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# Late Jurassic (Upper Kimmeridgian) Heterobranchia (Gastropoda) of the coral-facies of Saal near Kelheim and the viciniy of Nattheim (Germany)

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## Abstract

Forty gastropod species of the subclass Heterobranchia are described from the Upper Jurassic (Upper Kimmeridgian) reefal limestones of South Germany, including ten species in open nomenclature and further ten species of uncertain identity. Six species are new to science: *Ceritella convexa* **sp. nov.**, *Nerinea donosa* **sp. nov.**, *Endoplocus acutus* **sp. nov.**, *Endoplocus inflatus* **sp. nov.**, *Pseudonerinea*? *pseudomelaniformis* **sp. nov.**, and *Itieroptygmatis cylindrata* **sp. nov.** A lectotype is designated for *Ptygmatis*? *tornata* (Quenstedt, 1852). With this final part of the study of the Late Jurassic gastropods from Saal and the Nattheim area, a total of 156 species have been reported. Of these species, 125 have been reported from Saal and 54 from the Nattheim area. Only 23 species occur in both Saal and the Nattheim area. The sample sizes (number of specimens) from Saal and the Nattheim area differ considerably and few species are shared. Diversity metrics suggest the same high diversity at both sites. The gastropod fauna from the Saal quarry has yielded particularly much new information – all new species are based on specimens from Saal. With 125 gastropod species from a single outcrop, the diversity at the Saal quarry is the highest from the Kimmeridgian worldwide. In total, up to 300 species of marine macro-invertebrates have been reported from this quarry, which is a very high point diversity. Gastropods are by far the most diverse group from Saal, which is a modern aspect of this fauna.

## Keywords

Gastropoda, Heterobranchia, Southern Germany, Kimmeridgian, coral reef facies, taxonomy

## Introduction

This is the fourth and final part of the description of the Late Jurassic (Upper Kimmeridgian) gastropods from the reefal limestones of South Germany (Saal und Nattheim) (Gründel et al. 2015, 2017, 2019). Meanwhile, an additional private collection from Saal (collection Sylla) has been obtained by the Bavarian State Collection (SNSB-BSPG) in 2017 (Werner et al. 2017). It yields numerous not yet studied gastropod specimens that potentially could complement our knowledge of the gastropods from Saal and also yields additional undescribed species, but the study of this collection will need time.

Nerineoidea probably originated in the Early Jurassic (Tracey et al. 1993) and were comparatively rare and of low diversity until the Callovian. They diversified from the

Oxfordian onward and continued to do so in the Kimmeridgian. They became extinct at the end-Cretaceous mass extinction event.

Generally, gastropods from Saal are re-crystallized and lack the early ontogenetic shell including the protoconch. The specimens from Nattheim are silicified, but the silicification is rather coarse. However, many species could be characterized in sufficient detail so that 156 species could be described making this fauna one of the most diverse known Late Jurassic gastropod faunas.

## Geological setting

The geological setting for the studied Late Jurassic gastropod fauna is provided by Gründel et al. (2015) in German. A complemented translation is provided herein: The gastropod faunas come from Upper Jurassic reefal limestones from the localities of Saal near Kelheim, Lower Bavaria and Nattheim in Baden-Württemberg. Almost all finds from Württemberg published to date are listed under the locality name "Nattheim". This information is a collective name for finds from small quarries that no longer exist and finds from fields in the wider area of Nattheim. The exact fossiliferous localities can no longer be determined. Today, most finds are made in the Gerstetten area (see below).

### Saal

By far most of the studied gastropod material comes from a quarry near Saal near the Danube River. The quarry of the Fels-Werke GmbH (right-high value: 4495500/5417000) exposes a more than 100 m thick section of massive limestone of Middle and Late Kimmeridgian age which possibly extends into the basal Tithonian (Meyer in Weber et al. 1978; Meyer and Schmidt-Kahler 1983). The massive limestones are unconformably overlain by sediments of the Danubian Cretaceous Group (Niebuhr and Pürner 2009). Up to 80 m deep karst fissures, which formed during the Early Cretaceous, are filled with colourful, terrestrial sediments, the pre-Cenomanian Schutzfelsschichten (kaolinite-bearing clays, sands and fine gravel). The erosive surface of the Upper Jurassic massive limestones (in some places with borings of lithophagous bivalves), together with its filled carst fissures, is transgressively overlain by marine sands of the Regensburg Formation (Gümbel 1854; Trusheim 1935). In the Regensburg-Kelheim area, this succession is up to 16 m thick, contains glauconite, fossil-bearing sandstones (Upper Cenomanian Unterer Grünsandstein (Lower Greensandstone): Saal-Member) with a glauconite content of over 30% (Meyer and Schmidt-Kahler 1983; Wilmsen et al. 2009). At the contact between to the Cretaceous Schutzfelsschichten, the otherwise very dense Upper Jurassic massive limestones have been intensively weathered in a zone of usually only a few millimetres to up to 60 mm in some cases. From this highly porous weathering layer, small fossils, in particular gastropods, bivalves, echinoderms, brachiopods, corals, etc., can be carefully washed out. The acidic karst waters have gently and meticulously etched the fossils free. In 2003 and 2014, one of the authors (Fritz Lang) was able to isolate more than 300 and 1,000 gastropods, respectively, by washing the loose material carefully scraped off the karst surfaces.

The massive Upper Jurassic limestones are subject to rapid vertical and lateral facies changes. The deeper part of the section (up to approximately 300 m above sea level) exposed in the quarry is dominated associations of siliceous sponges and microbes. Then, platy corals (*Microsolena*) are increasingly intercalated during the Upper Kimmeridgian until a continuous transition into a pure coral reef facies is reached at the middle quarrying level, about 380 m above sea level (Meyer in Weber et al. 1978). In the upper 40–50 meters of the reef limestone from which the gastropod fauna was retrieved, the switch from the deeper-water association dominated by siliceous sponges to a shallow water coral facies is completed. The reefal facies consist of individual in situ reef bodies yielding a highly diverse coral fauna, as well as reef debris limestone and typical lagoon sediments (facies with coated grains, dasycladaceans, gastropods: "Breistein"="Porridge-Stone") containing pocket-like shell accumulations dominated by terebratulid brachiopods.

The stratigraphic age of the massive limestones is disputed. Rare ammonite finds reported by Schairer and Sylla (1996) from different levels of the Saal quarry confirmed a Late Kimmeridgian age, supported by finds of *Hybonoticeras beckeri*, *Sutneria subeumela* and a *Virgataxioceras* that cannot be determined in more detail between 335 and 415 m above sea level, i.e., up to the upper quarry level. From the top 15 meters of the reef limestone exposed in the quarry, no exactly localized ammonites have been described so far. Meyer (in Weber et al. 1978) assumed that the highest proportions of the Kelheim reef limestone reach into the basal Tithonian. However, direct evidence of this (*Lithacoceras* cf. *ulmensis*) is not available from Saal, but from the abandoned quarry near Ofenstetten, about 10 km SW. Meyer and Schmidt-Kaler (1983) base the presumed Lower-Tithonian age of the highest reefal limestones at Saal on the alleged occurrence of *Neochetoceras steraspis* with the unspecified locality information "above the middle working level." This ammonite is also a characteristic faunal element of the Obere Schiefer (Upper Slate) of the Solnhofen Plattenkalke (Solnhofen Lithographic Limestone) (Schweigert 2007).

### Gerstetten

The fossils from the Nattheim coral facies are silicified, i.e., originally aragonitic and calcitic shells were diagenetically converted into siliceous material. Thus, fossils can be freed from the dense limestone with acetic or formic acid. In addition to a very diverse coral association comprising more than 130 species, the massive limestones contain an equally rich reef dwelling fauna consisting of coralline sponges, tube worms, brachiopods, molluscs and echinoderms (e.g., Benz 1979; Reif 1988; Sauerborn 1988).

During the 19th century, in the course of bean ore mining, numerous outcrops on the Swabian Jura in the Nattheim/Blaubeuren/Gerstetten area were sampled for fossils. Today, finds are essentially limited to cobbles from fields or to temporary outcrops in connection with construction work. In the older descriptive literature (Goldfuss 1844; Quenstedt 1856–1858, 1881–1884; Brösamlen 1909) usually only "Nattheim" is mentioned as a locality name.

The massive coral facies in that area is part of the more than 120 m thick Mergelstetten Formation. It lies at the border to the Unterer Massenkalk (Lower Massive Limestone) that underlies the Mergelstetten Formation. It can thus be regarded as a chronological equivalent of the Liegende Bankkalk-Formation (Schweigert and Franz 2004). The Mergelstetten Formation is bounded by sedimentary discontinuities and may interfinger with the Brenztal-Trümmerkalken (Brenztal Debris-Limestones) in the East and with the bedded units of the Liegende Bankkalke (Lying Bedded Limestones) or the Zementmergel-Formation (Cement-Marl Formation) in the West (Reif 1988; Schweigert and Franz 2004; Schmid et al. 2005). As the rare finds of ammonites show, the Mergelstetten Formation belongs stratigraphically to the uppermost Kimmeridgian (Beckeri Zone, Ulmense Subzone) and is therefore contemporaneous with the Nusplinger Plattenkalk (Nusplingen Lithographic Limestone). Fischer and Weber (1997) erroneously considered the occurrences of Nattheim to be contemporaneous with the Transversarium to Bimammatum (Middle to Upper Oxfordian) zone – a range from which d'Orbigny (1851–1860) has described numerous species.

## Repository

Most of the illustrated and type material is reposited at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (SNSB-BSPG) (collections by Lang, Schäfer, Neubauer, and Keupp). Material from the Lang collection that has been examined but not figured herein has been returned to this collector. However, not illustrated specimens that are designated as type specimens of new taxa is also reposited at SNSB-BSPG. The material from the collection Sauerborn remains entirely in his private collection. The collection of Quenstedt is housed at the Universität Tübingen (Fachbereich Geowissenschaften, Paläontologische Forschungs-, Schau- und Lehrsammlung).

## Systematic palaeontology

Shell shape, ornament, number and morphology of plaits, ontogenetic change of shell morphology, and other shell characters have been used for taxonomy in Nerineoidea. However, the various authors used these characters in an inconsistent way, and thus the supraspecific classification is commonly also inconsistent. Due to a lack of a consistent concept, the generic or family assignments of species may differ strongly from author to author. Taxonomy and systematics of Nerineoidea are obviously still unstable. The most recent comprehensive treatment on the family level is that by Kollmann (2014). The present taxonomical treatment and classification is largely based on the contributions by Gründel and Nützel (2012), Kollmann (2014), and Bouchet et al. (2017).

The identification and systematics of the present Nerineoidea turned out to be especially challenging and needs further study. The preservation of nerineoid specimens is commonly insufficient and poorer than in other taxa. This is true of both the calcareous re–crystallized specimens from Saal and the silicified ones from Nattheim. Commonly, the ornamentation of the whorls is not or insufficiently preserved in Nerineoidea. Many Nerineoidea are relatively large and slender (turreted), and specimens are present as fragments of a few whorls only. Since both ornamentation and inner plaits are commonly subject to ontogenetic change, it was often impossible to attribute these fragments to any taxon with higher resolution. Previous students of these gastropods faced the same problems and therefore some of the species are characterized in a contradictionary way in the literature (see e.g., 'Remarks' for *Cossmannea desvoidyi*).

### Subclass Heterobranchia Gray, 1840
### Superfamily Nerineoidea Zittel, 1873
### Family uncertain

#### Genus *Cossmannea* Pchelintsev, 1927

**Type species.** *Nerinea desvoidyi* d'Orbigny, 1851; OD, Middle Oxfordian; France.

**Remarks.** Again declared as new by Pchelintsev (1931).

#### *Cossmannea desvoidyi* (d'Orbigny, 1851)

Plate 1: figs 1–3

?*1836 – *Nerinea grandis* Voltz in litt. – Bronn: 549, pl. 6, fig. 1.
*1851 – *Nerinea desvoidyi* d'Orbigny – d'Orbigny: 107, pl. 261, figs 1–3.
*1858 – *Nerinea grandis concava* – Quenstedt: 766, pl. 94, fig. 3.
v1881–1884 – *Nerinea grandis concava* – Quenstedt: 524, pl. 205, fig. 60.
part1901 – *Nerinea desvoidyi* d'Orb. – Geiger: 283, pl. 11, fig. 5.
1979 – *Cossmannea desvoidyi desvoidyi* (d'Orbigny, 1850) – Wieczorek: 321, fig. 11, pl. 7, figs 1, 4; pl. 8, figs 1, 6.
1997 – *Cossmannea desvoidyi* (d'Orbigny, 1851) – Fischer and Weber: 42, pl. 11, figs 1–3.
1997 – *Cossmannea* (*Cossmannea*) *desvoidyi* (d'Orbigny, 1850) – Hägele: 129, fig. p. 129 upper left.
2014 – *Cossmannea desvoidyi* (d'Orbigny, 1850) – Kollmann: 354, fig. 2B.

**Material.** A specimen from the area near Nattheim (collection Sauerborn) and a specimen from the Quenstedt collection, possibly the specimen figured by Quenstedt (1858, pl. 94, fig. 3) from Nattheim.

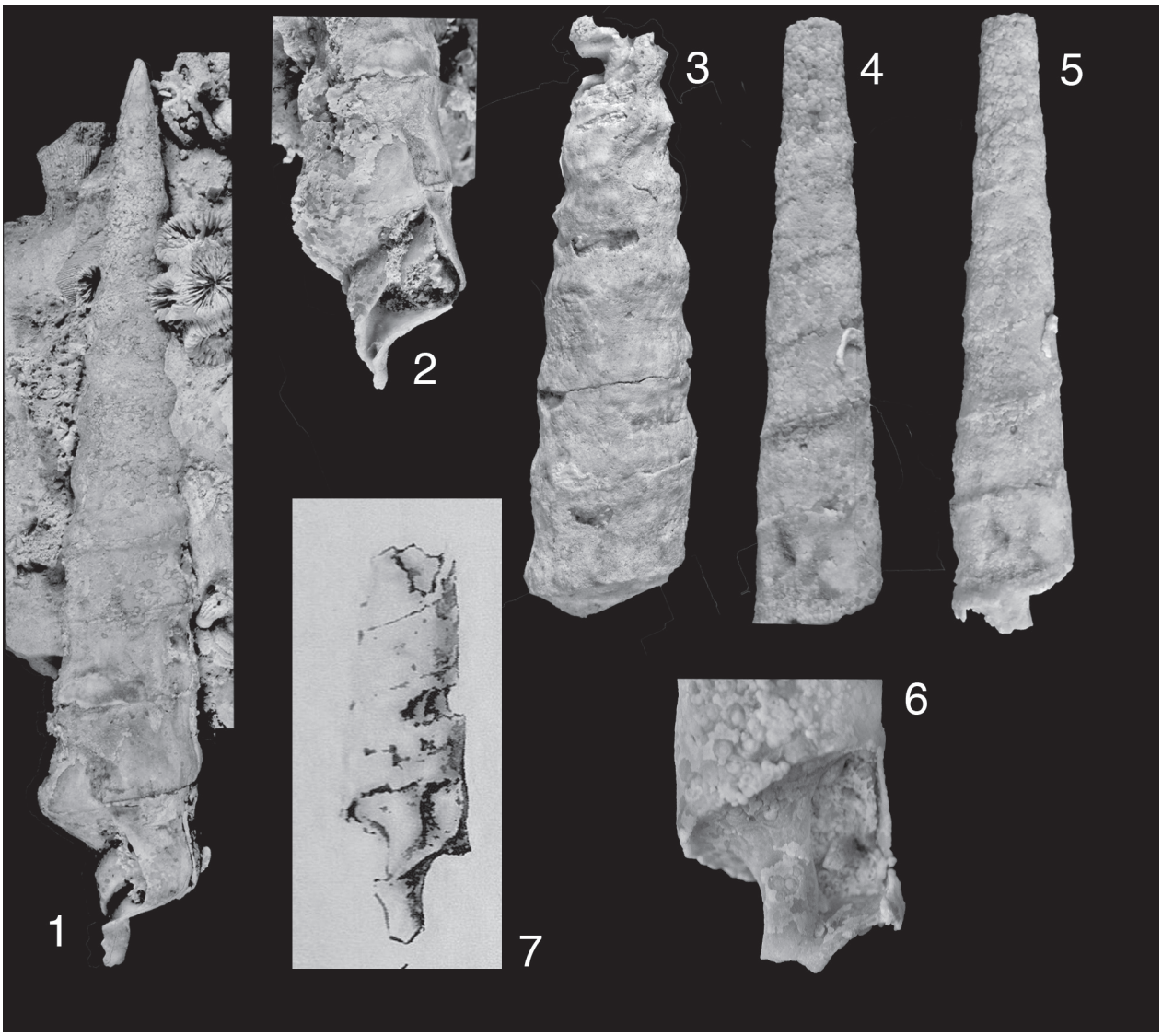


**Plate 1. (1–3)** *Cossmannea desvoidyi* (d'Orbigny, 1851). **(1–2)** collection Sauerborn, Nattheim area; **(1)** lateral view, height 23.8 cm; **(2)** last whorls with aperture, height 8 cm. **(3)** University Tübingen, collection Quenstedt), Nattheim, lateral view, height 130 mm (original of Quenstedt 1881–1884, pl. 205, 60). **(4–6)** *Aptyxiella planata* (Quenstedt, 1858), SNSB-BSPG 2021 XV 1, Nattheim–Rinderberg; **(4–5)** lateral views, height 70 mm; **(6)** aperture, height of detail 70 mm. **(7)** *Aptyxiella quenstedti* Geiger, 1901, Nattheim, lateral view (copy from Geiger 1901, pl. 11, fig. 1).

**Description.** The specimen from the Sauerborn collection is 23.8 cm high. The shell is slender with relatively high whorls. The whorl face is concave and lacks any visible ornament. The suture is distinct but shallow, situated at the lower side of an abapical, rounded bulge forming the transition to the flat, seemingly smooth base. The periphery is situated directly above abapical suture. The aperture is rhomboid with a large, oblique siphonal canal. Two columellar plaits are visible.

**Remarks.** According to Fischer and Weber (1997), *Cossmannea desvoidyi* has a long range from the middle Oxfordian to lower Portlandian. The type specimen is from the middle Oxfordian of France. Considering this long range, *Nerinea grandis* Voltz in Bronn, 1836 (Portlandian?) and *Nerinea grandis concava* Quenstedt, 1858 (upper Kimmeridgian) could represent *C. desvoidyi*. If true, then *Nerinea grandis* would be the oldest available name for this species.

The identity of *C. desvoidyi* is unclear, especially regarding the plaits, because there are conflicting reports in the literature: According to Geiger (1901), Cox (1947), and Fischer and Weber (1997), *C. desvoidyi* has a single columellar and a single palatal plait. In the present specimen from Nattheim, two columellar plaits are visible. The outer lip is not sufficiently well-preserved to show or exclude the presence of palatal plaits. Bronn (1836) and Kollmann (2014) mention the presence of only a single columellar plait. It is unclear whether these differences are results of variability, preservation, ontogenetic change, or whether two or more species are present.

There are also contradictory statements about the morphology of the aperture of *C. desvoidyi*. Kollmann (2014)

reported that a siphonal canal is absent in specimens from the type locality of St. Mihiel. However, Fischer and Weber (1997: pl. 11, fig. 1) figured a specimen from the same locality that has a siphonal canal. The present specimen from Nattheim (Sauerborn collection) has a very distinct oblique canal. Furthermore, this species is generally said to lack ornamentation, but the illustration by Geiger (1901: pl.11, fig. 5) shows numerous spiral cords covering the entire whorls, which is, however, not mentioned in Geiger's (1901) description of this species.

The present contribution cannot solve these problems. We assume that the upper Kimmeridgian specimens described herein represent the same species as the middle Oxfordian holotype of *C. desvoidyi* from France. In order to avoid nomenclatorial confusion, we include only the reference to the type material and to Kimmeridgian material in the synonymy and chresonymy list.

## Genus *Aptyxiella* P. Fischer, 1885

**Type species.** *Nerinea sexcostata* d'Orbigny, 1852; Oxfordian–Kimmeridgian; France.

### *Aptyxiella planata* (Quenstedt, 1858)

Plate 1: figs 4–6

*1858 – *Nerinea planata* – Quenstedt: p. 770, pl. 94, figs 31, 32.
v1881–1884 – *Nerinea planata* Qu. – Quenstedt: p. 554, pl. 207, figs 5–7, 8?
1901 – *Aptyxiella planata* Quenstedt – Geiger: p. 276.
1997 – *Aptyxiella planata* (Quenstedt) – Hägele: p. 133, fig. p. 133 upper right.

**Material.** One specimen (SNSB-BSPG 2021 XV 1) and four questionable fragments from Nattheim (Tübingen, Quenstedt collection).

**Description.** The shell is high–spired and very slender. It is 70 mm high (apex missing). The whorls are high with a straight to slightly concave whorl face and slowly increasing in width. The suture is oblique and situated on a slightly elevated bulge formed by two adjoined whorls. No ornament is visible (due to preservation?). The base is flat and demarcated from whorl face by a sharp angulation, and lacks visible ornament. The aperture is elongated, higher than wide, rhomboid, and has a distinct, oblique siphonal canal (partially broken). Plaits are absent.

**Remarks.** The four fragments from the Tübingen collection are poorly preserved and might represent different species. According to Geiger (1901, p. 277), the whorls are ornamented with numerous spiral cords of various strength which are, however, destroyed by the coarse silicification of the specimens from Nattheim (if they were present at all).

*Aptyxis planata* Quenstedt sensu Schlosser (1882) differs from the studied specimens by having spiral cords, a broader shape, lower whorls and more oblique sutures. According to Schlosser (1882, p. 77) "the only specimen housed in the Munich Museum" shows ornamentation. However, our study of the specimen could not confirm this. The very similar (identical?) *Cossmannea*? *quenstedti* Geiger, 1901 has a columellar plait.

### *Aptyxiella quenstedti* Geiger, 1901

Plate 1: fig. 7

part v1858 – *Nerinea grandis nuda* – Quenstedt: 766, pl. 94, fig. 4 (non fig. 5).
part v1881–1884 – *Nerinea grandis nuda* – Quenstedt: p. 553, pl. 207, fig. 2 (non fig. 1).
*1901 – *Aptyxiella quenstedti* sp. nov. – Geiger: p. 278, pl. 11, fig. 1.
1997 – *Aptyxiella quenstedti* Geiger, 1901 – Hägele: 133, fig. p. 133 lower right.

**Material.** One specimen from Nattheim (Tübingen: Quenstedt collection).

**Description.** The specimen illustrated by Quenstedt (1881–1884: pl. 207, fig. 2) is a 29 mm high fragment consisting of three whorls. Geiger (1901, pl. 11, fig. 1; copied herein in Plate 1: fig. 7) used another, better preserved specimen. In Quenstedt's (1881–1884) specimen, approximately half of shell wall is broken off. The flanks are straight. The suture is slightly impressed. No ornament is visible. The base is anomphalous. The aperture has a weak columellar plait.

**Relationships.** *Nerinea grandis nuda* Quenstedt, 1858 is much larger and has seemingly no plaits. The very similar and maybe identical *Aptyxiella planata* (Quenstedt) lacks a columellar plait. Hägele (1997) also claimed that *Aptyxiella quenstedti* has a more convex whorl face, but the specimen illustrated by Geiger (1901) does not show this.

## Family Pseudonerineidae Pchelintzev, 1965

## Genus *Pseudonerinea* Loriol in Loriol & Koby, 1890

**Type species.** *Pseudonerinea blauensis* Loriol in Loriol & Koby, 1890; Oxfordian; France.

### *Pseudonerinea*? *pseudomelaniformis* sp. nov.

https://zoobank.org/0A09158-5B82-45A5-B516-C04A5FF7943D

Plate 2: figs 1–7

**Derivatio nominis.** For being similar to *Pseudomelania* Pictet & Campiche, 1862 in regard to shell shape.

**Holotype.** SNSB-BSPG 2021 XV 23 (collection Lang).

**Locus typicus.** Saal quarry near Kelheim.

**Stratum typicum.** Upper Kimmeridgian.

**Paratypes.** Thirty-three specimens from Saal, collection Lang: SNSB-BSPG 2021 XV 24–26, 183–212.

**Additional material.** Three specimens from Saal, without type status (collection Lang).

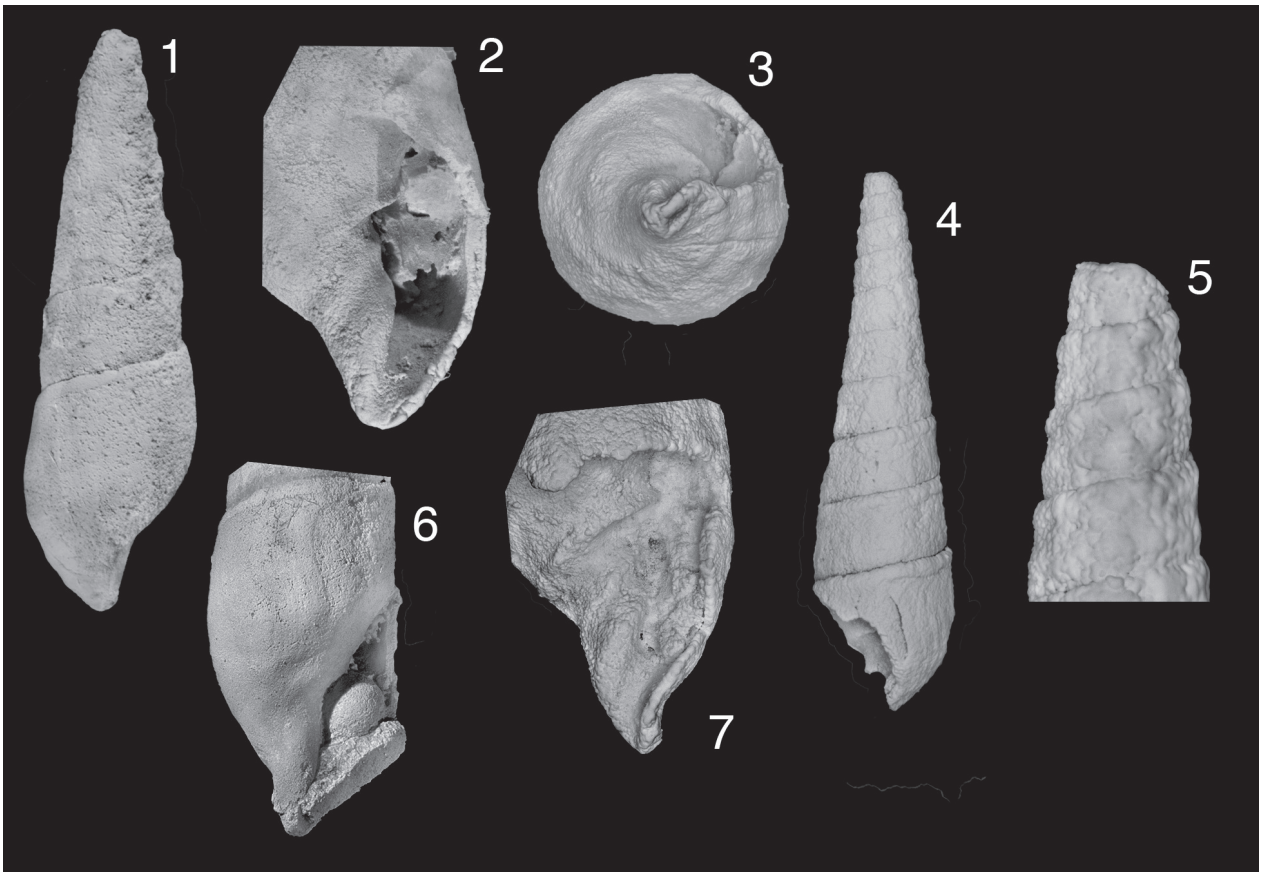


**Plate 2. (1–7)** *Pseudonerinea*? *pseudomelaniformis* sp. nov. **(1–3)** Holotype, SNSB-BSPG 2021 XV 23, Saal (collection Lang); **(1)** lateral view, height 22 mm; **(2)** aperture, height 8.5 mm; **(3)** base, width 6.5 mm. **(4–5)** Paratype, SNSB-BSPG 2021 XV 24, Saal (collection Lang); **(4)** lateral view, height 13.7 mm; **(5)** apex, height 2.8 mm. **(6)** Paratype, SNSB-BSPG 2021 XV 25, Saal (collection Lang), last whorl with aperture, height 10 mm. **(7)** Paratype, SNSB-BSPG 2021 XV 26, Saal (collection Lang); aperture, height 7 mm.

**Diagnosis.** Shell slender; spire high in relation to last whorl; whorl face straight with narrow ramp; weak spiral furrow present below ramp; aperture with distinct siphonal canal, two columellar, and one parietal plait.

