On Triassic *Murchisonia*-like gastropods—surviving the end-Permian extinction to become extinct in the Late Triassic

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High-spired *Murchisonia*-like slit-band gastropods are an important component of late Paleozoic gastropod faunas. Twenty-seven genera of such gastropods have been reported from the Permian, most of which representing the caenogastropod family Goniasmatidae. Only four genera, *Trypanocochlea, Wannerispira*, *Laschmaspira*, and *Altadema* crossed the Permian/Triassic boundary. Based on the study of newly collected specimens and material from natural history collections, we studied the surviving genera as well as the Triassic recovery of this group. Two new species (*Laschmaspira lirata* sp. nov. and *Altadema hausmannae* sp. nov.) and one new subfamily (Cheilotomoninae) are introduced. *Murchisonia*-like caenogastropods, chiefly Goniasmatidae, were diverse and abundant until the Permian, barely survived the end-Permian extinction, regained a certain generic diversity within the Triassic with the evolution of several new genera but failed by far to regain their Permian generic diversity. This once successful and diverse group shares a similar fate (surviving the end-Permian extinction, a reduced Triassic diversity and extinction during Late Triassic crises) as conodonts, orthoceratids, conulariids, and others. This diversity pattern does not qualify for the "Dead Clade Walking" phenomenon, i.e., the extinction shortly after a major mass extinction event (survival without recovery) because they have survived for ca. 30 Ma (at least until the Norian) and even produced a number of new genera. The exact time of their extinction is unknown but there are no safe Rhaetian occurrences. Their extinction is part of a long-term selective trend against the character "shell-slit".

Key words: Gastropoda, Goniasmatidae, diversity, recovery, end-Permian extinction, Triassic, Italy, Austria.

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Introduction

High-spired gastropods with selenizone (slit-band, closed shell slit) are a typical component of Paleozoic gastropod faunas from the Ordovician onwards. Like many typical Paleozoic gastropod groups, they were severely affected at the end-Permian mass extinction (Erwin 1990; Nützel 2005; Karapunar and Nützel 2021) and became a minor element in the Triassic until their demise in the Late Triassic. Due to their rarity in most of the Triassic faunas, studies on *Murchisonia*-like gastropods from the Triassic are scarce and the Triassic representatives of the group are less known compared to their Paleozoic representatives. Herein, we revise Triassic *Murchisonia*-like gastropods to better understand the diversity of this group in the Triassic and their possible relationships to Paleozoic forms.

High-spired slit-bearing gastropods have been traditionally assigned to the family Murchisoniidae or to the superfamily Murchisonioidea (e.g., Knight et al. 1960) and many of such gastropods ranging from the Ordovician to the Triassic were placed in the genus *Murchisonia*. However, there is a considerable number of *Murchisonia*-like genera and the composition of the group is quite complex. *Murchisonia*-like gastropods are considered either as exceptionally high-spired Pleurotomariida (Vetigastropoda) or as slit-bearing Caenogastropoda depending on the larval shell morphology and shell microstructure (Koken 1889; Knight et al. 1960; Nützel 1998; Nützel and Bandel 2000; see also Mazaev 2011). However, these characters are still unknown for many genera and hence their classification is doubtful. *Murchisonia*, the type genus of the group, has a Devonian type species, *M. bilineata* (Dechen, 1832), which is a highly variable species (Heidelberger 2001; Heidelberger and Koch 2005). Its early ontogeny, including protoconch morphology, is largely unknown and this hinders a correct taxonomic and systematic assessment of *Murchisonia* and Murchisoniidae in general. Several late Paleozoic *Murchisonia*-like gastropods (Goniasmatidae) have been reported with well-preserved early ontogenetic shells possessing caenogastropod-type larval shells (Yoo 1988, 1994; Nützel 1998; Nützel and Bandel 2000; Bandel 2002; Bandel et al. 2002; Pan and Erwin 2002; Nützel and Pan 2005; Karapunar et al. 2022). The specimens from the Pennsylvanian Buckhorn Asphalt deposit (USA, Oklahoma) further revealed that their Carboniferous representatives lack nacre but have an aragonitic crossed lamellar shell microstructure (Bandel et al. 2002). The absence of nacre supports a placement of these gastropods in Caenogastropoda because vetigastropods including Pleurotomariida commonly possess nacre, and only some vetigastropods are known to lack nacre (e.g., Skeneidae, Fissurelloidea; Ponder et al. 2020). By contrast, nacre is unknown in Gastropoda outside Vetigastropoda. As already stated by Koken (1889), *Murchisonia*-like gastropods commonly develop an anterior siphonal canal, a character that is absent in true Pleurotomariida. This character also brings the entire group closer to caenogastropods. On the other hand, Frýda and Manda (1997) and Frýda et al. (2008) documented well-preserved *Murchisonia*-like gastropods that have a protoconch typical of Vetigastropoda (i.e., consisting of about one whorl) suggesting placement in Vetigastropoda. The presence of nacre in the Ordovician "*Murchisonia*" (Mutvei 1983) further corroborates such a placement at least of early members assigned to this group. Murchisonioidea, in its present composition, is likely polyphyletic and holds members of both, Vetigastropoda and Caenogastropoda. There is no modern phylogenetic analysis including shell microstructure and larval shell characters of *Murchisonia*-like gastropods; hence, the importance of these characters in inferring the phylogeny of Murchisonioidea are not yet assessed.

