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A remarkable invertebrate fossil assemblage from the Lower Triassic Werfen Formation of the Totes Gebirge (Styria, Austria)

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3 Text-Figures, 3 Plates

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Cubozoa
Medusae
Gastropoda
Ammonoidea
Bivalvia
Xiphosura
Northern Calcareous Alps

Contents

Abstract

Invertebrate fossil assemblage yielded by siltstone and fine-grained sandstone beds of the Werfen Formation ("Werfener Schichten") exposed along Zauchenbach Creek near Bad Mitterndorf is briefly described and illustrated. Occurrence of the ammonite *Tirolites cassianus* (Quenstedt, 1849) indicates an early Spathian (late Early Triassic) age of the fauna. In addition to mollusc (gastropod, ammonite and bivalve) species characteristic of the "Campil Level" often mentioned from the Alpine-Carpathian region in the older literature, the assemblage consists also of ichnofossils (*Asteriacites* sp., *Cruziana* sp. and a coprolite) as well as coalified *Araucaria*-like and other plant fragments. Sedimentary features and composition of the fossil assemblage indicates that the Werfen beds exposed along Zauchenbach Creek have been deposited in nearshore and shallow marine environment.

Until now, unique peculiarities of the fauna are horseshoe crabs [*Limulitella* cf. *bronni* (Schimper, 1853)] and cnidarian medusae interpreted as box jellyfish (Cubozoa), i.e. *Anthracomedusa*? *hoferhauseri* n. sp. In addition, a new bivalve species *Avichlamys hoferhauseri* n. sp. is introduced.

Eine bemerkenswerte Invertebraten-Vergesellschaftung in den Werfener Schichten (Untertrias) des Toten Gebirges (Steiermark, Österreich)

Zusammenfassung

Aus einer siltig-feinsandigen Abfolge der Werfener Schichten des Zauchenbachgrabens bei Bad Mitterndorf wird eine Invertebraten-Vergesellschaftung beschrieben und illustriert. Das Vorkommen des Ammoniten *Tirolites cassianus* (Quenstedt, 1849) weist auf ein spätes Untertrias-Alter (Spathium) hin. Zusätzlich zu diversen Mollusken (Gastropoden, Ammoniten und Bivalven), die im „Campil" der Alpen-Karpaten-Region häufig erwähnt werden, konnten Lebensspuren (*Asteriacites* sp., *Cruziana* sp. und ein Koprolith) sowie nicht näher bestimmte inkohlte *Araucaria*-ähnliche und andere pflanzliche Reste nachgewiesen werden. Die Zusammensetzung der Fossilien-Vergesellschaftung sowie die Sedimentstrukturen sprechen für küstennahe, seicht marine Ablagerungsbedingungen der Werfener Schichten des Zauchenbach-Profils.

Bislang einzigartige Funde sind Pfeilschwanzkrebse [*Limulitella* cf. *bronni* (Schimper, 1853)] und zu den Würfelquallen (Cubozoa) zählende Nesseltiere: *Anthracomedusa*? *Hoferhauseri* n. sp. Zudem wird die Muschel-Art *Avichlamys hoferhauseri* n. sp. beschrieben.

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Introduction

The last three and a half decades saw a renewed interest in various aspects of Lower Triassic marine fossil assemblages. Studies carried out in the Southern Alps and the Balaton Highland of Hungary, both known as classical areas of the Alpine Triassic, for example, have resulted in several papers (e.g. Broglio Loriga et al., 1990; Hofmann et al., 2015; Kolar-Jurkovšek et al., 2013; Neri & Posenato, 1985; Posenato, 1992, 2008). Northern Calcareous Alps have received much less attention from this point of view and apparently, no Lower Triassic macrofossil has been illustrated from there in the last seven decades. The richly fossiliferous locality (Text-Fig. 1) discovered (or more probably re-discovered) some years ago by the enthusiastic fossil collector Helmut Meierl vulgo Hoferhauser of Zauchen (Bad Mitterndorf) thus seemed to serve as a good starting point for the study of the macrofossil assemblage of the Lower Triassic of the Northern Calcareous Alps.