**Description.** The holotype is 22 mm high. The shell is slender, high–spired, and consists of many whorls. The whorl face is straight. The sutures are accentuated by a narrow ramp. The early whorls are poorly preserved, seemingly with two spiral cords near sutures and having a concave whorl face between the cords. Later whorls have a subsutural bulging spiral cord (weakly nodular?) that is demarcated by an abapical spiral furrow. This furrow is rarely distinct or frequently not visible at all probably due to preservation. No other ornament is present. The transition from whorl face to the strongly convex base is evenly rounded. The base has several, weakly defined, bulging spiral cords. It is anomphalous. The growth lines are indistinct; they are strongly curving backward adapically. The aperture is narrow with a weakly convex outer lip; parietal and columellar lip meet at an angle. The aperture has a distinct siphonal canal, a distinct parietal and two columellar plaits. The columellar plaits are commonly weak or not visible even in seemingly well-preserved specimens (variability or due to preservation).

**Remarks.** It is possible that the studied material represent two species. The type species of *Pseudonerinea* lacks plaits. Therefore, the generic assignment of *P.*? *pseudomelaniformis* is tentative.

**Relationships.** *Phaneroptyxis fusiformis* (d'Orbigny) sensu Gemmellaro (1870), Blake and Hudleston (1877), Cossmann (1898), Loriol in Loriol and Koby (1895), and Fischer and Weber (1997) is less slender, has a higher last whorl in relation to spire height, a narrow umbilicus, and only a single columellar plait is visible. *Cerithium pellati* Loriol in Loriol & Pellat, 1874 is very similar but lacks plaits and the siphonal canal is less pronounced. *Itieria melanioides* Zittel, 1873 has only a single columellar plait as well as one parietal and one palatal plait; it lacks a siphonal canal, and its whorl face is weakly convex with impressed sutures. *Phaneroptyxis sulejovensis* Wieczorek, 1979 is larger, has a more pronounced ramp and deeper sutures, its base is demarcated by an edge, and it has a single columellar plait. *Nerinea eichwaldiana* d'Orbigny, 1845 has only a single columellar plait and a palatal plait; it lacks a ramp and the sutures are barely impressed. *Phaneroptyxis grayensis* Maire, 1927 is larger, its whorls are lower and increase more rapidly in width, and it has only a single columellar plait.

## Family Ceritellidae Wenz, 1938

Kollmann (2014) used a broad concept of the family Ceritellidae, and besides *Ceritella* included also closely related genera, even those that deviate considerably, such as *Cossmannea* Pchelintsev, 1931, *Aptyxiella* P. Fischer, 1885, *Aphanoptyxis* Cossmann, 1896, and others. Guzhov (2017) included only the genera *Ceritella* Morris & Lycett, 1851 and *Ceritellopsis* Fischer, 1961. Until recently, Ceritellidae have been considered to represent basal Nerineoidea (e.g., Kollmann 2014; Bouchet et al. 2017). However, according to Guzhov (2017), the genera *Ceritella* and *Ceritellopsis* belong to Acteonoidea d'Orbigny, 1843. We cannot contribute to this debate because the present material attributed to this family is too fragmentary. The species assigned to Ceritellidae and Nerineidae commonly appear as pairs of species lacking plaits (Ceritellidae) and having plaits (Nerineidae): *Ceritellopsis gramanni*/*Nerinea donosa*, *Ceritella* sp. 1/*Endoplocus acutus*, *Ceritella convexus*/*Endoplocus inflatus*. This could indicate that both families are closely related to each other or share similar environmental requirements. However, the species in question differ strongly from each other in size, i.e., Ceritellidae being small and Nerineidae large.

## Genus *Ceritellopsis* J.–C. Fischer, 1961

**Type species.** *Cerithium petri* d'Archiac, 1843; Bathonian; France.

### *Ceritellopsis gramanni* Huckriede, 1967

Plate 3: figs 1–4

?1895 – *Ceritella plicata* Zittel and Goubert – Cossmann: 102, pl. 4, figs 66, 67.

*1967 – *Ceritella* (*Ceritellopsis*) *gramanni* sp. nov. – Huckriede: 198, pl. 19, figs 4–9.

**Material.** Twenty-five specimens from Saal (collection Lang), three of which are illustrated herein: SNSB-BSPG 2021 XV 2–4.

**Description.** A large specimen is 3.2 mm high. The shell is fusiform, relatively slender with a high spire. The whorls are rather high and have a distinct, oblique ramp, demarcated from whorl face by a spiral cord. The whorl face is straight. The suture is distinct and is accentuated by the ramp. The whorls are ornamented with straight, slightly opisthocline, rounded axial ribs separated by wide interspaces. The ribs become weaker and may fade entirely on the last preserved whorl. The transition from whorl face to base is evenly rounded. The ribs do not continue onto the smooth base. The aperture is oval, higher than wide, with a weak, short canal and an acute posterior part. The inner lip is reflexed in the columellar portion.

**Remarks.** Most of the specimens of *Ceritellopsis gramanni* figured by Huckriede (1967) have a broader shell. However, in general the present specimens fall into the variation of this species as reported by Huckriede (1967: figs 7 and 8 on pl. 19).

**Relationships.** The differences to *Ceritellopsis plicatula* are discussed under the treatment of that species. *Actaeonina plicata* Zittel & Goubert, 1861 has a broader, stouter shell and its spire is not as slender and with a lower whorl face of the spire whorls. *Ceritella rissoides* Buvignier sensu Cossmann (1895) has a broader shell, its last whorl is higher in relation to the spire height and its ramp is not as sharply demarcated. *Cerithium lorteti* Loriol sensu Loriol and Pellat (1874) has more axial ribs, the whorl face of the spire whorls is higher and the aperture is narrower. *Ceritellopsis huckriedei* Gründel & Kaim, 2006 is slenderer, its spire is distinctly higher than the last whorl, and it has more axial ribs bent backwards adapically.

### *Ceritellopsis plicatula* Huckriede, 1967

Plate 3: figs 5, 6

*1967 – *Ceritella* (*Ceritellopsis*) *plicatula* sp. nov. – Huckriede: 197, pl. 18, figs 31–50.

?1971 – *Ceritella elata* Loriol, 1889 – Dmoch: 17, pl. 2, fig. 1.

**Material.** Five specimens from Saal (collection Lang), two of which are illustrated herein: SNSB-BSPG 2021 XV 5, 6.

**Description.** The largest specimen is 5.3 mm high. The shell is slender with a high and acute spire. The whorls are high and have a distinctly oblique ramp accentuating the sutures. The ramp is demarcated from whorl face by an angulation. The whorls are ornamented with broad axial ribs, that are fading on the last preserved whorls. The transition from whorl face to base is evenly rounded. The base is smooth. The damaged aperture is oval, acute adapically, and has a siphonal canal.

**Relationships.** *Ceritellopsis gramanni* Huckriede, 1967 is much stouter, has lower whorls and a nearly horizontal ramp. *Ceritellopsis huckriedei* Gründel & Kaim, 2006 has lower whorls, a horizontal ramp and its axial ribs are bent backward adapically. *Orthostoma longiscata* Buvignier sensu Buvignier (1852) is distinctly slenderer. The species with the same name, *Orthostoma longiscata*, sensu Buvignier (1843) resembles *C. plicatula* more closely in shape but has a horizontal ramp and more axial ribs. *Ceritella elata* de Loriol var. *striata* Maire, 1927 has a spiral ornament and lower whorls.

## Genus *Ceritella* Morris & Lycett, 1851

**Type species.** *Ceritella acuta* Morris & Lycett, 1851; Bathonian; England.

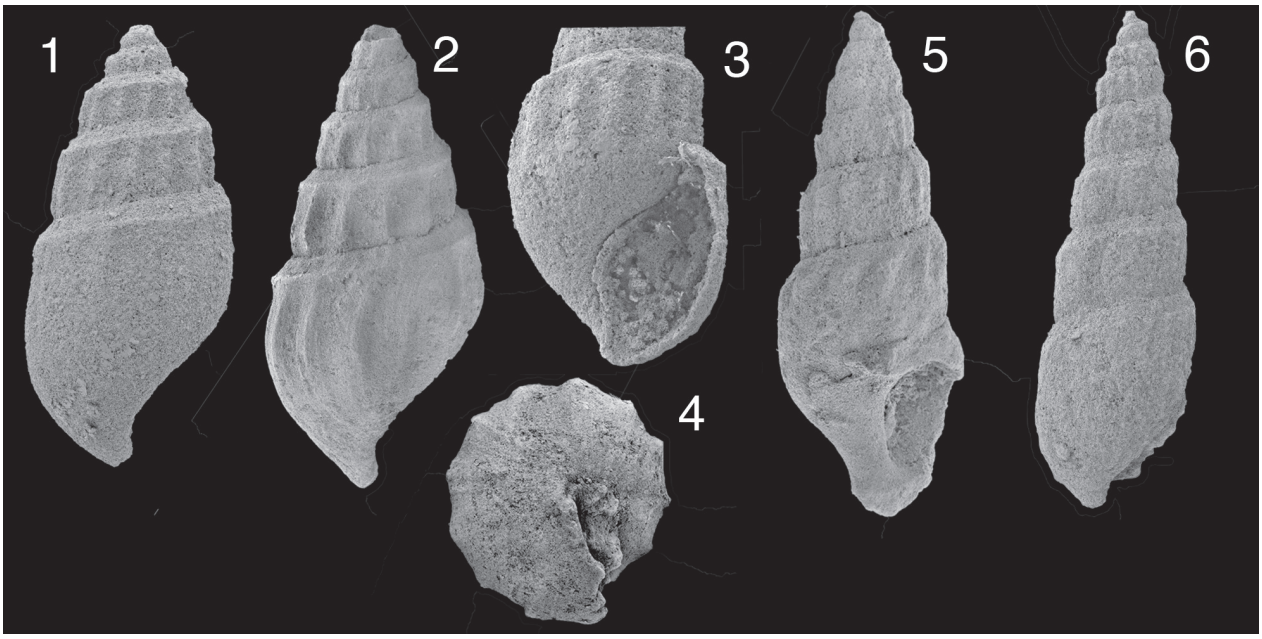


**Plate 3. (1–4)** *Ceritellopsis gramanni* Huckriede, 1967. **(1)** SNSB-BSPG 2021 XV 2, Saal (collection Lang), lateral view, height 2.5 mm. **(2, 4)** SNSB-BSPG 2021 XV 3, Saal (collection Lang); **(2)** lateral view, height 2.7 mm; **(4)** base, width 1.3 mm. **(3)** SNSB-BSPG 2021 XV 4; Saal (collection Lang), aperture, height of detail 1.3 mm. **(5–6)** *Ceritellopsis plicatula* Huckriede, 1967. **(5)** SNSB-BSPG 2021 XV 5, Saal (collection Lang), lateral view, height 3.3 mm. **(6)** SNSB-BSPG 2021 XV 6, Saal (collection Lang), lateral view, height 4.8 mm.

### *Ceritella convexa* sp. nov.

https://zoobank.org/154A9E44-1AEB-42FC-B0B6-0526AA853724

Plate 4: figs 1–5

**Derivatio nominis.** Lat. *convexus* – convex; for the convex, somewhat inflated whorls.

**Holotype.** SNSB-BSPG 2021 XV 9, collection Lang.

**Locus typicus.** Quarry Saal near Kelheim.

**Stratum typicum.** Upper Kimmeridgian.

**Paratypes.** Twenty-two mostly juvenile specimens from Saal (collection Lang) SNSB-BSPG 2021 XV 8, 147–167.

**Additional material.** Three specimens from Saal, without type status (collection Lang).

**Diagnosis.** Shell broadly fusiform; whorls with distinctly oblique ramp; larger specimens have a somewhat inflated last whorl; early whorls with axial ribs changing to strengthened growth lines in later whorls; ribs curve backward below ramp edge; spiral cords absent.

**Description.** A large specimen is 4.3 mm high. The shell is broadly oval, fusiform with an acute spire. The shell width is variable. Larger specimens have a somewhat inflated last whorl. The sutures are distinct. The whorls have a relatively broad, strongly oblique ramp, demarcated from whorl face by an edge. The spire whorls are broad and low. The early whorls have opisthocline axial ribs which weaken during ontogeny and finally change to strengthened growth lines. The ribs or strengthened growth lines run prosocyrt opisthocline from edge near ramp to base, and curve strongly backward at the edge that demarcates the ramp. The course of the growth lines is not visible on the ramp. Spiral ornament is absent. The base is strongly convex and smooth except of growth lines. The aperture is narrow and acute adapically. It has a short, oblique siphonal canal.

**Relationships.** *Ceritella pupoides* (d'Orbigny) sensu Fischer and Weber (1997) is slenderer, has a higher spire, and lacks axial ribs. Ribs are also absent in *Ceritella lauretana* Guirand and Ogérien, *C. dolium* Loriol (both sensu Cossmann 1895), *Orthostoma granum* Loriol in Loriol and Pellat (1866), and *Acteonina lauretana* Guirand and Ogérien sensu Loriol in Loriol and Bourgeat (1886–1888). *Acteonina terebra* Étallon sensu Loriol in Loriol and Bourgeat (1886–1888) is slenderer, lacks an oblique ramp, has a higher spire and its axial ribs are not reduced during ontogeny. *Ceritella* (*Ceritellopsis*) *parvula* (F. A. Roemer) sensu Huckriede (1967) has a horizontal ramp and therefore a gradate spire; it has fewer axial ribs that are stronger and not bent backward adapically.

### *Ceritella* sp. 1

Plate 4: figs 6–8

**Material.** Nine specimens from Saal (collection Lang), one of which is illustrated herein: SNSB-BSPG 2021 XV 7.

**Description.** The illustrated specimen is 3.2 mm high. The shell is moderately slender with high, acute spire. The whorls are distinctly broader than high. The sutures are impressed. The whorls have a strongly inclined ramp, separated from whorl face by a spiral cord. The growth lines are strengthened and weakly prosocyrt from ramp to base. The base and aperture are as in *Ceritella convexa* sp. nov.

**Relationships.** The shell of *Ceritella convexa* sp. nov. is broader than that of *Ceritella* sp. 1. *Ceritella convexa* sp. nov. has axial ribs whereas *Ceritella* sp. 1 lacks ribs. *Ceritella lorteti* Loriol sensu Cossmann (1895) has a higher last whorl in relation to the spire and its ramp is less pronounced. *Ceritella pupoides* (d'Orbigny) sensu Fischer and Weber

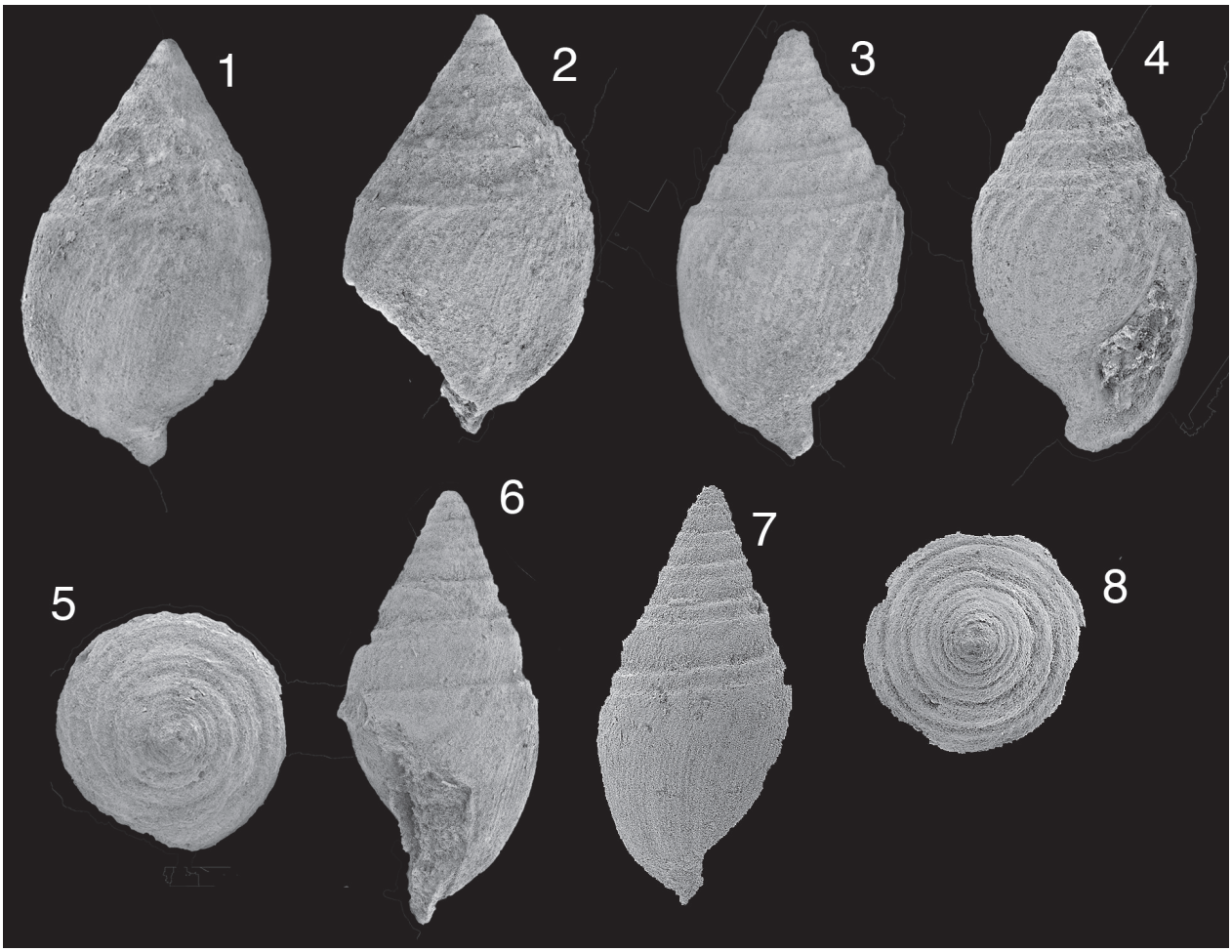


**Plate 4. (1–5)** *Ceritella convexa* sp. nov. **(1–2)** Paratype, SNSB-BSPG 2021 XV 8, Saal (collection Lang), lateral views, height 4.3 mm. **(3–5)** Holotype, SNSB-BSPG 2021 XV 9, Saal (collection Lang); **(3–4)** lateral views, height 3.5 mm; **(5)** apical view, width 1.8 mm. **(6–8)** *Ceritella* sp. 1, SNSB-BSPG 2021 XV 7, Saal (collection Lang); **(6–7)** lateral views, height 3.2 mm; **(8)** apical view, width 1.3 mm.

(1997) and *Actaeonina lauretana* Guirand and Ogérien. sensu Loriol in Loriol and Bourgeat (1886–1888) have a distinctly stouter shell and a less pronounced ramp. *Actaeonina miliola* d'Orbigny sensu Loriol in Loriol and Bourgeat (1886–1888) is broader and lacks a ramp entirely.

## Family Nerineidae Zittel, 1873

## Genus *Nerinea* Deshayes, 1827

**Type species.** *Nerinea mosae* Deshayes, 1827; Oxfordian; France.

### *Nerinea donosa* sp. nov.

https://zoobank.org/0351A026-965F-4B49-8FEB-714BAEF2B779

Plate 5: figs 1–5

2017 – Nerineoidea Nr. 7 – Gründel: 33, pl. 14D.

**Derivatio nominis.** Anagram of Latin *nodosa*, referring to the subsutural rows of nodes.

**Holotype.** SNSB-BSPG 2021 XV 11, collection Lang.

**Locus typicus.** Quarry Saal near Kelheim.

**Stratum typicum.** Upper Kimmeridgian.

**Paratypes.** Six incomplete or juvenile specimens from Saal: five specimens collection Lang (SNSB-BSPG 2021 XV 10, 13, 168–170), one specimen collection Keupp (SNSB-BSPG 2021 XV 12).

**Additional material.** Three specimens without type status from Saal (collection Lang).

**Diagnosis.** Shell moderately slender; subsutural row of strong nodes forming distinct ramp; spire gradate; transition from whorl face to base at distinct spiral, crest–like cord; base convex, with narrow umbilicus; aperture with two columellar plaits, one strong parietal and partly a palatal plait; with siphonal canal.

**Description.** The largest specimen is 20 mm high. The shell is moderately slender with relatively rapidly increasing whorls. The whorls are more than twice as wide as high. The whorls are ornamented with a subsutural row of strong nodes (8–10 nodes per whorl) occupying 1/2 to 2/3 of whorl height. The nodes demarcate the distinct ramp producing a gradate spire. The suture is accentuated by the ramp. The transition from whorl face to base is marked by a distinct, crest-like spiral cord which is not nodular, and is covered by the following whorls in spire whorls. The incompletely

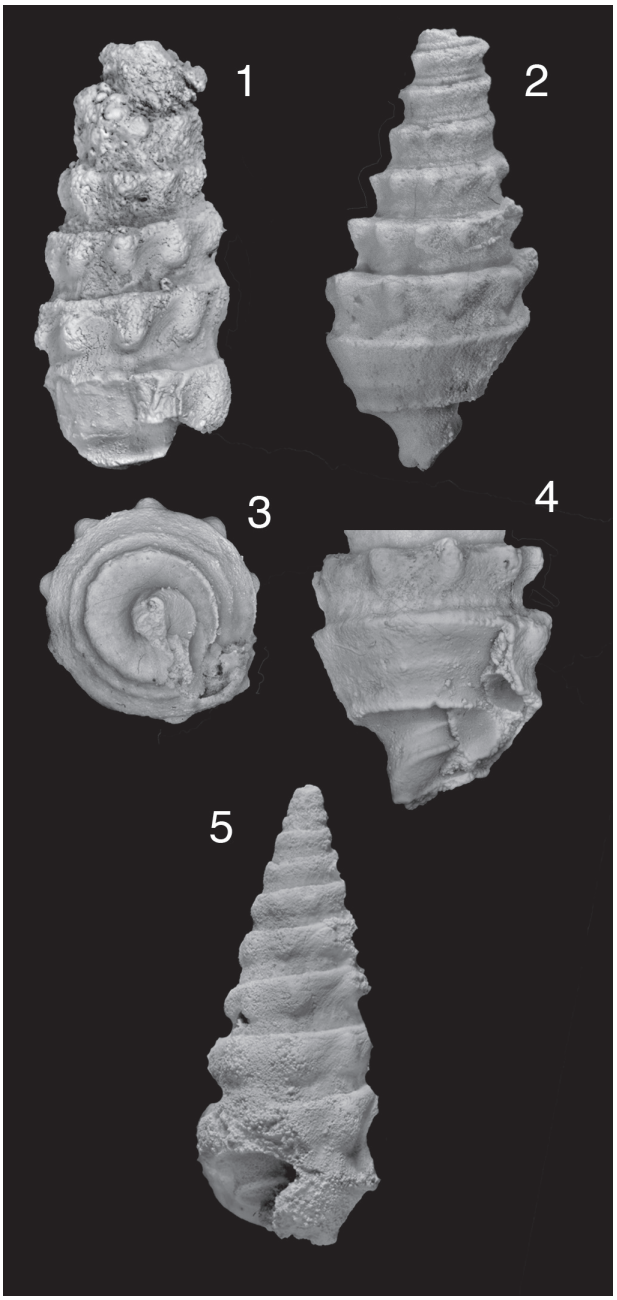


**Plate 5. (1–5)** *Nerinea donosa* sp. nov. **(1)** Paratype, SNSB-BSPG 2021 XV 10, Saal (collection Lang), lateral view, height 18 mm. **(2–4)** Holotype, SNSB-BSPG 2021 XV 11, Saal (collection Lang); **(2)** lateral view, height 8.8 mm; **(3)** base, width 4.5 mm; **(4)** last whorl, height 4.5 mm. **(5)** Paratype, SNSB-BSPG 2021 XV 11, Saal (collection Keupp), lateral view, height 20 mm.

preserved aperture is narrow and has a siphonal canal. It has two columellar plaits, 1–2 parietal plaits and in some specimens a palatal plait. If two columellar plaits are present, the adapical one is weaker as the abapical. The outer lip is not preserved. The base is distinctly convex.

**Relationships.** *Nerinea mosae* Deshayes, 1827 has weaker subsutural nodes and lacks a strong spiral cord at the transition to the base. *Nerinea* (respectively *Ptygmatis*) *nogreti* Guirand & Ogérien, 1865 has, according to these authors and according to Loriol in Loriol and Bourgeat (1886–1888), a similar shape but is larger and lacks a nodular ornament. *Cerithium kelheimense* Schlosser, 1882 lacks plaits and a spiral cord at the transition to the base. *Itieria* (respectively *Nerinea*) *moreana* d'Orbigny sensu Buvignier (1852) and Schlosser (1882) has a higher last whorl in relation to the spire height and it lacks a spiral cord at the transition to the base. *Nerinea margaritifera* d'Archiac, 1843 and *Itieria multicoronata* Zittel, 1873) lack a spiral cord at the transition to the base. *Nerinea catalloi* Gemmellaro, 1870 is broader and stouter and has a higher last whorl in relation to the spire.

## Genus *Acrostylus* Cossmann, 1896

**Type species.** *Nerinea trinodosa* Voltz, 1836; Portlandien.

### *Acrostylus*? sp. 1

Plate 6: figs 1, 2

v2017 – Nerineoidea Nr. 1 – Gründel: 33, pl. 13, fig. 13 C.

**Material.** Two specimens from Saal, collection Lang, one of which is illustrated (SNSB-BSPG 2021 XV 73).

**Description.** The present material is poorly preserved and only fragmentary. The illustrated specimen is 23 mm high. The whorl face is weakly concave. The whorls are ornamented with a subsutural row of knobs and two strong, knobby spiral cords below it, followed by one or two weak spiral cords and a strong, knobby suprasutural spiral cord. The knobby sub- and suprasutural cords form a bulge on which the suture is situated. The base is flat and its

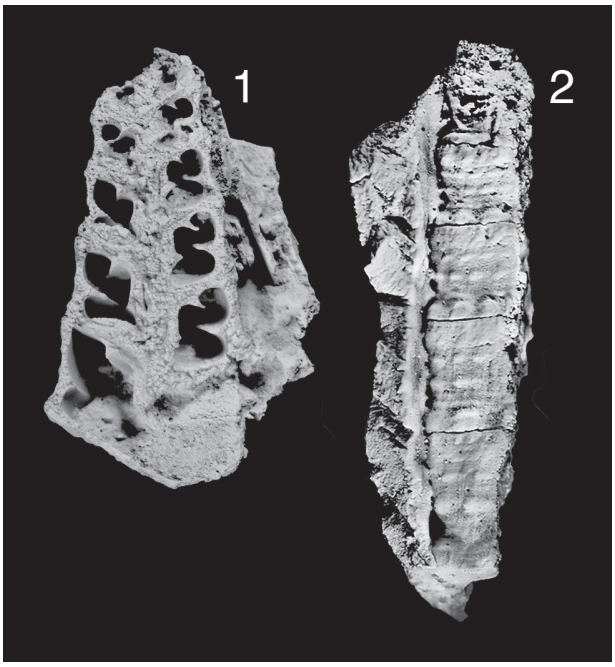


**Plate 6. (1–2)** *Acrostylus*? sp. 1., SNSB-BSPG 2021 XV 73, Saal (collection Lang), (original to Gründel 2017, fig. 13 C); **(1)** section of shell, height 23 mm; **(2)** lateral view, height 23 mm.

transition to the whorl face is angulated. A distinct umbilicus is present. The aperture is rhomboid. It is unclear whether a siphonal canal is present. The aperture has a parietal, a columellar, and a palatal plait.

**Relationships.** *Nerinella subscalaris* Münster sensu Schlosser (1882) has bulges that lack knobs and lacks an umbilicus. *Nerinea danubiensis* Zittel sensu Schlosser (1882) has lower whorls, the bulges have stronger knobs, and it lacks distinct spiral cords between the bulges. *Nerinella subtricincta* (d'Orbigny) sensu Fischer and Weber (1997) has an almost straight whorl face, its bulges are weaker and only weakly knobby (Fischer and Weber 1997, p. 54: „faiblement granuleux"). *Nerinella* (cf.) *laufonensis* Thurmann sensu Loriol in Loriol and Koby (1895) and Hägele (1997) is slenderer and has weaker bulges. *Nerinea chantrei* Loriol and *Nerinea ornata* d'Orbigny, both sensu Loriol in Loriol and Bourgeat (1886–1888), have a slenderer shell with higher and more concave whorls. *Nerinea hoheneggeri* Peters sensu Zittel (1873) has a slenderer shell, more spiral cords on the whorl face between the bulges, and lacks an umbilicus. *Nerinea roemeri* Philippi sensu Goldfuss (1844) is slenderer, has higher whorls; its whorls are not concave and the bulges are rather weak.

## Genus *Endoplocus* Cox, 1954

**Type species.** *Actaeon staszycii* Zeuschner, 1849; Tithonian; Poland.

**Remarks.** Cox (1954) reported that this genus is characterized by having 4–5 plaits (2 columellar, 1 parietal, and 1–2 palatal plaits). The present species assigned to *Endoplocus* shows only three plaits: two columellar and one parietal plait. The apparent lack of palatal plaits could be due to preservation.

