Latest Triassic bivalves and gastropods from South Germany – implications for the end-Triassic mass extinction and the early evolution of veneroid bivalves

Alexander Nützel, Martin Nose & Michael Hautmann

A fossil assemblage of small bivalves and gastropods from the latest Triassic (Rhaetian) Kössen Formation at the Brauneck Mountain in the Bavarian Alps is reported. It consists of the bivalve species *Pseudocorbula alpina* (Winkler, 1859) and at least three gastropod species including *Ampezzopleura brauneckensis* sp. nov. and *Jurilda stoppanii* (Winkler, 1861) comb. nov. The fossils are well-preserved including protoconch preservation in the gastropods and preserved hinges in the bivalves. The gastropod genera *Ampezzopleura* and *Jurilda* are reported from the Rhaetian for the first time. Both genera are also known from pre-Rhaetian and post-Triassic strata and hence they survived the end-Triassic mass extinction event. Their occurrence in the Rhaetian fills a gap in their stratigraphic distribution and removes them from the list of Rhaetian Lazarus taxa. The new material of *Pseudocorbula alpina* (Winkler, 1859) demonstrates a dentition of the AI, AIII, 3b, PI, PIII / AII, AIV, 2, 4b, PII type, which was possibly ancestral to the isocyprinid hinge of early veneroids. Therefore, *Pseudocorbula alpina* provides insights into the early evolution of the Venerida, which are among the most specious bivalve clades today. • Key words: Kössen Formation, Northern Calcareous Alps, Rhaetian, Euheterodonta, Caenogastropoda, Heterobranchia.

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The Northern Calcareous Alps are the classical area for the palaeontology of the latest Triassic. It is here, where Gümbel (1859) named the Rhaetian Formation, which today is the Rhaetian Stage. These latest Triassic strata consist of thick reef carbonates and argillaceous basin sediments – the latter represent the Kössen Formation.

At least locally, these sediments are very fossiliferous and hence, this region and formation is a key area for the understanding of the end-Triassic mass extinction event (*e.g.* Hautmann 2004, McRoberts *et al*. 2012, Mette *et al.* 2012). Numerous papers on the fauna of the latest Triassic of the Northern Calcareous Alp have been published since the 19th century (Winkler 1859, 1861; Schafhäutl 1863; Dittmar 1864), but, as demonstrated in this paper, the knowledge of this fauna is nevertheless incomplete and commonly lacks detail.

An assemblage of relatively well-preserved small gastropods and bivalves from the latest Triassic (Rhaetian) Kössen Formation at the Brauneck Mountain in the Bavarian Alps is described herein. The study of that sample is complemented by the documentation of previously collected material from the Kössen Formation of the Kotalm (Wendelstein). Although the Kössen Formation is fossiliferous and rich in molluscs, modern faunistic studies are scarce. In the light of its age, right before the end-Triassic mass extinction event, studies that improve taxonomy and document hitherto unknown taxa are needed for a better understanding of the impact of this important event.

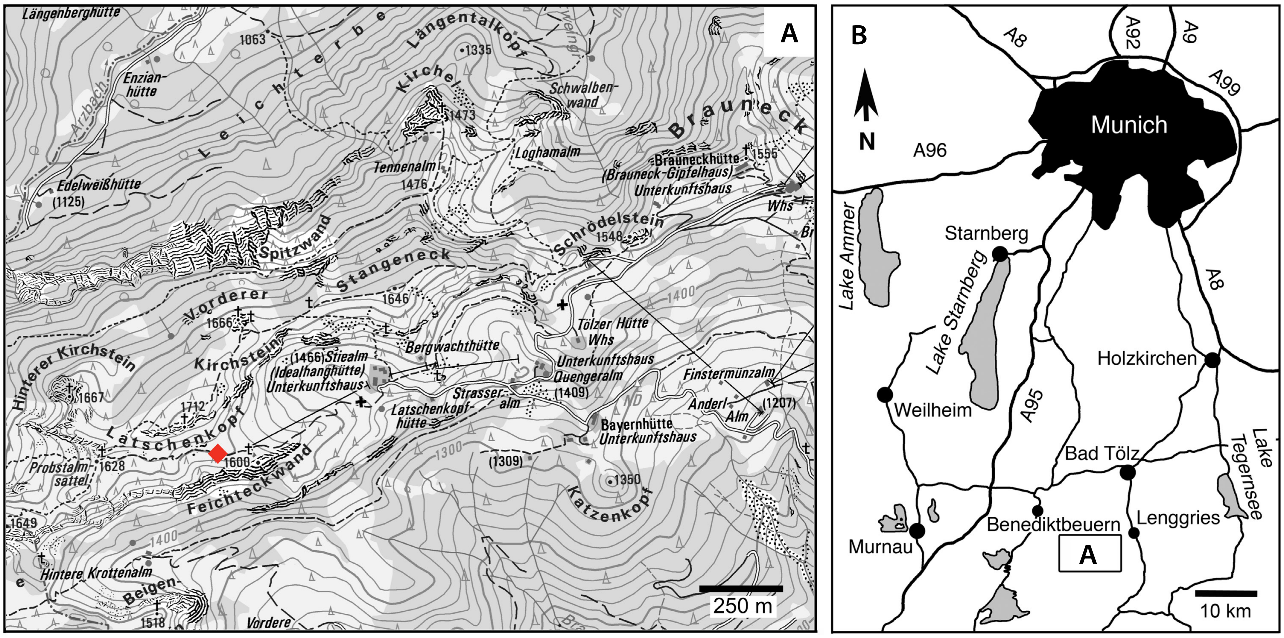


Figure 1. Locality of the study site in the Brauneck area (B), south of the Latschenkopf summit, marked with red diamond. • A – Bayerische Vermessungsverwaltung, CC-BY 4.0, modified, (*https://creativecommons.org/licenses/by/4.0/deed.de*).

Geological setting

The mollusc fauna described herein stems from the Upper Triassic Kössen Formation in the Brauneck-Benediktenwand mountain range between Lenggries and Benediktbeuern, approximately 50 km south of Munich (Fig. 1). This area is part of the Northern Calcareous Alps (NCA), which are one of the most prominent tectonic nappe complexes in the Eastern Alps. They represent a 500 km long and 20–50 km wide thrust belt of sedimentary rocks overlying the European basement. Important tectonic units of the NCA in the Brauneck-Benediktenwand mountain range are the Bajuvaric nappes including the Allgäu Nappe ("Tiefbajuvarikum") and the Lechtal Nappe ("Hochbajuvarikum"). The Lechtal Nappe is characterized by an extensive folding style, where the so-called 'Great Syncline' (Großer Muldenzug) represents a prominent synclinal fold element extending more than 80 km from the Lech valley in the west to the Fockenstein peak in the east, including the Brauneck-Benediktenwand ridge.

Within the 'Great Syncline' of the Lechtal Nappe, the Kössen Formation consists of an alternation of dark grey, bedded to laminated mudstones and marlstones with frequent thin shell beds yielding densely packed bivalve faunas. Locally, up to 1 m thick biostromal *Retiophyllia* coral limestones are intercalated. The Kössen Formation is overlain by reefal limestone facies of the Oberrhät Formation ("Oberrhätkalk"), which also interfingers laterally with the Kössen beds (Doben 1985, 1991; McRoberts *et al*. 2012). Locally, the Kössen Formation has black-shale-like marly horizons intercalated, which are rich in molluscs, mainly bivalves, and yielded the fauna described herein. The samples were taken in the southern branch of the 'Great Syncline', southwest of the Latschenkopf peak at the hiking path west of the Idealhang mountain hut (decimal degrees WGS84: N 47.655592, E 11.497907, elevation: 1625 m a.s.l.) (Fig. 1).

Characteristic marker beds in the Kössen Formation can be traced over 200 km along the E–W strike of the basin, evidencing largely isochronous sedimentation (Golebiowski 1991). The Kössen Formation is subdivided into the Hochalm Member and the Eiberg Member (Golebiowski 1989). Each of these two members consists of four informal lithostratigraphic units. The Hochalm Member is composed of small-scale sequences consisting of fine silciclastic and carbonate intervals with tempestitic shell beds. Deposits of the Hochalm Member mostly reflect depositional environments above maximum storm wave base. The Eiberg Member (correlates to the Restental member in the northern part of the basin, *i.e.* "Bajuvaricum") is characterized by a deeper marine, carbonate poor facies dominated by marls. Deposits of the Eiberg and Restental Member developed below storm wave base (Golebiowski 1991; Tomašových 2006a, b; Mandl *et al*. 2009).

Descriptions of the sedimentary successions and lithostratigraphy of the Kössen Formation are available from Austria (states of Tyrol and Salzburg; Golebiowski 1991) but also from the Brauneck-Benediktenwand area of Bavaria. The latter comprise accounts from east of the Tutzing mountain hut (Fabricius 1966) and south of the Latschenkopf peak, close to the study site (Schmidt

1991). By comparison, the mollusc bearing layer described herein most likely corresponds to the Hochalm Member (unit 2, "oberer Lumachellen-Bereich", *cf.* Mette *et al.* 2012), partly equivalent to the 'bivalve layer' (= "Lamellibranchiaten-Schicht") of Fabricius (1966). According to the stratigraphic overview of Krystyn *et al.* (2007) and Krystyn (2008), based on conodonts and ammonites, the Hochalm Member unit 2 and the lowermost part of unit 3 refer to the lower Rhaetian (Tethyan Substage Rhaetian 1; *cf.* Mette *et al.* 2012, 2016). The Rhaetian age is further corroborated by the occurrence of the bivalve *Rhaetavicula contorta* (Portlock) close to the study area.

The Rhaetian succession within the Bajuvaric (and Tyrolic) Nappe complexes developed in the Eiberg Basin, which is a subbasin of the Kössen Basin, and extends from the Salzkammergut in the east to the Lahnwiesengraben near Garmisch-Partenkirchen today. This basin was part of an expansive shallow marine carbonate platform at the northwestern margin of the Tethys. To the southeast, the Eiberg Basin was bordered by an extensive lagoon – today's Dachstein Formation – fringed by coral reefs, including those of the Steinplatte and the Adnet quarries). To the north, it was bounded by the carbonate ramp of the Oberrhät Formation ("Oberrhät limestone") (Mette *et al.* 2012, 2016).