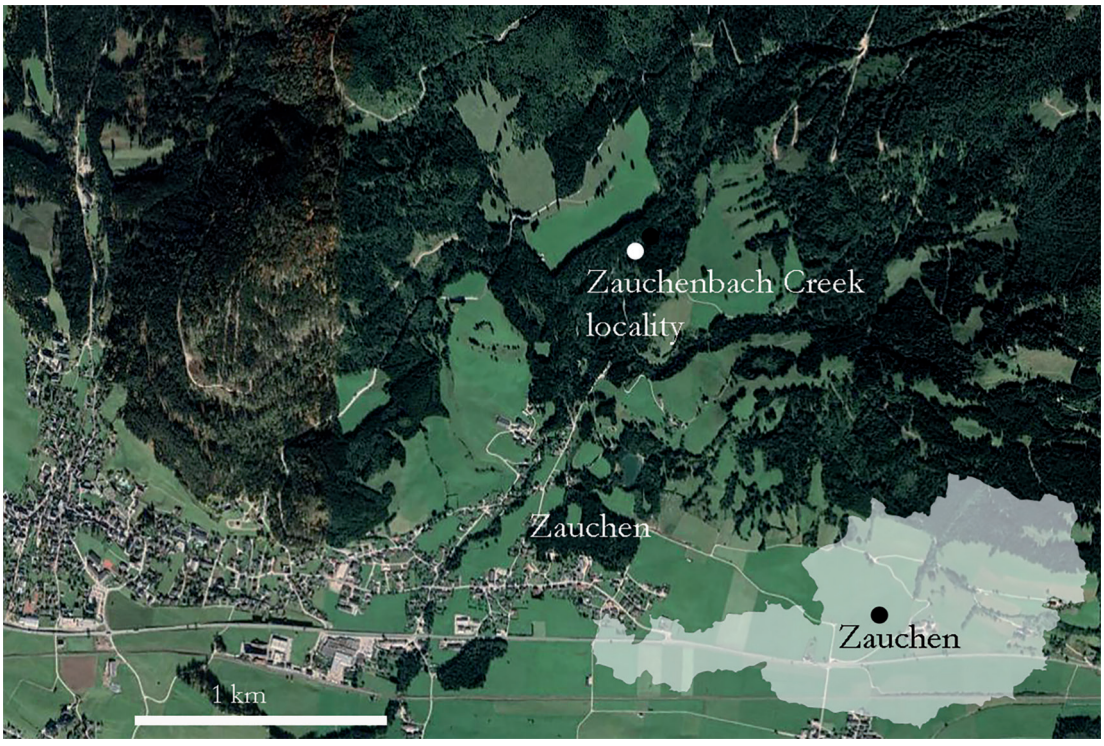
Previous studies

Fossiliferous beds of the Lower Triassic Werfen Formation have been known to crop out in the vicinity of Bad Mitterndorf since the pioneering work of Geyer (1915), who recorded "*Tirolites spinosus* Mojsisovics", "*Naticella costata* Münster" and "*Myacites fassaensis* Wissmann". Subsequent authors (Tollmann, 1960; Steiger, 1980; Mostler & Rossner, 1984) published results of investigations of the Zauchenbach Creek section and added some bivalve taxa, such as myophoriids and bakevelliids ("Gervilleen"), to the above-mentioned ones. The fauna, however, was not studied in detail or, at least, has remained undocumented in the literature except the report of Szente (2014).