### *Endoplocus acutus* sp. nov.

https://zoobank.org/3FF77922-9E93-4BA4-9B75-0176AAE61CA4

Plate 7: figs 1–7

part?1898 – *Phaneroptyxis clymene* d'Orbigny – Cossmann: 16, questionable pl. 8, fig. 35, non pl. 1, figs 23, 24.

**Derivatio nominis.** Latin *acutus* – acute; because of the acute spire.

**Holotype.** SNSB-BSPG 2021 XV 14 (collection Lang).

**Locus typicus.** Saal quarry near Kelheim.

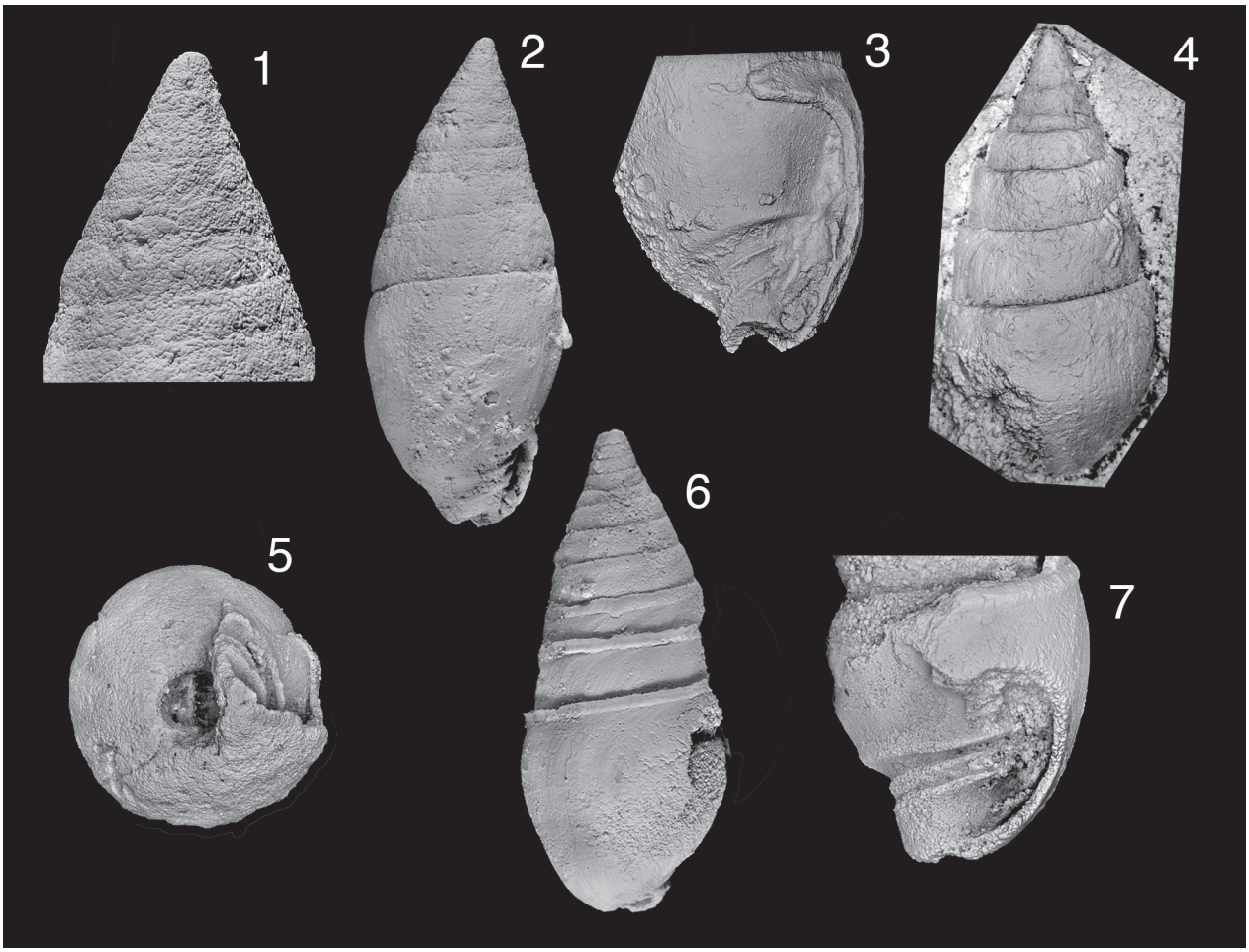


**Plate 7.** *Endoplocus acutus* sp. nov. **(1–3)** Holotype, SNSB-BSPG 2021 XV 14, Saal (collection Lang); **(1)** apical whorls in lateral view, height 11 mm; **(2)** lateral view, height 29 mm; **(3)** aperture, height 14 mm. **(4)** Paratype, SNSB-BSPG 2021 XV 15, Saal (collection Keupp), lateral view, height 18.5 mm. **(5)** Paratype, SNSB-BSPG 2021 XV 16, Saal (collection Lang), base, width 11 mm. **(6–7)** *Endoplocus acutus* sp. nov. var., paratype, SNSB-BSPG 2021 XV 17, Saal (collection Lang); **(6)** lateral view, height 23 mm; **(7)** last whorl, height 10 mm.

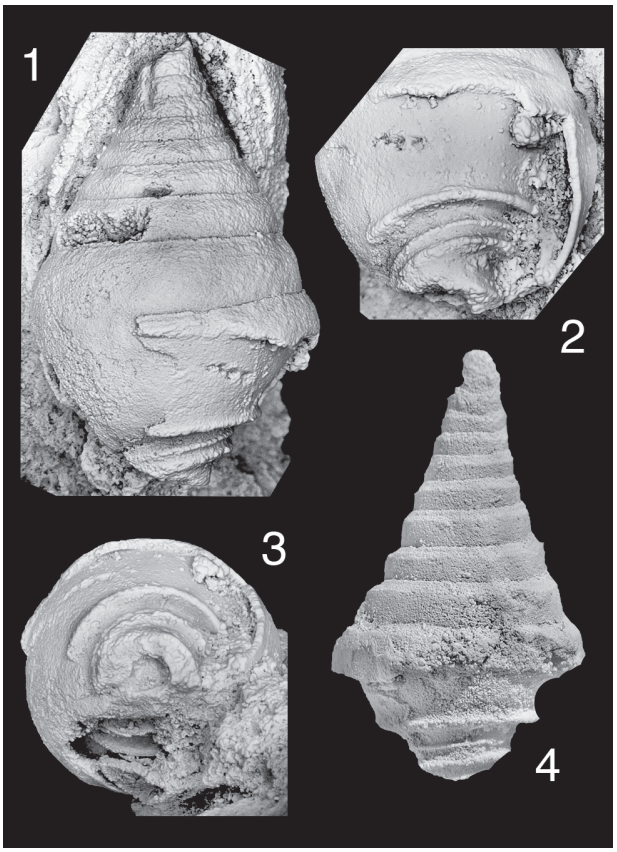


**Plate 8.** *Endoplocus inflatus* sp. nov. **(1–3)** Holotype, SNSB-BSPG 2021 XV 20, Saal (collection Lang); **(1)** lateral view, height 16 mm; **(2)** aperture, height 6.5 mm; **(3)** base, width 9 mm. **(4)** Paratype, SNSB-BSPG 2021 XV 108, Saal (collection Lang), juvenile specimen showing ramp on early whorls, height 9 mm.

**Stratum typicum.** Upper Kimmeridgian.

**Paratypes.** Thirteen specimens from Saal, collection Lang and Keupp: SNSB-BSPG 2021 XV 15–19, 171–178.

**Additional material.** Three specimens from Saal, without type status (two specimens collection Neubauer, one specimen collection Lang).

**Diagnosis.** The shell has a high, multi-whorled, acute spire; last whorl of large specimens distinctly lower than spire; last whorl somewhat constricted (slightly pupoid outline); no ornament visible.

**Description.** The holotype is 29 mm high. The shell has a high, multi-whorled, acute spire. The whorls are low with a slightly convex to straight whorl face. The sutures are somewhat impressed. In some specimens, a narrow ramp accentuates the sutures. The whorls lack visible ornament. The last whorl of large specimens is slightly tapering in an abapical direction resulting in a slightly pupoid shell shape. The last whorl is distinctly lower than the spire. The transition from whorl face to the strongly convex base is fluent and evenly rounded. The base is smooth and has a distinct umbilicus that is surmounted by an indistinct cord. The aperture is narrow. The inner lip has a strong parietal and two columellar plaits. The adapical columellar plait is weaker than the abapical one.

**Remarks.** The specimen illustrated by Cossmann (1898, pl. 8, fig. 35; specimens in pl.1, figs 23, 24 differ more strongly) as *Phaneroptyxis clymene* d'Orbigny from the Rauracien resembles *Endoplocus acutus* sp. nov. However, the specimen illustrated by Cossmann (1898) differs from *Endoplocus acutus* sp. nov. by having a slenderer shell, a higher last whorl in relation to the spire height, and by having only a single columellar plait. Fischer and Weber (1997) illustrated the holotypes of *Phaneroptyxis moreana* (d'Orbigny, 1851) (Fischer and Weber 1997, pl. 13, fig. 4) and of *P. clymene* (d'Orbigny, 1851) (Fischer and Weber 1997, pl. 13, fig. 5). These taxa were interpreted to represent a single variable species by Fischer and Weber (1997), both differ significantly from *Endoplocus acutus* sp. nov. and are not conspecific with the specimen illustrated by Cossmann (1898, pl. 8, fig. 35) as *Phaneroptyxis clymene*.

*Endoplocus acutus* sp. nov. var. (Plate 7: figs 6, 7): Two specimens from Saal agree with *E. acutus* in shell shape, size (specimen illustrated in Plate 7: figs 6, 7 is 23 mm high), and in the morphology of the plaits. However, these specimens have a subsutural spiral cord which accentuates the sutures. These specimens are considered to represent a variant of *Endoplocus acutus* sp. nov.

**Relationships.** *Endoplocus staczycii* (Zeuschner, 1849) has a stouter shell, more strongly convex whorls, deeper sutures, and the last whorl is higher in relation to spire height. *Endoplocus staczycii* sensu Hägele (1997) shows the same differences. *Endoplocus staczycii* is very variable according to Peters (1855). The specimen illustrated by Peters (1855, pl. 2, fig. 6) most closely resembles *Endoplocus acutus* sp. nov.. However, this specimen has a stouter shell, a less slender spire, and the last whorl is higher in relation to spire height. *Nerinea clymene* d'Orbigny sensu Gemmellaro (1870, pl. 4, fig. 4, 5; non fig. 3) is much larger and has deep sutures that are accentuated by a narrow ramp; its shell is slenderer and has higher whorls.

### *Endoplocus inflatus* sp. nov.

https://zoobank.org/03411E75-CB23-4ADB-B736-262D700F4E2E

Plate 8: figs 1–4

**Etymology.** Latin *inflatus* – inflated, according to the inflated last whorls of large specimens.

**Holotype.** SNSB-BSPG 2021 XV 20, Lang collection.

**Locus typicus.** Saal Quarry near Kelheim.

**Stratum typicum.** Upper Kimmeridgian.

**Paratypes.** Seven specimens from Saal, collections Lang and Keupp: SNSB-BSPG 2021 XV 21, 22, 108, 179–182.

**Additional material.** Two specimens from Saal, without type status (one specimen collection Neubauer, one specimen collection Lang).

**Diagnosis.** Spire conical, acute, coeloconoid, consisting of numerous whorls with low whorl face; last whorl of larger specimens inflated with convex whorl face; nodes absent.

**Description.** The holotype is 15 mm high. The early teleoconch is conical, acute, coeloconoid, slender, and consists of numerous very low whorls. A relatively well-preserved juvenile paratype (Plate 8: fig. 4) has a flat ramp demarcated by a distinct angulation. Later whorls

increase more rapidly in width producing coeloconoid shape. The last part of the last whorl is deflected downward so that the height of the whorl increases more rapidly. The transition from whorl face to the strongly convex base is evenly rounded. The last whorl is strongly convex and somewhat inflated. The shell is smooth, except in rare cases (due to preservation?) with a narrow subsutural spiral furrow. The base is narrowly phaneromphalous. The aperture is strongly damaged in all specimens; it has a strong parietal plait and two columellar plaits (adapical one weaker).

**Relationships.** *Phaneroptyxis proboscidea* Cossmann, 1898 has an even more inflated last whorl and is ornamented with nodes. *Phaneroptyxis* cf. *nogreti* (Guirand and Ogérien) sensu Hägele (1997) has fewer and higher whorls, a narrow ramp that accentuates the sutures, and its last whorl is not inflated. *Phaneroptyxis obtusiceps* Zittel sensu Hakobjan (1962) has a nodular ornament. *Endoplocus staczycii* (Zeuschner) sensu Wieczorek (1998) is similar but is slenderer, its last whorl is not as inflated, and its whorls are higher. According to Wieczorek (1998) this species is very variable. *Nerinea clymene* d'Orbigny sensu Gemmellaro (1870: pl. 4, fig. 3, non figs 4, 5) has a higher and less inflated last whorl and higher spire whorls.

## Family Ptygmatididae Pchelintsev, 1960
## Subfamily Ptygmatidinae Pchelintsev, 1960

### Genus *Ptygmatis* Sharpe, 1850

**Type species.** *Nerinea bruntrutana* Thurmann, 1832; Oxfordian; Switzerland.

### *Ptygmatis mandelslohi* (Bronn, 1836)

Plate 9: figs 1–5

*1836 – *Nerinea mandelslohi* sp. nov. – Bronn: 553, pl. 6, fig. 26.
1844 – *Nerinea mandelslohi* Bronn – Goldfuss: 39, pl. 175, fig. 4.
non v1881–1884 – *Nerinea mandelslohi* Bronn – Quenstedt: 535, pl. 206, figs 11, 12.
?1882 – *Ptygmatis mandelslohi* Bronn – Schlosser: 81, pl. 11, fig. 14.
1893 – *Ptygmatis bruntrutana* (Thurmann), Zittel – Loriol in Loriol and Lambert: 25, pl. 2, figs 6, 7.
?part1979 – *Ptygmatis bruntrutana* (Thurmann, 1832) – Wieczorek: 324, pl. 8, figs 2–5, 7; textfig. 10, 14, 19–21.
1997 – *Nerinea bruntrutana* (Thurmann, 1832) – Hägele: 128, fig. p. 128 upper left.
part 1997 – *Cryptoplocus depressus* (Bronn ex Voltz, 1836) - Fischer and Weber: 41, pl. 10, fig. 5 (non fig. 4).
2017 – Nerineoidea Nr. 6 – Gründel: 33, pl. 14C.

**Material.** Four specimens from Saal: three specimens, collection Lang, two of which are illustrated (SNSB-BSPG 2021 XV 27, 28), one specimen collection Keupp, SNSB-BSPG 2021 XV 29, and one additional questionable specimen from Saal (collection Lang).

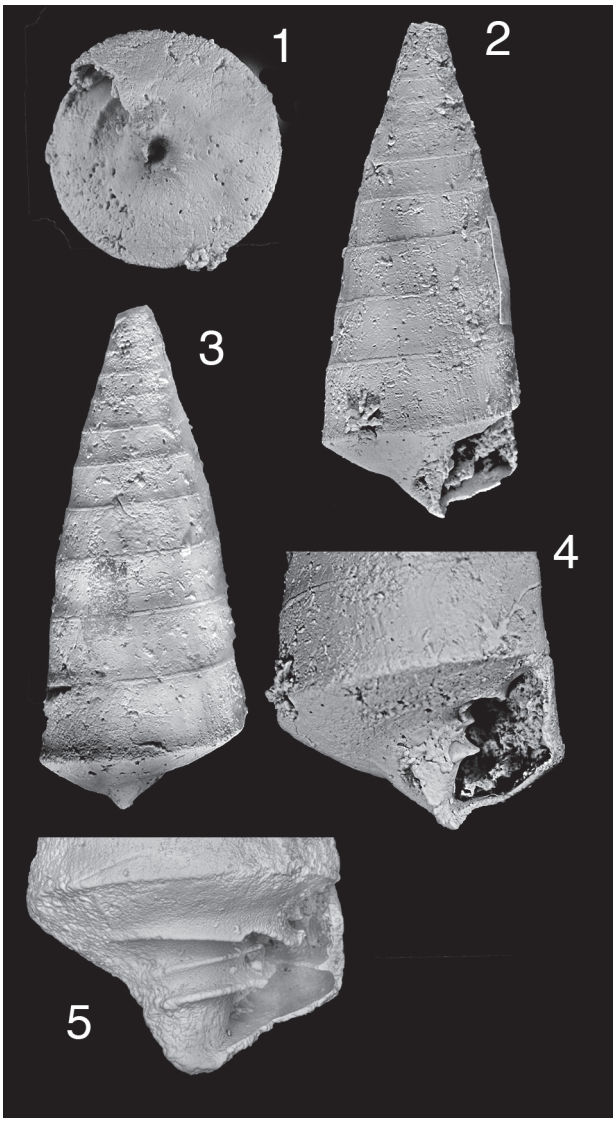


**Plate 9.** *Ptygmatis mandelslohi* (Bronn, 1836). **(1–4)** SNSB-BSPG 2021 XV 27, Saal (collection Lang); **(1)** base, width 15 mm; **(2–3)** lateral views, height 35 mm; **(4)** last whorl with aperture, height 12 mm (original to Gründel 2017, fig. 14 C). **(5)** SNSB-BSPG 2021 XV 28, Saal (collection Lang), last whorl with aperture, width 10 mm.

**Description.** The illustrated specimen (Plate 9: figs 1–4) is 35 mm high. The shell is moderately wide. The early whorls increase more rapidly in width than later ones producing slightly cyrtoconoid outline. The whorls are much wider than high. The whorl face is straight to slightly concave. The sutures are hardly impressed but visible. The whorls have a weak subsutural spiral furrow; apart from that, the whorls are smooth. The base is weakly convex and demarcated from whorl face by a sharp, almost rectangular edge. The base is smooth and narrowly phaneromphalous. The aperture is rhomboid. The inner lip has a strong parietal plait and two columellar plaits. The adapical columellar plait is weaker than the abapical one. A weak palatal plait is visible.

**Remarks.** According to Fischer and Weber (1997), *P. mandelslohi* is a junior synonym of *P. bruntrutana*. The specimen figured as *P. bruntrutana* by Fischer and Weber

(1997, pl. 10, fig. 6) is slenderer and has higher whorls than *Ptygmatis mandelslohi*. Regarding these characters, this specimen agrees with *Nerinea bruntrutana* as illustrated and described by Thurmann and Étallon (1861–1864).

The cyrtoconoid shape (produced by slower increase in width during ontogeny) is particularly characteristic of *P. mandelslohi*. This character is absent in most otherwise similar species. However, it is commonly unclear whether the lack of a cyrtoconoid shape is real or has not been recognized (e.g., due to preservation). This makes the differentiation of *P. mandelslohi* from similar species difficult. Otherwise similar species that also have a cyrtoconoid shape may have an entirely different plait-pattern in the aperture, i.e., having only a single, strong parietal plait as is typical for the genus *Cryptoplocus* (for instance *Cryptoplocus picteti* Gemmellaro, 1870: 39, pl. 6, fig. 8). As a consequence, a correct generic assignment of such species is impossible if the plait-pattern is unknown.

**Relationships.** *Cryptoplocus depressus* (Voltz, 1836) is distinctly larger, has whorls that are regularly increasing in width so that the shell is not cyrtoconoid, a wider umbilicus, and only a single parietal plait. *Ptygmatis carpathica* Zeuschner sensu Zeuschner (1850) and Zittel (1873) has a distinct bulge at the transition from whorl face to base, a wider umbilicus, and a weakly concave whorl face. *Ptygmatis carpathica* (Zeuschner) and *P. salomoniana* Cotteau, both sensu Loriol in Loriol and Lambert (1893), are slenderer, have a distinct bulge at the transition from whorl face to base, and a more or less distinctly concave whorl face.

*Ptygmatis carpathica* (Zeuschner) sensu Gemmellaro (1870) shows similar differences. Moreover, it is distinctly larger and the abapical spiral bulge is visible distinctly above the suture. *Nerinea carpathica* Zeuschner sensu Thurmann and Étallon (1861–1864) is slenderer and has a concave whorl face. *Cryptoplocus depressus* (Bronn ex Voltz, 1836) sensu Fischer and Weber (1997: pl. 10, fig. 5, non fig. 4) is slenderer and has higher whorls. *Cerithium climax* Zittel sensu Blaschke (1911) has more and lower whorls; its transition to the base is seemingly more strongly rounded. *Ptygmatis submirabilis* Pchelintsev, 1965 is larger and slenderer, its spiral bulge at the transition from whorl face to base is more pronounced and visible above the suture.

### *Ptygmatis*? *tornata* (Quenstedt, 1852)

Morphotype 1
Plate 10: figs 1–10

?*1830–1833 – *Nerinea terebra* Schübler – Zieten: 48, pl. 36, fig. 2.
?*1836 – *Nerinea incavata* sp. nov. – Bronn: 553, pl. 6., fig. 22.
1836 – *Nerinea terebra* Schübl. – Bronn: 557.
v*1852 – *Nerinea tornata* – Quenstedt: 429, pl. 34, fig. 36.
1852 – *Nerinea constricta* – Quenstedt: pl. 34, fig. 32.
1858 – *Nerinea tornata* – Quenstedt: 757, pl. 94, figs 12, 13.
v 1881–1884 – *Nerinea tornata* – Quenstedt: 527, pl. 205, figs 67, 68.
v1881–1884 – *Nerinea cochlearis* – Quenstedt: 556, pl. 207, figs 14, 15.
1901 – *Nerinea tornata* Quenst. – Geiger: 295.
1997 – *Nerinella tornata* (Quenstedt, 1852) – Hägele: 132, fig. p. 132 lower left.
1997 – *Nerinella partschi* (Peters, 1855) – Hägele: 132, pl. 13, fig. 2; fig. p. 132 upper left.
2017 – Nerineoidea Nr. 3 – Gründel: 33, pl. 13E.

**Lectotype designation.** Quenstedt (1852) based *Nerinea tornata* on a specimen from Nattheim (Quenstedt 1852, pl. 34, fig. 36). This illustration is somewhat schematic. It is probably the same specimen that was illustrated by him elsewhere (Quenstedt 1881–1884, pl. 205, fig. 67) and that is also illustrated herein (Plate 10: figs 8, 9). This specimen is herewith designated as the lectotype.

**Material.** Thirty-one specimens representing the typical form from Saal (collection Lang) of which five specimens are illustrated (SNSB-BSPG 2021 XV 32–36) and seven specimens representing the morphotype 2 from Saal: five specimens collection Lang of which two are illustrated (SNSB-BSPG 2021 XV 37, 38), one specimen collection Keupp (SNSB-BSPG 2021 XV 39), one specimen collection Neubauer); three specimens from Nattheim: *Nerinea tornata*, Tübingen (collection Quenstedt); two fragments from Nattheim: *Nerinea cochlearis*, Tübingen (collection Quenstedt).

**Description.** The shell is very slender; a fragmentary specimen (incomplete ad- and abapically) is 62 mm high; the shell illustrated in Plate 10: fig. 6 is ca. 50 mm high. If the assignment of the specimen illustrated in Plate 10: fig. 1 is correct, then the juvenile shell is very long, slender, and consists of numerous whorls. The whorls are generally wider than high but the height/width ratio varies. The whorls increase only slowly in width. The whorl face is concave. The only recognizable ornament is a subsutural bulge forming the whorl periphery. The subsutural bulge forms a sharp crest and ramp in well-preserved specimens. The whorls have a subsutural bulge bordered by the adapical suture. The base is flat, smooth and joins the whorl face at an angular edge. The base has a narrow umbilicus. The growth lines are generally opisthocline and curve backward strongly immediately below the adapical suture. The damaged aperture has a rhomboid outline and an oblique siphonal canal, two columellar plaits, one parietal, and one palatal plait.

### *Ptygmatis*? *tornata* (Quenstedt, 1852)

Morphotype 2
Plate 10: figs 11, 12

2017 – Nerineoidea Nr. 2 – Gründel: 33, pl. 13D.

**Note.** In some specimens, the ramp is not bordered by a sharp crest, but by a more or less pronounced band that is demarcated from the concave part of the whorl face by another edge; there seem to be transitions between both varieties.

**Remarks.** Two poorly preserved fragments of *Nerinea cochlearis* Quenstedt, 1881–1884 are present in the Quenstedt collection (Tübingen), both probably representing juveniles. Shape and ornament match the description

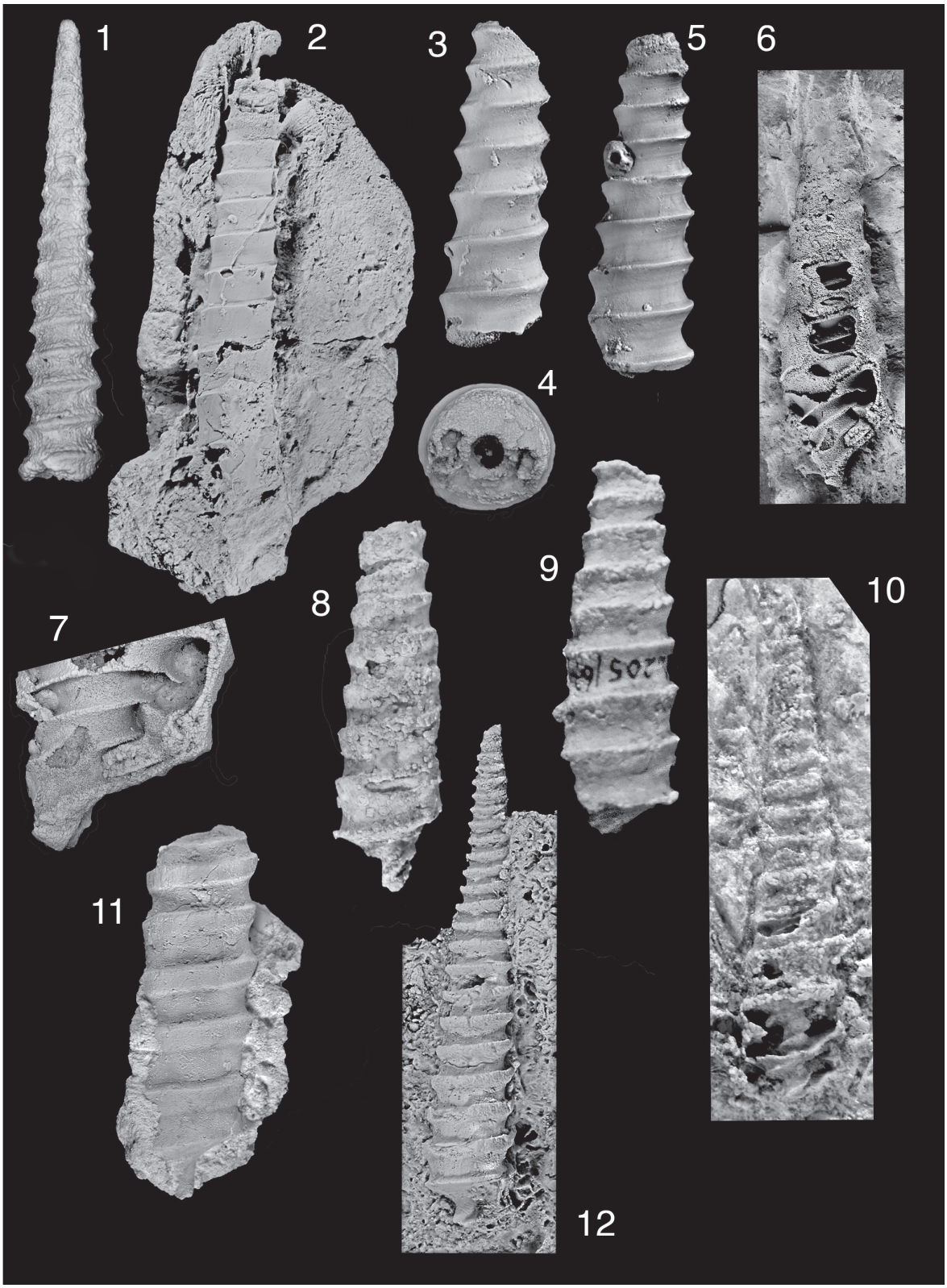


**Plate 10.** *Ptygmatis*? *tornata* (Quenstedt, 1852). **(1–10)** *Ptygmatis*? *tornata* (Quenstedt, 1852) morphotype 1. **(1)** SNSB-BSPG 2021 XV 32; Saal (collection Lang); lateral view, height 14 mm. **(2)** SNSB-BSPG 2021 XV 33, Saal (collection Lang), lateral view, height 65 mm (original to Gründel 2017, fig. 13 E). **(3–4)** SNSB-BSPG 2021 XV 34, Saal (collection Lang); **(3)** lateral view, height 20 mm; **(4)** base, width 7 mm). **(5)** SNSB-BSPG 2021 XV 35, Saal (collection Lang), lateral view, height 19 mm. **(6–7)** SNSB-BSPG 2021 XV 36, Saal (collection Lang); **(6)** lateral view, height ca. 50 mm; **(7)** aperture, width 15 mm. **(8–9)** Lectotype; University Tübingen (collection Quenstedt), Nattheim, shell in lateral views, height ca. 30 mm (original Quenstedt 1881–1884, pl. 205, fig. 67). **(10)** University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 45 mm (original Quenstedt 1881–1884, pl. 206, fig. 68). **(11–12)** *Ptygmatis*? *tornata* (Quenstedt, 1852) morphotype 2; **(11)** SNSB-BSPG 2021 XV 37, Saal (collection Lang), lateral view, height 29 mm. **(12)** morphotype 2, SNSB-BSPG 2021 XV 38, Saal (collection Lang), lateral view, height 42 mm (original to Gründel 2017, fig. 13 D).

of *Ptygmatis tornata* given above, as does the number and position of the plaits. Their base is umbilicated. However, these two specimens are too poorly preserved for a safe identification as *Ptygmatis tornata*.