Tomašových (2006a) interpreted shell beds within the Hochalm Member as usually distal, partly proximal tempestites in a storm-dominated environment, the composition of which was controlled by between-habitat differences in body size. This is in contrast to the interpretation of Golebiowski (1991), who argued that shell beds were dominated by small or large bivalves, due to differential sorting of a single community. The mollusk-rich, black shale like marls considered here most probably represent autochthonous shell beds developed during short term improved living conditions in an otherwise oxygen-depleted habitat hostile for life (Fabricius 1961, 1966). Furthermore, the bivalve associations in unit 2 of the Hochalm Member also reflect restricted conditions. The occurrence of bivalves within laminated bituminous shales indicates at least occasional oxygenation alternating with periods of dysoxic to anoxic conditions just below the sediment surface (Golebiowski 1991, Mette *et al.* 2012).

Material and methods

The fossil assemblage described herein comes from a bulk sample of dark claystones from an outcrop near the hiking trail west of the Idealhang mountain hut (coordinates see above, Fig. 1). Surface collection produced only a few fossils, but loose rock slabs of shell beds with abundant small bivalves and fewer gastropods were also collected. These slabs are approximately 1 cm thick, with bivalve shells oriented convex-up. Usually, the top surface of the bed has the convex exterior side of the bivalve shells exposed, while the lower side shows predominantly the interior sides. Two such slabs with well-preserved bivalves were studied in detail (slab 1 and 2, Fig. 4). Approximately 3 kg of bulk sediment from the claystones was treated with hydrogen peroxide solution and sieved under rinsing water down to 0.5 mm mesh size. Part of the dried residue was picked quantitatively under a stereomicroscope. The residue yielded fairly abundant fossils, almost entirely consisting of small gastropods and bivalves, the latter usually fragmented. Selected specimens were studied under an SEM. The fossil material is well-preserved. The gastropods have preserved protoconchs and some of them show morphological details of the larval shells. All newly collected material is housed at the Bayerische Staatssammlung für Paläontologie und Geologie, Munich under the collection number SNSB-BSPG 2025 III. In addition, material of the Kössen Formation from the Kotalm at Wendelstein (*ca.* 36 km East of the study area) from previous collections at SNSB-BSPG was studied.

Systematic palaeontology

Class Bivalvia Linnaeus, 1758
Subclass Heteroconchia Hertwig, 1895
Superorder Heterodonta Neumayr, 1884
Order Veneroida Rafinesque, 1815
Superfamily Veneroidea Rafinesque, 1815
Family Isocyprinidae Gardner, 2005

Genus *Pseudocorbula* Philippi, 1898

Type species. – Nucula gregaria Münster, 1837 *in* Goldfuss (1837), by subsequent designation of Diener (1923).

***Pseudocorbula alpina* (Winkler, 1859)**
Figures 2–6

*1859 *Corbula alpina* sp. nov.; Winkler, pp. 15, 16, pl. 2, fig. 2.
1861 *Corbula alpina* Winkl. – Winkler., p. 26 (484), pl. 8, fig. 1a–c.
? 1917 *Corbula alpina* Winkl. – Goetel, p. 200.
1923 *Corbula alpina* Winkler. – Diener, p. 240. [cum syn.]
1930 *Lucina* (non *Corbula*) *alpina* Winkl. – Osswald, p. 746, pl. 53, figs 16–20.
1962 *Corbula alpina* Winkler. – Allasinaz, p. 355, pl. 25, figs 10, 11.
1978 *Pseudocorbula alpina* (Winkler, 1859). – Tichy, p. 341, fig. 1.
1989 *Isocyprina* (*Eotrapezium*) *alpina* (Winkler, 1859). – Golebiowski, p. 171. [cum syn.]

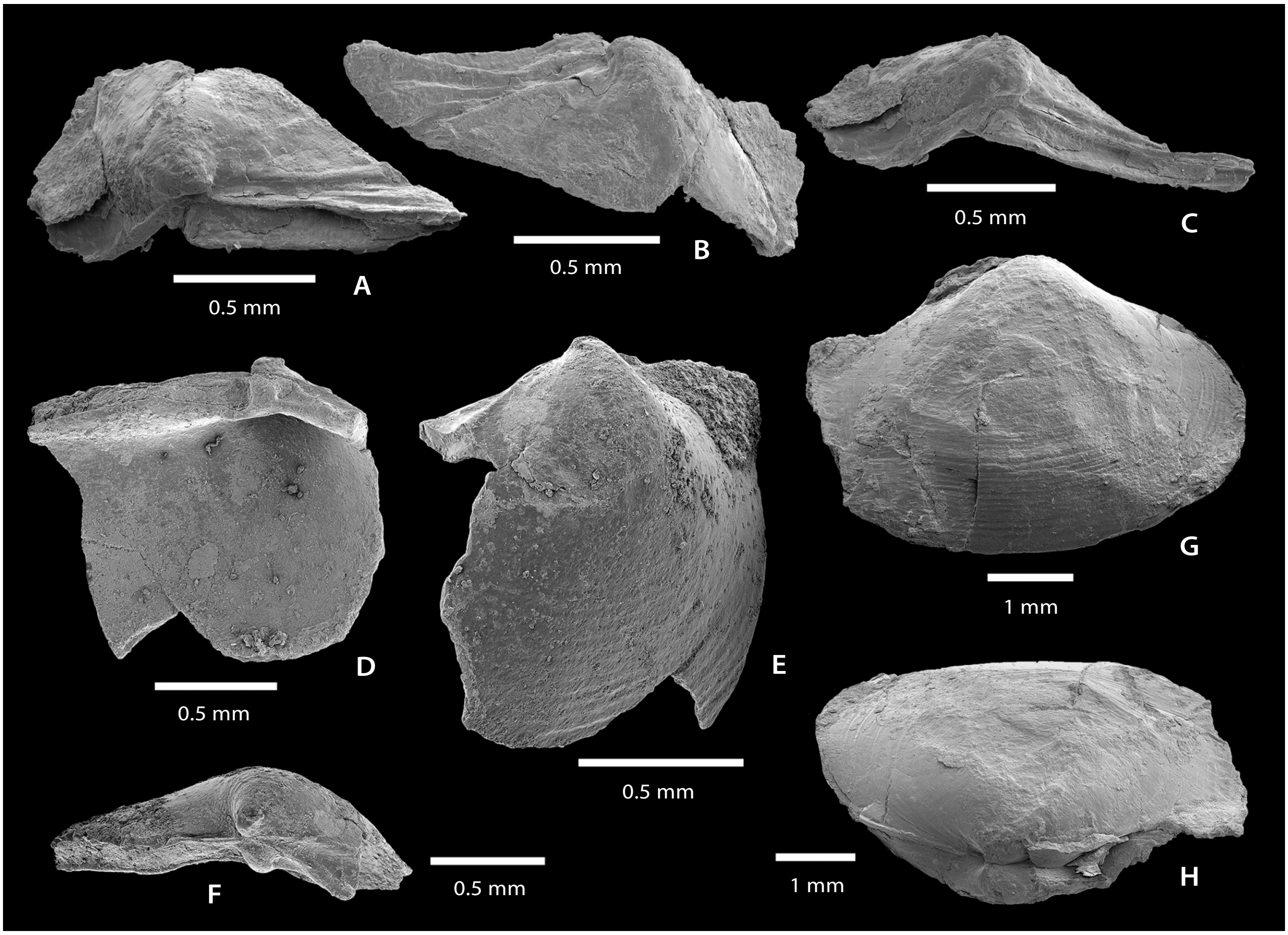


Figure 2. *Pseudocorbula alpina* (Winkler, 1859), from bulk sample. A–C – SNSB-BSPG 2025 III 14, fragment of a left valve in dorsal, exterior and interior view, showing details of the hinge. D–F – SNSB-BSPG 2025 III 15, fragment of a right valve in internal, external and dorsal view. G, H – complete specimen with conjoined valves, SNSB-BSPG 2025 III 28; G – view of right valve, H – beaks and right valve.

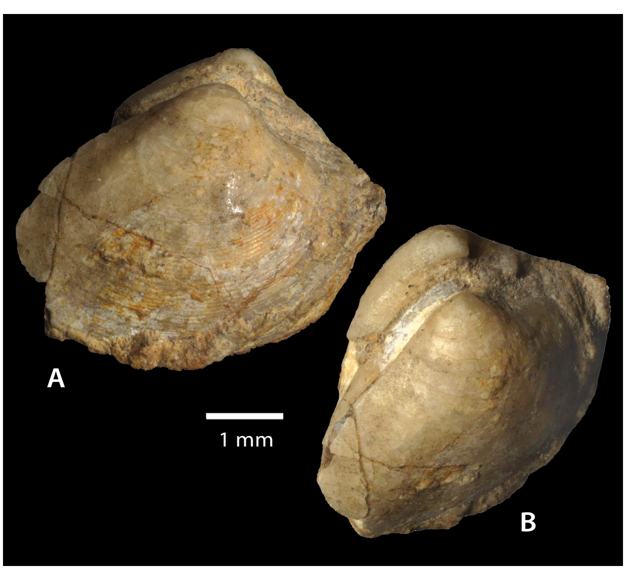


Figure 3. *Pseudocorbula alpina* (Winkler, 1859), SNSB-BSPG AS XV 490, original specimen of Winkler (1861, pl. 8, fig. 1a, b). A – view of right valve. B – oblique dorsal view, illustrating equivalve shell and prosogyrate umbones.

Material. – In the bulk sample, this species is represented by numerous, often fragmented specimens; two isolated valves with partly preserved hinges (Fig. 2A–F; SNSB-BSPG 2025 III 14, 15) and one specimen with conjoined valves (Fig. 2G, H; SNSB-BSPG 2025 III 28) were studied by SEM. In addition, one slab from a shell bed (slab 1, SNSB-BSPG 2025 III 39; Fig. 4A) from the same locality was studied, which provides a right valve that shows the complete details of the hinge dentition (Fig. 5A). A second slab (SNSB-BSPG 2025 III 40; Fig. 4B) shows abundant specimens including two specimens with preserved hinges (Figs 5B, 6A). We have also studied the only available original specimen of Winkler (1861, pl. 8, fig. 1a, b) (Fig. 3A, B).