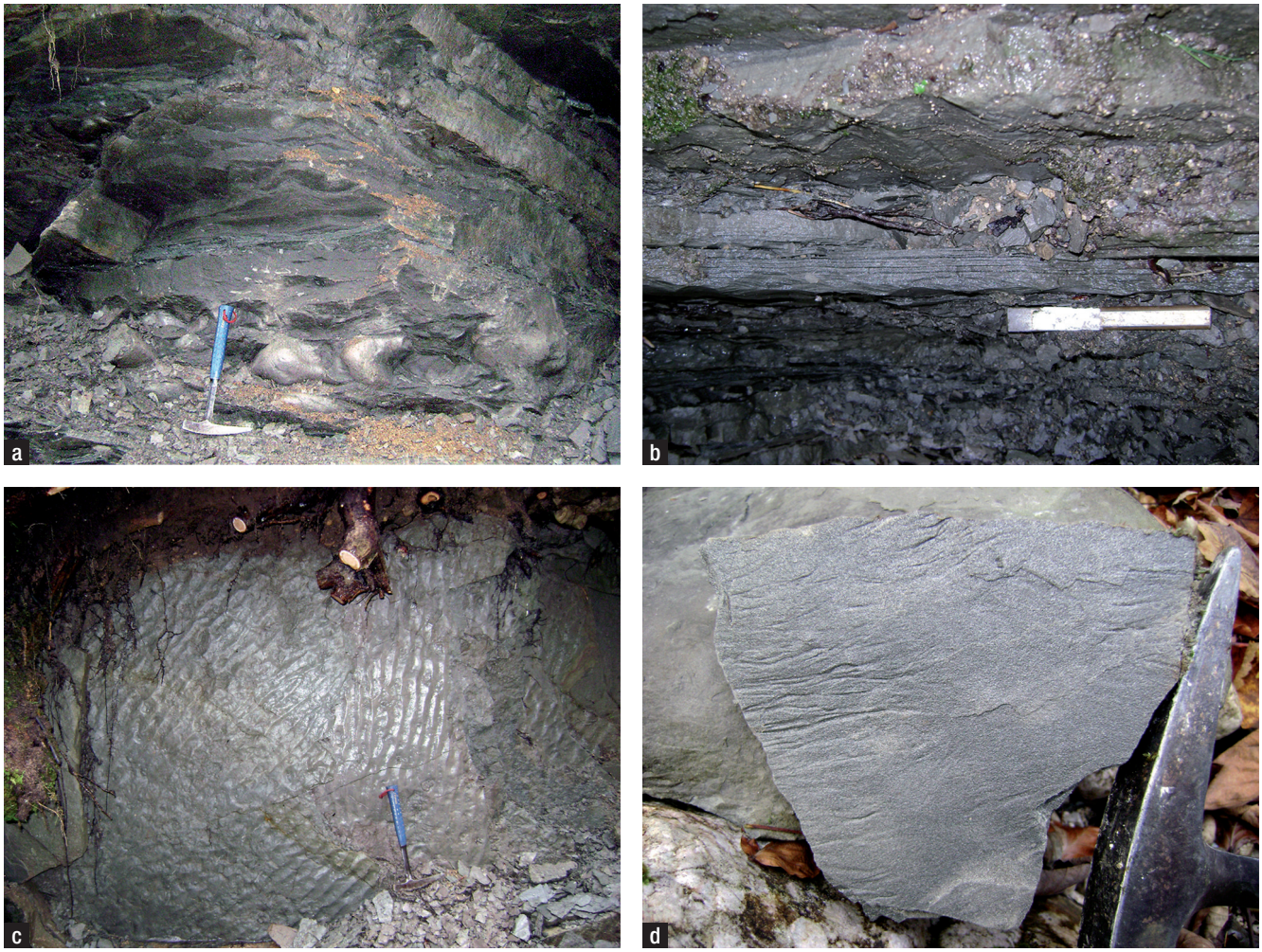
Locality and material

Werfen Formation represented by both "Werfen Shale" and Werfen Limestone" crops out for approximately 100 m along Zauchenbach Creek to the North of Zauchen village, about 1.5 km of the road No. 145 (Steiger, 1980). The outcrop is formed by isolated exposures of beds dipping in different directions and at various angles. The main fossil locality (Text-Figs. 2a, b) is situated on the right side of the ravine and displays siltstone and fine-grained sandstone beds steeply dipping to the Northwest. Sedimentary structures observed include ball and pillow structures (Text-Fig. 2a) and wrinkle structures (Text-Fig. 2d) as well. At another point situated around 20 meters to the Northeast of the former one on the left side of the ravine spectacular bedding planes with wave-formed ripples are exposed (Text-Fig. 2c). No desiccation cracks have been observed. Some more outcrops of smaller size are also scattered along the ravine. Their actual conditions, however, depends on the spring runoff of Zauchenbach Creek.

The macrofossil assemblage of the Werfen Shale consists of cnidarian medusae, gastropods, bivalves, ammonites and xiphosuran arthropods. The fossils are poorly preserved as a rule: aragonite shells such as those of gastropods, most bivalves and ammonites, have been completely dissolved during diagenesis. Remnants of calcite shell layers have been encountered only in bivalves *Eumorphotis* and *Avichlamys*. Most of the specimens are affected by deformation to a variable degree. About four outcrops, yielding fossil assemblages of slightly different taxonomic composition, were sampled. Fossils are scattered in the sediment or occur as densely packed pavements formed by usually fragmented fossils. These accumulations are interpreted as tempestites. Moldic preservation of cnidarian medusae (see below) can be explained by rapid infilling and burial of bells due to storm flows. In addition to invertebrate remains, the locality has yielded a low-diversity



Text-Fig. 1.
Location of the outcrop studied (map generated with Google Earth © 2020, image taken on 28.07.2020; Austria Map by Vemaps.com).



Text-Fig. 2.
Outcrop details and characteristic sedimentary structures. a: siltstone and fine-grained sandstone beds with ball and pillow structures; b: cross-section of fine-grained sandstone beds approximately perpendicular to the direction of ripples. The chisel is 12 cm long; c: bedding plane with wave-formed ripples; d: wrinkle structures.

ichnofossil assemblage consisting of *Asteriacites* sp., *Cruziana* sp. and a coprolite. Very rarely, coalified *Araucaria*-like and other plant fragments are also encountered. Sedimentary features and composition of the fossil assemblage indicates that the Werfen Shale exposed along Zauchenbach Creek has been deposited in nearshore and shallow marine environment.

Systematic palaeontology

In the following, an annotated list of invertebrate taxa encountered is given. In order to give a semi-quantitative picture on relative abundances, numbers of specimens collected by the author and handed to the Collection of the Geologische Bundesanstalt (thereinafter GBA) or studied and identified in the collection of HELMUT MEIERL (thereinafter HMC) are indicated, along with remarks on the mode of preservation, morphology, or taxonomy. Note that specimens housed at HMC are obviously biased towards well-preserved, spectacular ones.

Cnidaria: Cubozoa

Anthracomedusa? *hoferhauseri* n. sp.

Text-Fig. 3; Pl. 1, Figs. 1–4

Derivation of name: After the collector HELMUT MEIERL, vulgo HOFERHAUSER, who kindly donated the holotype to GBA.

Material: Four specimens including the holotype (GBA 2020/004/0001) housed in GBA (Pl. 1, Fig. 1) along with five poorly preserved specimens, four specimens (HMC).

Type locality and horizon: Zauchenbach Creek, Werfen Formation (*Cassianus* Zone, Spathian, Lower Triassic), Totes Gebirge, Northern Calcareous Alps, Austria.

Diagnosis: Cuboidal bell of sub-quadrangular outline, with protuberant axial and radial structures.

Description: Specimens are preserved as internal moulds and no traces of soft body can be studied. Features observable from aboral view include protruding, circular axial structure as well as four well-developed radial swells, in-

terpreted as traces of radial canals, connected to it. The areas between radial swells bear weak diagonal swells, which cannot be attributed to any features of cubozoan body and may be of diagenetic origin.