It remains unclear whether *N. terebra* Schübler in Zieten and *N. incavata* Bronn are conspecific with *N. tornata* Quenstedt. At least for *N. terebra* this is likely, because this species was described from Nattheim as is also the case for *Nerinea cochlearis*. Both, *N. terebra* and *N. incavata*, would have priority over *N. tornata* Quenstedt.

**Relationships.** Numerous similar species have been described which are hardly distinguishable based on study of the literature alone. In the following, differences to middle Oxfordian and to early Tithonian taxa are discussed.

*Nerinea mandelslohi* Bronn sensu Zeuschner (1850) has higher whorls that are more rapidly increasing in width. *Nerinea suevica* Quenstedt sensu Schlosser (1882) has higher whorls, and only 3 apertural plaits are known for this species. *Aptyxis paradoxa* Schlosser, 1882 lacks plaits and also shows other differences. *Bactroptyxis cassiope* d'Orbigny sensu Fischer and Weber (1997) has higher whorls, its whorl face is less concave and it has less pronounced bulges; its sutures are situated on the bulge. *Nerinea partschi* Peters, 1855 closely resembles *Ptygmatis*? *tornata* but has higher whorls and lacks an open umbilicus. *Nerinea gosae* Roemer sensu Goldfuss (1844) resembles the present material in shell shape but its sutures are situated on the bulge. The latter is also the case in *Nerinea acteon* d'Orbigny sensu Cossmann (1898), *Nerinea baillei* Maire, 1913, and *N. castor* d'Orbigny sensu Maire (1927). *Nerinea bruntrutana* Thurmann sensu Goldfuss (1844) resembles *Ptygmatis tornata* morphotype 2 in having a band–like, broadened bulge; however, its whorls increase more rapidly in width so that its shape is more broadly conical and it has two palatal plaits.

### *Ptygmatis nodosa* (Voltz, 1836)

Plate 11: figs 1–15

*1836 – *Nerinea nodosa* (Voltz) – Voltz: 542.
1836 – *Nerinea nodosa* Voltz – Bronn: 561, pl. 16, fig. 9.
1851 – *Nerinea nodosa* Voltz – d'Orbigny: 95, pl. 254, figs 3–5.
*1852 – *Nerinea calypso* d'Orbigny – d'Orbigny: 136, pl. 274, figs 4–6.
*1852 – *Nerinea elegans* Thurm. – d'Orbigny: 146, pl. 278, figs 4–6.
?1870 – *Nerinea plassenensis* Pet. – Gemmellaro: 25, pl. 4, figs 14, 15.
1889 – *Nerinea nodosa* Voltz – Loriol in Loriol and Koby: 32, pl. 4, figs 5–11.
1997 – *Ptygmatis nodosa* (Bronn ex Voltz, 1836) – Fischer and Weber: 37, pl. 11, figs 4–6.
1997 – *Ptygmatis nodosa* (Bronn ex Voltz, 1836) – Fischer and Weber: 54.
?1997 – *Nerinella elegans* (Bronn ex Thurmann, 1836) – Fischer and Weber: 58, pl. 8, fig. 5.
2017 – Nerineoidea Nr. 8 – Gründel: 33, pl.15A.

**Material.** 142 fragments and juvenile specimens from Saal: 138 specimens collection Lang, of which eight are illustrated ( SNSB-BSPG 2021 XV 40–45, 47, 48), four specimens collection Keupp (SNSB-BSPG 2021 XV 46, 49–51).

**Description.** The present material consists of fragments of larger specimens and juvenile specimens. The largest specimen is 32 mm high. The apical whorls are not preserved. The shell is slender with a somewhat variable apical angle. The ornament consists of a nodular adapical bulge forming a narrow ramp. The suture is situated on the adapical portion of the bulge. The nodular spiral cord (in some specimens only very weakly developed) is mostly close to the abapical suture or – more rarely – about half way between adapical bulge and abapical suture. The number of nodes per whorl is strongly variable (only in part due to preservation). In few specimens, an additional weakly nodular spiral cord is present between the nodular spiral cord and the adapical bulge. The base is weakly convex with a pronounced spiral cord at the almost rectangular transition to the whorl face. This bordering spiral cord is sometimes nodular. The base is covered with spiral cords. The aperture has a rhomboid outline and a distinctly oblique siphonal canal. The plait pattern is only visible in few specimens. It consists of one or two columellar plaits, one strong parietal plait, while a palatal is plait very rarely visible – perhaps due to the preservation.

**Remarks.** In the present material, some specimens have one and others have two columellar plaits. The references listed in the chresonymy and synonymy list above probably refer to material from older strata (Oxfordian, with the exception of Gründel 2017). These references note the presence of four plaits (two columellar plaits, one parietal and one palatal plait).

**Relationships.** See Remarks for *Eunerinea* sp. 1 for relationships with *Ptygmatis nodosa*. *Ptygmatis nodosa* Voltz sensu Cossmann (1898) has higher whorls, its whorl face is more concave, its basal spiral rib is not as pronounced and widened, and it has three spiral cords on the base. *Nerinea danubiensis* Zittel sensu Schlosser (1882) has more rapidly increasing whorls in width, its second nodular spiral cord is situated directly above the suture and forms the basal spiral cord at the transition from whorl face to base instead of having a non-nodular bulge/cord at this position. Moreover, this spiral cord is stronger than the subsutural row of knobs. *Nerinea plassenensis* Peters, 1855 has a more convex base and stronger subsutural knobs and therefore a more concave whorl face. In *Nerinea nodosa* Voltz sensu Thurmann and Étallon (1861–1864), the spiral cord at the transition from whorl face to base is distinctly knobby. *Ptygmatis nodosa* Voltz sensu Maire (1913, 1927) has fewer but larger subsutural knobs, the edge from whorl face to base is at least partly knobby (Maire emphasized the great variability of this species), and it has some spiral cords on the base. *Nerinea paronae* Stefano, 1884 has more and smaller subsutural knobs, more weak, knobby spiral cord on the whorl face, knobs on the edge demarcating whorl face and base and it has spiral cords on the base.

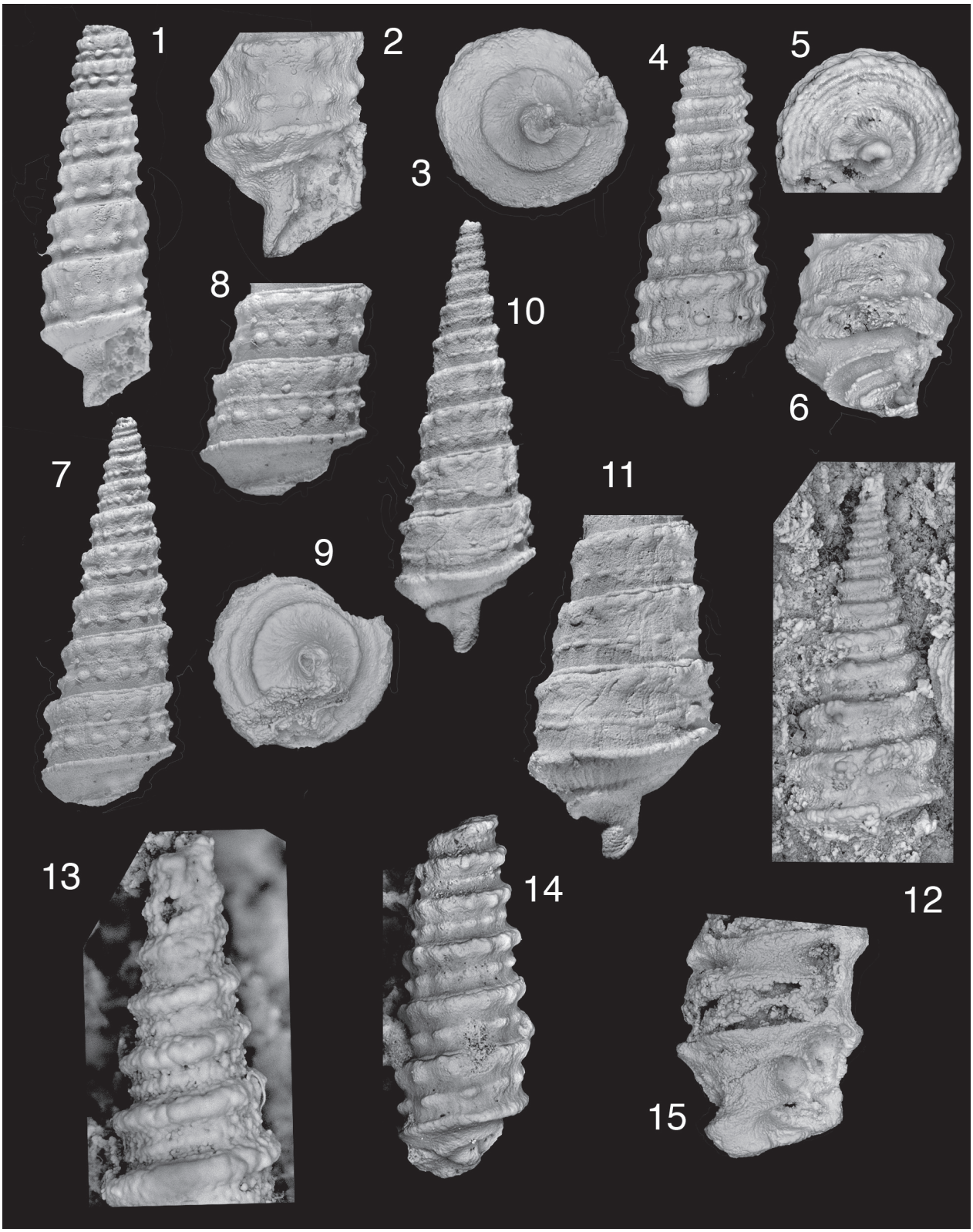


**Plate 11.** *Ptygmatis nodosa* (Voltz, 1836). **(1–3)** SNSB-BSPG 2021 XV 40, Saal (collection Lang); **(1)** lateral view, height 22 mm; **(2)** last whorl with aperture, width 6.6 mm; **(3)** base, width 6.6 mm. **(4–5)** SNSB-BSPG 2021 XV 41; Saal (collection Lang); **(4)** lateral view, height 9 mm; **(5)** base, width 3.5 mm. **(6)** SNSB-BSPG 2021 XV 42, Saal (collection Lang), aperture, width of whorl 3.7 mm. **(7–8)** SNSB-BSPG 2021 XV 43, Saal (collection Lang); **(7)** lateral view, height 11.5 mm; **(8)** last two whorls in lateral view, width 4.2 mm. **(9)** SNSB-BSPG 2021 XV 44, Saal (collection Lang), base, width 6 mm. **(10–11)** SNSB-BSPG 2021 XV 45, Saal (collection Lang); **(10)** lateral view, height 16 mm; **(11)** last whorls in lateral view, width 5.2 mm. **(12–13)** SNSB-BSPG 2021 XV 46, Saal (collection Keupp); **(12)** lateral view, height 9 mm; **(13)** apex in lateral view, height 2.9 mm. **(14)** SNSB-BSPG 2021 XV 47, Saal (collection Lang), lateral view, height 10 mm. **(15)** SNSB-BSPG 2021 XV 48, Saal (collection Lang), last whorls with aperture, width 7.8 mm.

### *Ptygmatis clio* (d'Orbigny, 1852)

Plate 12: figs 1–3

*1852 – *Nerinea clio* d'Orbigny – d'Orbigny: 139, pl. 275, figs 3–5.
1886–1888 – *Ptygmatis clio* d'Orbigny – Loriol in Loriol and Bourgeat: 84, pl. 7, figs 1–3.
1898 – *Ptygmatis clio* d'Orbigny – Cossmann: 72, pl. 6, figs 18, 19.
1997 – *Polyptyxisella clio* (d'Orbigny, 1852) – Fischer and Weber: 55, pl. 12, figs 9, 10.

**Material.** Two illustrated specimens (SNSB-BSPG 2021 XV 59, 60) and a questionable one, all from Saal, collection Lang.

**Description.** The largest specimen (Plate 12: fig. 3) is 108 mm high. The shell is slender. The whorl face is straight. The last whorl of the largest specimen has a weak, indistinctly delimited subsutural furrow. The sutures are distinct. The whorls lack visible ornament. The basal edge is pronounced and forms an angular transition to the base. The base is incompletely preserved, and is seemingly smooth with a distinct umbilicus. The aperture is not preserved. A columellar section shows the presence of a parietal, two columellar, and one palatal plaits.

**Remarks.** Fischer and Weber (1997) designated a lectotype (section of a shell, Fischer and Weber 1997: pl. 12, fig. 9) that agrees well with the sectioned shell illustrated herein (Plate 12: figs 1, 2). The lateral view provided by Fischer and Weber (1997: pl. 12, fig. 10) also agrees well with the present material. The specimens illustrated by Fischer and Weber (1997) are from the middle Oxfordian of St. Mihiel, but these authors noted that the species is also present in the Kimmeridgian. The illustration given by d'Orbigny (1852: pl. 275, figs 3–5) deviates more strongly from our specimens: the shell is slenderer and the whorl face is distinctly concave.

**Relationships.** *Aptyxiella planata* (Quenstedt) sensu Hägele (1997), *A. quenstedti* Geiger, 1901, and *A. ewaldi* Geiger, 1901 lack plaits. *Cossmannea nantuacensis* (d'Orbigny) sensu Fischer and Weber (1997) is much larger, lacks an umbilicus and columellar and parietal plaits. *Megaptyxis caucasica* Pchelintsev, 1965 has a concave whorl face and more oblique sutures.

### *Ptygmatis*? *polyspira* (Quenstedt, 1884)

Plate 12: fig. 4

v*1881–1884 – *Nerinea polyspira* – Quenstedt: 554, pl. 207, fig. 3.
1901 – *Aphanoptyxis polyspira* Quenstedt – Geiger: 301.
1997 – *Aphanoptyxis polyspira* (Quenstedt, 1884) – Hägele: 133, fig. p.133, lower left.

**Material.** Quenstedt's (1881–1884) figured specimen (holotype by monotypy) from Nattheim (Tübingen, Quenstedt collection).

**Description.** The specimen consists of 7 whorls and is 32 mm high (apex missing). The shell is moderately slender and the whorls are increasing regularly in width. The sutures are somewhat pronounced by a subsutural bulge. The whorl face is straight and entirely covered by spiral cords (7–8 spiral cords on last whorl). The transition from whorl face to base is angular. The aperture is not preserved, plaits are not visible.

**Remarks.** The studied holotype of *Nerinea polyspira* Quenstedt, 1884 is a poorly preserved specimen. Its systematic and taxonomic position remain unclear because aperture and plaits are unknown.

**Relationships.** *Nerinea ursicina* Thurmann, 1861 (in Thurmann and Étallon 1861–1864) differs in having a strong adapical bulge, making the whorl face distinctly concave, fewer spiral cords, and four apertural plaits. *Nerinea punctata* Voltz sensu Bronn (1836) has a narrow but distinct ramp, and only three spiral cords on its whorl face. *Nerinella calliope* d'Orbigny sensu Cossmann (1898) has 5–6 spiral cords on the whorl face, some of them having fine knobs. Its aperture has three plaits. *Nerinella turritella* Voltz sensu Cossmann (1898) lacks a bulge and has four strong, knobby spiral cords on the whorl face and additional weaker cords between them. *Nerinella cyane* Loriol in Loriol & Pellat, 1874 has higher whorls with a smooth portion above the suture.

### *Ptygmatis*? *ursicina* (Thurmann, 1861 in Thurmann and Étallon 1861–1864)

Plate 12: figs 5–7

?1844 – *Nerinea visurgis* Röm. – Goldfuss: 44, pl. 176, fig. 6.
1852 – *Nerinea visurgis* Roemer, 1836 – d'Orbigny: 122, pl. 268, figs 5–7.
*1861–1864 – *Nerinea ursicina* Th. – Thurmann and Étallon: 103, pl. 8, fig. 50.
?1872 – *Nerinea pseudospeciosa* P. de Loriol, 1871 – Loriol, Royer and Tombeck: 89, pl. 6, fig. 7.
1889 – *Nerinea ursicina* Thurmann – Loriol and Koby: 37, pl. 6, figs 1–8.
1898 – *Nerinea ursicinensis* Thurmann – Cossmann: 37, pl. 3, figs 11, 12.
1927 – *Nerinea ursicinensis* Thurmann – Maire: 142, pl. 7, figs 15, 16.
1997 – *Cossmannea* (*Eunerinea*) *ursicina* (Thurmann, 1861) – Fischer and Weber: 40, pl. 9, fig. 2.

**Material.** Nineteen juvenile specimens from Saal (collection Lang), of which two are illustrated (SNSB-BSPG 2021 XV 30, 31).

**Description.** The largest specimen from Saal is 9 mm high. The shell is slender to very slender. The whorls are regularly increasing in width. The whorl face is concave, with a strong, sometimes ramp-like bulge. The bulge is formed at the suture by both whorls. The suture is situated somewhat above the middle of the bulge. The whorl face between the bulges is initially ornamented with one spiral cord, later whorls with 4–5 spiral cords: two of these spiral cords may be stronger than the others. The bulges and stronger spiral cords are possibly nodular (unclear

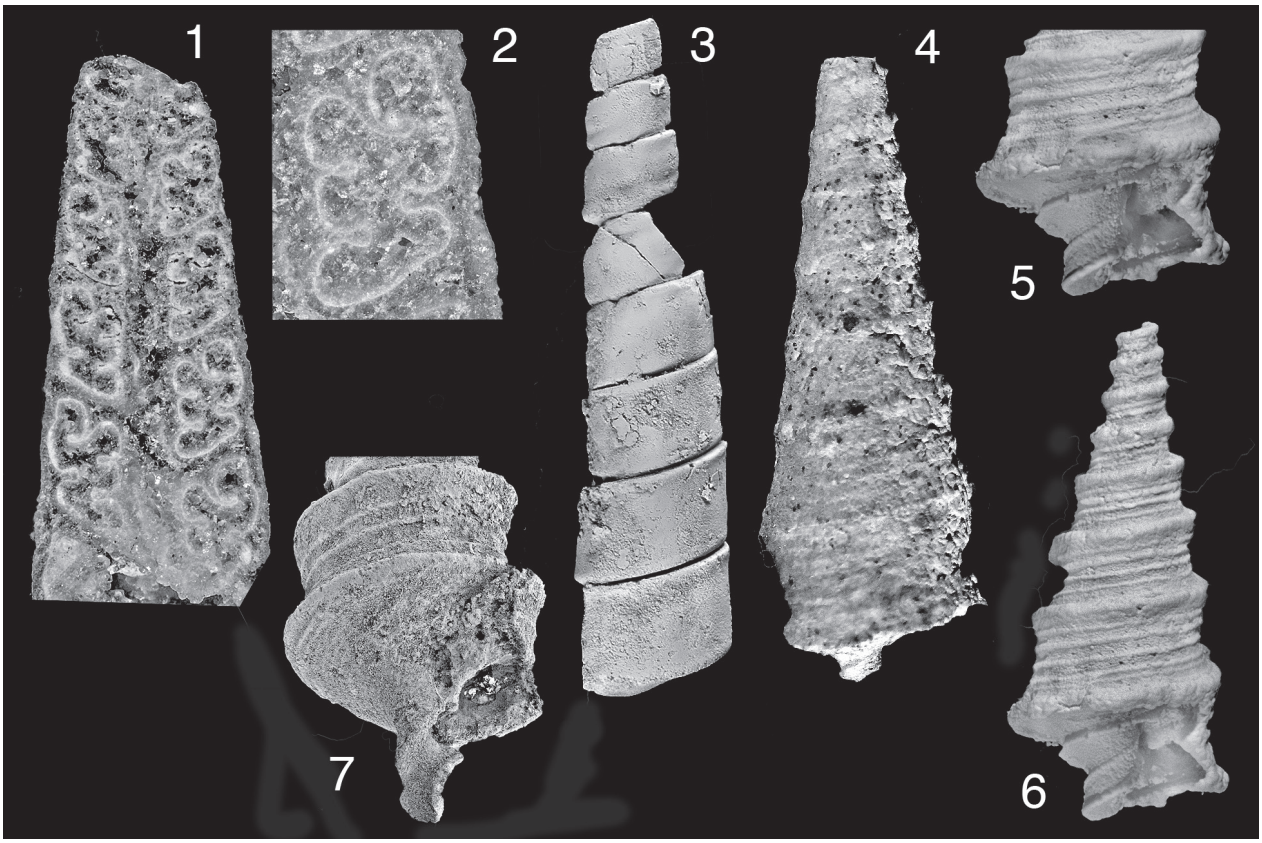


**Plate 12. (1–3)** *Ptygmatis clio* (d'Orbigny, 1852). **(1–2)** SNSB-BSPG 2021 XV 59, Saal (collection Lang); **(1)** section of fragment, height 21 mm; **(2)** detail, height 3.7 mm. **(3)** SNSB-BSPG 2021 XV 60, Saal (collection Lang), lateral view, height 108 mm. **(4)** *Ptygmatis*? *polyspira* (Quenstedt, 1881–1884), holotype, collection University Tübingen (collection Quenstedt); Nattheim, lateral view, height 32 mm (original to Quenstedt 1881–1884, pl. 207, fig. 3. (11–12) *Bactroptyxis teres* (Münster in Goldfuss, 1844), collection Sauerborn, Nattheim area. **(5–7)** *Ptygmatis*? *ursicina* (Thurmann in Thurmann & Étallon, 1861). **(5–6)** SNSB-BSPG 2021 XV 30, Saal (collection Lang); **(5)** last whorl with aperture, height 4 mm; **(6)** lateral view, height 9.5 mm. **(7)** SNSB-BSPG 2021 XV 31, Saal (collection Lang), aperture and ornament of base, width 2.5 mm.

due to preservation). The base is flat, with an almost rectangular transition to the whorl face. The transition has a strong, protruding bulge that is largely covered by the following whorls of the spire. The base is densely covered with weak spiral cords. The aperture has an approximately rectangular outline and distinct oblique siphonal canal. The aperture has a single parietal plait, two columellar plaits, and a palatal plait.

**Remarks.** The identity of the present juvenile shells with much larger growing taxa is uncertain (see synonymy list). Thurmann in Thurmann and Étallon (1861–1864) reported that *Nerinea ursicina* has distinct knobs on the bulges and partly also on the spiral cords between the bulges. Such a knobby ornament could not be substantiated for the present material, due perhaps to preservation.

**Relationships.** Differences to *Ptygmatis*? *polyspira* (Quenstedt, 1881–1884) are herein discussed in the treatment of this taxon. *Nerinea subscalaris* Münster in Goldfuss (1844) has higher whorls in relation to whorl width and it has more oblique sutures. *Nerinea*? *lafayettensis* Imlay, 1945 has, among other differences, only two spiral cords between the bulges. *Nerinea speciosa* Voltz sensu Maire (1927) has a broader shell with lower whorls and its bulges are not as much protruding. *Nerinea mariae* d'Orbigny sensu Cossmann (1898) is slenderer and has higher whorls.

## Genus *Bactroptyxis* Cossmann, 1896

**Type species.** *Nerinea implicata* d'Orbigny, 1851; Bathonian; France.

### *Bactroptyxis teres* (Münster in Goldfuss, 1844)

Plate 13: figs 1, 2

*1844 – *Nerinea teres* Münster – Goldfuss: 43, pl. 176, fig. 3.
?1997 – *Nerinea teres* (Münster, 1844) – Hägele: 136, fig. p. 136 lower left, pl. 13, fig. 6.

**Material.** Two specimens from the Nattheim area (collection Sauerborn).

**Description.** A specimen is 28 mm high. The shell is very slender. The sutures are indistinct and hardly recognizable. The whorl face is straight. The ornament is weak (due to preservation?) consisting of four spiral cords on

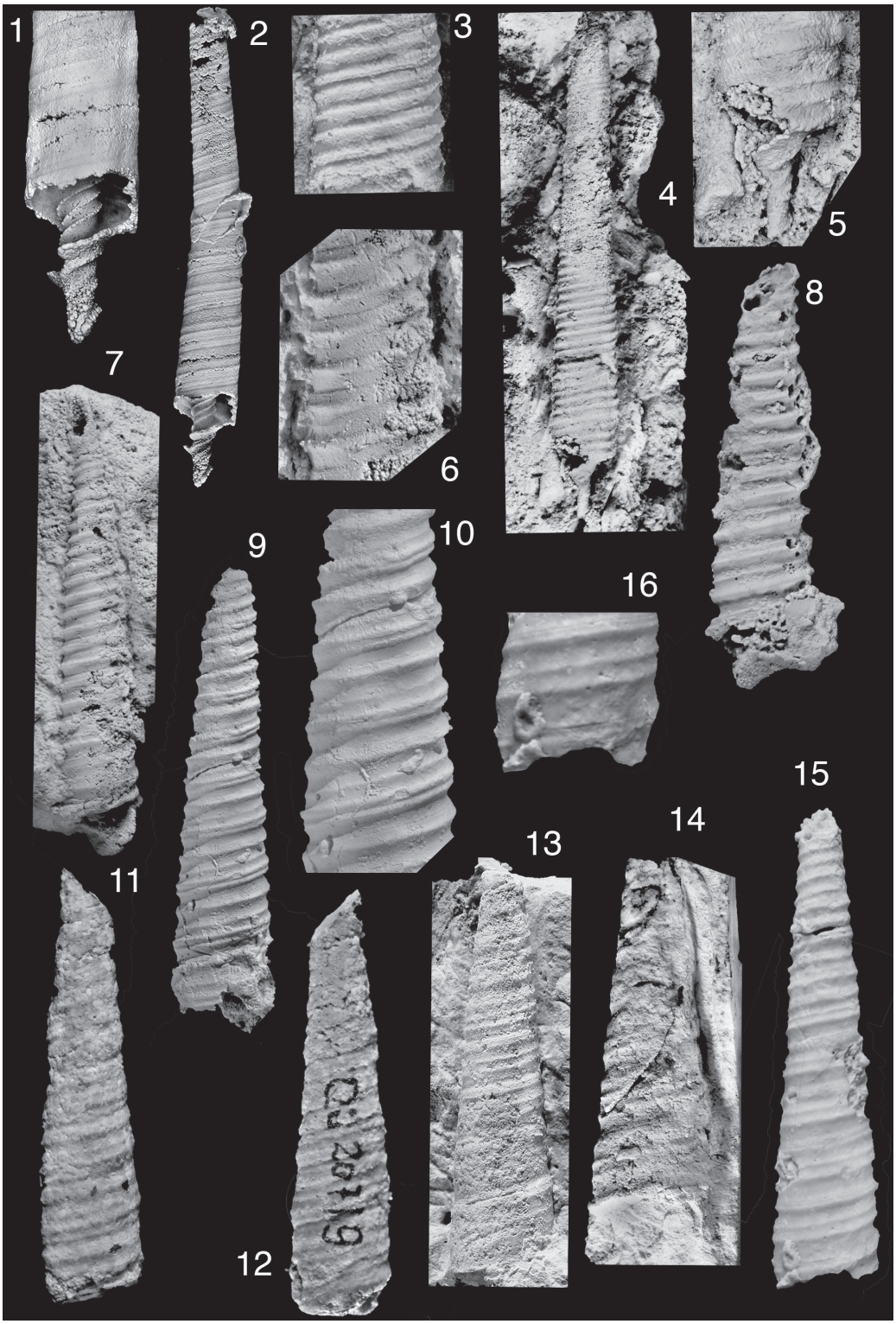


**Plate 13. (1–2)** *Bactroptyxis teres* (Münster in Goldfuss, 1844), from the Nattheim area (collection Sauerborn); **(1)** last whorl with aperture, height 11 mm; **(2)** lateral view, height 29 mm. **(3–5)** *Bactroptyxis* cf. *fasciata* (Voltz, 1836), SNSB-BSPG 2021 XV 56, Saal (collection Lang); **(3)** detail of ornament, width 4.5 mm; **(4)** lateral view, height 36 mm; **(5)** aperture, width of whorl 4.6 mm. **(6–8)** *Bactroptyxis*? *subcochlearis* (Münster in Goldfuss, 1844). **(6–7)** SNSB-BSPG 2021 XV 57, Saal (collection Neubauer); **(6)** detail of ornament, height 11.5 mm; **(7)** lateral view, height 55 mm. **(8)** SNSB-BSPG 2021 XV 58, Saal (collection Lang), lateral view, height 29 mm. **(9–10)** *Bactroptyxis*? *tricincta* (Münster in Goldfuss, 1844). **(9)** SNSB-BSPG 2021 XV 52, Saal (collection Lang), lateral view, height 48 mm (original to Gründel 2017, fig. 14 B). **(10)** SNSB-BSPG 2021 XV 52, Saal (collection Lang), detail of shell in lateral view, height 21 mm. **(11–16)** *Bactroptyxis*? *tricincta* (Münster) sensu Quenstedt (1881–1884). **(11–12)** Collection University Tübingen (collection Quenstedt); Nattheim, lateral views, height 29 mm (original to Quenstedt 1881–1884, pl. 207, fig. 9). **(13)** SNSB-BSPG 2021 XV 53, Saal (collection Lang), lateral view, height 64 mm. **(14)** SNSB-BSPG 2021 XV 54, Saal (collection Lang), lateral view, height 55 mm. **(15–16)** SNSB-BSPG 2021 XV 55, Saal (collection Lang); **(15)** lateral view, height 72 mm; **(16)** last whorl, width 17 mm.

the whorl face at about same distance to each other. Two spiral cords are situated directly near the sutures, two other cords are in the middle portion of the whorl face. The transition from whorl face to base is angular. The aperture has two columellar, two palatal plaits, and one parietal plait.