Description. – Shell small (generally less than 1 cm long), equivalve, umbones prosogyrate. Valves suboval in outline, with blunt posterior ridge, externally covered with commarginal ribs that are rather fine and very regularly and densely spaced. Hinge of right valve (Fig. 5A, B) with elongated anterior lateral tooth AI, which extends to the

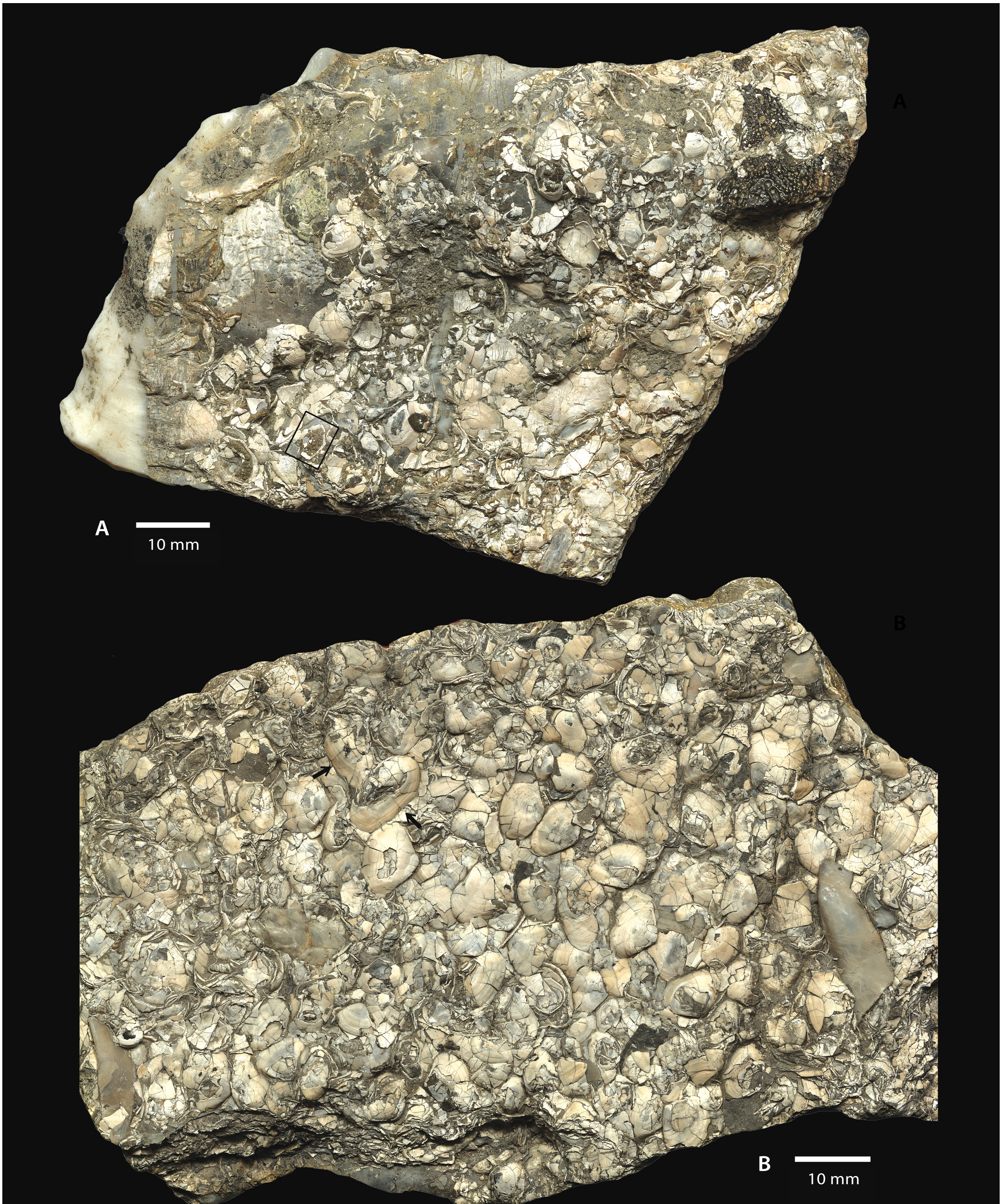


Figure 4. Slabs of shell beds from the Brauneck with numerous specimens of *Pseudocorbula alpina* (Winkler, 1859), illustrating the shape variation of this species. A – slab 1, rectangle indicates specimen with preserved hinge depicted in Fig. 5A, SNSB-BSPG 2025 III 39. B – slab 2 of shell bed from the Brauneck with numerous specimens of *Pseudocorbula alpina* (Winkler, 1859); specimens oriented primarily exposing convex outer sides; arrows indicate valves with unusually elongated shapes; specimens exposing interior side with preserved hinges from other side of shell bed illustrated in Figs 5 and 6, elongate shell on the right side is *Gervillia wagneri* Winkler, 1861, SNSB-BSPG 2025 III 40.

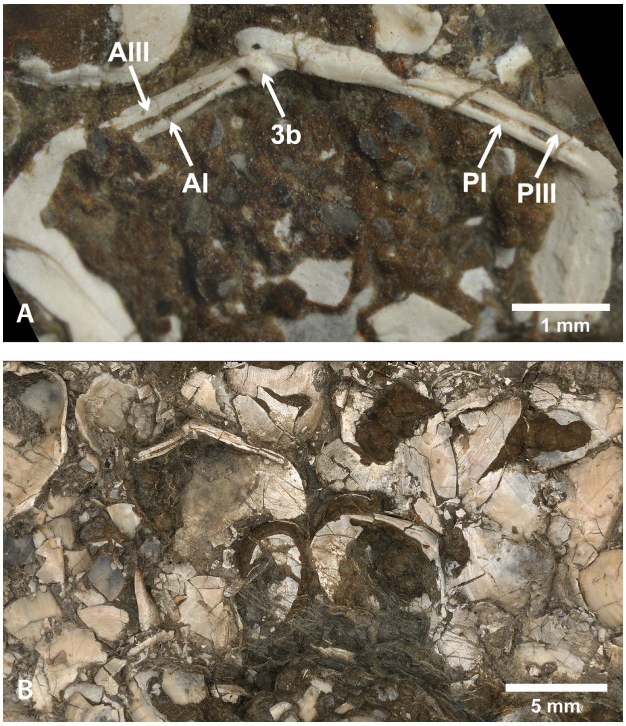


Figure 5. Hinge details of *Pseudocorbula alpina* (Winkler, 1859). A – specimen from slab 1 (SNSB-BSPG 2025 III 39) showing details of the right valve interior with complete hinge dentition; indication of hinge teeth (AI, AIII: anterior lateral teeth; 3b cardinal tooth; PI, PIII posterior lateral teeth) according to Bernard (1895). B – details of lower side of slab 2 (SNSB-BSPG 2025 III 40) with a left and a right valve of *Pseudocorbula alpina* (Winkler, 1859) showing hinge details.

area below the umbo. Anterior lateral tooth AIII giving rise to cardinal tooth 3b in the pivotal position below the umbo. Posterior lateral tooth PI elongated, extending to a position close to the posterior end of dorsal margin; posterior lateral tooth PIII paralleling PI, formed by shell margin. Hinge of left valve (Figs 2C, 6) with two anterior lateral teeth (AII and AIV) giving rise to two cardinal teeth interpreted as 2 and 4b. Posterior lateral tooth PII elongated, formed by hinge margin (Fig. 6A). Nymph short, inserting below umbo and running approximately parallel to shell margin (Fig. 6A).

Remarks. – As noted by Osswald (1930), the original descriptions and figures of Winkler (1859, 1861) are inaccurate in some regards. Reexamination of Winkler's (1861, pl. 8, fig. 1a, b) specimen with conjoined valves shows that *Corbula alpina* is equivalve (Fig. 3A), not inequivalve as stated by Winkler (1861, p. 26). The isolated left valve of Winkler (1861, pl. 8, fig. 1c) that shows details of the hinge area seems to be lost, but it was obviously available to Osswald (1930), who noted (p. 747) that its hinge morphology was comparable with the specimens that he assigned to the same species. Although Winkler's (1861, pl. 8, fig. 1c) illustration of this left valve is not entirely clear, it agrees with our material (*e.g*. Fig. 6A) in the presence of two anterior lateral teeth AII and AIV, the nature of the AII–2 transition (see below), and the presence of a central, triangular socket below the umbo.

Although this species is possibly the most abundant macrofossil in the Kössen Formation (Osswald 1930, Golebiowski 1989), there has been much uncertainty about its taxonomic identity. Golebiowski (1989, p. 169) suggested that this uncertainty results from the presence of several (probably three) small bivalve species with similar shapes, combined with the scarcity of individuals with preserved hinges. More precisely, Golebiowski (1989) distinguished among the "small, circular bivalves" of the Kössen Formation (1) *Myophoriopis isoceles* (Stoppani, 1857), which has a sharp posterior carina, (2) *Pseudocorbula* cf. *ewaldi* (Bornemann, 1854), which lacks a sharp posterior carina and is externally smooth, and (3) Winkler's *Corbula alpina*, which he assigned to *Isocyprina* (*Eotrapezium*). Golebiowski's (1989, p. 172) criteria for the separation of Winkler's species from the two similar ones are quite vague and refer to subtle differences in the shape ("rounded shape, absence of an area"). It appears that Golebiowski (1989) has not seen any specimens with preserved hinges for his study.

Winkler (1859) originally assigned this species to *Corbula* Bruguière, 1797, but Osswald's (1930) study revealed the presence of a heterodont hinge that led him to assign it to *Lucina* Bruguière, 1797. He tentatively suggested a new subgenus *Raetolucina* "if a new name should be required for the distinction from other groups (= subgenera of *Lucina*)". However, Casey (1952, p. 134) pointed out that *Lucina* is only superficially similar to *Corbula alpina* and dismissed *Raetolucina* as a synonym of *Isocyprina* Röder, 1882. In the *Treatise on Invertebrate Paleontology* (Cox & Chavan 1969, Keen & Casey 1969), *Raetolucina* Osswald, 1930 is tentatively placed in the synonymy of both *Eotrapezium* Douvillé, 1913 and *Pseudocorbula*. Without citing the *Treatise*, Tichy (1978) advocated an assignment of *Corbula alpina* to *Pseudocorbula* on the basis of Osswald's (1930) illustrations of the hinge, whereas Golebiowski (1989) assigned the species on the same basis to *Isocyprina* (*Eotrapezium*).