Discussion: The fossil record of box jellyfish is extremely incomplete (YOUNG & HAGADORN, 2010). Three genera, *Anthracomedusa* JOHNSON & RICHARDSON, 1968, as well as *Bipedalia* GAILLARD & GOY, 2006 and *Paracarybdea* GAILLARD & GOY, 2006 have been introduced to accommodate Upper Carboniferous and Upper Jurassic forms, respectively (JOHNSON & RICHARDSON, 1968; GAILLARD et al., 2006). Comparison of Zauchenbach Creek medusae with previously described forms is, due to the fundamental difference in the mode of their preservation, rather difficult. Specimens of *Anthracomedusa turnbulli* JOHNSON & RICHARDSON, 1968, the only species attributed to the genus have been preserved as impressions in early diagenetic siderite concretions while Upper Jurassic forms are represented by 2D moulds in lithographic limestone. Their descriptions are partly based on preserved features of the soft body.

The specimen most similar to *Anthracomedusa*? *hoferhauseri* n. sp. is *A. turnbulli* as figured by YOUNG & HAGADORN (2010: Fig. 3e). It displays, however, relatively shorter radial swells not reaching the corners (see also https://ucmp.berkeley.edu/cnidaria/Anthracomedusa.html).

Mollusca: Gastropoda

Natiria costata (MÜNSTER, 1841)

Pl. 1, Figs. 5–9

Material: 26 specimens (GBA), dozens of specimens (HMC).

The Zauchenbach Creek specimens of this characteristic "Campilian" gastropod species agree well in form and size with those figured in the literature (e.g. FRECH, 1911: Pl. 7, Figs. 8, 9; BROGLIO LORIGA et al., 1990: Pl. 5, Fig. 10.).

Werfenella rectecostata (HAUER, 1851)

Pl. 1, Figs. 10–15

Material: 17 specimens (GBA), dozens of specimens (HMC).

The Zauchenbach Creek specimens are internal moulds, so the shell ornamentation consisting of axial ribs and nodes, displayed by better preserved specimens (see NÜTZEL, 2005), is indistinct or completely lacking.

Text-Fig. 3.
Field occurrence of *Anthracomedusa*? *hoferhauseri* n. sp. immediately after finding. The chisel is 12 cm long.

Mollusca: Ammonoidea

Dalmatites morlaccus Kittl, 1903

Pl. 1, Figs. 16–19; Pl. 2, Figs. 1, 2

Material: Seven specimens (GBA), about a dozen specimens (HMC).

D. morlaccus is a rare species at the type area around the village of Muć in Dalmatia (Golubić, 2000) and its stratigraphical range is poorly known. Co-occurrence of *D. morlaccus* and *Tirolites cassianus* (see below) is worth mentioning because Posenato (1992) supposed that the first-mentioned species appeared after the disappearance of *Tirolites cassianus*, in other words, ranges of these species do not overlap.

Tirolites cassianus (Quenstedt, 1849)

Pl. 2, Figs. 3–14

Material: 17 specimens extracted and some further ones on a slab (GBA), around 20 specimens (HMC).

The umbilical diameter/maximum diameter ratio of the specimens, considered as characteristic of *Tirolites* species by Krystyn (1974) and Posenato (1992), is around 0.45, well within the range of *T. cassianus*. The Zauchenbach Creek *Tirolites* display remarkable variability in their ornamentation, i.e. in the number and nature of ribs. Some specimens (e.g. Pl. 2, Figs. 6, 11, 14) bear spines on their inner whorls. A few, presumably adult specimens (Pl. 2, Figs. 3, 5, 6, 13), although incompletely preserved, made the estimation of the number of nodes ("Marginalknoten") on their last whorl possible. In each case more than ten nodes could be counted, a value well within the range of *T. cassianus*, which is 12–22, mean 16.3 in specimens from Muć (Krystyn, 1974) and 8–18, mean 13.34 in specimens from the Dolomites (Posenato, 1992).

Mollusca: Bivalvia

Bakevellia exporrecta (Lepsius, 1878)

Pl. 2, Figs. 15, 17–20

Material: seven specimens (GBA), five specimens (HMC).

Bivalves referred to as "Gervillien" in the older literature and currently assigned to *Bakevellia* s.l. display remarkable morphological variability in the Werfen Formation. Due to the work of Ehrlich (1946), a plethora of species names is available for them. The prevailing poor preservation, however, seems to have hindered the sound revision of this group until now. The majority of recent authors (e.g. Neri & Posenato, 1985; Hautmann et al., 2013; Hofmann et al., 2013) assigned most of bakevelliids encountered in the Lower Triassic to *B. exporrecta* and their taxonomic opinion is shared here. The twisted nature of valves (i.e. commissure not in a plane), observed recently in *B. exporrecta* by Hautmann et al. (2013), is not displayed by the Zauchenbach Creek specimens.

Bakevellia castelli (Wittenburg, 1908)

Pl. 2, Fig. 16

Material: One specimen (HMC).

B. castelli differs from *B.* cf. *exporrecta* by having much more elongated form. The Zauchenbach Creek specimen clearly displays the trace of a posterolateral tooth. Generic assignment of "*Edentula*" *castelli* to *Bakevellia* s.l. is thus confirmed.

Eumorphotis telleri (Bittner, 1898)

Pl. 2, Figs. 21–25

Material: Four specimens (GBA), a few specimens (HMC).

