MATERIAL: One poorly preserved articulated specimen (AMSN).

REMARKS: It is not possible to assign the single Neuburg terebratulid safely to a genus from its external morphology. Both valves are relatively poorly preserved but the lateral view of the pedicle valve shows fine, very closely-spaced growth lines. The genus *Concinnithyris* is suggested from the equally biconvex cross section and the weakly developed asymmetric biplication of the anterior commissure. However, in contrast to this feature in typical species of this genus, such as C. obesa (see Sahni 1929; Owen 1988, 2002), the ventral umbo is upturned, revealing indications of a symphytium, rather than incurved and more or less adpressed to the dorsal umbo. Moreover, the pedicle opening is relatively large for the genus, suggesting an adaptation to high energy, shallow water conditions and attachment to a hard, rather than a relatively soft substrate. The relatively narrow, elongate-ellipsoidal shape in dorsal view differs from that of any of the known Cenomanian and Lower Turonian species of this genus and is similar to that of Praelongithyris. However, the anterior commissure of this genus is initially rectimarginate, later becoming sulciplicate and is not usually biplicate.

#### Echinoidea (Andreas Kroh)

The echinoid fauna of the Neuburg Siliceous Earth is relatively poor, both in terms of diversity and abundance. Preservation is also rather poor and identification was only possible due to the large amount of data available on the European Upper Cretaceous echinoid fauna. A majority of the specimens, however, could not be addressed at genus or species level. Classification follows Kroh and Smith (2010).

Class Echinoidea Leske, 1778 Subclass Eucchinoidea Bronn, 1860 Atelostomata von Zittel, 1879 Order Holasteroida Durham and Melville, 1957 Infraorder Cardiasterina Pomel, 1883 Genus *Pseudholaster* Pomel, 1883 ? *Pseudholaster bicarinatus* (Agassiz in Agassiz and Desor, 1847) (Text-fig. 19A, B) 2003. *Pseudholaster bicarinatus* (L. Agassiz, in Agassiz & Desor, 1847); Smith and Wright, p. 462, text-figs 184, 185, pl. 145, figs 1–14, pl. 146, figs 4–11, pl. 148, figs 8–9.

MATERIAL: A single, partially preserved specimen (HMC).

DESCRIPTION: The single specimen available represents an internal cast of the anterior aboral side of the corona only, partially enclosed in hard siliceous matrix, so that most details are obscured. The estimated length of the specimen is about 50-60 mm, the width is 53 mm. The outline of the test is cordate, with a deep frontal sulcus flanked by well-developed keels in interambulacral columns 2b and 3a. In lateral view the highest point of the test seems to have been anterior of the centre, slightly in front of the apical disc. The anterior face was steeply inclined. The frontal groove starts close to the apex and is deepest at the ambitus. The pore pairs of ambulacrum III appear to be small and uniserial, being more densly crowded adapically than ambitally and placed close to the outer edge of the groove. The paired ambulacra are flush with the test, petaloid, featuring numerous, closely spaced and transversely elongate pore pairs, which extend at least 70 % of the corresponding test radius towards the ambitus. The pores of the posterior pore columns of ambulacra II and IV are about twice as wide as the anterior columns. As far as preserved, the anterior and posterior petals appear to be equally developed. The apical disc is partially preserved and of the usual holasteroid type: elongate, with a single gonopore on each genital plate.

**REMARKS:** Without information on plastron structure and presence/absence of a marginal fasciole around the posterior part of the test, it is impossible to firmly identify the material to genus level. However, based on the shape of the aboral side, with marked keels flanking ambulacrum III and the presence of petaloid paired ambulacra with numerous elongate pore pairs, an attribution to either Pseudholaster or Cardiaster seems most likely. Among Pseudholaster, the present material appears to be closest to P. bicarinatus (Agassiz, 1847), as evidenced by the presence of well-defined carinae flanking the frontal groove, the crowded pores in adapical ambulacrum III and the marked inequality of the pore columns in the anterior paired ambulacra (compare Smith and Wright 2003, p. 462-465). P. sequanicus (Bucaille, 1883) shares the characteristics of

\* 1847. [Holaster] bicarinatus Agass.; Agassiz and Desor, p. 29.