Our sample contains numerous fragments of a small subovate bivalve species with a blunt posterior ridge (rather than a sharp carina) and pronounced commarginal ribs. Applying Golebiowski's (1989) concept, these external characters suggest an assignment to *Corbula alpina*, but we note that his concept was based solely on subtle differences in shape and external morphology. This is critical, because the three superficially similar species discussed by Golebiowski (1989) have been assigned by him to three different genera. Fortunately, our material includes three left and three right valves that show details

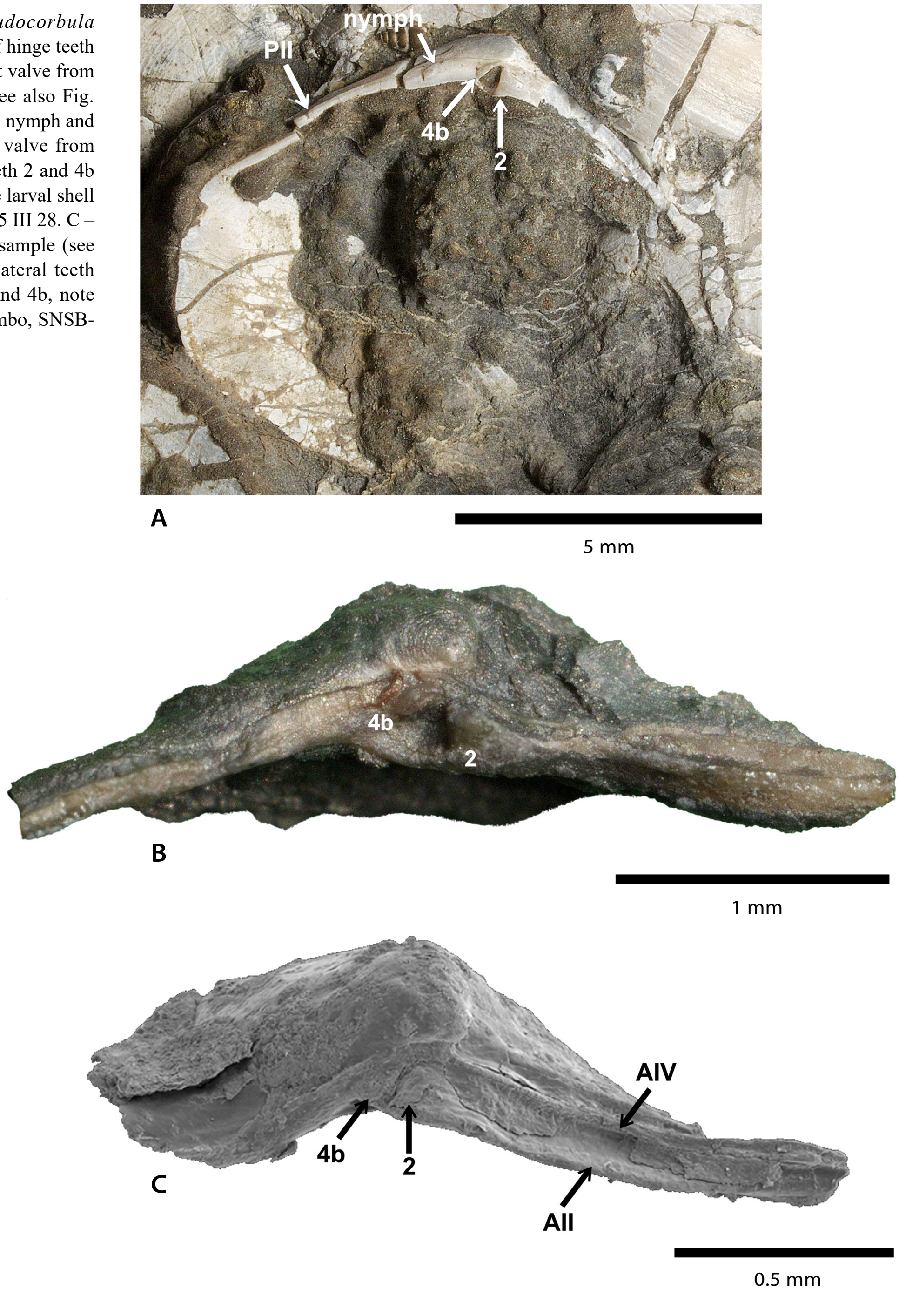


Figure 6. Hinge details of *Pseudocorbula alpina* (Winkler, 1859), indication of hinge teeth according to Bernard (1895). A – left valve from slab 2 (SNSB-BSPG 2025 III 40; see also Fig. 5B) showing cardinal teeth 2 and 4b, nymph and posterior lateral tooth PII. B – left valve from bulk sample, illustrating cardinal teeth 2 and 4b and central tooth socket, note minute larval shell at the tip of umbo, SNSB-BSPG 2025 III 28. C – fragment of a left valve from bulk sample (see also Fig. 2C) illustrating anterior lateral teeth AII and AIV and cardinal teeth 2 and 4b, note the upward-bending of AII below umbo, SNSB-BSPG 2025 III 14.

of the shell interior, which allow for a clarification of the generic identity of *Corbula alpina*.

As described above, the hinge formula of *Corbula alpina* is AI, AIII, 3b, PI, PIII / AII, AIV, 2, 4b, PII. Both *Isocyprina* (including its subgenus *Eotrapezium*) and *Pseudocorbula* have hinges that correspond to this type, which is unusual in the presence of lateral tooth AI and the absence of cardinal tooth 3a in the right valve. However, there is a notable difference between *Isocyprina* (including *Eotrapezium*) and *Pseudocorbula* in the details of the AII–2 transition in the left valve. In *Pseudocorbula*, the left valve has an anterior, stout cardinal tooth 2 that is formed by a swelling of the proximal end of lateral tooth AII (Cox & Chavan 1969; Hautmann in press), whereas the anterior cardinal tooth (generally interpreted as 2b) in the left valve of *Isocyprina*/*Eotrapezium* forms an obtuse chevron with the anterior lateral tooth AII (Cox 1947, p. 144; see also hinge illustrations in Böhm 1901 and Douvillé 1913).

As shown in Fig. 2C and Fig. 6, our material conforms to the hinge morphology of *Pseudocorbula*, rather than that of *Isocyprina*/*Eotrapezium*. However, we note that in the smallest studied specimen (Figs 2C, 6C), lateral tooth AII seems to bend upward below the umbo, as in *Isocyprina*/*Eotrapezium*. Unfortunately, adhering sediment covers the structural relationship with cardinal tooth 2, but we do not exclude that the hinge of *Pseudocorbula* showed an *Isocyprina*/*Eotrapezium* type AII–2 transition in its very early ontogeny. If confirmed, this observation would suggest an evolutionary transition from *Pseudocorbula* to *Isocyprina*/*Eotrapezium* that included the neotenous retention of the hinge morphology, and consequently, *Pseudocorbula* would be the oldest known member of the Venerida (see Cox 1947 and Gardner 2005 for the role of *Eotrapezium* and *Isocyprina* in the evolution of the veneroid hinge dentition).

The clarification of the generic identity of *Pseudocorbula alpina* does not resolve the question whether morphologically similar species, either belonging to *Pseudocorbula* or to different genera, co-occurred in the Kössen Formation. The slabs of shell beds with abundant *Pseudocorbula alpina* that we studied (Fig. 4) provide an impression of the broad morphological variation of this species. Through visual inspection, only two elongated valves with nearly straight ventral margins, possibly belonging to the same individual, seem to fall outside the general variation in shell shape (Fig. 4B). In absence of information about the shell interior, the taxonomic identity of these outliers remains unresolved.

Class Gastropoda Cuvier, 1795

The gastropod systematics follows Bouchet *et al*. (2017).

Subclass Neritimorpha Koken, 1897

Neritimorpha indet.
Figure 7

Material. – Three specimens in total, illustrated specimen SNSB-BSPG 2025 III 9.

Remarks. – Three specimens of a smooth-shelled egg-shaped, low-spired neritimorph with smooth protoconch occur in the studied assemblage. All specimens are deformed and the aperture, which is a particularly important character complex in this group, is not preserved. Hence, an identification of this material below subclass level is impossible.

Subclass Caenogastropoda Koken, 1897
Superfamily Pseudozygopleuroidea Knight, 1930
Family Zygopleuridae Wenz, 1938

Genus *Ampezzopleura* Bandel, 1991

Type species. – *Ampezzopleura tenuis* Nützel, 1998; SD under ICZN Art. 70.3, Bouchet & Rocroi, 2017 *in* Bouchet *et al.* (2017); from the lower Carnian St. Cassian Formation.

***Ampezzopleura brauneckenis* sp. nov.**
Figure 8
LSID. – urn:lsid:zoobank.org:act:36156FBA-0F50-4ADF-9E40-9C6C4FCE1CEA

Holotype. – SNSB-BSPG 2025 III 2.

Paratypes. – Ten specimens, SNSB-BSPG 2025 III 5, 6, 8, 19, 21, 22, 29–32.

Type horizon and locality. – Hochalm Member, Kössen Formation; Late Triassic, Rhaetian; Brauneck, South of the Latschenkopf summit.

Material. – Types only.

Etymology. – After the type locality near the Brauneck Mountain.

Diagnosis. – *Ampezzopleura* species with a conical larval shell of the planktotrophic type. The larval shell has an ornament of axial ribs, which are restricted to the abapical portion of the whorls.

Description. – Shell high-spired, slender; largest specimen (holotype) consisting of *ca*. 3 teleoconch and 5 protoconch whorls, 1.6 mm high, 0.6 mm wide; teleoconch whorls convex with periphery below mid-whorl, ornamented with broad, wavy, slightly opisthocline axial ribs (8–10 per whorl), which are as wide as their interspaces; protoconch consisting of *ca*. 5 whorls, 0.61 mm high,

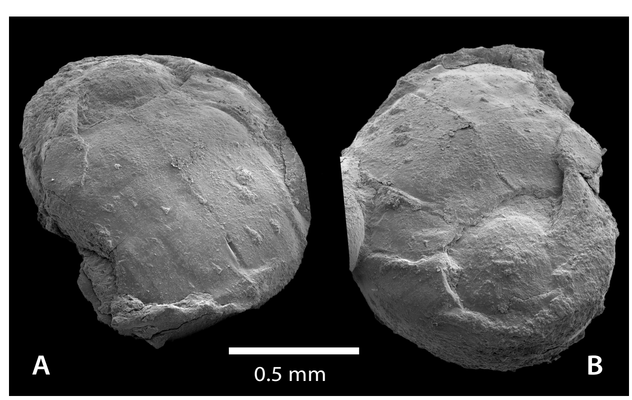


Figure 7. Neritimorpha indet. from bulk sample, SNSB-BSPG 2025 III 9. A – oblique laterview. B – apical view.