The Zauchenbach Creek specimens of this species are the largest bivalves found at the locality and agree well in shape with *E. telleri* figured in the literature (e.g. Bittner, 1898: Pl. 15, Figs. 11–15; Bittner, 1901: Pl. 22. Figs. 1–5; Broglio Loriga et al., 1990: Pl. 5, Fig. 6, Pl. 7, Fig. 15). *E. telleri* was considered as the index fossil of the stratigraphically youngest subzone of the "Eumorphotis Zone" distinguished in the Lower Triassic of the Dolomites (e.g. Broglio Loriga et al., 1990).

Eumorphotis multiformis (Bittner, 1899)

Pl. 2, Fig. 26; Pl. 3, Figs. 1–4

Material: Two specimens (GBA), two specimens (HMC).

The orbicular to arched outline of the specimens as well as their ornamentation consisting of a relatively few first-order radial ribs intercalated by finer second-order and third-order ones agree to *E. multiformis* figured in the literature (e.g. Bittner, 1899: Pl. 2, Figs. 11–22; Kumagae & Nakazawa, 2009: Fig. 144.17; Hautmann et al., 2013: Fig. 6R; Hofmann et al., 2014: Fig. 11J–L).

Eumorphotis sp.

Pl. 3, Fig. 5

Material: One specimen (HMC).

E. sp. differs from *E. telleri* and *E. multiformis* by bearing relatively few, robust, spiny radial ribs.

Avichlamys hoferhauseri n. sp.

Pl. 3, Figs. 6, 7

Derivation of name: After Helmut Meierl, known as Hoferhauser, discoverer of the type locality.

Material: Two specimens including the holotype (GBA 2020/004/0002) housed in GBA, two specimens (HMC).

Type locality and horizon: Zauchenbach Creek, Werfen Formation (*Cassianus* Zone, Spathian, Lower Triassic), Totes Gebirge, Northern Calcareous Alps, Austria.

Diagnosis: Sub-ovate disc ornamented with radial ribs whose number increases towards the margin by intercalation, distinguished from other species of *Avichlamys* by the higher number of radial ribs.

Description: Only features of left valve can be studied in detail in the specimens available. Medium-sized *Avichlamys* with sub-ovate disc outline. Inaequilateral, longer than high. Umbonal angle around 85°. Auricles well demarcated from disc, anterior slightly larger than posterior. Exterior of valve exhibiting 17 radial ribs at shell height 1 cm, and around 30 at height 2 cm.

Discussion: On the basis of general shape and especially the length and well demarcated nature of auricles this rare form seems to represent the pectinid genus *Avichlamys* Allasinaz, 1972, confined to the Olenekian (Posenato, 2008). Apart from a few poorly known forms of doubtful affinity, four species have been assigned to this genus. These are: *Pecten csopakensis* Frech, 1905; *Pecten nicolensis* Ogilvie Gordon, 1927; *Chlamys tellinii* Tommasi, 1896 and *Pecten voelseckhofensis* Wittenburg, 1908 (Allasinaz, 1972; Neri & Posenato, 1985; Hofmann et al., 2015). Ribbing pattern of them, however, differs from that of *Avichlamys hoferhauseri* n. sp.

Costatoria costata (Zenker, 1833)

Pl. 3, Fig. 8

Material: Some small-sized specimens on a rock slab (GBA).

In the Dolomites, *C. costata* is the index fossil of the "*Costatoria costata* Local-Range-zone", corresponding to the upper Spathian (or uppermost Olenekian). At the base of the "zone" *C. costata* specimens are reported to be small-sized and bear 7–10 ribs while stratigraphically younger ones are larger in size and are more ribbed (12–15 ribs) (Broglio Loriga et al., 1990). The Zauchenbach Creek specimens are small-sized and bear relatively few (about 10) radial ribs. It is worth mentioning that "*Costatoria costata* zone" in the Dolomites is stratigraphically younger than the beds with *Tirolites cassianus*.

Neoschizodus laevigatus (Zieten, 1830)

Pl. 3, Fig. 9

Material: Two specimens (GBA).

N. laevigatus, whose remains are widespread in Lower and Middle Triassic rocks, was a morphologically highly variable species (Hofmann et al., 2013). The Zauchenbach Creek specimens are slightly more elongated than most *N. laevigatus* figured in the literature.

Unionites? *fassaensis* (Wissmann in Münster, 1841)

Pl. 3, Figs. 10–12

Material: More than 40 specimens (GBA), numerous specimens (HMC).

U.? *fassaensis* is one of the most frequently reported and most variable Lower Triassic bivalve species. It often occurs associated with *U.*? *canalensis* (Catullo, 1846), a species of similar shape. Although both are very variable in shape, most authors consider them as distinct species. Problems of distinguishing these forms were discussed recently by Neri & Posenato (1985), Kumagae & Nakazawa (2009), and Hautmann et al. (2013).

According to Kumagae & Nakazawa (2009), *U.*? *canalensis* has more elongated shape and more developed umbonal ridge. Another diagnostic feature is the position of the umbo, which is more or less at the half of the length in *U.*? *fassaensis.* Based on these criteria, most – if not all – *Unionites* yielded by the Zauchenbach Creek locality represent *U.*? *fassaensis.*

Arthropoda: Xiphosura

Limulitella cf. bronni (Schimper, 1853)

Pl. 3, Figs. 13–16

Material: Four specimens (HMC).