Text-fig. 19. Echinoidea. A, B. – ? *Pseudholaster bicarinatus* (Agassiz, in Agassiz and Desor, 1847). A – Aboral view. B – Right lateral view. HMC. C–G – *Epiaster brevipetalus* Smith and Wright, 2008. HMC. C, E – Aboral view. F. Oral view. D, G – Left lateral view. H–J. *E – distinctus* (Agassiz, in Agassiz and Desor, 1847) H – Aboral view. I – Oral view. J – Left lateral view. HMC. Scale bar = 10 mm



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the unequally developed pore columns, but has a different profile (highest point subcentrally) and less pronounced keels (compare Smith and Wright 2003, p. 465-468). Other Cenomanian species of Pseudholaster [P. cenomanensis (Orbigny, 1855), P. suborbicularis (Brongniart, 1822)] can clearly be ruled out due to widely differing test shape (Orbigny 1854-1860; Smith and Wright 2003). Likewise, most species of Cardiaster differ in test profile, development of keels flanking the frontal sulcus, and the more posterior location of the apical disc. Moreover, Cardiaster, according to our present knowledge (Smith 2004; Smith and Kroh 2012) first appears in the Turonian, while the material studied is slightly older, being Cenomanian in age. Protocardiaster, another genus with a similar shape, can be ruled out due to its smaller pore pairs and shorter petals.

# Order Spatangoida L. Agassiz, 1840a Family Hemiasteridae H. L. Clark, 1917 Suborder Micrasterina Fischer, 1966 Genus *Epiaster* Orbigny, 1855 *Epiaster brevipetalus* Smith and Wright, 2008 (Text-figs 19C–G, 20A)

2008. *Epiaster brevipetalus* sp. nov.; Smith and Wright, p. 633, text-figs 249, 275, 276, pl. 207, fig. 2, pl. 209, figs 1, 2.

MATERIAL: Three internal casts (HMC), plus a partially enclosed internal cast of uncertain affinity (NMA).

#### MEASUREMENTS (in mm):

Specimen	length	width	height*
HMC (Text-fig. 19C, D)	46.5	45.4	15.8
HMC (not figured)	32.1	31.6	13.2
HMC (Text-fig. 19E–G)	c. 24	25.7	14.4
* specimens deformed, values	s do not	correspond to	full original

\* specimens deformed, values do not correspond to full origina height

DESCRIPTION: The specimens available range from c. 24 to 46.5 mm in test length. Test outline is subcircular to slightly cordiform, with a very shallow frontal sulcus. All except the smallest specimens are strongly deformed and thus their original profile cannot be observed; test height, however, clearly was at least 50– 60 % of test length. In the specimen of Text-fig. 19E– G, the highest point is situated just posterior of the apical disc on the rounded keel formed by interambulacrum 5. The anterior end is gently sloping towards the ambitus, while the posterior end seems to be vertically truncated. The apical disc is situated subcentrally and is not well preserved in any of the specimens.

Ambulacrum III is distinctly sunken, most strongly so close to the apical disc and less so towards the ambitus. The ambulacral pores are relatively large, marginal and extend slightly more than halfway towards the ambitus. In a c. 24 mm test length specimen there are approximately 15 pore pairs in each column, in the largest specimen (TL 46.5 mm), albeit not clearly visible, there are at least 30 pore pairs per column.

The paired ambulacra are petaloid and distinctly sunken adapically. The petals close distally and terminate abruptly, at about 67 % of the corresponding test radius (anterior paired petals), respectively at about 44 % (posterior petals in large specimens) to 56 % (small specimens). The anterior petals diverge at about 110°, while the posterior ones diverge at about 70°. The ambulacral pores are closely spaced elongate pore pairs (possibly conjugate), consisting of two widely spaced horizontally elongated pores each. The pore columns are more or less equally developed, although the posterior column in each petal is slightly wider than the anterior column adapically. The interporiferous zone is about the width of a single pore column. In the anterior paired petals there are 32-35 pore pairs per column in a 32.1 mm length individual and 35 pores in the largest specimen (46.5 mm length). In the posterior petals, there are distinctly fewer pores (c. 20 in a 32.1 mm length individual).

Of the oral plating only the plastron structure is clearly visible on the internal casts (Text-fig. 20A). The labrum is triangular with a strongly concave posterior end. It abuts both sternal plates, but only barely touches sternal plate 5.a.2. The sternal plates are much larger and have a highly oblique median suture. The episternal plates are much smaller than the sternal plates, being biserially offset.