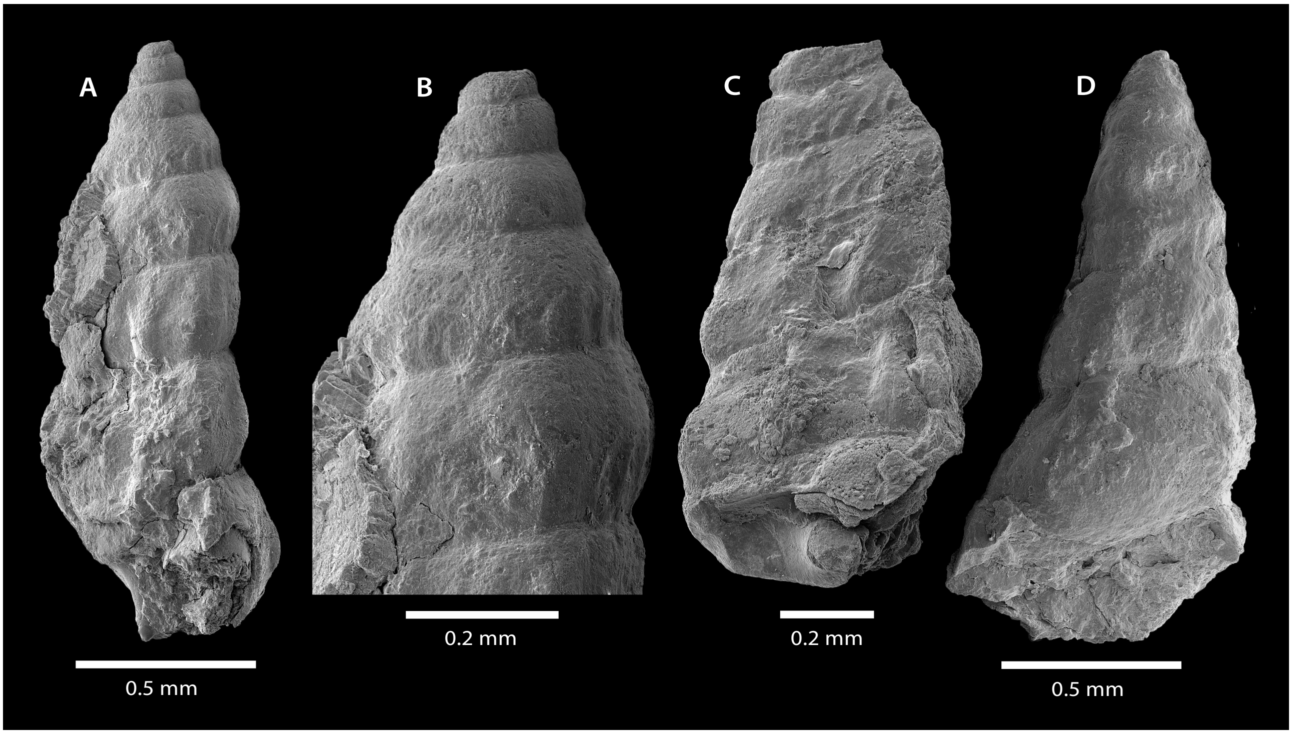


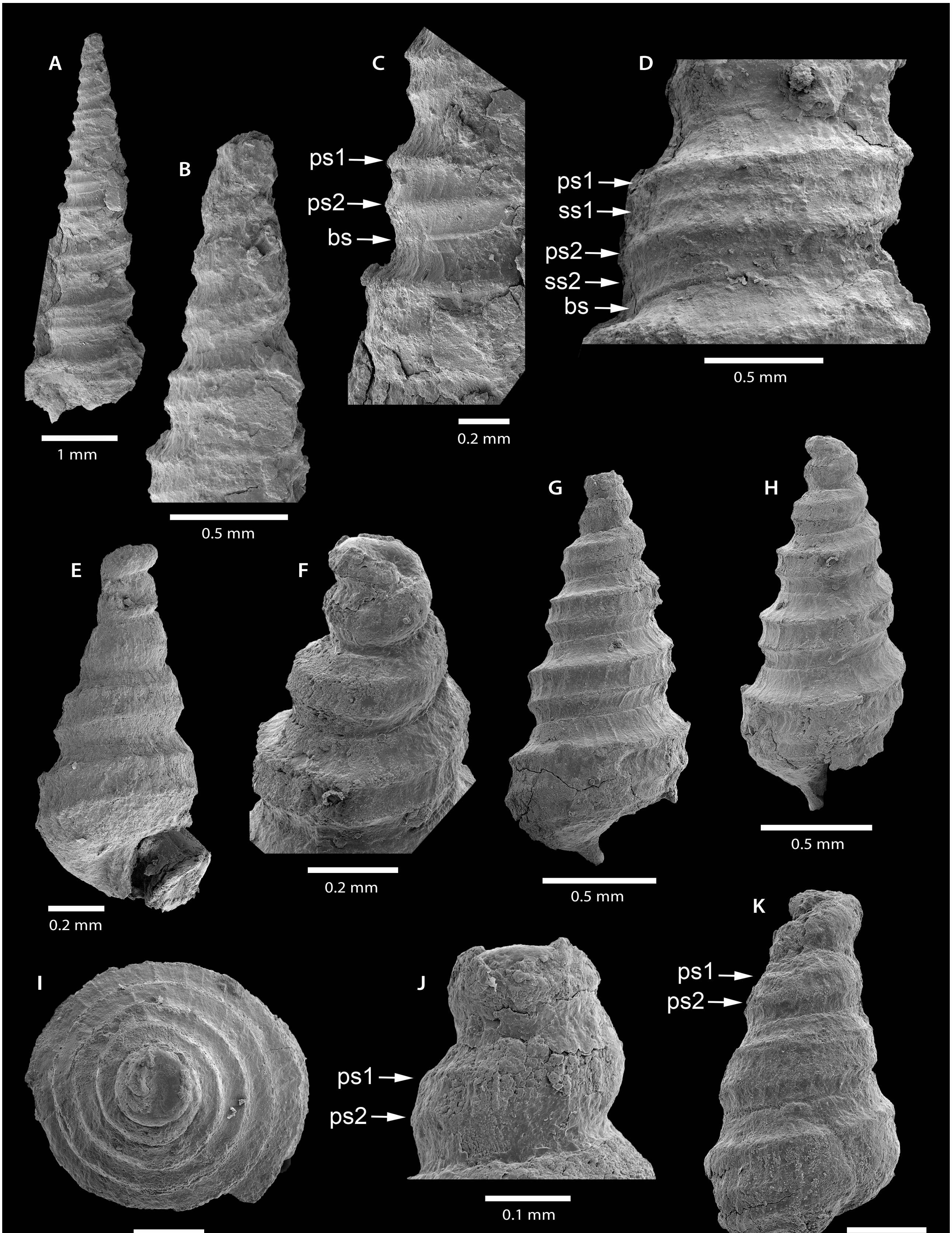
Figure 8. *Ampezzopleura brauneckenis* sp. nov. from bulk sample, A, B – holotype, SNSB-BSPG 2025 III 2; A – lateral view; B – protoconch in lateral view; with short riblets in abapical half of larval whorls. C – paratype, SNSB-BSPG 2025 III 21, adapical two whorls are larval, with short riblets in abapical half. D – paratype SNSB-BSPG 2025 III 6, adapical whorls are larval with short riblets in abapical half.

0.47 mm wide, conical with apical angle somewhat larger than that of teleoconch; protoconch whorls ornamented with numerous (> 20 per whorl) axial ribs occupying the abapical of the whorls; ribs strongly curving backward in their adapical portion; adapical half of protoconch whorl smooth.

Remarks. – Although the preservation of the present material is not ideal, the described characters are clearly visible and justify the description of a new species of *Ampezzopleura*. This is the only known species of this genus that has ribs on the larval shell, which are restricted to the abapical half of the whorls. However, the larval ornament has clearly the character of ribs and hence assignment to the genus *Ampezzopleura* is justified. All other known species of *Ampezzopleura* have continuous axial ribs (uninterrupted from suture to suture) on the larval shell. *Zygopleura* is very similar with regard to morphology, but has subsutural nodes.

Ampezzopleura sp. indet., reported by Kaim *et al.* (2014) *in* Shigeta *et al.* (2014) from the Bac Thuy Formation in northeastern Vietnam is an isolated axially ribbed larval shell. In contrast to *A. brauneckensis*, its larval ribs are continuous. Its teleoconch is unknown. *Ampezzopleura rugosa* (Batten & Stokes, 1986) from the Early Triassic of the USA has a coarser, more irregular ribbing on the teleoconch whorls (Nützel 2005, Nützel & Schulbert 2005). The type species of the genus, *Ampezzopleura tenuis* Bandel, 1991 from the St. Cassian Formation, has sharper, narrower teleoconch ribs (see also Nützel 1998). *Ampezzopleura bandeli* Nützel, 1998 and *Ampezzopleura mammilata* Nützel, 1998 have much smaller larval shells (Nützel 1998, Hausmann & Nützel 2015). *Ampezzopleura hybridopsis* Nützel, 1998 has continuous ribs on the larval shell that are later reduced to subsutural nodes (Nützel 1998, Hausmann *et al.* 2021). *Ampezzopleura slovenica* Kaim, Jurkovsek & Kolar-Jurkovsek, 2006 has a greater apical angle and the larval shell is smaller (0.23 mm high, 0.33 wide). *Ampezzopleura barremica* Isaji, Haga & Kashiwagi, 2022 from the Cretaceous (Barremian) of Japan is unusual for the genus by having a spiral cord on the teleoconch and could thus represent a different genus. "*Palaeorissoina*" *sokolovensis* Golovinova & Guzhov, 2009 from the Early Cretaceous of Russia actually represents *Ampezzopleura* and differs in having continuous ribs on the larval shell and stronger teleoconch ribs.

This is the first report of *Ampezzopleura* from the Rhaetian. Other species are known from the Carnian of the Alps (Bandel 1991, Nützel 1998, Kaim *et al.* 2006), the Early Triassic of the Western US (Nützel 2005, Nützel & Schulbert 2005), and the Early Cretaceous of Russia [*Ampezzopleura sokolovensis* (Golovinova & Guzhov, 2009) (new combination)].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0.2 mm

Subclass Heterobranchia Burmeister, 1837
Superfamily Mathildoidea Dall, 1889
Family Mathildidae Dall, 1889

Genus *Jurilda* Gründel, 1973

Type species. – *Mathilda* (*Jurilda*) *crasova* Gründel, 1973 (= subjective junior synonym of *Promathilda* (*Teretrina*) *concava* Walther, 1951); original designation, Bajocian to Bathonian, Poland.