**Remarks.** *Bactroptyxis teres* (Münster) sensu Hägele (1997) is probably identical but has three columellar and three palatal plaits according to Hägele (1997).

**Relationships.** *Bactroptyxis*? *tricincta* Goldfuss sensu Quenstedt (1881–1884) is distinctly larger, not as slender and has only three spiral cords (suprasutural spiral cord lacking). *Bactroptyxis* sp. cf. *fasciata* (Voltz, 1836) (see below) is very similar to *Bactroptyxis teres* but has much more distinct spiral cords. However, this could be due to preservation and both taxa could represent a single species. *Nerinella bipunctata* (Quenstedt) sensu Hägele (1997) has nodular spiral cords and it has only one columellar and one parietal plait. *Aptyxiella ewaldi* Geiger, 1901 closely resembles *Bactroptyxis teres* in shape and ornament but lacks plaits in the aperture according to Geiger (1901). *Nerinea vallonia* Loriol in Loriol and Cotteau (1868) differs by having 7–8 spiral cords on the whorl face and only a weak columellar plait. *Aptyxiella inornata* d'Orbigny sensu Maire (1913) has an ornament of five spiral cords of unequal strength and lacks plaits in the aperture.

### *Bactroptyxis* cf. *fasciata* (Voltz, 1836)

Plate 13: figs 3–5

?1836 – *Nerinea fasciata* Voltz – Bronn: 554, pl. 16, fig. 21.

**Material.** One specimen (SNSB-BSPG 2021 XV 56) and one questionable specimen, both from Saal, collection Lang.

**Description.** The bona fide specimen is 36 mm high. The shell is very slender. The whorl face is straight. The sutures are not impressed and only occasionally visible. The ornament is only preserved on the last whorl. It consists of four spiral cords of equal strength that are equally distant from each other. A knobby ornament is absent. An abapical spiral cord, probably representing the bordering spiral cord, is visible above the suture and marks the angular transition to the flat base. Only the inner lip of the aperture is preserved; it shows one parietal plait and two columellar plaits.

**Remarks.** *Nerinea fasciata* sensu Bronn (1836) has the same shell shape as the present species and it has also four spiral cords, which are, however, of unequal strength.

**Relationships.** *Bactroptyxis teres* (Münster in Goldfuss, 1844) differs from *Bactroptyxis* cf. *fasciata* by having four strong spiral cords of equal strength and at equal distances. *Bactroptyxis teres* (Münster) sensu Hägele (1997) has more and weaker spiral cords of unequal strength. *Aptyxiella rupellensis* d'Orbigny sensu Pchelintsev (1965) has higher whorls and more spiral cords. *Aptyxiella inornata* d'Orbigny sensu Maire (1913) has five spiral cords on the whorl face and a subsutural bulge; apertural plaits are not visible. *Nerinea quadricincta* Münster sensu Maire (1913, pl. 11, fig. 7) has two stronger spiral cords on the whorl face (unlike in Maire's 1913, p. 93 description) and allegedly additional weak spiral cords that are unrecognizable, and it shows swellings near the sutures. These swellings form bulges on which the sutures are situated.

### *Bactroptyxis*? *subcochlearis* (Münster in Goldfuss, 1844)

Plate 13: figs 6–8

*1844 – *Nerinea subcochlearis* Münster – Münster in Goldfuss: 42, pl. 175, fig. 14.

1858 – *Nerinea subcochlearis* Goldfuss – Quenstedt: 769, pl. 94, fig. 24.

v1881–1884 – *Nerinea subcochlearis* Goldf. – Quenstedt: 555, pl. 207, figs 12, 13.

non1997 – *Aptyxiella subcochlearis* (Münster, 1844) – Hägele: 134, fig. 134 upper right.

**Material.** One relatively large specimen (collection Neubauer) and four fragments (collection Lang), of which two are illustrated (SNSB-BSPG 2021 XV 57, 58) from Saal; two specimens from Nattheim (Tübingen: collection Quenstedt).

**Description.** The large specimen is 55 mm high. The shell is slender. The whorls increase regularly in width. The sutures are hardly recognizable. The whorl face is ornamented with two strong spiral cords lacking knobs. The upper spiral cord is in directly subsutural position. The lower spiral cord lies somewhat above the abapical suture. The adapical spiral cord is somewhat stronger than the abapical one. At least on the last whorl, another much weaker spiral cord is intercalated. The base and the aperture are not preserved. The base has a narrow umbilicus.

**Relationships.** In *Aptyxiella nattheimensis* (d'Orbigny) sensu Hägele (1997), the suture lies on a bulge formed by adapical and abapical swelling of neighbouring whorls; its whorl face has two spiral cords. *Nerinea quadricincta* Münster sensu Geiger (1901) has a gradate spire, a subsutural bulge and at least two distinct spiral cords on the whorl face. The ornament reported by Geiger (1901: 293) cannot be seen in the illustration provided by this author. *Nerinea sulcata* Schübler in Zieten 1830 has whorls that are more rapidly increasing in width (conical shape), higher whorls and more distinct sutures. *Nerinea bicostata* Gemmellaro, 1870 has a broader shell and lacks an umbilicus.

### *Bactroptyxis*? *tricincta* (Münster in Goldfuss, 1844)

Plate 13: figs 9, 10

*1844 – *Nerinea tricincta* Münster – Münster in Goldfuss: 42, pl. 176, fig. 1.

2017 – Nerineoidea Nr. 5 – Gründel: 33, pl. 14 B.

**Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 52.

**Description.** The specimen is 47 mm high. The apical whorls, aperture, and base are missing. The shell is very slender. The whorl face is concave. The sutures are

indistinct. The earliest preserved whorls have three spiral cords: a strong subsutural cord and a pair of closely spaced, somewhat weaker spiral cords below mid-whorl, close to the abapical suture. The area between the upper cord and the lower pair of cords is strongly concave. On late whorls, a fourth, weak spiral cord is intercalated between the upper cord and the lower pair of cords. The subsutural spiral cord is strong and crest-like on the latest preserved whorls. The base has an umbilicus.

**Remark.** The aperture as well as number and arrangement of the plaits are unknown, therfore the generic assignment is doubtful.

### *Bactroptyxis*? *tricincta* (Münster) sensu Quenstedt, 1881–1884

Plate 13: figs 11–16

1844 – *Nerinea turritella* Voltz – Goldfuss: 43, pl. 176, fig. 5.
1852 – *Nerinea nattheimensis* sp. nov. – d'Orbigny: 144.
v1881–1884 – *Nerinea tricincta* Goldfuss – Quenstedt: 555, pl. 207, fig. 9.

**Material.** Three specimens from Saal, collection Lang: SNSB-BSPG 2021 XV 53–55, one specimen from Nattheim (Tübingen: collection Quenstedt).

**Description.** The largest specimen is 72 mm high. The shell is slender. The whorl face is straight. The suture is weakly impressed. The whorls are ornamented with a strong subsutural spiral cord, two somewhat weaker spiral cords at mid–whorl which are close to each other. The adapical cord of this pair is either weaker or both cords have about the same strength. The spiral cords are weakly knobby (knobby ornament indistinct due to preservation). The base is flat. The transition from base to whorl face is sharply angular at a pronounced bordering spiral cord. The base is umbilicated. Other details are not preserved.

**Relationships.** *Bactroptyxis*? *tricincta* (Münster in Goldfuss, 1844) is smaller. It has four spiral cords on the whorl face. As in the present material, two of these cords are close to each other, of which the adapical one is stronger, and both are close to the abapical suture. *Nerinella subtricincta* (d'Orbigny) sensu Fischer and Weber (1997: 54, pl. 5, figs 21, 22) is slenderer and has two spiral cords at mid-whorl that are distinctly nodular. *Nerinella* cf. *laufonensis* (Thurmann, 1859) and *N. subtricincta* (d'Orbigny, 1850) sensu Hägele (1997) are both slenderer and have higher, more concave whorls, and their nodular ornament is more pronounced.

## Subfamily Cryptoplocinae Pchelintsev in Pchelintsev & Korobkov, 1960

### Genus *Cryptoplocus* Pictet & Campiche, 1861

**Type species.** *Nerinea depressa* Voltz, 1836; Kimmeridgian?

### *Cryptoplocus depressus* (Voltz, 1836)

Plate 14: figs 1–5

*1836 – *Nerinea depressa* Voltz – Voltz: 540.
1836 – *Nerinea depressa* Voltz – Bronn: 549, fig. 17.
?1858 – *Nerinea depressa* Voltz – Quenstedt: 765, pl. 94, figs 1, 2.
1874 – *Trochalia depressa* (Voltz) Sharpe – Loriol in Loriol and Pellat: 312, pl. 7, fig. 2.
v1881–1884 – *Nerinea depressa* Voltz, 1836 – Quenstedt: 546, pl. 206, figs 48–53.
1898 – *Cryptoplocus depressus* Voltz – Cossmann: 158, pl. 11, figs 33, 34; pl. 12, figs 3, 4, 7, 11, 12.
non 1997 – *Cryptoplocus depressus* (Bronn ex Voltz, 1836) – Fischer and Weber: 41, pl. 10, figs 4, 5.
?1998 – *Cryptoplocus* cf. *picteti* Gemmellaro, 1864 – Wieczorek 316, pl. 1, fig. 5.

**Material.** Seven fragments from Nattheim (Tübingen, collection Quenstedt), three specimens from the vicinity of Nattheim (collection Sauerborn) and three specimens from Saal (collection Lang), one of which illustrated herein (SNSB-BSPG 2021 XV 106).

**Description.** The largest specimen is 96 mm high. The shell is moderately broad. The whorls are regularly increasing in width throughout ontogeny. They are distinctly wider than high. The whorl face is straight. The sutures are not impressed and hardly visible. No ornament is visible on whorl face. The base is weakly convex. The transition from base to whorl face forms a pronounced angular edge. The base has a wide umbilicus that is surmounted by a bulge. The base is otherwise smooth. The aperture is strongly damaged in all studied specimens, only a strong parietal plait is visible.

**Remarks.** Quenstedt's (1881–1884) material of *Cryptoplocus depressus* from Nattheim consists of seven poorly preserved fragments. Their shell shape is mostly not recognizable. The specimen illustrated by Quenstedt (1881–1884: pl. 206, fig. 52) (here: Plate 14: figs 3, 4) is a fragment of 37 mm height. It has a strong parietal plait.

**Relationships.** Differences to *Ptygmatis mandelslohi* are discussed where that species is treated. *Nerinea depressa* Voltz sensu Zeuschner (1850) has a distinct subsutural furrow, and its whorl face has a concave zone in lateral view. *Cryptoplocus depressus* Voltz sensu Yin (1931) is slenderer and has lower whorls. *Ptygmatis meneghini* Gemmellaro sensu Yin (1931) is slenderer and has a suprasutural bulge that is delimited adapically by a furrow. *Nerinea terebra* Schübler in Zieten, 1830 is slenderer, has a bulge at the sutures and its whorl face is concave.

### *Cryptoplocus subpyramidalis* (Münster in Goldfuss, 1844)

Plate 14: fig. 6

1844 – *Nerinea subpyramidalis* Münster – Münster in Goldfuss: 40, pl. 175, fig. 7.

1882 – *Cryptoplocus subpyramidalis* Münster – Schlosser: 86, pl. 12, fig. 10.

?1931 – *Cryptoplocus pyramidalis* Münster – Yin: 66, pl. 7, figs 11–15.

1931 – *Cryptoplocus subpyramidalis* Münster – Yin: 67, pl. 8, fig. 1.

**Material.** Three specimens from Saal: two specimens collection Lang, one of which is illustrated (SNSB-BSPG 2021 XV 61), one specimen collection Keupp: SNSB-BSPG 2021 XV 62).

**Description.** The larger specimen (composed of numerous fragments) is incomplete and is 103 mm high. The shell is conical with regularly increasing whorls. The whorls are very low in relation to their height. The whorl face is weakly concave. A weak subsutural bulge with narrow ramp accentuates the sutures. No ornament is visible on the whorls. The base is moderately convex. The transition from base to whorl face forms a distinct edge. No other morphological details are preserved.

**Relationships.** *Cryptoplocus pyramidalis* (Münster in Goldfuss) sensu Yin (1931) and *Trochalia subpyramidalis* Sharpe sensu Loriol in Loriol and Pellat (1874) lack a subsutural bulge. *Nerinea pyramidalis* Münster in Goldfuss, 1844 has a distinctly concave whorl face. In *Trochalia engeli* Geiger sensu Geiger (1901) and Hägele (1997), *Nerinea pyramidalis* sensu Quenstedt (1881–1884), Peters (1855), Gemmellaro (1870), and Münster in Goldfuss (1844) the bulge is situated above the suture (not subsutural).

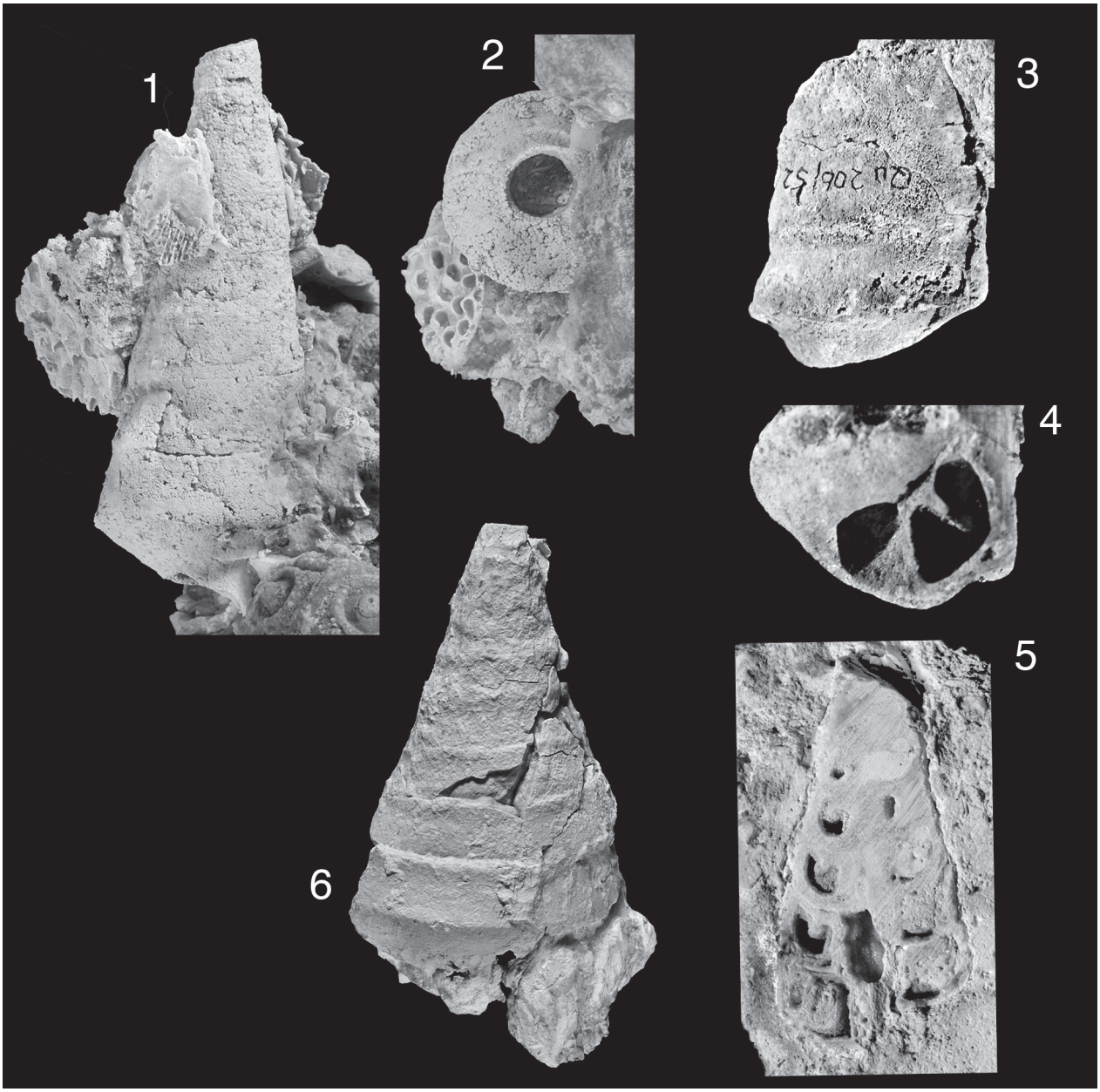


**Plate 14. (1–5)** *Cryptoplocus depressus* (Voltz, 1836). **(1–2)** Collection Sauerborn, Nattheim area; **(1) l**ateral view, height 78 mm; **(2)** base, width 29 mm. **(3–4)** University Tübingen (collection Quenstedt), Nattheim; **(3)** lateral view, height 37 mm; **(4)** last whorls with aperture, width 25 mm. **(5)** SNSB-BSPG XV 106, Saal (collection Lang), columellar section, height 47 mm. **(6)** *Cryptoplocus subpyramidalis* (Münster in Goldfuss, 1844), SNSB-BSPG 2021 XV 61, Saal (collection Lang), lateral view, height 103 mm.

## Family Nerinellidae Pchelintsev in Pchelintsev & Korobkov, 1960

### Genus *Nerinella* Sharpe, 1850

**Type species.** *Nerinea dupiniana* d'Orbigny, 1842–1843; Lower Cretaceous; France.

### *Nerinella ornata* (d'Orbigny, 1852)

Plate 15: figs 1–5

*1852 – *Nerinea ornata* d'Orbigny – d'Orbigny: 135, pl. 274, figs 1–3.
v1881–1884 – *Nerinea ornata* Orb. – Quenstedt: 528, pl. 205, figs 74, 75.
1997 – *Nerinella subtricincta* (d'Orbigny, 1852) – Fischer and Weber: 54, pl. 5, figs 21, 22.

**Material.** Two specimens from Nattheim (Tübingen: collection Quenstedt), one specimen certainly representing this species (SNSB-BSPG 2021 XV 72) and a questionable juvenile specimen from Saal (both collection Lang).

**Description.** The specimen illustrated in Plate 15: figs 1–3 is 33 mm high and that in Plate 15: fig. 4 is 18 mm high. The shell is very slender and consists of many whorls. The whorls are high with concave whorl face. The most conspicuous sculptural feature is a bulge lacking knobs (or weakly knobby?) forming the periphery which is formed by two neighbouring whorls. The suture is not clearly visible on this bulge. A weak spiral cord is present directly below the bulge followed by two stronger spiral cords in abapical direction. All spiral cords are knobby. Base and aperture are incompletely preserved. At least one columellar and a parietal plait are present. The aperture seemingly has an abapical canal.

**Remarks.** Fischer and Weber (1997) designated a neotype for *N. ornata* and illustrated it (pl. 5, fig. 22). They considered this species to represent a synonym of *Nerinella subtricincta* d'Orbigny, 1852.

**Relationships.** *Nerinella elatior* d'Orbigny juv. sensu Fischer and Weber (1997) has more concave whorls, only a single strong, knobby spiral cord at mid-whorl and a distinctly weaker one above it. *Nerinella chantrei* Loriol sensu Cossmann (1898) is similar and has the same ornamentation but differs in having higher whorls, the whorl face is more concave, and besides knobby spiral cords it also has smooth ones. *Nerinea satagea* Loriol in Loriol and Pellat (1874) has a knobby bulge, the spiral cords on the whorls are of approximately equal strength, and the whorls are higher. *Nerinea greppini* Loriol, 1889 (in Loriol and Koby 1889–1892) has two knobby and two smooth spiral cords. *Nerinea* sp. sensu Hudleston (1880) has three approximately equally strong knobby spiral cords and its shell is slenderer. *Nerinea punctata* Quenstedt sensu Fiebelkorn (1893) has higher and more concave whorls; the knobs on the spiral cords are weaker (due to preservation?). *Nerinea subscalaris* Münster sensu Schlosser (1882) has a stronger bulge (knobby?), a more concave whorl face and two knobby spiral cords. *Nerinella subtricincta* (d'Orbigny) sensu Hägele (1997) has a weaker but knobby bulge and three equally strong knobby spiral cords. *Nerinea ornata* d'Orbigny sensu Loriol in Loriol and Lambert (1893) is slenderer and has higher whorls and the abapical spiral cord is weakest. *Nerinea fasciata* Voltz sensu Fiebelkorn (1893) has lower whorls that increase more rapidly in width, and it has more spiral cords.

### *Nerinella*? *subscalaris* (Münster in Goldfuss, 1844)

Plate 15: figs 6–12

*1844 – *Nerinella subscalaris* Münster – Goldfuss: 41, pl. 175, fig. 12.
*v1852 – *Nerinea uniplicata* – Quenstedt: 429, pl. 34, fig. 22.
?1852 – *Nerinea suprajurensis* – Quenstedt: 429, pl. 34, fig. 24.
v part1858 – *Nerinea punctata* Voltz, 1836 – Quenstedt: 767, pl. 94, figs 7–9 (original of fig. 8 seen).
v1858 – *Nerinea uniplicata* – Quenstedt: 766, pl. 94, fig. 6.
v*1858 – *Nerinea suevica* – Quenstedt: 767, pl. 94, fig. 10.
v1881–1884 – *Nerinea suevica* Quenstedt – Quenstedt: 525, pl. 205, figs 63–64.
v1881–1884 – *Nerinea uniplicata* – Quenstedt: 526, pl. 205, fig. 65.
v1881–1884 – *Nerinea subscalaris* Goldfuss – Quenstedt: 526, pl. 205, fig. 66.
vpart1881–1884 – *Nerinea punctata* Bronn, 1836 – Quenstedt: 527, pl. 205, figs 69–73 (original to fig. 73 seen).
1997 – *Cossmannea* (*Eunerinea*) *subscalaris* (Münster, 1844) – Hägele: 130, pl. 12, fig. 6 left, p. 130 fig. lower left.
1997 – *Nerinella suevica* (Quenstedt, 1858) – Hägele: 132, fig. p. 132 left middle.

**Material.** Thirteen specimens from Nattheim/Rinderberg, eight of which housed at BSPG (SNSB-BSPG 2021 XV 63–70), six specimens Tübingen: collection Quenstedt).

**Description.** A large specimen is 63 mm high. The shell is very slender. The whorls are high and separated by oblique sutures. They have a broad, nearly horizontal ramp that is demarcated from whorl face by a sharp edge forming the periphery. The whorl face is straight, somewhat tapering abapically. The details of the ornament are commonly obscured by poor preservation. The whorls are ornamented by a spiral cord at about mid-whorl. The originals of Quenstedt (1881–1884) show further spiral cords. The transition from whorl face to base is demarcated by a rounded bulge that is covered by the following whorl of the spire whorls. The base is moderately convex. The aperture is elongated, rhomboid with a long, almost vertical canal. The aperture has a strong parietal plait, one somewhat weaker columellar plait, and one palatal plait.

**Remarks.** Quenstedt (1858) erected *Nerinea constricta suevica* as a subspecies separate from *Nerinea suevica* that was introduced in the same year and in the same publication. The latter species, *Nerinea suevica*, is considered to represent a synonym of *Nerinella subscalaris* (Münster in Goldfuss, 1844) as is indicated in the synonymy list, whereas *Nerinea constricta suevica* is seen as a nomen dubium herein (see *Nerinea constricta dubia* Quenstedt).

**Relationships.** *Eunerinea* sp. 1 differs from *Nerinella*? *subscalaris* by having lower whorls, a row of stronger

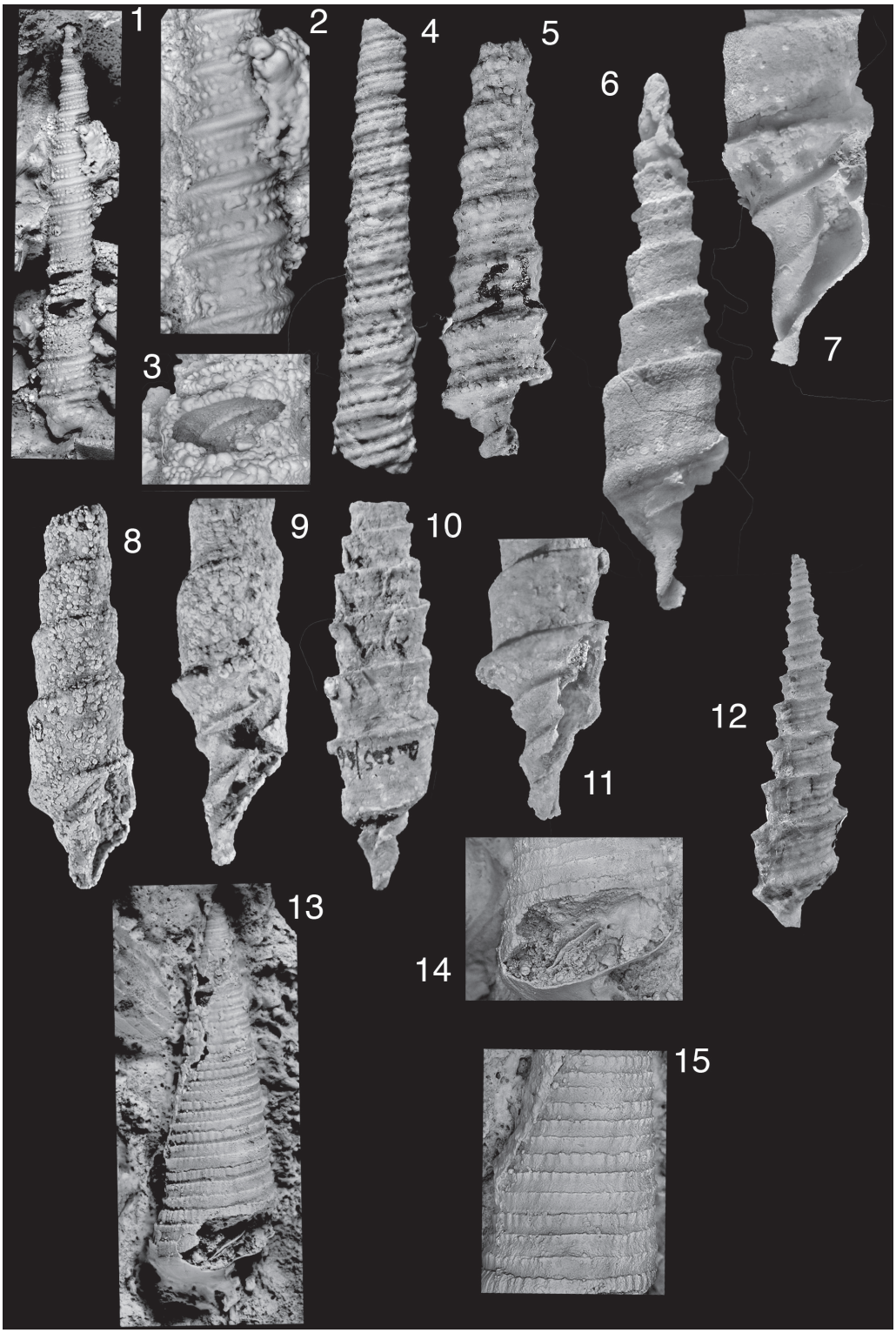


**Plate 15. (1–5)** *Nerinella ornata* (d'Orbigny, 1852). **(1–3)** SNSB-BSPG 2021 XV 72, Saal (collection Lang); **(1)** lateral view, height 33 mm; **(2)** detail of ornament, height 10 mm; **(3)** whorl with plait, height 3 mm. **(4)** University Tübingen (collection Quenstedt), Nattheim, lateral view, height 18 mm (original Quenstedt 1881–1884, pl. 205, fig. 74). **(5)** University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 14 mm (original to Quenstedt 1881–1884, pl. 205, fig. 75). **(6–12)** *Nerinella*? *subscalaris* (Münster in Goldfuss, 1844). **(6–7)** SNSB-BSPG 2021 XV 63, Nattheim–Rinderberg; **(6)** lateral view, height 64 mm; **(7)** last whorls with aperture, height 38 mm. **(8)** University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 40 mm (original Quenstedt 1881–1884, pl. 205, fig. 63). **(9)** University Tübingen (collection Quenstedt), Nattheim, lateral view, height ca. 30 mm (original to Quenstedt 1881–1884, pl. 205, fig. 64). **(10–11)** Collection University Tübingen (collection Quenstedt), Nattheim; **(10)** lateral view, height ca. 38 mm (original to Quenstedt 1881–1884, pl. 205, fig. 66); **(11)** last whorls with aperture, height ca. 20 mm. **(12)** Collection University Tübingen (collection Quenstedt), Nattheim, 26 mm, lateral view, height ca. 26 mm (original Quenstedt 1881–1884, pl. 205, fig. 73). **(13–15)** *Nerinella*? sp. 1, SNSB-BSPG 2021 XV 78, Saal (collection Lang); **(13)** lateral view, height 43 mm; **(14)** whorl with plaits, width 17 mm; **(15)** detail of ornament, height 17 mm.

nodes at mid-whorl, a less pronounced ramp and a more pronounced spiral cord at the transition from whorl face to base. *Nerinella turriculata* d'Orbigny sensu Cossmann (1898) has higher whorls in relation to their width, lacks a pronounced spiral cord at mid-whorl and also lacks a palatal plait. *Nerinella jollyana* d'Orbigny sensu Cossmann (1898) has four stronger and additional weak spiral cords on the whorl face. *Nerinella subelegans* Étallon sensu Cossmann (1898) has lower whorls and its whorl face is ornamented by alternating weak and strong spiral cords.