The peristome lies close to the anterior margin, about 15 % of TL away from it and is kidney shaped. The periproct is not well preserved in the specimens available, but seems to have been positioned high on the posterior face of the corona.

Tuberculation and fascioles unknown.

REMARKS: The present specimens are difficult to identify due to their preservation as internal moulds. Based on general shape and plastron structure, *Hemiaster*, *Epiaster* and *Pliotoxaster* are the most likely candidates. Most species of *Hemiaster*, however, can be ruled out by their petal shape and lack of a frontal sulcus. *Pliotoxaster* and *Epiaster* can be told apart by their differing number of pores in ambulacrum III (Smith and Wright 2008, p. 586, 629). The present

species shows the characteristics of *Epiaster* in this respect (few and widely spaced pores). Among European species of *Epiaster* it fits best with *E. brevipetalus*, based on petal shape and the lack of a subanal projection (typical for *E. crassissimus*).

## *Epiaster distinctus* (Agassiz in Agassiz and Desor, 1847) (Text-figs 19H–J, 20B)

- \* 1847. [*Micraster*] distinctus Agass.; Agassiz and Desor, p. 23.
- ? 1933. Epiaster crassissimus Defr.; Lehner, p. 465.
- ? 1937b. *Epiaster crassissimus* (Defrance 1827); Lehner, p. 184, pl. 17, figs 29–31.
  - 1958a. *Epiaster Polygonus* d'Orbigny; Kempcke, p. 9, fig. 13.
  - 1991. Epiaster polygonus D'Orb.; Mörs, p. 79, fig. 3.
  - 2008. *Epiaster distinctus* (Agassiz, in Agassiz & Desor, 1847); Smith and Wright, p. 631, text-figs 249, 274, 275, pl. 208, figs 1–4.

MATERIAL: A single internal cast (HMC).

DESCRIPTION: The single specimen available has a test length of 50.3 mm, a width of 48.6 mm and a height of 24.4 mm. In outline the corona is ovate, with a shallow and wide frontal sulcus. In profile the test is low, with the highest point situated just posterior of the apical disc on the rounded keel formed by interambulacrum 5. The anterior end slopes gently towards the ambitus, while the posterior end is vertically truncated.

The apical disc is situated very slightly posterior of the centre, about 51.7 % from the anterior margin. Apical disc plating structure is not well preserved, but shows a tetrabasal disc with 4 gonopores, the posterior pair being wider apart than the anterior pair.

Ambulacrum III is distinctly sunken, most strongly so in the upper half of the aboral side, shallowing towards the ambitus. The ambulacral pores are relatively large, marginal and extend slightly more than halfway towards the ambitus. In the single specimen available there are approximately 20 pore pairs in each column.

The paired ambulacra are petaloid. The petals are distinctly sunken and closing distally, where they terminate abruptly. The anterior pair extends about 63 % of the corresponding test radius, the posterior pair about 56 %. The ambulacral pores are closely-spaced elongate pore pairs (possibly conjugate), consisting of two widely-spaced horizontally-elongated pores each. The pore columns are more or less equally developed, although the posterior column in each petal is slightly wider than the anterior column adapically. The interporiferous zone is about the width of a single pore column. The anterior petals diverge at about 105°, while the posterior ones diverge at about 60°. In the single specimen available there are about 40 pore pairs per column in the anterior paired petals and about 30 in the posterior ones.

The oral plating is not well preserved, but the structure of the plastron is clear (Text-fig. 20B): the labrum is triangular and has a strongly concave posterior end. It abuts both sternal plates, but only barely so in case of 5.a.2. The sternal plates are much larger



Text-fig. 20. Echinoidea; camera lucida drawings of the oral plating patterns. A – *Epiaster brevipetalus* Smith and Wright, 2008. HMC. B – *E. distinctus* (Agassiz, in Agassiz and Desor, 1847). HMC. Interambulacra shaded in grey

and have a highly oblique median suture. The episternal plates are poorly visible but are much smaller than the labral plates, being biserially offset.

The peristome is kidney-shaped and situated anteriorly, about 20 %TL away from the margin of the test. The periproct is more or less circular and lies high on the posterior face of the corona.