Jurilda stoppanii **(Winkler, 1861) comb. nov.**
Figures 9–10

1861 *Turritella Stoppanii* Winkl.; Winkler, p. 466, pl. 5, fig. 8.
1926 *Loxonema Stoppanii* Winkler. – Diener, p. 171.

Material. – Thirteen specimens from bulk sample, SNSB-BSPG 2025 III 1, 3, 4, 13, 16, 20, 24, 33–38; several specimens on the two shell bed slabs (SNSB-BSPG 2025 III 39, 40); 3 specimens from the Kotalm, Holinka collection, SNSB-BSPG 1963 VI 152, 192, 193.

Description. – Shell high-spired, slender; largest specimen from washed residue consisting of *ca*. 12 teleoconch whorls (apex missing) 4.9 mm high, 1.4 mm wide (Fig. 9A–D); specimen from Kotalm (Fig. 10A) 7.1 mm high, 2.5 mm wide; whorl face angulated at two primary spiral cords (ps1 and ps2); spiral cords approximately equally spaced between ad- and abapical sutures; adapical spiral cord at a somewhat greater distance from the upper suture than abapical spiral cord from lower suture; two secondary spiral cords (ss1 and ss2) present in centres between primary spiral cords (ss1), and abapical primary spiral and abapical suture cord (ss2) on mature teleoconch whorls; secondary spiral cords distinctly weaker than primary spiral cords; further spiral cord (bs) emerges at suture, forming angular edge towards transition to base; outer whorl face concave, steeply inclined, almost vertical, parallel to shell axis between primary spiral cords, more strongly inclined, and concave towards sutures; protoconch co-axially heterostrophic.

Remarks. – The original illustration by Winkler (1861, pl. 5, fig. 8) is too sketchy for safe identification. We tried in vain to find the type material in Munich (SNSB-BSPG) in order to corroborate its identity with our material. The high-spired shell with two main spiral cords, and an additional, later appearing spiral cord in Winkler's (1861) figure seem to indicate that our material is conspecific. The type locality of "*Turritella*" *stoppanii*

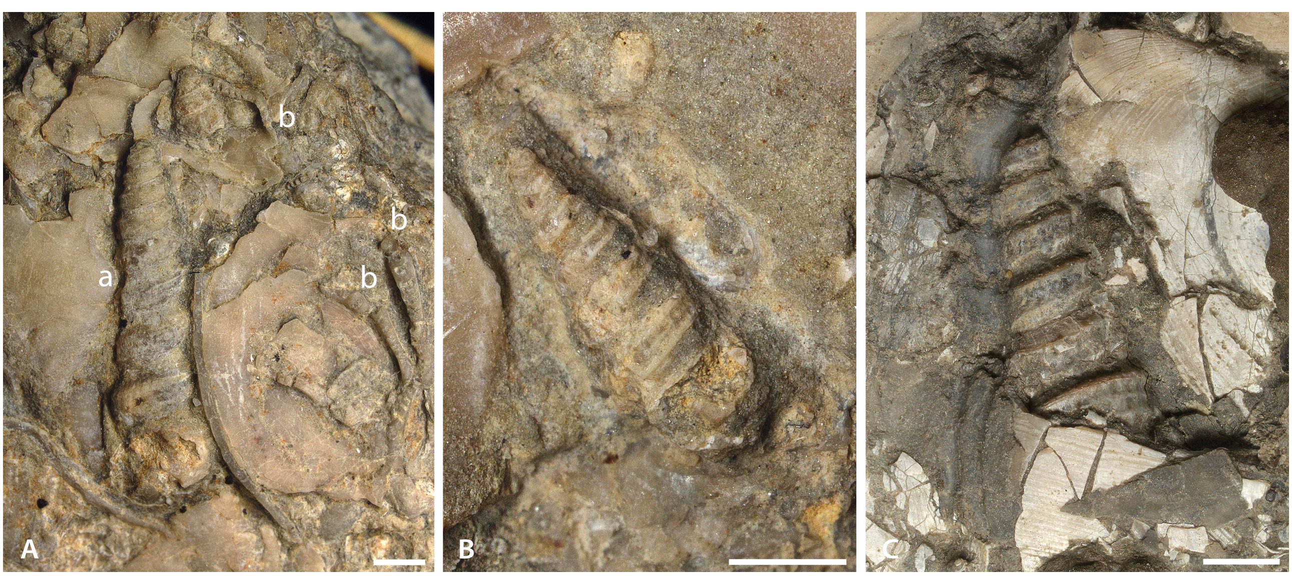

Figure 10. *Jurilda stoppanii* (Winkler, 1861). A – small slab with fossils from the Kössen Formation at Kotalm, collection Holinka, SNSB-BSPG 1963 VI 192. Legend: a – *Jurilda stoppanii*; b – three nuculid bivalves showing taxodont hinges. B – from the Kössen Formation at Kotalm, collection Holinka, SNSB-BSPG 1963 VI 193. C – from slab 2 of shell bed from the Brauneck, SNSB-BSPG 2025 III 40C. Scale bars 1 mm.

< **Figures 9.** *Jurilda stoppanii* (Winkler, 1861), from bulk sample. A–D – SNSB-BSPG 2025 III 13; A – lateral view; B – apical whorls (early teleoconch) in lateral view; C – detail early teleoconch; D – detail late teleoconch whorl. E – SNSB-BSPG 2025 III 1, juvenile whorls including heterostrophic protoconch in lateral view. F–J – SNSB-BSPG 2025 III 3, juvenile whorls including heterostrophic protoconch; F, J – earliest whorls including protoconch in lateral view; G, H – lateral views; I – apical view; K – SNSB-BSPG 2025 III 4, juvenile shell including heterostrophic protoconch, lateral view. Abbreviations: bs – basal spiral cord; ps – primary spiral cord; ss – secondary spiral cord.

is the Kotalm ("Kothalpe bei Fischbachau", at the Wendelstein Mountain) in the Bavarian Alps, where the Kössen Formation is exposed. We found three specimens from the Kotalm at the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG 1963 VI 152, collection Holinka), identified as "*Turritella*" *stoppanii*, which seem to be conspecific with the present material but are poorly preserved. Two of these specimens are illustrated herein (Fig. 10A, B).

Our material represents the first Rhaetian mathildoid with preserved protoconch and the second certain Triassic member of the mathildoid genus *Jurilda*, which is diverse in the Jurassic. Another representative of this genus, *Jurilda elongata* (Leonardi & Fiscon, 1959) was reported from the Carnian St. Cassian Formation (Hausmann *et al.* 2021). In *Jurilda elongata*, the primary spiral cords are much more distant from each other and it has a denser ribbing than *J. stoppanii. Jurilda stoppanii* resembles specimens from the St. Cassian Formation, which were identified as *Mathilda biserta* (Münster, 1841) by Bandel (1995, especially pl. 1, fig. 6 from Alpe di Specie). However, comparison with Münster's (1841) type material revealed that Bandel's (1995) material is misidentified. *Mathilda biserta* (Münster, 1841) has a median angulation, as is also visible in Münster's (1841, pl. 13, fig. 44) illustration. Although similar, Bandel's (1995) material differs from *Jurilda stoppanii* by lacking secondary spiral cords and by having a denser, coarser axial ribbing. *Promathildia acedesta* Healy, 1908 from the Rhaetian of Myanmar is similar but has fewer and stronger axial ribs. *Promathildia hemes* (*Cerithium hemes* d'Orbigny, 1850, p. 128) was reported to be Toarcian in age and derives from Bellagio at Lago di Como, Italy. According to Stoppani (1863), the material is not of Toarcian but of Rhaetian age. The images of the syntypes, provided by the Muséum national d'Histoire naturelle (MNHN, Chagnoux 2025) clearly show a species different from our material (it has a prominent knobby median crest), but also from the Rhaetian species illustrated and described by Stoppani (1863, p. 121, pl. 28, figs 11, 12) from Bellagio. Stoppani's material bears fine tubercles on the carination and in a subsutural position.

Discussion

We report a Rhaetian mollusc assemblage including a new gastropod species from the Bavarian Alps. It consists of one bivalve and at least three gastropod species. More species seem to be present in the sample, but the preservation of the specimens is too poor for a taxonomic identification. In addition, a nuculid bivalve is documented on a shell bed slab from the Kössen Formation at the Kotalm near the Wendelstein Mountain (Fig. 10A) and *Gervillia wagneri* Winkler, 1861, in a shell bed from the Brauneck (Fig. 4B). The identified fossils are relatively well-preserved including protoconch preservation in the gastropods, which is almost unique for Rhaetian gastropods. Both the bivalve *Pseudocorbula alpina* and the gastropod *Jurilda stoppanii* are abundant in the studied bulk sample and in the shell beds. Although a comprehensive quantitative paleoecological analysis is beyond the scope of this contribution, it is clear that both species form an important part of the communities of the Kössen Formation of the Brauneck, with a strong dominance of *Pseudocorbula alpina.*

Our study highlights the potential for new and taxonomically relevant discoveries in supposedly well-studied rock units such as the Kössen Formation. The present fauna consists of soft-bottom dwellers occurring in the basins between coeval carbonate platforms with intense reef-growth. All specimens of the investigated sample are small and were recovered by disaggregation and sieving of the relatively low-grade lithified shales. Therefore, this occurrence qualifies as a Liberation Lagerstätte *sensu* Roden *et al.* (2021). By contrast, the Rhaetian reefal fauna of the Northern Alps (Austria) described by Nützel *et al.* (2023) derives from strongly lithified and diagenetically altered carbonate rocks. Only large molluscs (> 10 mm) could be recovered from these rocks, whereas small, delicate specimens and species were not found, although they were primarily present, as was seen in thin sections.

Bivalves are represented by a small heterodont species in the studied samples, which we assign to *Pseudocorbula alpina* (Winkler, 1859). The new material as well as unpublished material from museum collections allows for a reconstruction and documentation of the hinge dentition of this species, which is suggestive of *Pseudocorbula* but possibly ancestral to *Eotrapezium* and thus potentially an early representative of the Venerida.