Although the specimens are relatively poorly preserved, incomplete internal and external moulds with remains of the carapace, they are assigned to *Limulitella* Størmer, 1952, on the basis of their size and gross morphology, with certainty. The distinctly triangular genal spine with a straight inner margin, as well as the acute angle made by it with the antero-lateral margin of the opisthosoma, are characteristic features of *Limulitella*. The Zauchenbach Creek specimens bear strong resemblance to and may be conspecific with *L. bronni* (Schimper, 1853), type species of *Limulitella,* described by Schimper (1853: Pl. 3) and illustrated by Gall (1971: Pl. 7, Fig. 1) from the early Middle Triassic *Voltzia* Sandstone of the Vosges Mountains of France.

According to Lamsdell (2016), *Limulitella* was a freshwater genus. The findings documented here, however, confirm the opinion of Błażejowski et al. (2017), who interpreted it as an environmentally highly tolerant form with the ability to exist in both marine and fresh/brackish water.

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Plate 1

Figs. 1–4: *Anthracomedusa* ? *hoferhauseri* n. sp. 1: holotype (GBA 2020/004/0001) (2–4: HMC). Note that the appearance of circular pits of the axial structure in Figures 1–3 is due to over-preparation.

Figs. 5–9: *Natiria costata* (MÜNSTER) (8, 9: GBA 2020/004/0003, 2020/004/0004) (5–7: HMC).

Figs. 10–15: *Werfenella rectecostata* (HAUER) (12–15: GBA 2020/004/0005–2020/004/0008) (10–11: HMC).

Figs. 16–19: *Dalmatites morlaccus* KITTL (HMC).

Specimens figured are housed in the Collection of the Geologische Bundesanstalt (Vienna) unless indicated as HMC (HELMUT MEIERL collection). All specimens are coated with ammonium chloride and figured in natural size.

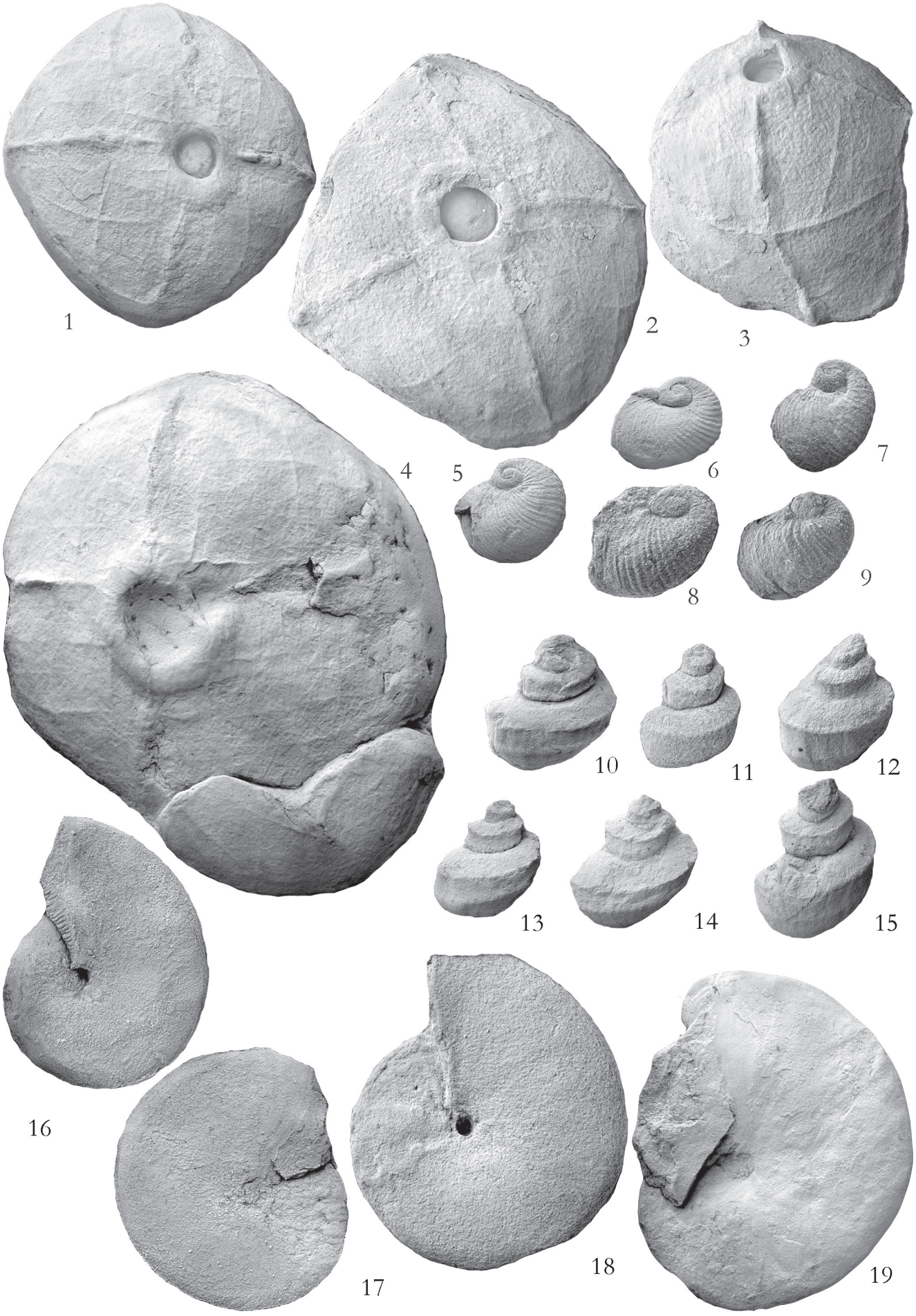
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Plate 2