### *Nerinella*? sp. 1

Plate 15: figs 13–15

**Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 78.

**Description.** The specimen is 45 mm high and has a moderately broad shape. The whorls increase regularly in width. They are distinctly wider than high. The sutures are hardly visible. The whorls are ornamented with three spiral cords. The subsutural spiral cord is the most prominent one. All spiral cords bear small knobs. The largest knobs are on the subsutural spiral cord. In the last whorls, the knobs on the middle and suprasutural spiral cord become weaker. The base is flat and has an angular transition to the whorl face which is demarcated by a spiral cord that is probably not knobby. The growth lines on the base are prosocyrt. The aperture is not preserved. Only a strong palatal plait can be recognized.

**Relationships.** *Aphanoptyxis polyspira* (Quenstedt) sensu Hägele (1997) has spiral cords of equal strength on the whorl face, the aperture lacks plaits, and the ornament does not become weaker during ontogeny. *Nerinea nodospira* Quenstedt, 1881–1884 has four spiral cords on the whorl face, the knobby ornament is stronger, and the ornament does not become weaker during ontogeny. *Nerinea punctata* Voltz sensu Bronn (1836) has a weak ramp so that the whorls are well separated from each other and its ornament does not become weaker during ontogeny.

## Family Eunerineidae Kollmann, 2005

### Genus *Eunerinea* Cox, 1947

**Type species.** *Nerinea castor* d'Orbigny,1852; middle Oxfordian; France.

### *Eunerinea*? *sequana* (Bronn ex Thirria, 1836)

Plate 16: figs 1, 2

*1836 – *Nerinea sequana* Thirr. – Bronn: 561, pl. 6, fig. 6.
?1852 – *Nerinea speciosa* Voltz – d'Orbigny: 123, pl. 269, figs 1, 2.
?1997 – *Cossmannea* (*Eunerinea*) *sequana* (Bronn ex Thirria, 1836) – Fischer and Weber: 49.

**Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 74.

**Description.** The almost complete specimen is 42 mm high. The shell is slender. The whorls are regularly increasing in width forming an acutely conical shell. The whorls are relatively low with concave whorl face. The earliest whorls are poorly preserved. Later whorls seem to have a subsutural, weakly knobby bulge. The suture is barely visible. One or two weak knobby spiral cords below the bulge are present. The knobs of the bordering spiral cord emerge from the abapical suture. The whorl face is ornamented with broad, barely visible axial ribs. The base is flat and its transition to the whorl face is almost rectangular with a distinctly knobby bodering spiral cord. The base is entirely covered with numerous densely spaced, fine spiral cords. The aperture is not preserved; it probably has at least a columellar and a parietal plait.

**Relationships.** *Nerinea visurgis* Roemer sensu Bronn (1836) lacks a subsutural bulge, the knobs on the bordering spiral cord are smaller, the base is more convex and seemingly devoid of any ornament. *Nerinea tuberculosa* Defrance sensu Cossmann (1896) has a slenderer shell with higher whorls, lacks a weakly knobby spiral cord at mid-whorl, the knobs on the bordering spiral cord are smaller but more numerous and its base is smooth. *Nerinea speciosa* Voltz sensu Cossmann (1898) is slenderer, its whorls increase less rapidly in width and are higher and it has five spiral cords on the whorl face. *Nerinea posthuma* Zittel sensu Cossmann (1898) is much larger, its whorls are higher and its base lacks spiral cords.

### *Eunerinea*? *biplicata* (Quenstedt, 1858)

Plate 16: figs 3–9

*1858 – *Nerinea biplicata* – Quenstedt: 766, pl. 94, fig. 11.
1881–1884 – *Nerinea biplicata* – Quenstedt: 529, pl. 205, figs 76–77.

**Material.** Five specimens from Saal, collection Lang, four of which are illustrated (SNSB-BSPG 2021 XV 75–77, 107).

**Description.** The largest fragment is 58 mm high. The shell is slender. The whorls increase regularly in width. The sutures are situated in the middle of a bulge that is formed by two neighbouring whorls. The whorl face is distinctly concave. The whorl face is ornamented with broad, orthocline axial ribs that reach from suture to suture in early whorls but may be reduced on late whorls except of nodes. They are thickened and node-like near the sutures. The whorls are deepened and pit-like between the axial ribs at mid-whorl. Juvenile specimens have two spiral cords between the nodes. The base is flat, smooth, and distinctly umbilicated. The transition from base to whorl face is sharply angulated. Sections show that the aperture is rhomboid and has two columellar plaits, a parietal, a palatal, and a basal plait.

**Relationships.** *Nerinea* or else *Cossmannea* (*Eunerinea*) *sculpta* Étallon sensu Loriol in Loriol and Bourgeat (1886–1888), Cossmann (1898) and Hägele (1997) has stronger and probably also more axial ribs, a more strongly concave whorl face and, according to Loriol, lacks an umbilicus.

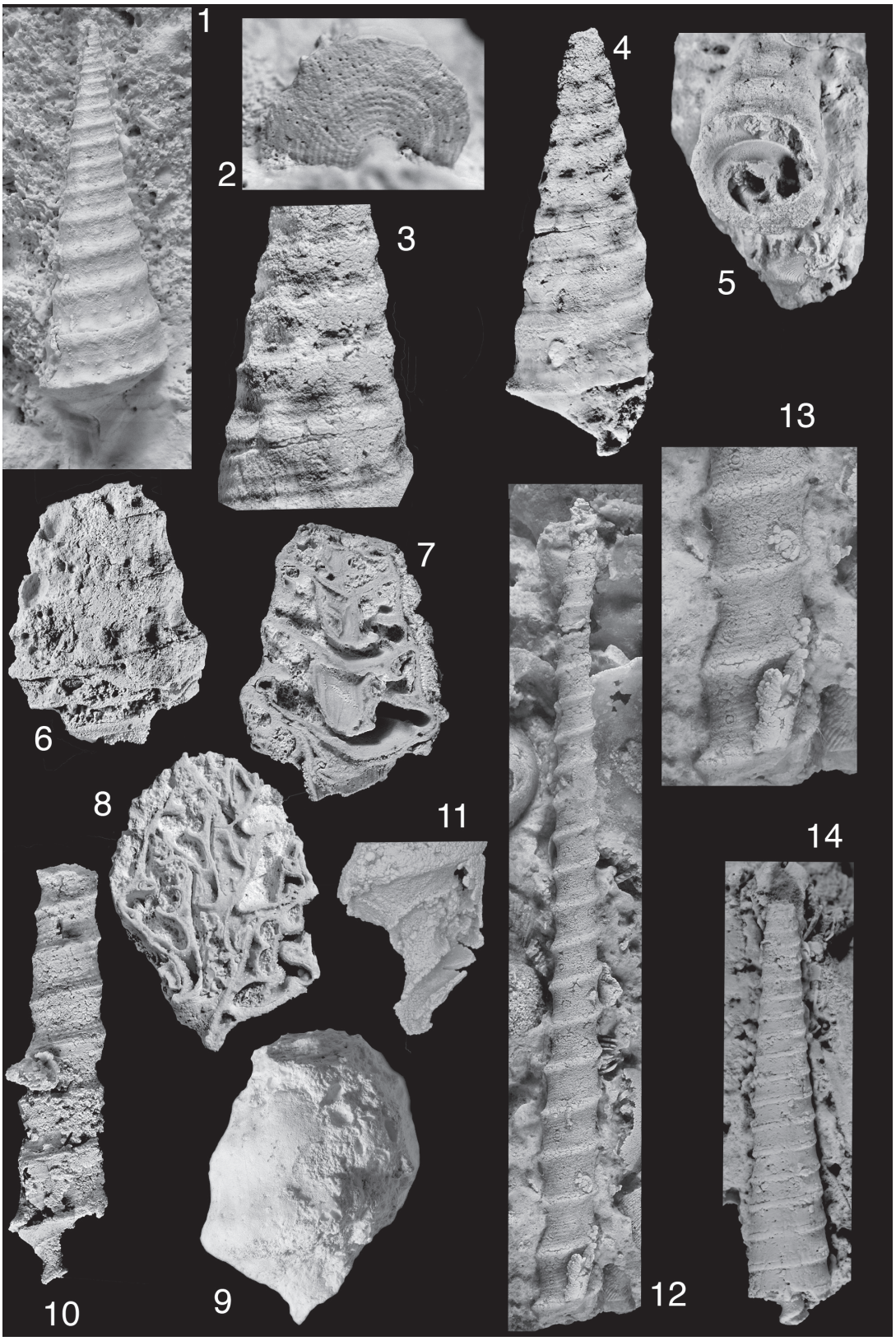


**Plate 16. (1–2)** *Eunerinea*? *sequana* (Bronn ex Thirria, 1836), SNSB-BSPG 2021 XV 74, Saal (collection Lang); **(1)** lateral view, height 42 mm; **(2)** base, width 13 mm. **(3–9)** *Eunerinea*? *biplicata* (Quenstedt, 1858). **(3–4)** SNSB-BSPG 2021 XV 75, Saal (collection Lang); **(3)** lateral view, height 36 mm; **(4)** shell detail, height 17 mm. **(5)** SNSB-BSPG 2021 XV 76, Saal (collection Lang), oblique view of base, width 16 mm. **(6–7)** SNSB-BSPG 2021 XV 77, Saal (collection Lang), lateral view and section, height 58 mm. **(8–9)** SNSB-BSPG 2021 XV 107, Saal (collection Lang), height 57 mm; **(8)** columellar section; **(9)** lateral view showing concave whorl face encrusted by colonial coral. **(10–13)** *Eunerinea* sp. nov. 1. **(10–11)** collection Sauerborn, Nattheim area; **(10)** lateral view, height 46.5 mm; **(11)** aperture, width 10 mm. **(12–13)** Collection Sauerborn, Nattheim area; **(12)** lateral view, height 120 mm; **(13)** detail of ornament, height 26 mm. **(14)** *Eunerinea* sp. 2; SNSB-BSPG 2021 XV 79 (collection Lang), lateral view, height 32 mm.

*Nerinea bicincta* Bronn sensu Goldfuss (1844) has stronger axial ribs, lacks spiral cords and seemingly also lacks an umbilicus. *Nerinea wosinskiana* Zeuschner, 1849 has lower whorls, stronger nodes and it allegedly has only two plaits. *Nerinea wosinskiana* Zeuschner sensu Gemmellaro (1870) has an only weakly concave whorl face, lacks spiral cords and has only a columellar plait. *Nerinea haidingeri* Peters, 1855 is slenderer, has higher whorls which increase less rapidly in width, lacks spiral cords, has stronger knobs, and lacks an umbilicus. *Nerinea incisa* Étallon sensu Cossmann (1898) has a slenderer shell, higher whorls, a more distinctly concave whorl face, and more spiral cords; the presence of an umbilicus was not mentioned for that species.

### *Eunerinea* sp. nov. 1

Plate 16: figs 10–13

**Material.** Three certain and a questionable specimen from the Nattheim area (all from the collection Sauerborn).

**Description.** A specimen is 120 mm high. The shell is very slender, needle-shaped. The shell has a pronounced bulge at the suture that is formed by two neighbouring whorls. The suture lies on this bulge. The whorl face is distinctly concave between the bulges where it is entirely covered with numerous weak spiral cords. Details of this ornament cannot be recognized because of insufficient preservation. The base is flat with an angular transition to the whorl face. The aperture is damaged in all specimens; it probably has a rhomboid outline and a distinct siphonal canal, a columellar plait that forms the adapical border of the canal, and a parietal plait.

**Remarks.** The illustrated specimen of *Nerinea terebra* Schübler sensu Goldfuss (1844) derives from Nattheim and could be identical with *Eunerinea* sp. nov. 1. The lack of spiral ornament in the specimen illustrated by Goldfuss (1844) and the lack of a palatal plait in *Eunerinea* sp. nov. 1 could be due to preservation. *Nerinea terebra* as described by Schübler (in Zieten 1830: pl. 36, fig. 3) is, however, not identical with the specimen figured by Goldfuss (1844): its shell is much broader, it has lower whorls and only a single, strong parietal plait in the aperture.

**Relationships.** *Nerinea contorta* Buvignier sensu Cossmann (1898) is even slenderer, has higher whorls, and its whorl face is more concave. Its whorl face is ornamented with four strong spiral cords and weaker ones between them. *Nerinella bononiensis* Loriol sensu Cossmann (1898) is somewhat less slender, its whorls are higher and the suture is not situated on the bulge. *Aptyxiella cottaldina* d'Orbigny sensu Cossmann (1898) has lower whorls and it lacks plaits in the aperture. *Nerinea contorta* Buvignier var. *sesostris* Krumbeck sensu Delpey (1939) has higher whorls, its whorl face is more concave, and it lacks distinct plaits.

### *Eunerinea* sp. 2

Plate 16: fig. 14

?part 1882 – *Aptyxis kelheimensis* sp. nov. – Schlosser: 77, ?pl. 11, figs 3, 7; non pl. 11, figs 4–6.

**Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 79.

**Description.** The specimen is 32 mm high. The early whorls are lacking. The shell is very slender. The whorls are very broad in relation to their height. The whorl face is concave. The suture is situated on a bulge that is formed by two neighbouring whorls. The bulge is demarcated abapically by a furrow-like deepening. There is no other ornament. The base and aperture are not preserved. Within the last preserved whorl, there are at least two columellar plaits. The aperture probably has a siphonal canal.

**Relationships.** *Aptyxis kelheimensis* Schlosser, 1882 is quite similar in part and possibly conspecific to the present specimen (Schlosser 1882, pl. 11, figs 3, 7; non figs 4–6). However, this species has several spiral cords and allegedly lacks plaits in the aperture. *Nerinea cincta* Münster in Goldfuss, 1844 is very similar but much younger (Gosau-Cretaceous) and has more concave whorls. *Nerinea goldfussi* d'Orbigny sensu Schlosser (1882) is much larger, has higher whorls and a spiral cord at mid-whorl. *Nerinea petersi* Gemmellaro, 1870 has a rounded transition from whorl face to base, the whorls are higher and the whorl face is less concave; the situation of the suture is unclear in this species. *Nerinea curmontensis* Loriol in Loriol, Royer and Tombek (1872) lacks a bulge, has a suprasutural row of knobs and a straight whorl face. *Nerinea cincta* Münster sensu Schafhäutl (1863) is much larger and has higher whorls. *Ptygmatis intermedia* Pchelintsev, 1926 and *P. exelsa* Pchelintsev, 1926 have higher whorls and a more convex base. *Nerinea bruntrutana* Thurmann sensu Zeuschner (1849) is larger, has a distinct umbilicus and its whorls increase more rapidly in width.

### *Eunerinea* sp. 1

Plate 17: figs 1–8

non1836 – *N. punctata* Voltz in litt. – Bronn: 559, pl. 6, fig. 23.

1886–1888 – *Nerinea subelegans* Étallon – Loriol in Loriol and Bourgeat: 110, pl. 11, figs 4–6.

1997 – *Nerinella elatior* (d'Orbigny, 1852), forme juvenile – Fischer and Weber: 52, pl. 5, fig. 5.

**Material.** Seven specimens from the Nattheim area (five specimens collection Quenstedt/Tübingen, two specimens collection Sauerborn), four specimens from Saal, collection Lang, one of which is illustrated (SNSB-BSPG 2021 XV 71).

**Description.** A large specimen is 30 mm high. The shell is very slender. The whorls are slowly increasing in width. The apical angle is somewhat variable. The whorl face is concave and ornamented with a subsutural bulge (smooth or knobby), with a strong and distinctly knobby spiral cord at approximately mid-whorl, and a narrow projecting bordering spiral cord that emerges above the suture. This cord demarcates the flat base from whorl face. Only very well preserved specimens show further weak spiral cords between adapical bulge and median spiral cord, and another between median spiral cord and abapical suture.

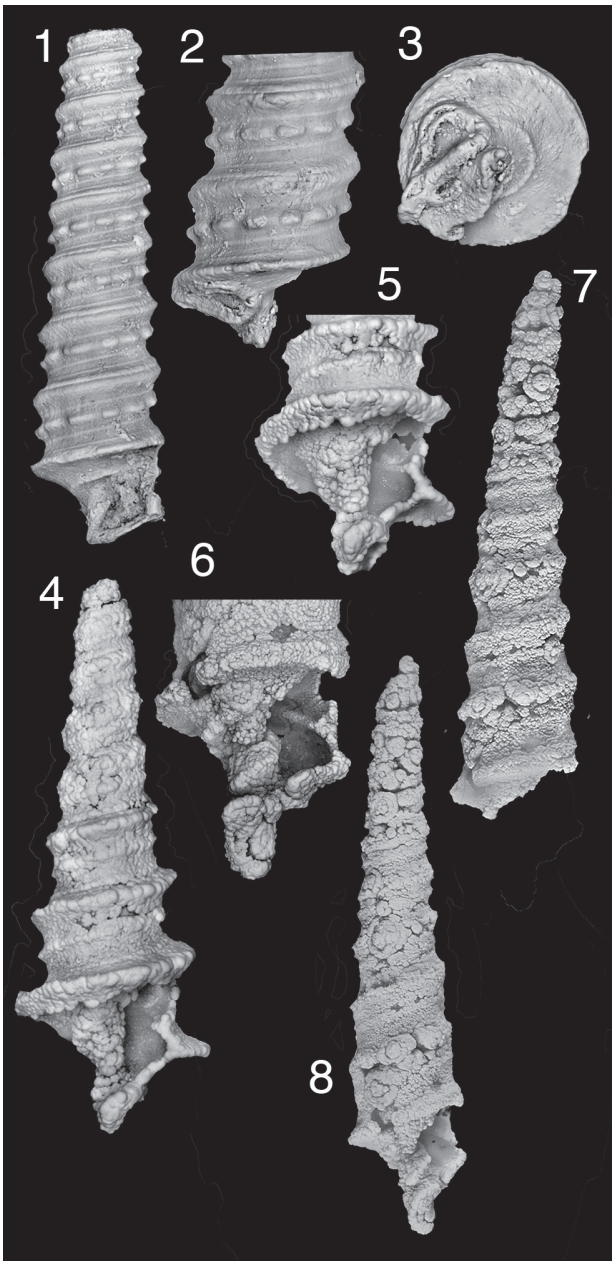


**Plate 17.** *Eunerinea* sp. 1. **(1–3)** SNSB-BSPG 2021 XV 71, Saal (collection Lang); **(1)** lateral view, height 15 mm; **(2)** last two whorls, height 4 mm; **(3)** base, width 3.7 mm. **(4–5)** Collection Sauerborn, Nattheim area; **(4)** lateral view, height 10.5 mm; **(5)** last whorls with aperture, height 3.4 mm. **(6–8)** Collection Sauerborn; Nattheim area; **(6)** last whorl with aperture, height of detail 6.5 mm; **(7–8)** lateral views, height 26 mm.

They are at least partly knobby. The base lacks ornament. The rhomboid aperture has a siphonal canal. It shows a columellar, a parietal, and a palatal plait.

**Remarks.** The present material assigned to this species is somewhat variable. The subsutural bulge is of various strength and, even if well preserved, is either smooth respectively knobby (in silicified specimens). It is possible that two very similar species are present. A possible identity with *Nerinella nodosa* (Voltz, 1836) remains unclear. This species differs from *Nerinella* sp. 1 by having a broader shell and more rapidly increasing whorls, an always knobby adapical bulge, a knobby spiral cord that is situated in most cases below mid-whorl, and a less projecting bordering spiral cord at the transition to the base. It is unclear whether these differences reflect preservation differences or not.

**Relationships.** Differences to *Nerinella subscalaris* (Münster in Goldfuss, 1844) are discussed under this taxon. *Nerinea punctata* Voltz, as described by Bronn (1836), with which Quenstedt (1881–1884) identified his species (*Nerinea punctata* Voltz sensu Quenstedt, 1858 and 1881–1884), has three knobby spiral cords of about equal strength and lacks the pronounced projection of the bordering spiral cord. *Nerinea ornata* d'Orbigny sensu Loriol in Loriol, Royer and Tombeck (1872) is similar but its subsutural bulge is less pronounced. *Nerinea hoheneggeri* Peters, 1855 has a row of knobs directly above the abapical suture and several crenulated, relatively weak spiral cords between the suprasutural row of knobs and a knobby spiral cord situated somewhat above mid-whorl. *Eunerinea hoheneggeri* Peters sensu Wieczorek (1998) has distinct knobs on the bulges. *Nerinea ornata* d'Orbigny and *N. tricincta* d'Orbigny sensu Cossmann (1898) have three strong knobby spiral cords as well as weaker not knobby spiral cords in their interspaces.

## Family Itieriidae Cossmann, 1896

### Genus *Itieroptygmatis* Charvet & Termier, 1971

**Type species.** *Itieroptygmatis ellipticata* Charvet & Termier, 1971; Jurassic/Cretaceous transition; Bosnia–Herzegovina.

### *Itieroptygmatis cylindrata* sp. nov.

https://zoobank.org/05FC3FC9-3FBE-4EE3-8FA8-0B64093E42EA
Plate 18: figs 1–14

?1882 – *Itieria austriaca* Zitt. – Schlosser: 84, pl. 12, figs 8, 9.
2017 – Nerineoidea Nr. 9a, b – Gründel: 33, pl. 15B–C.

**Derivatio nominis.** Latin *cylindratus* – cylindrical; according to the approximately cylindrical shell shape of the late teleoconch of this species.

**Holotype.** SNSB-BSPG 2021 XV 80, collection Lang.

**Locus typicus.** Saal Quarry near Kelheim.

**Stratum typicum.** Upper Kimmeridgian.

**Paratypes.** 45 specimens from Saal (43 specimens collection Lang, BSPG (SNSB-BSPG 2021 XV 81–84, 86, 109–146); one specimen collection Keupp, SNSB-BSPG 2021 XV 87, one specimen collection Schäfer, BSPG SNSB-BSPG 2021 XV 85; additional specimens on block with *Cassianopsis quenstedti* SNSB-BSPG 2015 VII 58.

**Material.** A total of 56 specimens from Saal, 46 types (see above) and 10 specimens without type status from private collections: 6 specimens collection Lang, 4 specimens collection Schäfer.

**Diagnosis.** The adapical part of the shell is slender with many whorls lacking a ramp. Later whorls are broad in relation to their height and have a ramp which becomes broader from whorl to whorl in most specimens. Below the

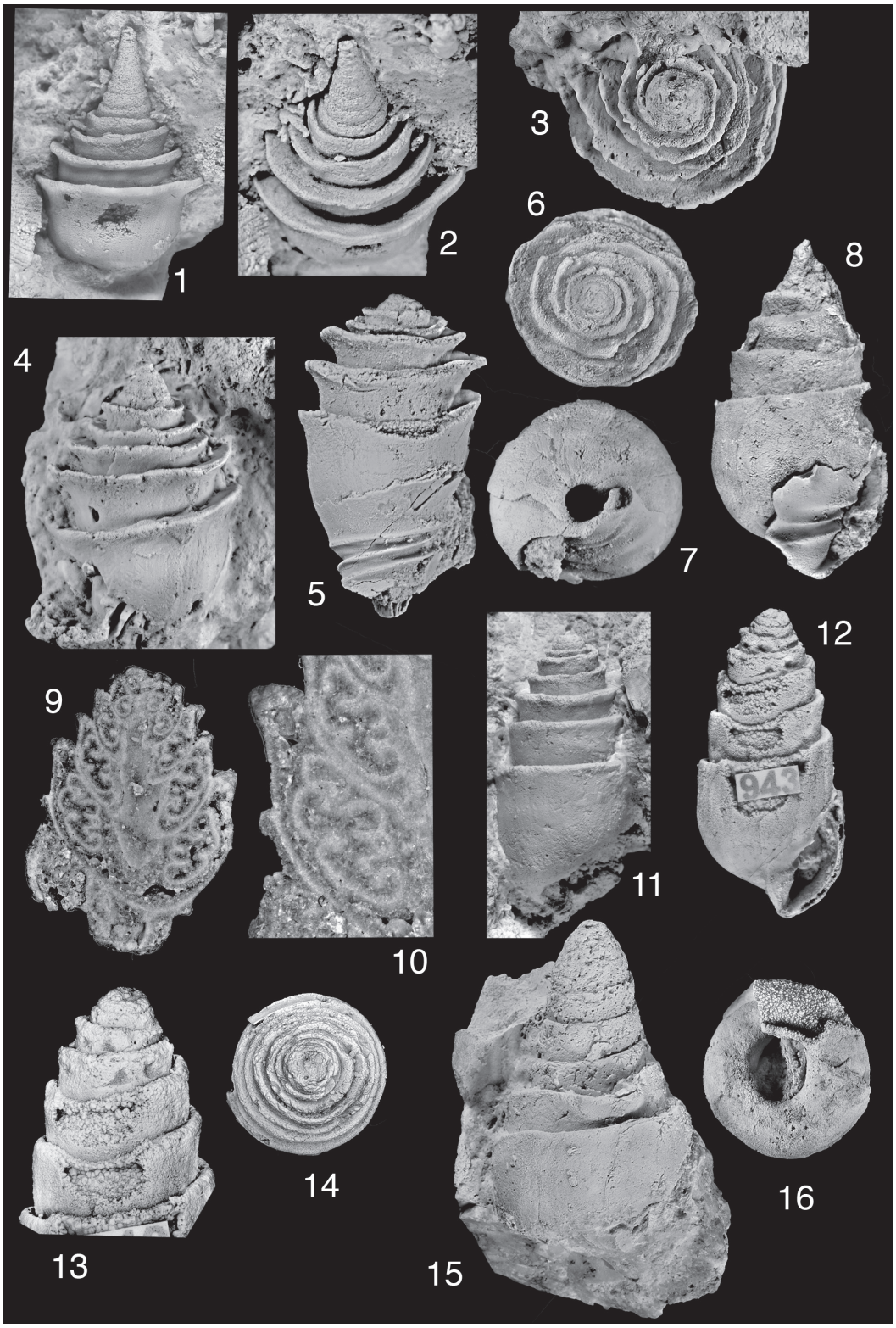


**Plate 18. (1–10)** *Itieroptygmatis cylindrata* sp. nov., morphotype 1. **(1–2)** Holotype, SNSB-BSPG 2021 XV 80, Saal (collection Lang); **(1)** lateral view, height 15 mm; **(2)** oblique view, width 5.5 mm (Gründel 2017, fig. 15 B). **(3–4)** Paratype, SNSB-BSPG 2021 XV 81, Saal (collection Lang), apical and lateral views, width 14 mm. **(5–6)** Paratype, SNSB-BSPG 2021 XV 82, Saal (collection Lang), apical and lateral views, width 16 mm (original Gründel 2017, fig. 15 C). **(7–8)** Paratype, SNSB-BSPG 2021 XV 83, Saal (collection Lang), basal and lateral views, width 15 mm. **(9–10)** Paratype, SNSB-BSPG 2021 XV 84, Saal (collection Lang); **(9)** columellar section, height 16 mm; **(10)** detail of (9), height 7.5 mm. **(11)** *Itieroptygmatis cylindrata* sp. nov., transition from morphotype 1 to morphotype 2, paratype, SNSB-BSPG 2021 XV 85, Saal (collection Schäfer), lateral view, height 33 mm. **(12–14)** *Itieroptygmatis cylindrata* sp. nov., morphotype 2, paratype, SNSB-BSPG 2021 XV 86, Saal (collection Lang), **(12)** lateral view, height 27 mm; **(13)** apex in lateral view, height 12 mm; **(14)** apical, width 13 mm. **(15–16)** *Itieroptygmatis* sp. 1. **(15)** SNSB-BSPG 2021 XV 88, Saal (collection Lang), lateral view, height 47 mm. **(16)** SNSB-BSPG 2021 XV 89, Saal (collection Lang), base, width 21 mm.

ramp, a weak concavity (lateral view) is developed; rarely, the ramp remains narrow and the concavity is lacking. The last whorls of large specimens increase only slowly in width and this part of the shell is more or less cylindrical. The transition from whorl face to base is evenly rounded without edge or spiral cord. Aperture with two columellar and palatal plaits and one parietal plait.