Details of the tuberculation and presence/absence of fascioles unknown.

REMARKS: Like the specimens of *Epiaster brevi*petalus discussed above, the present specimen is an internal mould, incompletely preserving the characters needed for classification. Again *Epiaster* and *Pliotoxaster* are the most likely genera. With c. 20 pores at a length of 50 mm, the specimen plots with members of the genus *Epiaster* (see Smith and Wright, 2008, p. 586, fig. 249). It differs from *E. brevipetalus* in its longer posterior paired petals and from *E. crassissimus* in its vertically truncated posterior end (forward sloping with a distinct subanal heel in *E. crassissimus*).

## DISCUSSION

#### **Taphonomy and diagenesis**

Within the Neuburg Kieselerde Member, fossils are usually preserved in opaline nodules (e.g., most of the bivalves and echinoids) or occur as isolated, predominantly entirely and densely silicified objects (a majority of the sponges and brachiopods). As noted above, aragonite skeletons usually were obviously dissolved during early diagenesis, and the aragoniticshelled groups, e.g., heterodont bivalves, gastropods and ammonites have been taphonomically excluded from the fossil record of the Neuburg Kieselerde Member. Moreover, silicification favours stable low-magnesium calcite (Mergl 2010; Niebuhr 2011a), and is thus selective even with regard to calcitic skeletons. As a result, a considerable number of taxa may have been not preserved or only rarely so. Given these circumstances, it is somewhat surprising to find nautilid fossils since their shells consist primarily of aragonite (Crick and Mann 1987). However, such specimens are very rare and we attribute their sporadic preservation to the fact that nautilid shells usually are very thick-walled (in contrast to most infaunal bivalve and ammonite shells), thus being more resistant to rapid early diagenetic dissolution. The thick shells facilitated the formation of internal nautilid moulds.

Based on petrographic analyses (thin-sections,

SEM), limestones and marly limestones that contained large amounts of biogenic silica (e.g., siliceous opoka; see Pożaryska 1952; Niebuhr et al. 1997) are regarded as the primary, unaltered sediment that was turned into the Neuburg Siliceous Earth during decalcification, and sagging into karst depressions in Cenozoic times. Silicification of fossils and sediment certainly occurred during early diagenesis in Cretaceous times, in a predominantly marine environment (see Niebuhr 2011, p. 54). Major silicification leading to the formation of abundant, dense opaline nodules obviously happened during emergence at sequence boundaries (i.e. the *crippsi* Event = SB Ce 1, and the Hornsand Unconformity = SB Tu 1), while porous nodules most likely formed under marine conditions. All kinds of transitional stages occur in abundance (Text-fig. 5E).

For sponges, SEM studies of numerous skeletons and the corresponding taphonomic data enable interpretation of the succession of the most prominent mineralisation processes: (1) During early diagenesis, the skeletons and spicules, formed of biogenic silica, were partly or completely desilicified and replaced by calcite. (2) In a second step, intense silicification forming opal-CT affected the sponge spicules, skeletons and sediment in the interspicular areas of the sponge skeletons, especially within the wall interiors (Text-fig. 8B, F, H). (3) Subsequent complete decalcification resulted in the formation of empty voids after (a) calcified spicules (Text-fig. 8H) and/or (b) calcareous sediment accumulations (Text-fig. 8B, D) within heavily silicified parts of the skeleton. (4) Finally, a single or several episode(s) of secondary silica accumulation led to the formation of spherical chalcedony within part of these empty voids (Text-fig. 8D, compare with Carson 1987). Partial desilicification process(es), affecting the surface of the original siliceous spicules, probably took place during these episodes of mineralization (Text-fig. 8G, H).