One of three gastropod species, *Ampezzopleura brauneckenis*, is described as new. In addition, the heterobranch *Jurilda stoppanii* (Winkler, 1861) and an unidentifiable neritimorph are present. As far as we know, the latter represents the first record of a neritimorph from the Kössen Formation. Most *Ampezzopleura* species are known from the Triassic, in particular from the Early Triassic (Nützel 2005, Nützel & Schulbert 2005, Kaim *et al.* 2014) and the Carnian (Bandel 1991, Nützel 1998, Kaim *et al*. 2006, Hausmann & Nützel 2015, Hausmann *et al*. 2021). This is the first report of *Ampezzopleura* from the Rhaetian. A Cretaceous species that was assigned to *Ampezzopleura*, *Ampezzopleura barremica* Isaji, Haga & Kashiwagi, 2022, does not represent this genus because it has a conspicuous spiral teleoconch ornament. However, "*Palaeorissoina*" *sokolovensis* Golovinova & Guzhov, 2009 from the Early Cretaceous of Russia actually represents *Ampezzopleura*. Consequently, the genus *Ampezzopleura* must have crossed the Triassic–Jurassic boundary. This is also the case for the mathildid *Jurilda* that is also known from the Jurassic (Gründel & Nützel 2013). *Jurilda* was previously reported from the Carnian St. Cassian Formation (Hausmann *et al*. 2021), but this is the first report from the Rhaetian. Hillebrandt & Urlichs (2023) reported that a mathildoid, *Tricarilda*, is common in the Rhaetian of the Bavarian Alps, but they neither described nor illustrated this material. We assume that it may be identical with *Jurilda stoppanii*. Ferrari & Hautmann (2022) found that Heterobranchia as a whole encountered low extinction rates in the Late Triassic and high origination rates in the Early Jurassic but few mathildoids were included in their database. Gründel & Nützel (2013, fig. 11) found that Mathildoidea crossed the Triassic-Jurassic boundary with up to eight genera and subgenera. Karapunar & Nützel (2021) reported that the generic diversity of Heterobranchia (to which *Jurilda* belongs) remained basically stable at a low level throughout the Triassic. However, Caenogastropoda (to which *Ampezzopleura* belongs) radiated until the Carnian, and declined considerably until the Rhaetian. Most of the mentioned gastropod diversity studies use the range-through method and Rhaetian data are extrapolations rather than based on actual occurrences. Karapunar *et al*. (2024) also showed a severe drop in generic gastropod diversity from the Carnian to the Pliensbachian. Especially in Caenogastropoda and Heterobranchia, the correct systematic placement requires knowledge of the protoconch morphology. In so far, the report of well-preserved representatives of both clades from the Rhaetian is of importance for a better understanding of gastropod diversity dynamics at the Triassic–Jurassic transition.

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References

Allasinaz, A. 1962. Il Trias in Lombardia (Studi geologici e paleontologici). III. Studio paleontologico e biostratigrafico del Retico del dintorni di Endine (Bergamo). *Rivista Italiana di Paleontologia e Stratigrafia 68(3)*, 307–376, pls 24–28.

Bandel, K. 1991. Über triassische 'Loxonematoidea' und ihre Beziehungen zu rezenten und paläozoischen Schnecken. *Paläontologische Zeitschrift 65*, 239–268. DOI 10.1007/BF02989844

Bandel, K. 1995. Mathildoidea (Heterostropha, Gastropoda) from the Upper Triassic St. Cassian Formation. *Scripta Geologica 111*, 1–83.

Batten, R.L. & Stokes, W.L. 1986. Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *American Museum Novitates 2864*, 1–33.

Bernard, F. 1895. Première note sur le développement et la morphologie de la coquille chez les Lamellibranches. *Bulletin de la Société Géologique de France, Troisième Série, 23*, 104–154.

Böhm, J. 1901. Ueber die Fauna der Pereiros-Schichten. *Zeitschrift der Deutschen Geologischen Gesellschaft 53*, 211–252.

Bornemann, J.G. 1854. *Über die Lias Formation in der Umgegend von Göttingen und ihre organischen Einschlüsse*. 77 pp. Wilhelm Hertz, Berlin.

Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia 61*, 1–526. DOI 10.4002/040.061.0201

Bruguière J.G. (1791–1797). *Tableau encyclopédique et méthodique des trois règnes de la nature. Vers, coquilles, mollusques et polypiers*. 180 pp. 92 pls. H. Agasse, Paris.

Burmeister, H. 1837. *Handbuch der Naturgeschichte. Zum Gebrauch bei Vorlesungen. Zweite Abtheilung: Zoologie*. 858 pp. [Zoology 369–858 pp.] T.C.F. Enslin, Berlin. DOI 10.5962/bhl.title.100177

Casey R. 1952. Some genera and subgenera, mainly new, of Mesozoic heterodont lamellibranches. *Proceedings of the Malacological Society 29*, 121–176.

Cox, L.R. 1947. The lamellibranch family Cyprinidae in the Lower Oolites of England. *Journal of Molluscan Studies 27(4)*, 141–184.

Cox, L.R. & Chavan, A. 1969. Family Myophoricardiidae Chavan in Vokes, 1967, N580–N582. *In* Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology, Pt. N, Mollusca 6, Bivalvia 2*. Geological Society of America and University of Kansas Press, Lawrence.

Cuvier, G. 1795. Second mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordre, lu à la société d'Histoire Naturelle de Paris, le 11 prairial an 3. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts 2*, 433–449.

Dall, W.H. 1889. On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group. *The American journal of science and arts, Series 3, 38*, 445–462. DOI 10.2475/ajs.s3-38.228.445

Diener, C. 1923. Lamellibranchiata triadica. *In* Diener, C. (ed.) *Fossilium catalogus I: Animalia. Pars 19.* 257 pp. W. Junk, Berlin.

Diener, C. 1926. Glossophora triadica. *In* Diener, C. (ed.) *Fossilium catalogus I: Animalia. Pars 19.* 242 pp. W. Junk, Berlin.

Dittmar, A. 1864. *Die* Contorta-*Zone (Zone der* Avicula Contorta *Portl.), Ihre Verbreitung und organischen Einschlüsse.* 217 pp. Herrmann Manz, München. DOI 10.5962/bhl.title.13972

Doben, K. 1985. *Geologische Karte von Bayern 1:25000, Erläuterungen zum Blatt Nr. 8334 Kochel*. 134 pp. Bayerisches Geologisches Landesamt, München.

Doben, K. 1991. *Geologische Karte von Bayern 1:25000, Erläuterungen zum Blatt Nr. 8335 Lenggries*. 120 pp. Bayerisches Geologisches Landesamt, München,

Douvillé, H. 1913. Classification des Lamellibranches. *Bulletin de la Societé Géologique de France 12*, 419–467.

Fabricius, F. 1961. Die Strukturen des Rogenpyrits (Kössener Schichten, Rät) als Beitrag zum Problem der "Vererzten Bakterien". *Geologische Rundschau 51*, 647–657. DOI 10.1007/BF01820027

Fabricius, F. 1966. Beckensedimentation und Riffbildung an der Wende Trias/Jura in den Bayrisch-Tiroler Kalkalpen. *International Sedimentary Petrographical Series 9*, 1–143. DOI 10.1163/9789004627796

Ferrari, M. & Hautmann, M. 2022. Gastropods underwent a major taxonomic turnover during the end-Triassic marine mass extinction event. *PLoS ONE 17(11)*, e0276329. DOI 10.1371/journal.pone.0276329

Gardner, R.N. 2005. Middle–Late Jurassic bivalves of the superfamily Veneroidea from New Zealand and New Caledonia. *New Zealand Journal of Geology and Geophysics 48(2)*, 325–376. DOI 10.1080/00288306.2005.9515119

Goetel, M.W. 1917. Die rhätische Stufe und der untere Lias der subtatrischen Zone in der Tatra. *Bulletin international de l´academie des sciences de Cracovie – Classe des sciences mathématiques et naturelles, série A: sciences mathématiques, Nov-Dez. 1916*, 1–222, pls 7–12.

Goldfuss G. A. 1837. *Petrefacta Germaniae*, *Part 2(3)*. 141–224 pp., Arnz, Düsseldorf.

Golebiowski, R. 1989. *Stratigraphie und Biofazies der Kössener Formation (Obertrias, Nördliche Kalkalpen)*. 254 pp. Ph.D. thesis, Universität Wien, Austria.

Golebiowski, R. 1991. Becken und Riffe der alpinen Obertrias – Lithostratigraphie und Biofazies der Kössener Formation. *Exkursionen im Jungpaläozoikum und Mesozoikum Österreich*, 80–11. Österreichische Paläontologische Gesellschaft, Wien.

Golovinova, M.A. & Guzhov, A.V. 2009. Early Cretaceous gastropods of the Middle–Lower Volga River region from P.A. Gerasimov's collection. *Paleontological Journal 43*, 506–513. DOI 10.1134/S0031030109050050

Gründel, J. 1973. Zur Gastropodenfauna aus dem Dogger. I. Die Gattungen *Mathilda* und *Eucycloidea*. *Zeitschrift für Geologische Wissenschaften 1*, 947–965.

Gründel, J. & Nützel, A. 2013. Evolution and classification of Mesozoic mathildoid gastropods. *Acta Palaeontologica Polonica 58*, 859–882. DOI 10.4202/app.2012.0052

Gümbel, C.W. 1859. Über die Gleichstellung der Gesteinsmassen in den nordöstlichen Alpen mit ausseralpinischen Flötzschichten. *Amtlicher Bericht über die vier und dreissigste Versammlung deutscher Naturforscher u. Ärzte in Carlsruhe im September 1858 34*, 80 – 88.

Hausmann, I.M. & Nützel, A. 2015. Diversity and palaeoecology of a highly diverse Late Triassic marine biota from the Cassian Formation at the Stuores Wiesen (North Italy, Dolomites). *Lethaia 48*, 235–255.

Hausmann, I.M., Nützel, A., Roden, V.J. & Reich, M. 2021. Diversity and palaeoecology of Late Triassic invertebrate assemblages from the tropical marine basins near Lake Misurina (Dolomites, Italy). *Acta Palaeontologica Polonica 66*, 143–192. DOI 10.4202/app.00659.2019

Hautmann, M. 2004. Effect of end-Triassic CO_2 maximum on carbonate sedimentation and marine mass extinction. *Facies 50*, 257–261. DOI 10.1007/s10347-004-0020-y

Hautmann, M. in press. An Early /Middle Triassic origin of the Venerida (Bivalvia). *Journal of Paleontology*. DOI 10.1017/jpa.2025.10139

Healey, M. 1908. The fauna of the Napeng-beds of the Rhaetic beds of Burma. *Palaeontologica Indica, New Series 2, Memoir 4*, 1–88.

Hertwig, C.W.T.R. 1895. *Lehrbuch der Zoologie (third edition)*. 599 pp. Fischer, Jena.