This species is present in two morphotypes and specimens that are intermediate:

- Morphotype 1: Plate 18: figs 1–10;
- Transition from morphotype 1 to morphotype 2: Plate 18: fig. 11;
- Morphotype 2: Plate 18: figs 12–14.

**Description.** A large specimen (early whorl missing) is 33 mm high. The early shell is very slender consisting of at least eight smooth whorls having a weakly convex whorl face and somewhat impressed sutures. The following 2–3 whorls increase rapidly in width and are very wide in relation to their height. As a result, the spire is coeloconoid. In the mentioned 2–3 whorls following the slender spire whorls, a broad, distinctly concave, funnel-shaped ramp is formed. From now on, the ontogenetic evolution of the shell follows different pathways leading to two varieties (morphotype 1 and 2 as well as to intermediate forms).

In morphotype 1 (much more abundant than morphotype 2), the wide ramp continues and becomes wider. It is delimited from whorl face by a broad concavity with indistinct borders. Initially, the whorls continue to rapidly increase in width. In large, more or less fully grown specimens, the increase in width decelerates, the last whorls are high and almost cylindrical in shape. The edge of the ramp is projecting abaxially and forms the whorl periphery.

In the other extreme form, morphotype 2, the rapid increase of the width of the whorls and the formation of a broad ramp is confined to 2–3 whorls. Afterwards, the whorls become wider and increase in width only slowly, but considerably increase in height. The ramp forms only a narrow band. The whorl face is straight and lacks a concavity below the ramp so that this part of the shell is almost cylindrical. As mentioned, there are transitional forms between varieties 1 and 2 (Plate 18: fig. 11).

All individuals have a continuous, rounded transition from whorl face to the strongly convex base. Base and whorl face are smooth. The base has a distinct umbilicus. The growth lines run straight and somewhat opisthocline on the whorl face and curve strongly backward below the ramp. The aperture is very narrow, adapically acute and has a weakly developed siphonal canal. The inner lip is broadened and detached in the columellar area; it partly covers the umbilicus. The inner lip bears a strong parietal and two columellar plaits. The adapical columellar plait is weaker than the abapical one. The aperture has two palatal plaits which are, however, rarely recognizable.

**Remarks.** *Itieria austriaca* Zittel as described by Schlosser (1882) closely resembles morphotype 2 of *Itieroptygmatis cylindrata* sp. nov. However, it has a distinctly lower last whorl in relation to its spire height. The real *Itieria austriaca* Zittel, 1873 differs distinctly from *Itieroptygmatis cylindrata* sp. nov. by lacking a ramp and by having a subsutural row of knobs.

**Relationships.** *Itieria* (*Campichia*) *pellati* Cossmann and *Itieria* (*Campichia*) *truncata* Pictet and Campiche, both sensu Cossmann (1916), resemble morphotype 1 of *Itieroptygmatis cylindrata* sp. nov. However, their spire is lower and has not as many whorls, the last whorl is much broader than the spire (having wide ramp only on a single whorl). *Itieria obtusiceps* Zittel, 1873 resembles morphotype 2 of *Itieroptygmatis cylindrata*. However, *I. obtusiceps* has a less distinct ramp, the spire is blunter, and the shell outline is more oval-shaped. *Phaneroptyxis nogreti* Guir. and Ogérien sensu Cossmann (1898) differs from morphotype 1 of *Itieroptygmatis cylindrata* sp. nov. by having a lower last whorl (in relation to spire height) in large specimens, lacking a wide ramp, and not having a cylindrical shape of the last whorl.

### *Itieroptygmatis* sp. 1

Plate 18: figs 15, 16

**Material.** Two juvenile specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 88, 89.

**Description.** A specimen is 47 mm high. The shell is moderately high-spired and coeloconoid. At least the first six whorls are moderately slender with whorls increasing slowly in width. The sutures are impressed. The whorls are smooth. The last two preserved whorls increase rapidly in width and at the same time, a furrow-like ramp is forming. The whorl face below the ramp is straight and the transition to the moderately convex base is evenly rounded. The base is smooth and has a wide umbilicus. The aperture is not preserved and it is unknown whether it has plaits.

**Remarks.** This incompletely preserved species shows the same ontogenetic change in shell shape as *I. cylindrata* sp. nov. but is distinctly larger.

**Relationships.** *Itieroptygmatis cylindrata* sp. nov. is considerably smaller and more gracile. *Phaneroptyxis* cf. *nogreti* sensu Hägele (1997) has whorls that are more regularly increasing in width across the entire shell and lacks a distinct ramp.

## Insufficienty known or problematic species of Nerineoidea

### *Nerinea constricta suevica* Quenstedt, 1858 nomen dubium

1852 – *Nerinea constricta* Roemer, 1836 – Quenstedt: 429, pl. 34, fig. 32.

*1858 – *Nerinea constricta suevica* – Quenstedt: 769, pl. 94, fig. 25.

*1881–84 – *Nerinea columelloides* – Quenstedt: 556, pl. 207, figs 16, 17.

**Remarks.** Two small fragments from the Nattheim area labelled *Nerinea constricta suevica* were found in the

collection of Quenstedt (1881–1884) of the Tübingen Institute. They probably represent two species because they have different apical angles (one very slender, the other distinctly broader). The slender specimen is probably the one illustrated by Quenstedt (1852: *N. constricta* Roemer, 1836; 1858: *Nerinea constricta suevica*; 1881–1884: *N. columelloides* Quenstedt). Because the original material is fragmentary, poorly preserved and probably represents two species, *N. constricta suevica* is herein considered a *nomen dubium*. It is (even according to Quenstedt 1881–1884) not identical with *Nerinea suevica* Quenstedt, 1858 (see under *Nerinella subscalaris* Münster, 1844 in Goldfuss).

### *Nerinea grandis nuda* Quenstedt, 1858 nomen dubium

part v*1858 – *Nerinea grandis nuda* – Quenstedt: 766, pl. 94, fig. 5 (non fig. 4).

part v1881–1884 – *Nerinea nuda* – Quenstedt: 553, pl. 207, fig. 1 (non fig. 2).

**Material.** One specimen (Tübingen: collection Quenstedt).

**Description.** The specimen illustrated by Quenstedt (1881–1884, pl. 207, fig. 1) is 77 mm high. It consists of well over two whorls. Half of the shell wall is broken off. The whorls are high, the whorl face is straight. The surface

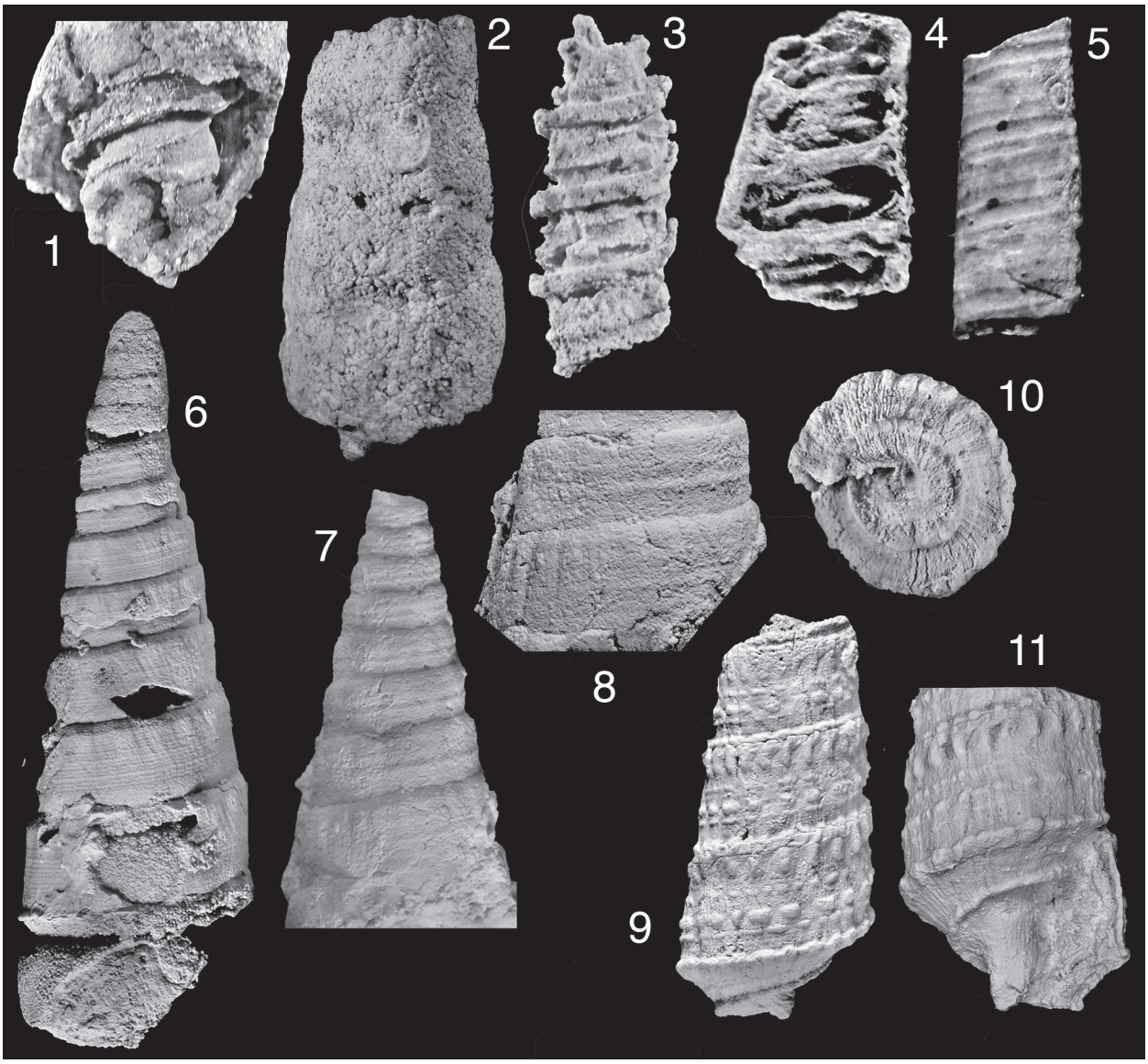


**Plate 19. (1–2)** *Nerinea bruntrutana* Thurmann, 1832 sensu Quenstedt (1881–1884); University Tübingen (collection Quenstedt), Nattheim; **(1)** aperture, height ca. 22 mm; **(2)** lateral view (original Quenstedt 1881–1884, pl. 206, fig. 2). **(3–4)** *Nerinea mandelslohi* Bronn sensu Quenstedt (1881–1884); **(3)** University Tübingen (collection Quenstedt), Nattheim, fragment in lateral view, height ca. 31 mm (original Quenstedt 1881–1884, pl. 206, fig. 11). **(4)** University Tübingen (collection Quenstedt), Nattheim, fragment in lateral view, height ca. 21 mm (original Quenstedt 1881–1884, pl. 206, fig. 12). **(5)** *Nerinea teres* (Goldfuss, 1844) sensu Quenstedt (1881–1884), collection University Tübingen (collection Quenstedt), Nattheim, fragment in lateral view, height 12 mm (original to Quenstedt 1881–1884, pl. 206, fig. 26). **(6–8)** *Nerinea*? sp. 1; **(6)** SNSB-BSPG 2021 XV 90, Saal (collection Lang), lateral view, height 67 mm. **(7–8)** SNSB-BSPG 2021 XV 91, Saal (collection Schäfer); **(7)** lateral view, height 21 mm; **(8)** detail of ornament, width 8.5 mm. **(9–11)** Gen. et sp. Indet, SNSB-BSPG 2021 XV 92, Saal (collection Lang); **(9)** lateral view, height 19 mm; **(10)** base, width 9 mm; **(11)** last whorls with aperture, height 12 mm.

of the whorls is completely encrusted. No ornament is visible. The suture is indicated with red ink but it is unclear whether this interpretation of the situation of the suture is correct. No plaits are visible inside the shell. Aperture and base are not preserved.

**Remarks.** Quenstedt (1858, 1881–1884) assigned two specimens to *Nerinea grandis nuda* which differ strongly from each other: a large and a small one. However, he considered only the specimen illustrated by him (Quenstedt 1858, pl. 94, fig. 5) as the „real *grandis nuda*" (p. 766). Referring to that, Geiger (1901) based *Aptyxiella quenstedti* Geiger, 1901 on the smaller specimen (see also treatment of that taxon herein). *Nerinea grandis nuda*, which is based on a fragment, cannot be sufficiently characterized and is here regarded as a *nomen dubium*. Geiger (1901) assigned this specimen to *Nerinea nantuacensis* d'Orbigny, 1851.

### *Nerinea bruntrutana* Thurmann, 1832 sensu Quenstedt (1881–1884)

Plate 19: figs 1, 2

v1881–1884 – *Nerinea bruntrutana* Thurmann – Quenstedt: 534, pl. 206, fig. 2.

**Remarks.** The fragmentary specimen from Nattheim that was assigned to *N. bruntrutana* by Quenstedt (1881–1884) consists of a single complete whorl and two whorls that are partially preserved. The shell is slender. The whorl face is weakly convex, without visible ornament. The sutures are weakly impressed. The base is not preserved. The aperture is strongly damaged. An umbilicus is present and filled with quartz. A strong and a weak columellar, a strong parietal, and a palatal plait are visible. A safe identification of this specimen is impossible. *Nerinea bruntrutana* Thurmann (in Thurmann and Étallon 1861–1864) differs significantly in having lower whorls that increase more rapidly in width, a straight whorl face, and weakly impressed suture.

### *Nerinea dilatata* d'Orbigny sensu Quenstedt (1881–1884)

1881–1884 – *Nerinea dilatata* d'Orbigny – Quenstedt: 550, pl. 206, fig. 61.

**Remarks.**Two indeterminable columella remains from Nattheim are present in the Quenstedt collection (Tübingen) and were assigned to *Nerinea dilatata* d'Orbigny. The whereabouts of the specimen illustrated by Quenstedt (1881–1884, pl. 206, fig. 61) is unknown.

### *Nerinea fasciata* Bronn, 1836 sensu Quenstedt (1858)

1858 – *Nerinea fasciata* Bronn, 1836 – Quenstedt: 770, pl. 94, fig. 18.

v1881–1884 – *Nerinea fasciata* Bronn – Quenstedt: 529, pl. 205, figs 78–81.

**Remarks.** Quenstedt's (1858, 1881–1884) material consists of four moderately to poorly preserved fragments that represent at least two to possibly three species. This material cannot be identified.

### *Nerinea mandelslohi* Bronn, 1836 sensu Quenstedt (1881–1884)

Plate 19: figs 3, 4

vpart 1858 – *Nerinea mandelslohi* Bronn, 1836 – Quenstedt: 767, pl. 94, figs 14, 15 (specimen in fig. 15 not seen).

v1881–1884 – *Nerinea mandelslohi* Bronn – Quenstedt: 535, pl. 206, figs 11, 12.

**Remarks.** The following statements are based on the study of the material from Nattheim figured by Quenstedt (1858, 1881–1884). The specimen illustrated by Quenstedt (1858, pl. 94, fig. 14 and 1881–1884, pl. 206, fig. 12) (herein Plate 19: fig. 4) is a fragment consisting of about two whorls. The shell wall is broken off at one side so that the columella with two plaits and a parietal plait are visible. The specimen illustrated by Quenstedt (1881–1884, pl. 206, fig. 11 (herein Plate 19: fig. 3) is a columellar fragment of about 2.5 whorls. Both mentioned specimens are undeterminable.

### *Nerinea pyramidalis* Münster in Goldfuss, 1844 sensu Quenstedt (1881–1884)

vpart 1881–1884 – *Nerinea pyramidalis* Münster in Goldfuss – Quenstedt: 549, pl. 206, figs 59, 60.

**Remarks.** Quenstedt (1881–1884) illustrated two specimens from Nattheim and assigned them to *Nerinea pyramidalis* Münster, 1844 in Goldfuss. The specimens illustrated by Quenstedt (1881–1884, pl. 206, fig. 59) could not be found. The other specimen is an undeterminable cast of an umbilicus.

### *Nerinea teres* Goldfuss, 1844 sensu Quenstedt (1881–1884)

Plate 19: fig. 5

v1881–1884 – *Nerinea teres* Goldfuss – Quenstedt: 540, pl. 206, fig. 26.

**Remarks.** The material representing *Nerinea teres* studied by Quenstedt (1881–1884) consists of five poorly preserved fragments. The best preserved one is figured here in Plate 19: fig. 5 (Quenstedt 1881–1884, pl. 206, fig. 26). It consists of about three whorls and is 12 mm high. Its whorl face is straight and ornamented with four equally strong spiral cords without knobs. The distance between the second and

third spiral cord is larger than the distance between the other cords. The sutures are barely impressed. The specimen illustrated by Quenstedt (1881–1884, pl. 206, fig. 25), which is of uncertain species identity, has a canal, two columellar plaits, and a parietal plait. The morphology of the outer lip is unknown. The fragment illustrated cannot be assigned with certainty to any of the species described herein.

### *Nerinea*? sp. 1

Plate 19: figs 6–8

**Material.** Two incomplete specimens from Saal (one specimen collection Lang, SNSB-BSPG 2021 XV 90, one specimen collection Schäfer, SNSB-BSPG 2021 XV 91).

**Description.** The larger specimen is 67 mm high. The multi-whorled shell is slender. The apical whorls are missing. The whorl height is about one third of its width. The whorl face is weakly convex to straight. The sutures are somewhat impressed. The early whorls are ornamented with 2–3 distinct spiral cords. The subsutural spiral cord is weakly knobby. Later whorls have numerous rather weak spiral cords (respectively lirae). Weak axial ribs emerge from the adapical suture and fade rapidly in an abapical direction. The base is flat with an angular transition to the whorl face. Other details are not preserved.

**Remarks.** The present material is too poorly preserved and cannot be identified.

**Relationships.** *Ptygmatis crassa* Étallon sensu Loriol in Loriol and Bourgeat (1886–1888) has higher whorls, a more distinct ramp and smaller knobs. *Nerinea guirandi* Loriol in Loriol & Bourgeat, 1886–1888 has higher whorls, a more distinct ramp and, at least on the early whorls, more distinct knobs. *Ptygmatis guirandi* Loriol sensu Cossmann (1898) has higher whorls, a more concave whorl face, and knobs are restricted to the early whorls.

### Gen. et sp. indet.

Plate 19: figs 9–11

**Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 92.

**Description.** The shell fragment is 19 mm high. The whorls are relatively high. The whorl face is straight. The sutures are indistinct. The whorls are ornamented with a subsutural row of axially elongated, opisthocline knobs. Below it, the whorl face is ornamented with three spiral cords: a weak upper one, then a stronger one and again a weak spiral cord. All spiral cords are knobby. The size of the knobs corresponds to the strength of the spiral cords. The knobs of the bordering spiral cord emerge from the abapical suture. The bordering spiral cord is strong and marks the angular transition from whorl face to the weakly convex base. The base is ornamented with at least one distinct spiral cord and possibly with additional weaker ones. The growth lines are weakly prosocyrt on the base and almost straight orthocline on the whorl face. They curve strongly backward immediately below the adapical suture. The aperture is rhomboid and has a siphonal canal. Only a single strong parietal plait is visible.

**Relationships.** *Nerinea binodosa* Étallon sensu Loriol in Loriol and Bourgeat (1886–1888: pl. 9, fig. 6) is larger, the adapical knobs are prosocline, it lacks a distinct row of knobs below mid-whorl, the knobs on the bordering spiral are larger, less numerous, almost fully exposed above the abapical suture, and the base is covered with distinct spiral cords. *Nerinea oppeli* Gemmellaro, 1870 is larger, the knobs on the bordering spiral are larger, almost fully exposed above the abapical suture, and the subsutural knobs are smaller and not as distinctly elongated. *Nerinea loreti* nom. mut. sensu Cossmann (1898) has higher whorls, a concave whorl face, the subsutural knobs are smaller and not elongated, the knobs on the bordering spiral are larger and almost fully exposed above the abapical suture, and its whorl face is covered with numerous spiral cords.

## Infraclass Euthyneura Spengel, 1881
## Superfamily Acteonoidea d'Orbigny, 1843
## Family Cylindrobullinidae Wenz, 1938

### Genus *Rugalindrites* Gründel & Nützel, 2012

**Type species.** *Acteon cuspidatus* Sowerby, 1824; Bathonian; England.

### *Rugalindrites cylindracea* (Cornuel, 1841)

Plate 20: figs 1–9

* 1841 – *Melania cylindracea* sp. nov. – Cornuel: 289, pl. 15, fig. 14.
1852 – *Actaeonina cylindracea* (Cornuel). – d'Orbigny: 179, pl. 288, fig. 9?
1874 – *Acteonina cylindracea* d'Orbigny (Cornuel) – Loriol in Loriol and Pellat: 295, pl. 6, fig. 7.
1895 – *Cylindrobullina cylindracea* Cornuel – Cossmann: 57, pl. 3, fig. 1, pl. 4, fig. 1, 2.
1997 – *Cylindrobullina cylindracea* (Cornuel, 1841) – Fischer and Weber: 69.
2017 – *Rugalindrites* sp. – Gründel: 33, pl. 15, fig. D

**Material.** Forty-eight mostly juvenile specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 93–97.

**Description.** A large specimen with damaged spire is 10 mm high. The shell is elongated fusiform. The last whorl is very high, cylindrical, tapering in abapical direction, embracing high on the previous whorl and covering most of it. The spire is relatively high for the genus and is acutely conical, consisting of several low whorls. A narrow but distinct horizontal ramp is formed early in ontogeny. The ramp is sharply demarcated from the whorl face by an edge. The shell is smooth. Growth lines are not visible, only on the ramp, remains of strengthened opisthocyrt growth lines are visible. The aperture is elongated, narrow and stretches over the entire height of the last whorl. Its adapical portion is narrow and acutely tapering. The abapical portion of the aperture is widened drop-shaped. The columellar portion of the

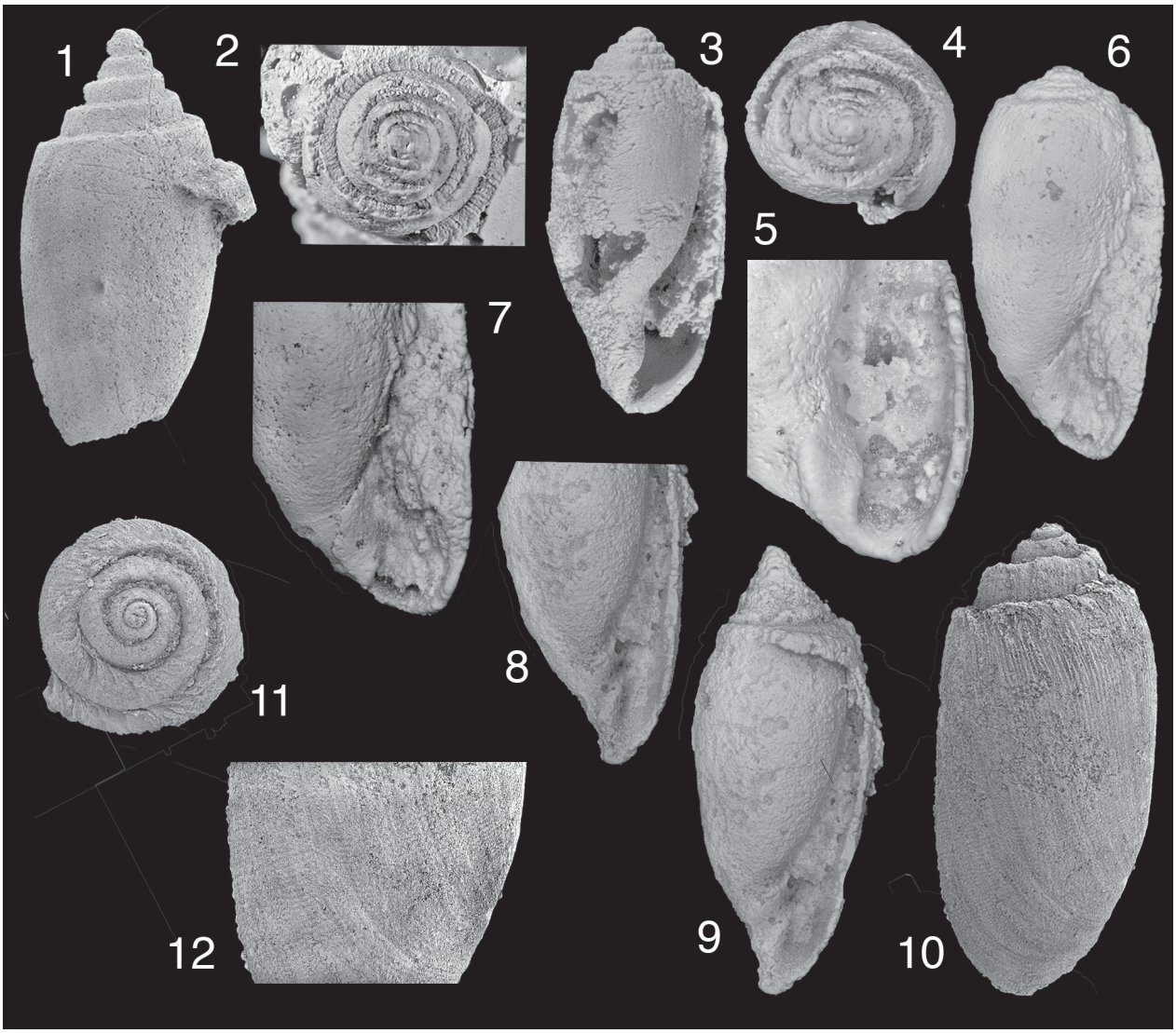


**Plate 20. (1–9)** *Rugalindrites cylindracea* (Cornuel, 1841). **(1)** SNSB-BSPG 2021 XV 93, Saal (collection Lang), lateral view, height 5 mm. **(2)** SNSB-BSPG 2021 XV 94, Saal (collection Lang), apical view, width 5.5 mm. **(3–4)** Saal (collection Lang), lateral and apical views (specimen lost). **(5)** SNSB-BSPG 2021 XV 95, Saal (collection Lang), aperture, height 3.5 mm. **(6–7)** SNSB-BSPG 2021 XV 96, Saal (collection Lang); **(6)** lateral view, height 8.5 mm; **(7)** aperture, height 3.5 mm. **(8–9)** SNSB-BSPG 2021 XV 97, Saal (collection Lang); **(8)** aperture, height 6 mm; **(9)** lateral view, height 9.5 mm. **(10–12)** *Rugalindrites* sp. 1, SNSB-BSPG 2021 XV 98, Saal (collection Lang); **(10)** lateral view, height 5.5 mm; **(11)** apical view, width 2.5 mm; **(12)** detail of ornament, height ca. 1.3 mm.

aperture is covered by callus which also covers parts of the base. The abapical delimitation of the callus is formed by a somewhat oblique plait which also demarcates the columellar area from the abapical edge of the aperture. A further weak plait forms the outer edge of the callus of the aperture.

**Remarks.** Columellar plaits are mostly not mentioned for *Rugalindrites cylindracea* possibly due to insufficient preservation of the specimens and due to the fact that the plaits are rather weak. Even in the present material, plaits are rarely visible.

**Relationships.** Differences to *Rugalindrites* sp. 1 are discussed below. *Cylindrobullina humbertina* Buvignier sensu Cossmann (1895) has a weaker and oblique ramp and its bordering edge is less pronounced. Moreover, it lacks a columellar callus with plaits. *Tornatina boutillieri* Cossmann, 1895 has a lower spire and the last whorl is cylindrical with straight whorl face. *Acteonina davidsoni* Loriol, 1874 (in Loriol and Pellat) has a lower spire, broader whorls, the last whorl is cylindrical and has a straight whorl face; columellar plaits have not been mentioned for this species.

### *Rugalindrites* sp. 1

Plate 20: figs 10–12

**Material.** Two specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 98.

**Description.** The larger specimen is 6 mm high. The overall shape closely resembles that of *Rugalindrites cylindracea*. The spire is distinctly elevated and gradate. The spire whorls increase more rapidly in height than in width due to a downward shift of the suture. The whorls have a narrow ramp with a more rounded transition to the whorl face. The growth lines are almost straight and weakly pro-

socline. In the upper part of the whorls, they are strengthened and thread-like. The growth lines are distinctly prosocyrt on the convex base. At about mid-whorl of the last whorl, there is a broad band with a micro-ornament of numerous spiral threads (Plate 20: fig. 12). The aperture is not preserved.