#### Palaeoecology

The fauna of the Neuburg Kieselerde Member has been assembled from several localities, which are, however, dispersed over a relatively small area. Taking into account that the sediments are generally preserved in post-depositional karst depressions, the original transgression surface may have been only moderately structured (see Wilmsen *et al.* 2010 and Wilmsen and Niebuhr 2010 for the regional distribution of the transgressive strata of the Danubian Cretaceous Group), resulting in relatively homogeneous level-bottom deposition. The fine-grained fabric of the sediments of the Neuburg Kieselerde Member suggests deposition predominantly below the fair-weather and even the storm-wave base. On the other hand, the palaeogeographic situation rules out a deep-water offshore setting. Thus, sheltered deposition within a largescale embayment on a very shallow shelf system of the Danubian Cretaceous Group, absorbing most of the water energy of the open ocean in the south, appears as a suitable scenario. The lack of significant coarsegrained terrigenous input and glauconite is also noteworthy and differentiates the depositional environment of the Wellheim Formation from those of contemporaneous deposits of the Regensburg-Kelheim area in the east. This difference can be attributed to the geological structure of the hinterland: elevated topography with strong riverine clastic input from the Bohemian Massif in the east in contrast to low-lying, karstified Jurassic carbonates of the Franconian Alb surrounding the Wellheim embayment in the west. We speculate that due to the karstification, no significant fluvial input occurred into the Wellheim embayment.

In general, the sediments of the lower Danubian Cretaceous Group document a 2nd-order trans-/regressive cycle starting with the Cenomanian transgression and ending in the Hornsand Unconformity in the Lower-Middle Turonian boundary interval with an intervening maximum flooding during the early Early Turonian (Niebuhr et al. 2009, 2011; Wilmsen et al. 2010; Richardt et al. 2013). The same development can be recognized in the lithostratigraphic pattern (Textfigs 3, 4) as well as the microfacies of the Wellheim Formation (i.e., the matrix of Late Cenomanian Inoceramus pictus pictus is much finer than that of Early Cenomanian I. crippsi crippsi; see Text-fig. 5B, E). Thus, shallow-water conditions should be expected during the (Early and Middle) Cenomanian and late Early Turonian, while somewhat deeper depositional environments should have prevailed during the Late Cenomanian and early Early Turonian (for the timeequivalent Eibrunn Formation of Regensburg-Kelheim area, 50-70 m of water depth were assumed by Wilmsen et al. 2010). In a broad sense, this environmental subdivision may be reflected by the fauna of the Neuburg Kieselerde Member, which can largely be grouped into two assemblages:

(1) A major part of the fauna including most of the bivalves, the nautilids and echinoids, the branching bryozoans, as well as the ichnofossils, driftwood and part of the serpulids, has been collected from the abundant opaline nodules of the basal to lower part of the Neuburg Kieselerde Member and is usually preserved on lithified rock matrix (Kempcke 1958a).

(2) In contrast, isolated fossils, i.e. most of the sponges preserved as body fossils, brachiopods, sabel-

lids, several serpulids, the globular bryozoan colonies, and several (cementing) bivalves are derived from levels higher up-section, where opaline nodules are scarce (Kempcke 1958a).

Certainly, exceptions may occur but the general pattern of a bivalve and echinoid-dominated lower assemblage and a sponge and brachiopod-dominated upper assemblage is evident. However, it also should be pointed out that due to the preservation in the karst depressions, fossils have usually been collected in no stratigraphic order. Furthermore, the stratigraphic and fossil record of the upper part of the Wellheim Formation will be limited to the central part of the structures where sediments were preserved from erosion; it will be dependent on the amount of post-depositional sag as well as post-sag erosion during the Cenozoic. In contrast, the lower and middle parts of the succession will normally be preserved because the sediments in question were protected from erosion.

#### Bivalve-echinoid assemblage

The composition of the fauna forming the bivalveechinoid assemblage clearly indicates shallow water conditions. The bivalve fauna comprises predominantly epifaunal taxa accompanied by a few semi-infaunal representatives. A majority of the bivalves, i.e. the abundant Inoceramus crippsi crippsi, most of the pectinids, as well as the pteriids, bakevelliids, limids and anomiids, lived epifaunally byssate. Specimens of I. crippsi crippsi are usually large and flat, obtaining stability as recliners on the soft substrate by means of the "snow-shoe-principle". They often occur doublevalved. Noteworthy is the complete absence of inoceramids of the group of I. virgatus Schlüter which occur abundantly in Lower Cenomanian arenaceous deposits of the Regensburg-Kelheim area (Tröger et al. 2009; Wilmsen and Niebuhr 2010) and elsewhere in NW Europe. Representatives of I. ex gr. virgatus likewise dwelled as epibyssate recliners (Wilmsen 2008) but, according to their inflated shell shapes, seemed to prefer more stable substrates (Wilmsen and Niebuhr 2010). Neithea and probably also Merklinia were not attached by byssus and lay freely on the sea bottom. Similar to their modern counterparts, the abundant Pinna cretacea and rare Modiolus lived as semiinfaunal mud-stickers, fixed by byssus threads. All the other bivalves are epifaunal taxa. Cementing bivalves, i.e., spondylids and small oysters occur in the sponge-brachiopod assemblage (see below) rather than in the bivalve-echinoid assemblage; only two specimens of Rastellum and several Rhynchostreon belong to this guild; the latter, however, were only attached to