Hillebrandt, A. von & Urlichs, M. 2023. Extinctions and recoveries in the Allgäu Basin (Northern Calcareous Alps) during the end-Triassic mass extinction. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 308(2)*, 91–111. DOI 10.1127/njgpa/2023/1132

Isaji, S., Haga, T. & Kashiwagi, K. 2022. Early Cretaceous small-sized gastropods from the shallow marine deposits of the Kimigahama Formation, Choshi Group, Japan. *Paleontological Research 26(1)*, 31–54. DOI 10.2517/PR20009

Kaim, A., Jurkovšek, B. & Kolar-Jurkovšek, T. 2006. New associations of Carnian gastropods from Mezica region in the Karavanke Mountains of Slovenia. *Facies 52*, 469–482. DOI 10.1007/s10347-005-0040-2

Kaim, A., Nützel, A. & Maekawa, T. 2014. Smithian gastropod assemblages of the Bac Thuy Formation, 63–64. *In* Shigeta, Y., Komatsu, T., Maekawa, T. & Dang, H.T. (eds) *Olenekian (Early Triassic) Stratigraphy and Fossil Assemblages in Northeastern Vietnam. National Museum of Nature and Science Monographs 45*.

Karapunar, B. & Nützel, A. 2021. Slit-band gastropods (Pleurotomariida) from the Upper Triassic St. Cassian Formation and their diversity dynamics in the Triassic. *Zootaxa 5042(1)*, 1–165. DOI 10.11646/zootaxa.5042.1.1

Karapunar, B., Höhna, S. & Nützel, A. 2024. Phylogeny of the longest existing gastropod clade (Pleurotomariida) reconstructed with Bayesian and parsimony methods and its implications on gastropod shell characters. *Journal of Systematic Palaeontology 22(1)*, 2384141. DOI 10.1080/14772019.2024.2384141

Keen, A.M. & Casey, R. 1969. Family Arcticidae Newton, 1891, N644–N650. *In* Moore, R.C. (ed.) *Treatise on Invertebrate Paleontology, Pt. N, Mollusca 6, Bivalvia 2*. Geological Society of America and University of Kansas Press, Lawrence.

Knight, J.B. 1930. The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: The Pseudozygopleurinae. *Journal of Paleontology 4*, 1–89.

Koken, E. 1897. Gastropoden der Trias um Hallstadt. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt 17(4)*, 1–111.

Krystyn, L. 2008. An ammonoid-calibrated Tethyan conodont time scale of the late Upper Triassic, 9–11. *In* Krystyn, L. & Mandl, G.W. (eds) *Upper Triassic Subdivisions, Zonations* *and Events. Meeting of the Late IGCP 467 and STS, Abstracts and Excursion guide, Sept. 28th–Oct. 2nd Bad Goisern (Upper Austria). Berichte der geologischen Bundesanstalt 76.*

Krystyn, L., Bouquerel, H., Kuerschner, W., Richoz, S. & Gallet, Y. 2007. Proposal for a candidate GSSP for the base of the Rhaetian stage, 189–198. *In* Lucas, S.G. & Spielmann, J.A. (eds) *The global Triassic. New Mexico Museum of Natural History and Science Bulletin 41*.

Leonardi, P. & Fiscon, F. 1959. La fauna Cassiana di Cortina d'Ampezzo. Parte III Gasteropodi. Ricerce Geo-Paleontologiche nelle Dolomiti. *Memorie degli Istituti di Geologia e Mineralogia dell'Università di Padova 21*, 1–103.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Tomus I. Editio Decima.* 824 pp. Laurentius Salvius, Stockholm. DOI 10.5962/bhl.title.542

Mandl, G.W., Bryda, G. & Pavlik, W. 2009. Der Dachsteinkalk im Großraum Hochkar – Hochschwab und seine Stellung in der kalkalpinen Karbonatplattform-Entwicklung. *Arbeitstagung der Geologischen Bundesanstalt 2009*, 70–80.

McRoberts, C.A., Krystyn, L. & Hautmann, M. 2012. Faunal response to the end-Triassic mass extinction in the west-Tethyan Kössen Basin, Austria. *Palaios 27*, 607–616. DOI 10.2110/palo.2012.p12-043r

Mette, W., Elsler, A. & Korte, C. 2012. Palaeoenvironmental changes in the Late Triassic (Rhaetian) of the Northern Calcareous Alps: Clues from stable isotopes and microfossils. *Palaeogeography Palaeoclimatology Palaeoecology 350–352*, 62–72. DOI 10.1016/j.palaeo.2012.06.013

Mette, W., Thibault, N., Krystyn, L., Korte, C., Clémence, M.-E., Ruhl, M., Rizzi, M. & Ullmann, C. 2016. Rhaetian (Late Triassic) biotic and carbon isotope events and intraplatform basin development in the Northern Calcareous Alps, Tyrol, Austria. *Geo Alp 13*, 233–256.

MNHN, Chagnoux, S. 2025. *The fossil collection (F) of the Muséum national d'Histoire naturelle (MNHN – Paris. Version 68.419*. MNHN – Museum national d'Histoire naturelle. Occurrence dataset *https://doi.org/10.15468/fjjmkb* accessed via GBIF.org on 2025-07-22. *https://www.gbif.org/occurrence/418889913*

Münster, G. zu 1841. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen, 25–152. *In* Wissmann, H.L. & Münster, G. zu (eds) *Beiträge zur Geognosie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. Beiträge zur Petrefacten-Kunde 4*.

Neumayr, M. 1884. Zur Morphologie des Bivalvenschlosses. *Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathematisch–Naturwissenschaftliche Klasse, Abteilung 88(1)*, 385–418.

Nützel, A. 1998. Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen, Reihe E 26*, 1–229.

Nützel, A. 2005. Recovery of gastropods in the Early Triassic. *Comptes Rendus Palevol 4*, 501–515. DOI 10.1016/j.crpv.2005.02.007

Nützel, A. & Schulbert, C. 2005. Gastropod lagerstätten in the aftermath of the end-Permian mass extinction – Diversity and facies of two major Early Triassic occurrences. *Facies 51*, 495–515. DOI 10.1007/s10347-005-0074-5

Nützel, A., Nose, M., Hautmann, M. & Hochleitner, R. 2023 (2022 online first). Latest Triassic (Sevatian–Rhaetian) reef carbonates from the Northern Calcareous Alps (Austria), their mollusc dwellers and their fate at the end-Triassic extinction event. *PalZ 97*, 265–309. DOI 10.1007/s12542-022-00631-9

Orbigny, A.D. d'. 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques & rayonnés, faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques. Vol. 1*. 394 pp. 60 pls. Masson, Paris. DOI 10.5962/bhl.title.62810

Osswald, K. 1930. Über einige Rätfossilien aus dem Risserkogelgebiet (südlich Tegernsee). *Jahrbuch der Preußischen geologischen Landesanstalt 50 (für 1929)*, 733–750.

Philippi, E. 1898. Die Fauna des unteren *Trigonodus*-Dolomits vom Hühnerfeld bei Schwieberdingen und des sogenannten 'Cannstatter Kreidemergels'. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 54*, 145–227.

Rafinesque, C.S. 1815. *Analyse de la nature ou tableau de l'a Univers et des corps organisés*. 224 pp. Jean Barravecchia, Palermo. DOI 10.5962/bhl.title.106607

Roden, V., Hausmann, I.M., Nützel, A., Seuss, B., Reich, M., Urlichs, M., Hagdorn, H. & Kiessling, W. 2020. Fossil liberation: a model to explain high biodiversity in the Triassic Cassian Formation. *Palaentology 63*, 85–102. DOI 10.1111/pala.12441

Röder, H.A. 1882. *Beiträge zur Kenntnis des Terrain à Chailles und seiner Zweischaler in der Umgegend von Pfirt im Ober-Elsass.* 110 pp. Inaugural-Dissertation der Mathematisch-naturwissenschaftlichen Fakultät der Kaiser-Wilhelm-Universität Straßburg. Schultz, Straßburg, Germany.

Schafhäutl, K.F.E. von 1863. *Südbayerns Lethea geognostica*. 487 pp. Leopold Voss, Leipzig.

Schmidt, M. 1991. *Mikrofazies und fazielle Entwicklung der Rhät/Lias-Sedimentation im Bereich zwischen Brauneck und Benediktenwand (Nördliche Kalkalpen, Isarwinkelgebirge, Lenggries, Oberbayern)*. 140 pp. Master thesis, Johannes Gutenberg Universität Mainz, Germany.

Stoppani, A. 1857. *Studi geologici e paleontologici sulla Lombardia*. 461 pp. 3 pls. Joseph Bernardoni, Milano.

Stoppani, A. 1860–1865. *Géologie et Paléontologie des Couches à Avicula contorta en Lombardie. Paléontologie Lombarde ou Description des Fossiles de Lombardie III*. 407 pp. Joseph Bernardoni, Milano.

Tichy, G. 1978. Der erste Fossilfund, *Pseudocorbula alpina* (Winkler), aus dem Hauptdolomit des Festungsberges (Stadt Salzburg). *Mitteilungen der Gesellschaft für Salzburger Landeskunde 118*, 341–344.

Tomašových, A. 2006a. Linking taphonomy to community-level abundance: Insights into compositional fidelity of the Upper Triassic shell concentrations (Eastern Alps). *Palaeogeography, Palaeoclimatology, Palaeoecology 235*, 355–381. DOI 10.1016/j.palaeo.2005.11.005

Tomašových, A. 2006b. Brachiopod and bivalve ecology in the

Late Triassic (Alps, Austria): onshore-offshore replacements caused by variations in sediment and nutrient supply. *Palaios 21*, 344–368. DOI 10.2110/palo.2005.P05-53e

Walther, H. 1951. Jurassische Mikrofossilien, insbesondere Gastropoden, am Südrand des Hils. *Paläontologische Zeitschrift 25*, 35–106. DOI 10.1007/BF03044009

Wenz, W. 1938–1944. *Gastropoda, Teil I. In* Schindewolf, O.H. (ed.) *Handbuch der Paläozoologie, vol. 6.* 1639 pp. Borntraeger, Berlin.

Winkler, G. 1859. *Die Schichten mit Avicula contorta inner- und außerhalb der Alpen*. 51 pp. Palm, München.

Winkler, G. 1861. Der Oberkeuper nach Studien in den bayerischen Alpen. *Zeitschrift der Deutschen Geologischen Gesellschaft 13*, 459–521.