Figs. 1, 2: *Dalmatites morlaccus* KITTL (GBA 2020/004/0009, 2020/004/0010).
Figs. 3–14: *Tirolites cassianus* (QUENSTEDT) (7–14: GBA 2020/004/0011–2020/004/0018) (3–6: HMC).
Figs. 15, 17–20: *Bakevellia exporrecta* (LEPSIUS) (18–20: GBA 2020/004/0019–2020/004/0021) (15, 17: HMC).
Fig. 16: *Bakevellia castelli* (WITTENBURG) (HMC).
Figs. 21–25: *Eumorphotis telleri* (BITTNER) (22, 24, 25: GBA 2020/004/0022–2020/004/0024) (21, 23: HMC).
Fig. 26: *Eumorphotis multiformis* (BITTNER) (GBA 2020/004/0025).

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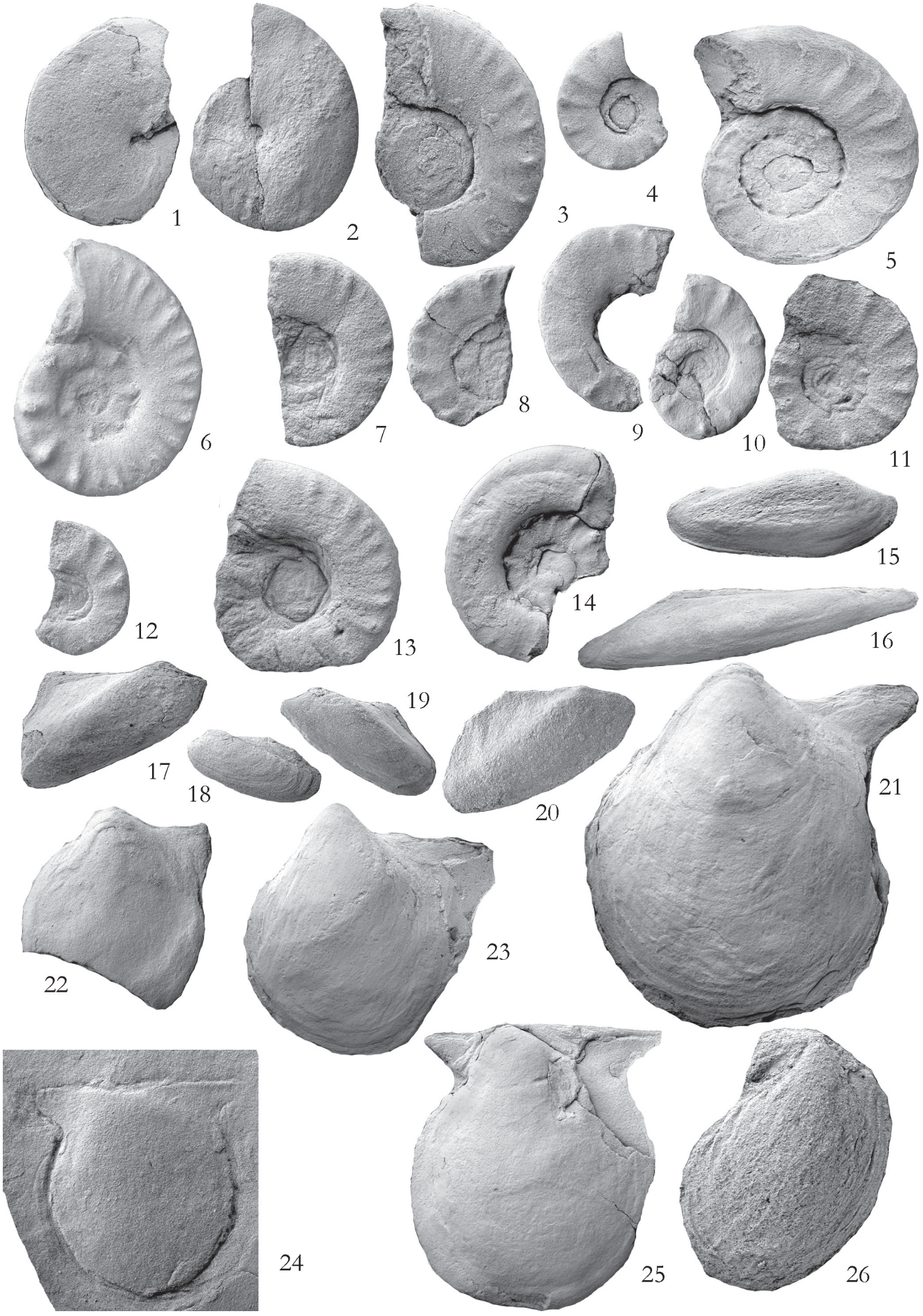
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Plate 3

Figs. 1–4: *Eumorphotis multiformis* (Bittner) (3, 4: GBA 2020/004/0026, 2020/004/0027) (1, 2: HMC).