some hard substratum as juveniles. A taxonomically and ecologically fairly similar bivalve-dominated benthic assemblage occurs in the Cenomanian Oberhäslich Formation of Saxony (Germany; Wilmsen and Richardt 2012).

Bryozoans are represented only by a few erect, branching colonies in the bivalve-echinoid assemblage. Generally, massive erect colonies are most abundant in quiet, slightly deeper water while encrusting forms dominate in shallow water (McKinney and Jackson 1989). However, bryozoans may grow in colony shapes characteristic of much deeper, open basin environments, when occurring in sheltered or cryptic habitats (Taylor 2005), which, in our case was realised in the embayment.

Evidence of the infauna is weak. The few specimens of *Planolites* that have been found in the collections may indicate that the animals creating these burrows were not particularly abundant. Generally, Planolites is interpreted as a trace of "a wandering deposit feeder backfilling behind it" (Bromley 1996, p. 203), which may, considering the small diameter of the burrows, apply to polychaetes or prosobranch bivalves. Additionally, a single shallow-burrowing Cucullaea? is preserved. Other infaunal bivalves that might have been expected to occur, e.g., glycymeridids, cardiids and tellinids, were probably subject to diagenetic loss (see above). Moreover, the two Epiaster species probably belonged to the burrowing infauna (based on the tuberculation pattern of well-preserved British specimens illustrated in Smith and Wright 2008). For ? Pseudholaster bicarinatus, in contrast, a semi-infaunal mode of life seems to be more likely, due to its rather heterogeneous aboral tuberculation and the lack of a dense, pseudofasciolelike groundmass of tubercles as observed in Epiaster. All echinoid taxa reported are typically known from Albian to Cenomanian deeper water chalk deposits of Great Britain and France, indicating that the substrate conditions (soft muds) were more important for their occurrence than water depth.

Nekton is represented only by the few nautilids. Modern *Nautilus*, although usually living at greater depths, is known to access shallow waters mainly during the night for preying (Saunders and Ward 1987), and Cretaceous ribbed ("cymatoceratid") nautilids may have behaved similar or even permanently inhabited shallow-water areas (Frank *et al.* 2013). Furthermore, shells of dead nautilids may have come up to the water surface driven by fermentation gas, and may have been floating over long distances, to finally become deposited far from their original habitat (e.g., House 1987).

#### Sponge-brachiopod assemblage.

With regard to abundance, the sponge-brachiopod assemblage is clearly dominated by almost equal numbers of lithistid demosponges and hexactinellids, albeit with a marked prevalence of the lithistids with regard to diversity. Wagner (1963) compared the Porifera from the Neuburg Kieselerde Member with numerous sponge faunas from other European Upper Cretaceous localities. As a result, the hexactinellid assemblage, in particular, has been found to be strikingly similar to other Cenomanian assemblages from northern France and southern England (Wagner 1963 and literature therein).

The skeletons of many of the siliceous sponges are still attached to their original substrate, which is represented mainly by (1) skeletons of other sponges and their fragments (e.g., Text-fig. 7I), (2) subangular quartz clasts, 1-9 mm in size (mainly in basal skeletons of hexactinellids) and (3) other invertebrate skeletons (juvenile oysters, serpulid tubes, bryozoans; Textfig. 12E). In turn, various epibionts occur on the surface of sponge skeletons, including bryozoans (preserved in the form of zoarium moulds on the dermal surface of Prokaliopsis danubica), agglutinated foraminifers (on the dermal surface of Brachiolites fenestratus), sabellids (Text-fig. 15A, D, E), serpulids (Text-fig. 15H) and bivalves (Text-fig. 12A). Small oyster shells are attached to skeletons of both lithistid demosponges (Text-fig. 7A) and hexactinellids. Usually, the material of the shells occurs in the form of beekite (see Carson 1987).