**Relationships.** *Rugalindrites cylindracea* (Cornuel, 1841) has a more convex whorl face, a higher spire, the edge that borders the ramp is more pronounced, it lacks spiral ornament and strengthened growth lines. *Cylindrobullina peroni* Cossmann, 1895, *Tornatina boutillieri* Cossmann, 1895, *Cylindrites nitidens* Loriol, 1889 (in Loriol and Koby 1889–1892), and *Actaeonina cylindracea* d'Orbigny sensu Loriol and Pellat (1874) are larger (some of them considerably larger), the edge that borders the ramp is more pronounced, and lack any visible ornament. *Cylindrobullina* cf. *disjuncta* Terquem and Jourdy sensu Nalivkin and Akimov (1917) has a stouter shell, is larger, and lacks ornament.

## Genus *Ptychocylindrites* Cossmann, 1895

**Type species.** *Bulla condati* Guirand & Ogérien, 1865; Kimmeridgian; Switzerland.

### *Ptychocylindrites condati* (Guirand & Ogérien, 1865)

Plate 21: figs 1, 2

* 1865 – *Bulla condati* sp. nov. – Guirand and Ogérien: 388, figs 38, 39.
1886–1888 – *Cylindrites condati* Guirand and Ogérien – Loriol in Loriol and Bourgeat: 51, pl. 3, figs 4, 5.
non 1893 – *Cylindrites condati* Guirand and Ogérien – Greppin: 26, pl. 3, fig. 9.
1895 – *Ptychocylindrites condati* Guir. et Ogér. – Cossmann: 89, pl. 4, figs 28–32.
1895 – *Ptychocylindrites condati* (Guir. et Og). – Cossmann: 72, pl. 3, figs 4–6.
1917 – *Ptychocylindrites caudati* Cossmann – Nalivkin and Akimov: 41, pl. 3, fig. 27.
1997 – *Cylindrites* (*Ptychocylindrites*) *condati* (Guirand & Ogérien, 1865) – Hägele: 120, fig. p. 121 upper right.
2012 – *Ptychocylindrites condati* (Guirand & Ogérien, 1865) – Gründel and Nützel: 37, fig. 3 d–f.

**Material.** One specimen from the Nattheim area (collection Sauerborn).

**Description.** The specimen is 13 mm high. The shell is slender, fusiforme and convolute with weakly convex flanks. The apex is blunt. The last whorl covers all previous ones in lateral view. Some of the earlier whorls can be seen in apical view. The adapical portion of the last whorl is bulging and possibly knobby (uncertain due to poor preservation). This portion of the shell is narrower than the portion below it and is demarcated by a shallow furrow. No ornament is visible. The damaged aperture stretches from the adapical furrow to the base. It is very narrow and somewhat broadened at its abapical termination. The columella has two strong plaits.

**Remarks.** Seemingly, only the type species *Ptychocylindrites condati* can be assigned to the genus *Ptychocylindrites* with certainty. It ranges from the Oxfordian to the Kimmeridgian according to the literature. It seems unclear whether this species was long-lived or several species have been identified as this taxon. *Cylindrites condati* sensu Greppin (1893) does not belong to this species. If Greppin's (1893) illustration is accurate, then this specimen represents a much slenderer, probably undescribed species. *Tornatellina corallina* sensu Quenstedt (1881–1884) differs significantly from *Ptychocylindrites condati*. It is slenderer and lacks a bulging adapical portion of the last whorl.

## Genus *Volvocylindrites* Cossmann, 1895

**Type species.** *Bulla marcousana* Guirand & Ogérien, 1865; Kimmeridgian; Switzerland.

### *Volvocylindrites marcousana* (Guirand & Ogérien, 1865)

Plate 21: figs 3–5

*1865 – *Bulla marcousana* sp. nov. – Guirand and Ogérien: 388, figs 40, 41.
1872 – *Volvula marcousana* Guirand et Ogérien – Loriol in Loriol, Royer and Tombeck: 72, pl. 5, fig. 8.
1886–1888 – *Volvula marcousana* Guirand et Ogérien – Loriol in Loriol and Bourgeat: 53, pl. 3, figs 6–9.
1893 – *Volvula marcousana* Guirand et Ogérien – Loriol in Loriol and Lambert: 13, pl. 1, fig. 4.
1895 – *Volvocylindrites marcousanus* Guir. et Ogér. – Cossmann: 87, pl. 4, fig. 14.
1927 – *Cylindrites extensus* nov. sp. – Maire: 122, pl. 6, figs 55–57.
2012 – *Volvocylindrites marcousana* (Guirand and Ogérien) – Gründel and Nützel: 37, fig. 3g–h.

**Material.** Thirty-nine mostly juvenile specimens from Saal, collection Lang, SNSB-BSPG 2021 XV 99, 100.

**Description.** The largest specimen is 12 mm high. The shell is slender cylindrical and convolute with tapering anterior portion. The last whorl completely covers all previous ones. No ornament is visible on the whorl face except of few spiral furrows on the abapical end of the shell in some specimens (not preserved in most specimens). The aperture stretches over the entire shell height. It is narrow and only somewhat widened anteriorly. It has a columellar callus with one or possibly two plaits.

**Remarks.** *Volvocylindrites marcousana* ranges from the (upper) Oxfordian to the upper Kimmeridgian according to the literature. Spiral furrows are not mentioned in published descriptions. According to the literature this species has one or two plaits on the columella. *Cylindrites*

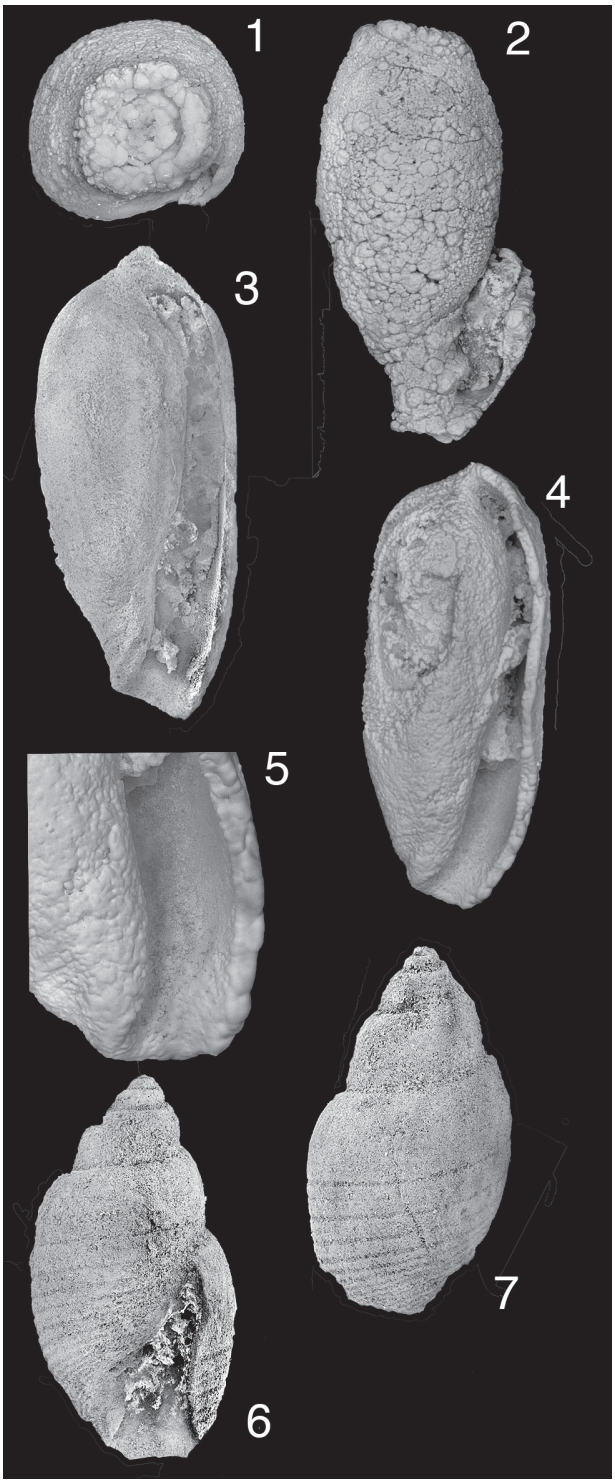


**Plate 21. (1–2)** *Ptychocylindrites condati* (Guirand & Ogérien, 1865), Nattheim (collection Sauerborn); **(1)** apical view, width 5 mm; **(2)** lateral view, height 12 mm. **(3–5)** *Volvocylindrites marcousana* (Guirand & Ogérien, 1865). **(3)** SNSB-BSPG 2021 XV 99, Saal (collection Lang), lateral view, height 5.5 mm. **(4–5)** SNSB-BSPG 2021 XV 100, Saal (collection Lang); **(4)** lateral view, height 8.8 mm; **(5)** aperture, height 3.2 mm. **(6–7)** *Sulcoactaeon* sp. 1, SNSB-BSPG 2021 XV 101, Saal (collection Lang), lateral views, height 3.7 mm.

*extensus* Maire, 1927 from the upper Rauracien (= middle Oxfordian) is similar but very slender. Similar slender forms have been illustrated by Loriol in Loriol and Bourgeat (1886–1888: pl. 3, figs 6–7) as *Volvula marcousana* from the upper Kimmeridgian of Valfin. These slender forms are interpreted herein as variations of *V. marcousana*.

### Familie Aplustridae Gray, 1847

### Genus *Sulcoactaeon* Cossmann, 1895

**Type species.** *Actaeon striatosulcatus* Zittel & Goubert, 1861; Oxfordian; France.

#### *Sulcoactaeon* sp. 1

Plate 21: figs 6, 7

?1997 –*Sulcoactaeon leblanci* (Loriol, 1875) – Hägele: 118, p. 118 below, 2nd fig. from left.

**Material.** One specimen from Saal, collection Lang, SNSB-BSPG 2021 XV 101.

**Description.** The shell is 4.2 mm high. It is slender oval. The last whorl is higher than the distinctly elevated and gradate spire. The whorl height increases rapidly by a downward shift of the suture. The sutures are accentuated by the presence of a narrow ramp. The whorl face is weakly convex. The spire whorls have a suprasutural spiral furrow. The transition from whorl face to the strongly convex base is evenly rounded. The base is entirely covered by spiral furrows (ca. 15). The furrows are widely distant to each other on the adapical portion of the base and become increasingly more narrowly spaced towards the abapical portion of the base. The aperture is elongated oval and acute posteriorly. The outer lip is convex. The inner lip consists of the parietal and columellar lips that meet at an obtuse angle. The columella terminates abruptly at the anterior margin of the aperture.

**Relationships.** *Sulcoactaeon leblanci* (Loriol) sensu Hägele (1997) is probably conspecific. However, its spire whorls are lower, it has a subsutural spiral cord, and the last whorl is broader and has a more convex outline.

## Discussion

With this final part or the study of the Late Jurassic gastropods from Saal and the Nattheim area, a total of five new families, 15 new genera, and all in all 156 species haven been reported (problematic species of Nerineoidea not included) (Gründel et al. 2015, 2017, 2019, herein) (Table 1). Of these species, 125 have been reported from Saal and 54 from the Nattheim area (Nattheim, Gerstetten, Gussenstadt, Blaubeuren, Bosler, all in Swabian Alb, about 140 km West of Saal). Only 23 species occur, both, at Saal and in the Nattheim area. A total of 100 nominate gastropod species have been identified, and among those 45 new species have been erected in this monographic series (Gründel et al. 2015, 2017, 2019, herein). The remainig 56 species were reported in open nomenclature, mainly due to insufficient preservation. The clade proportions are as follows:

**Table 1.** Species list of gastropods from the Saal quarry and the Nattheim area with abundances (number of specimens) and sublass attribution (Pat = Patellogastropoda, Vet = Vetigastropoda, Ner = Neritimorpha, Cae = Caenogastropoda, Het = Heterobranchia).

| | | Saal | Nattheim area |
|---|---|---|---|
| Pat | *Hennocquia saalensis* Gründel et al., 2017 | 3 | |
| Vet | *Emarginula* (*Tauschia*) sp. 1 | 1 | |
| Vet | *Rimulopsis broesamleni* Gründel et al., 2017 | 7 | 1 |
| Vet | *Rimulopsis perforata* Gründel et al., 2017 | 3 | |
| Vet | *Pleurotomaria agassizii* Münster in Goldfuss, 1844 | | 5 |
| Vet | *Bathrotomaria reticulata* (Sowerby, 1821) | | 2 |
| Vet | *Leptomaria goldfussi* (Sieberer, 1907) | 2 | 3 |
| Vet | *Leptomaria tuberosa* Gründel et al., 2017 | 3 | |
| Vet | *Pyrgotrochus* sp. 1 | | 2 |
| Vet | *Placostoma suevica* (Quenstedt, 1881–1884) | 6 | 1 |
| Vet | *Valfinia qinquecincta* (Zieten, 1830–1833) | 12 | 2 |
| Vet | *Scissurella*? sp. 1 | 1 | |
| Vet | *Falsotectus parvus* Gründel et al., 2017 | 76 | |
| Vet | *Falsotectus* sp. nov. 1 | 9 | |
| Vet | *Discotectus crassiplicatus* (Étallon, 1859) | 9 | |
| Vet | *Undatotectus glaber* Gründel et al., 2017 | 9 | |
| Vet | *Wernerocutus angulatoplicatus* (Münster in Goldfuss, 1844) | 5 | 11 |
| Vet | *Ambercyclus longinquus* (Quenstedt, 1881–1884) sensu Brösamlen (1909) | | 1 |
| Vet | *Eucycloscala*? *filifer* (Brösamlen, 1909) | | 4 |
| Vet | *Eucycloscala*? *anchura* (Münster in Goldfuss, 1844) | | 1 |
| Vet | *Marloffsteinia*? *funatoides* (Quenstedt, 1881–1884) | | 3 |
| Vet | *Eucycloscalidae*? gen. inc. sp. 1 | 1 | |
| Vet | *Chilodonta quadratofoveata* Gründel et al., 2017 | 3 | 1 |
| Vet | *Chilodonta haegelei* Gründel et al., 2017 | 1 | |
| Vet | *Odontoturbo suevicus* Brösamlen, 1909 | | 2 |
| Vet | *Onkospira ranellata* (Quenstedt, 1852) | 1 | 25 |
| Vet | *Onkospira*? *gussenstadtensis* (Quenstedt, 1881–1884) | | 5 |
| Vet | *Proconulus aequilineatus* (Münster in Goldfuss, 1844) | | 11 |
| Vet | *Proconulus*? sp. 1 | 3 | |
| Vet | *Amphitrochus muensteri* Gründel et al., 2017 | 1 | |
| Vet | *Amphitrochus*? *gerberi* Gründel et al., 2017 | 1 | |
| Vet | *Nododelphinula magnotuberosa* Gründel et al., 2017 | 2 | |
| Vet | *Heliacanthus*? sp. 1 | 1 | |
| Vet | *Nododelphinulidae*? gen. et sp. inc. 1 | 1 | |
| Vet | *Torusataphrus inornatus* (Quenstedt, 1858) | 1 | 3 |
| Vet | *Cochleochilus*? *longinquoides* (Quenstedt, 1881–84) | | 1 |
| Vet | *Metriomphalus parvotuberosus* Gründel et al., 2017 | 8 | |
| Vet | *Metriomphalus* sp. 1 | 8 | |
| Vet | *Planiturbo funatus* (Goldfuss, 1844) | | 1 |
| Vet | *Planiturbo procerus* Gründel et al., 2017 | 6 | |
| Vet | *Planiturbo validotuberosus* Gründel et al., 2017 | 7 | |
| Vet | *Caryomphalus funatoplicosus* (Quenstedt, 1858) | | 6 |
| Vet | *Caryomphalus concavus* Gründel et al., 2017 | 11 | |
| Vet | Metriomphalidae n. gen.? sp. 1 | 4 | 1 |
| Vet | Metriomphalidae? gen. et sp. inc. | | 2 |
| Vet | *Asperilla longispina* (Rolle, 1861) | | 5 |
| Vet | *Metriacanthus crenocarina* (Rolle, 1861) | | 1 |
| Vet | *Tegulacanthus tegulatus* (Münster in Goldfuss, 1844) | 1 | 22 |
| Vet | *Sclarotrarda coronilla* (Brösamlen, 1909) | 6 | 2 |
| Vet | *"Scalaria" tenuis* Brösamlen, 1909 | | 1 |
| Vet | gen. inc., sp. inc. | 9 | |
| Ner | *Dauterria rotundata* Gründel et al., 2015 | 110 | |
| Ner | *Dauterria variocostata* Gründel et al., 2015 | 100 | |
| Ner | *Pileopsella biconvexa* Gründel et al., 2015 | 6 | |
| Ner | *Neridomus laevis* (Gerasimov, 1955)? | 112 | |
| Ner | *Neridomus* sp. 1 | 2 | |
| Ner | *Parvulatopsis quinquecostatus* Gründel et al., 2015 | 33 | |
| Ner | *Wallowiella* (*Plicaropsis*) *cancellata* (Stahl, 1824) | 28 | 19 |
| Ner | *Wallowiella* (*Plicaropsis*) *compacta* Gründel et al., 2015 | 2 | |
| Ner | *Cassianopsis quenstedti* (Brösamlen, 1909) | 7 | 1 |
| Ner | *Cassianopsis ratua* Gründel et al., 2015 | 2 | |
| Ner | *Cassianopsis eversi* Gründel et al., 2015 | 5 | |
| Ner | *Hayamiella schaeferi* Gründel et al., 2015 | 12 | 1 |
| Ner | *Hayamiella decussata* (Münster in Goldfuss, 1844) | | 3 |
| Ner | *Hayamiella semiplicata* (Brösamlen, 1909) | 2 | 2 |
| Ner | *Bipartopsis robustus* Gründel et al., 2015 | 8 | |
| Cae | *Rugosacyclus rugosus* (Brösamlen, 1909) | | 1 |
| Cae | *Pseudomelania* sp. 1 | 8 | |
| Cae | *Pseudomelania*? sp. 2 | 7 | |
| Cae | *Saalensia birugata* Gründel et al., 2015 | 42 | 1 |
| Cae | *Petersia* sp. 1 | 1 | |
| Cae | *Costazygia* sp. 1 | 3 | |
| Cae | *Erratopleura* sp. 1 | 1 | |
| Cae | *Ampullina* sp. 1 | 7 | |
| Cae | *Pictavia silicea* (Quenstedt, 1858) | 1 | |
| Cae | *Pictavia lactera* Gründel et al., 2019 | 2 | |
| Cae | *Pictavia*? sp. 1 | 1 | |
| Cae | *Gymnocerithium*? *convexoconcavum* Gründel et al., 2019 | 10 | |
| Cae | *Metacerithium nodospirum* (Quenstedt, 1881–1884) | | 5 |
| Cae | *Metacerithium* sp. 1 | 15 | |
| Cae | *Tylostoma* sp. 1 | 6 | |
| Cae | *Ditretus* sp., cf. *rostellaria* (Buvignier, 1852) | 3 | |
| Cae | *Coninoda strekwera* Gründel et al., 2019 | 10 | |
| Cae | *Coninoda*? sp. 1 | 5 | |
| Cae | *Maoraxis* sp. 1 | 1 | |
| Cae | *Cryptoptyxis rarenodosa* Gründel et al., 2019 | 21 | |
| Cae | *Nudivagus* sp. 1 | 5 | |
| Cae | *Nudivagus*? sp. 2 | | 1 |
| Cae | *Uchauxia* ex gr. *limaeforme* (Roemer, 1836) | 44 | |
| Cae | *Provolibathra*? sp., cf. *septemplicata* (Roemer, 1836) | 69 | |
| Cae | *Cryptaulax*? *parvum* Gründel et al., 2019 | 3 | |
| Cae | *Cryptaulax*? *triangulare* Gründel et al., 2019 | 3 | |
| Cae | *Tyrnoviella* sp. 1 | 1 | |
| Cae | *Exelissa* sp. 1 | 2 | |
| Cae | *Shurovites robustus* Gründel et al., 2019 | 5 | |
| Cae | *Shurovites* sp. 1 | 1 | |
| Cae | *Tropacerithium cumaritum* Gründel et al., 2019 | 9 | |
| Cae | *Tropacerithium danubii* Gründel et al., 2019 | 15 | |
| Cae | *Bleytonella saalensis* Gründel et al., 2019 | 10 | |
| Cae | Juvenile cerithioid | 1 | |
| Cae | *Palaeorissoina* sp. 1 | 1 | |
| Cae | *Boreomica costaspiralis* Gründel et al., 2019 | 10 | |
| Cae | *Boreomica* sp. | 1 | |
| Cae | *Boreomica* sp. 2 | 1 | |
| Cae | *Buvignieria* sp. nov. 1 | 2 | |
| Cae | *Buvignieria racitana* Gründel et al., 2019 | 106 | |
| Cae | *Buvignieria convexa* Gründel et al., 2019 | 14 | |
| Cae | Palaeorissoinidae? gen. inc., sp. 1 | 1 | |
| Cae | *Falsobuvigna peregrina* Gründel et al., 2019 | 24 | |
| Cae | *Columbellaria corallina* (Quenstedt, 1852) | 7 | |
| Cae | *Columbellaria* sp. 1 | 1 | |
| Cae | *Columbellaria globosa* (Brösamlen, 1909) | | 1 |
| Cae | Strombidae gen. inc., sp. 1 | 1 | |
| Cae | *Diarthema* sp. 1 | | 2 |
| Cae | *Diempterus* sp. 1 | 4 | |
| Cae | *Diempterus*? *fusiformis* (Münster in Goldfuss, 1844) | 5 | 6 |
| Het | *Cossmannea desvoidyi* (d'Orbigny, 1851) | | 2 |
| Het | *Aptyxiella planata* (Quenstedt, 1858) | | 2 |
| Het | *Aptyxiella quenstedti* Geiger, 1901 | | 1 |

| | | Saal | Nattheim area |
|---|---|---|---|
| Het | *Ceritellopsis gramanni* Huckriede, 1967 | 25 | |
| Het | *Ceritellopsis plicatula* Huckriede, 1967 | 5 | |
| Het | *Ceritella convexa* Gründel et al., 2022 | 26 | |
| Het | *Ceritella* sp. 1 | 9 | |
| Het | *Nerinea donosa* Gründel et al., 2022 | 10 | |
| Het | *Endoplocus acutus* Gründel et al., 2022 | 17 | |
| Het | *Endoplocus inflatus* Gründel et al., 2022 | 10 | |
| Het | *Ptygmatis pseudomelaniformis* Gründel et al., 2022 | 37 | |
| Het | *Ptygmatis mandelslohi* (Bronn, 1836) | 4 | |
| Het | *Ptygmatis tornata* (Quenstedt, 1852) | 37 | 3 |
| Het | *Ptygmatis nodosa* (Voltz, 1836) | 142 | |
| Het | *Ptygmatis*? *polyspira* (Quenstedt, 1884 | | 1 |
| Het | *Ptygmatis*? *ursicina* Thurmann in Thurmann & Étallon, 1861 | 19 | |
| Het | *Bactroptyxis teres* (Münster in Goldfuss, 1844) | | 2 |
| Het | *Bactroptyxis*? *tricincta* (Münster, 1844) | 1 | |
| Het | *Bactroptyxis*? *tricincta* (Münster, 1844) sensu Quenstedt 1881–1884 | 3 | 1 |
| Het | *Bactroptyxis* cf. *fasciata* (Voltz, 1836) | 1 | |
| Het | *Bactroptyxis*? *subcochlearis* (Münster in Goldfuss, 1844) | 5 | 2 |
| Het | *Polyptyxisella clio* (d'Orbigny, 1852) | 2 | |
| Het | *Cryptoplocus depressus* (Voltz, 1836) | 3 | 10 |
| Het | *Cryptoplocus subpyramidalis* (Münster, 1844 in Goldfuss) | 3 | |
| Het | *Nerinella subscalaris* (Münster, 1844 in Goldfuss) | | 19 |
| Het | *Nerinella* sp. 1 | 4 | 7 |
| Het | *Nerinella ornata* (d'Orbigny, 1852) | 1 | 2 |
| Het | *Nerinella* sp. 2 | 2 | |
| Het | *Nerinella sequana* (Bronn ex Thirria, 1836) | 1 | |
| Het | *Nerinella biplicata* (Quenstedt, 1858) | 4 | |
| Het | *Nerinella*? sp. 3 | 1 | |
| Het | *Eunerinea* sp. 1 | | 3 |
| Het | *Eunerinea* sp. 2 | 1 | |
| Het | *Itieroptygmatis cylindrata* Gründel et al., 2022 | 57 | |
| Het | *Itieroptygmatis* sp. 1 | 2 | |
| Het | *Rugalindrites cylindracea* (Cornuel, 1841) | 48 | |
| Het | *Rugalindrites* sp. 1 | 2 | |
| Het | *Ptychocylindrites condati* (Guirand & Ogérien, 1865) | | 1 |
| Het | *Volvocylindrites marcousana* (Guirand & Ogérien, 1865) | 39 | |
| Het | *Sulcoactaeon* sp. 1 | 1 | |
| | | 1663 | 224 |

| | |
|---|---|
| Patellogastropda | 1 species |
| Vetigastropoda | 50 species |
| Neritimorpha | 15 species |
| Caenogastropoda | 50 species |
| Heterobranchia | 40 species. |

Vetigastropoda and Neritimorpha are rather diverse when compared with Early to Late Jurassic soft-bottom communities from shales of South Germany that were studied in the last years (e.g., Schröder 1995; Gründel et al. 2011; Schulbert and Nützel 2013; Gründel and Nützel 2015; Nützel and Gründel 2015). Especially the high neritimorph diversity is remarkable when compared with other faunas and is probably due to their hard substrate, shallow water preference. The generic diversity of Pleurotomariida (Vetigastropoda) is also still relatively high, given that this group is today restricted to deeper water settings. Pleurotomariida occur in shallow water settings until the Late Cretaceous (Kiel and Bandel 2004). Middle and Late Jurassic faunas reported from clays (soft bottom) of Poland and Russia are, however, dominated for the most part by small caenogastropods and heterobranchs, whereas Vetigastropoda and Neritimorpha are mostly rare (Guzhov 2004; Kaim 2004). It is likely that the strong lithification of the calcareous rocks in Saal produces a bias against small caenogastropod and heterobranch species when compared with faunas from shales that can be easily disaggregated so that such species can be retrieved (liberation effect sensu Roden et al. 2020). Moreover, neritimorphs and vetigastropods commonly have calcitic outer shell layers which facilitate preservation. However, abundance and diversity of Vetigastropoda and Neritimorpha preserves an original signal. The abundance and diversity of nerineoids (Heterobranchia) in the calcareous rocks of South Germany is typical of Late Jurassic shallow water carbonates.

The sample sizes (number of specimens) from Saal and the Nattheim area differ considerably and few species are shared. Diversity indices and rarefaction analysis suggest the same high diversity at both sites (Tables 1, 2). Diversity indices suggest a very high gastropod diversity which can be expected for a tropical reef associated fauna. The gastropod diversity of both studied Late Jurassic sites even exceeds that of the reef associated Late Triassic gastropod fauna of the St. Cassian Formation (N Italy) as is indicated by rarefaction at sample size of 200 individuals (around 40 expected species in the St. Cassian samples from Stuores Meadows and Alpe di Specie (Hausmann and Nützel 2015), and ca. 50 at Saal and Nattheim).

The gastropod fauna from the Saal quarry has yielded particularly much new information – all new species are based on specimens from Saal with only two of the new species also being present in the Nattheim area. The considerable sampling effort including the sample technique applied by one of us (FL, see Methods section above) resulted in the recovery of large numbers of mostly small and well-preserved specimens.

With 125 gastropod species from a single outcrop, the diversity at the Saal quarry is the highest from the Kimmeridgian worldwide that we are aware of. Moreover, a new collection from Saal currently under study will yield even more gastropod species so that likely more than 150 gastropod species are present in the Saal quarry. In addition, numerous other macro-invertebrates have been recovered from the Saal quarry; the following species (or genus) numbers were reported by Lang et al. (2017):

**Table 2.** Diversity of the gastropod fauna from Saal and from the Nattheim area (Nattheim, Gerstetten, Gussenstadt, Blaubeuren, Bosler, all in Swabian Alb); number of indiduals, species richness, Simpson- and Shannon index, rarefaction at 200 specimens: expected species richness; both gastropod faunas have the same diversity although few species are shared.

| | Individuals | Species | Simpson | Shannon | Rarefaction at 200 spcms. |
|---|---|---|---|---|---|
| Saal | 1663 | 125 | 0.96 | 3.864 | 50 exp. Species |
| Nattheim | 224 | 54 | 0.95 | 3.417 | 52 exp. Species |

bivalves: 33 (up to 50 according to Werner oral communication 2022)
ammonites: 6
brachiopods: 13
serpulids: 8
echinids: 7
corals: 27 (genera)
arthropods: 19
and others (e.g. sponges)

In total, up to 300 species of macro-invertebrate species have been reported from this quarry, which is a very high point diversity. Gastropods are by far the most diverse group from Saal, which is a modern aspect of this fauna (see also Roden et al. 2020, who found another example for early gastropod dominance in the Late Triassic St. Cassian Formation).

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