Fig. 5: *Eumorphotis* sp. (HMC).

Figs. 6, 7: *Avichlamys hoferhauseri* n. sp. 6: holotype (GBA 2020/004/0002) (plaster cast) (7: GBA 2020/004/0028).

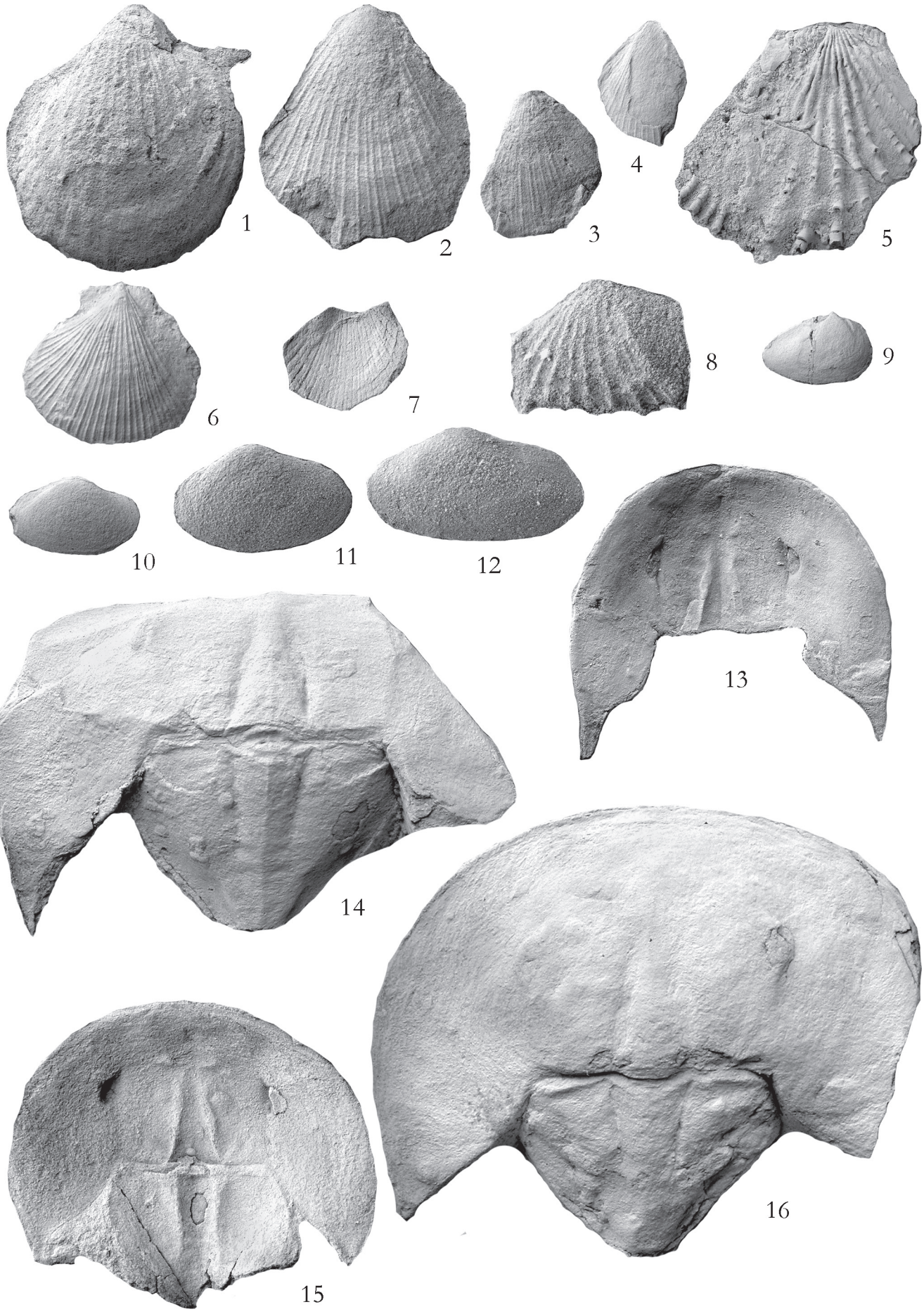
Fig. 8: *Costatoria costata* (Zenker), 4X, (GBA 2020/004/0029).

Fig. 9: *Neoschizodus laevigatus* (Zieten) (GBA 2020/004/0030).

Figs. 10–12: *Unionites* ? *fassaensis* (Wissmann in Münster) (GBA 2020/004/0031–2020/004/0033).

Figs. 13–16: *Limulitella* cf. *bronni* (Schimper, 1853) (HMC). The specimens depicted in Figures 13 and 15 are external moulds.

Specimens figured are housed in the Collection of the Geologische Bundesanstalt (Vienna) unless indicated as HMC (Helmut Meierl collection). All specimens are coated with ammonium chloride and figured in natural size except Plate 3, Figure 8.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