While serpulids occur exclusively attached to shells or sponge skeletons, sabellids of the genus Glomerula may be found both cementing to sponges or growing in isolated clusters. The sabellid and serpulid assemblage from the Neuburg Siliceous Earth generally resembles the common Late Cretaceous offshore fauna typical of fine-grained sediments, which has been detailed by Jäger (1983, 2005). It is noteworthy that well-developed Glomerula plexus clusters consisting of a large number of tubes as well as members of Serpula (Cementula)? are relatively common. In contrast, none of the specific serpulid taxa that characterize the Cenomanian coarsegrained nearshore sediments along the southwestern margin of the Münsterland Cretaceous Basin (Lommerzheim 1979) has been recorded from the Neuburg Siliceous Earth. Notwithstanding the specific post-diagenetic lithology of the Kieselerde, the polychaete assemblage is rather similar to those assemblages found in other Upper Cretaceous offshore sediments, e.g., in England or northern Germany.

In the sponge-brachiopod assemblage, bryozoans are usually represented by globular colonies, which are

characteristic of very shallow habitats exposed to high water energy (Holcová and Zágoršek 2008). However, due to their rounded shape and low weight, globular bryozoan colonies are easily transported and often deposited in deeper environments. Due to abrasion or destruction of the substratum (Zágoršek *et al.* 2012) encrusting bryozoans may have a lowered preservation potential. Anyway, the low abundance of encrusting forms in the studied material may suggest relatively quiet marine conditions, since abrasion is not evident.

The brachiopod assemblage is dominated by Cyclothyris, which commonly is abundant in marginal coarse-grained arenaceous deposits of Cenomanian age such as the Wilmington Sands of England. The degree of costation thus does not really correlate with the relatively fine-grained sediment and the inferred lowenergy and relatively deep water depositional setting of the Neuburg Kieselerde Member. This is perhaps the first record of Cyclothyris from relatively fine-grained sediments, rather than from sandstones and calcarenites, reinforcing the idea expressed above that they may represent a new, yet undescribed taxon. The more generalist Grasirhynchia grasiana may occur in chalk and limestone as well as argillaceous facies. For Concinnithyris, the large pedicle opening suggests attachment to a hard substrate and adaptation to a high energy, shallow water habitat.

Depth distribution ranges of various groups of living sponges have frequently been used to interpret fossil sponge assemblages with regard to water depth (e.g., Reid 1968; Vodrážka and Crame 2011 and literature therein). Likewise, Wagner (1963) has discussed the taxonomic composition of the sponge assemblage from the Neuburg Kieselerde Member with regard to this aspect, and suggested that the sponges may have lived at a water depth of 100 to 150 m. These estimates contrast with interpretations based on the sedimentology and sequence stratigraphy of the Danubian Cretaceous Group, assuming a water depth of 50 to 70 m during the maximum flooding interval in the Late Cenomanian (Wilmsen et al. 2010). Furthermore, the ecologic requirements of Cretaceous sponges may have been somewhat different from those of taxonomically similar Recent sponge faunas, as Cretaceous siliceous sponge faunas may also occur in nearshore depositional environments (e.g., Kauffman et al. 2000). The abundant spicules that can be recognized in thin-sections from the Wellheim Formation, ranging from the Lower Cenomanian sandy basis beds into the uppermost Lower Turonian Hornsand facies (see Text-fig. 5B-E), furthermore show that loosespicule demosponges were common faunal elements in most parts of the Wellheim embayment.

#### CONCLUSIONS

In conclusion, the fauna from the Neuburg Kieselerde Member can be characterized as a bivalve- and sponge-dominated soft-bottom community, which lived in a neritic, shallow to moderately deep, fully marine environment of low water energy. A large-scale embayment on the wide shelf system of the Danubian Cretaceous Group, absorbing most of the water energy of the open ocean in the south, integrates all palaeoecological and palaeogeographic constraints. The lack of significant coarse-grained terrigenous input can be attributed to the geological structure of the hinterland, with low-lying, karstified Jurassic carbonates of the Franconian Alb surrounding the protected Wellheim embayment. With few exceptions, the fauna is composed of common and widespread Cenomanian-Turonian species, and thus resembles several faunas of similar age throughout western and central Europe. Although not collected stratigraphically, the fauna may largely be grouped into a lower bivalve-echinoid assemblage and a succeeding sponge-brachiopod assemblage, basically reflecting the Cenomanian-Turonian 2<sup>nd</sup>-order sea-level development.

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The peculiar preservation of the fossils, best seen in the sponge skeletons, provides evidence of an exceptional diagenetic pathway, involving multiple steps of dissolution and silicification, which also led to the formation of a unique type of sediment. Although the general preservation of the fossils is relatively poor, the Neuburg Kieselerde Member of the Wellheim Formation provides evidence of approximately 100 species and thus preserves the probably most diverse and complete fauna of the Danubian Cretaceous Group. As a result, the Neuburg Kieselerde Member is certainly one of the most important archives of life in the peri- and epi-continental shelf seas around the Mid-European Island during the early Late Cretaceous.

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## Appendix.

Revised list of Porifera from the Neuburg Kieselerde Member, arranged in systematic order. Names of species depicted in Text-figures 7 and 8 are written in bold letters.

Class Demospongea Sollas, 1885

Subclass Choristida Sollas, 1880 Order Pachastrellida Reid, 2004

Propachastrella sp.

Order uncertain

Ophiraphidites annulatus Schrammen

Subclass Lithistida Schmidt, 1870

Order Tetralithistida Lagneau-Hérenger, 1962 Suborder Tetracladina Zittel, 1878 Jerea pyriformis Lamouroux Siphonia tubulosa (Roemer) Polvierea arbuscula Hinde Thecosiphonia torgeri Schrammen *Thecosiphonia neoburgensis* Wagner Turonia constricta Zittel Turonia cerebriformis Schrammen Turonia globosa Wagner Kalpinella pateraeformis Hinde Astrocladia subramosa (Roemer) Acrochordonia ramosa Schrammen *Phyllodermia antiqua* (Schrammen) Phyllodermia kempckei Wagner *Phyllodermia* aff. *galloprovincialis* (Moret) Ragadinia rimosa (Roemer) Ragadinia laccophora Wagner Pseudojerea excavata Moret Leiophyllum cf. panniculosum Schrammen Thamnospongia cf. reticulata Hinde Prokaliapsis schrammeni Wagner *Prokaliapsis danubica* Wagner Prokaliapsis bulbosa Wagner Polyrhipidium cristagalli Schrammen Pholidocladia incrustans Moret Pholidocladia tuberculata Moret Pholidocladia cf. tuberculata Moret Pycnodesma globosa Schrammen Phymaplectia cribrata Hinde Suborder Dicranocladina Schrammen, 1924

Procorallistes polymorphus Schrammen Phrissospongia hoffmanni Wagner

Order Megalithistida Reid, 2004

Suborder Megamorina Zittel, 1878 Doryderma roemeri Hinde Homalodoriana benetti (Hinde) Heterostinia obliqua (Benett)

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Order Monalithistida Lagneau-Hérenger, 1955 Suborder Sphaerocladina Schrammen, 1924 *Lecanella*? aff. *pateraeformis* Zittel *Regnardia* cf. *lapparenti* Moret Ozotrachelus cf. *exspectatus* (Schrammen)

> Suborder Rhizomorina Zittel, 1895 *Laosciadia mantellii* (Goldfuss) *Laosciadia columna* (Schrammen)

Class Hexactinellida Schmidt, 1870

Subclass Hexasterophora Schulze, 1887

Order Hexactinosa Schrammen, 1903

Laocoetis cf. tenuis (Roemer) Laocoetis fittoni (Mantell) Laocoetis vulgata (Počta) Guettardiscyphia stellata (Michelin) Guettardiscyphia alata (Pomel) Guettardiscyphia cf. roemeri (Pomel) Guettardiscyphia diptera Wagner Guettardiscyphia sp.

Order Lychniscosa Schrammen, 1903

Ventriculites sp. Napaeana sp. Pleuropyge plana Schrammen Ubiquiradius mirus (Schrammen) Leiostracosia sp. **Exanthesis reticulatus (Hinde) Brachiolites fenestratus T. Smith** Kentrosia incrustans Schrammen **Stauronema carteri Sollas** Stauronema cf. planum Hinde

Class Calcarea Bowerbank, 1864 Subclass Calcaronea Bidder, 1898 Order Stellispongiida Finks and Rigby, 2004 *Elasmoierea* sp.