There are several Triassic holdovers of high-spired, selenizone-bearing gastropods. To date, six of these *Murchisonia*-like genera comprising a total of 30 nominate species have been reported from the Triassic: "*Murchisonia*", *Pseudomurchisonia*, *Cheilotomona*, *Trypanocochlea*, *Wannerispira*, and *Vistilia.* Batten (1973) and Hallam and Wignall (1997) stated that Murchisonioidea became extinct at the end-Triassic mass extinction event. Based on new material and the re-study of type material of several species, we discuss the diversity of Triassic *Murchisonia*-like gastropods, their link to late Paleozoic taxa, and revise their classification.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: http://zoobank.org/urn:lsid:zoobank.org:pub:3B3057AC-62DC-4B94-A557-5A4099947A6F.

Institutional abbreviations.—GBA, Geologische Bundesanstalt, Vienna, Austria; GPIT-PV, former Geologisch-paläontologisches Institut Tübingen (PV, Petrefaktenverzeichnis), now Senckenbergische Sammlungen in Tübingen, Germany; MUSE, Museo delle Scienze, Trento, Italy; NHMW, Naturhistorisches Museum Wien, Vienna, Austria; SNSB-BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Systematic palaeontology

Subclass Caenogastropoda Cox in Knight et al., 1960

Family Goniasmatidae Nützel and Bandel, 2000

Included genera: *Laschmaspira* Mazaev, 2003, and *Altadema* Kues, 2002; these genera have been placed in Orthonematidae. However, they clearly possess a selenizone and hence they are placed in Goniasmatidae. *Pseudomurchisonia* Koken, 1896, has only a weak sinus in the upper whorl portion; it is possible that it would develop into a selenizone. Therefore, it is tentatively placed in Goniasmatidae*. Murchisonietta* Nützel, Kaim, and Grădinaru, 2018, a subjective younger synonym of *Wortheniopsis* Böhm, 1895, has also been placed tentatively in Goniasmatidae (Nützel et al. 2018).

Genus *Laschmaspira* Mazaev, 2003

Type species: *Laschmaspira rara* Mazaev, 2003, Pennsylvanian, Russia.

Remarks.—To date, *Laschmaspira* has been known only from a few Pennsylvanian and Permian species (Mazaev 2003). Here we place two Late Triassic species in this genus: *Laschmaspira euglypha* Koken, 1896 comb. nov. (previously *Murchisonia euglypha* Koken, 1896), and *Laschmaspira lirata* sp. nov., both from the Feuerkogel, Austria. *Laschmaspira lirata* sp. nov. and the type species of *Laschmaspira* have a spiral ornament on the teleoconch whorls. However, *Laschmaspira euglypha* Koken, 1896, seems to lack spiral ornament.

Stratigraphic and geographic range.—Permian (Asselian) of Southern Fergana (Uzbekistan), middle Carboniferous of Central Russia– Carnian (Upper Triassic).

Laschmaspira lirata sp. nov.

Figs. 1, 2.

Zoobank LCID: urn:lsid:zoobank.org:act:361FE73E-A4F1-4E81-A9A2-042103EE645F

Etymology: From Latin *lirata*, ridged; for the spiral lirae on the teleoconch,

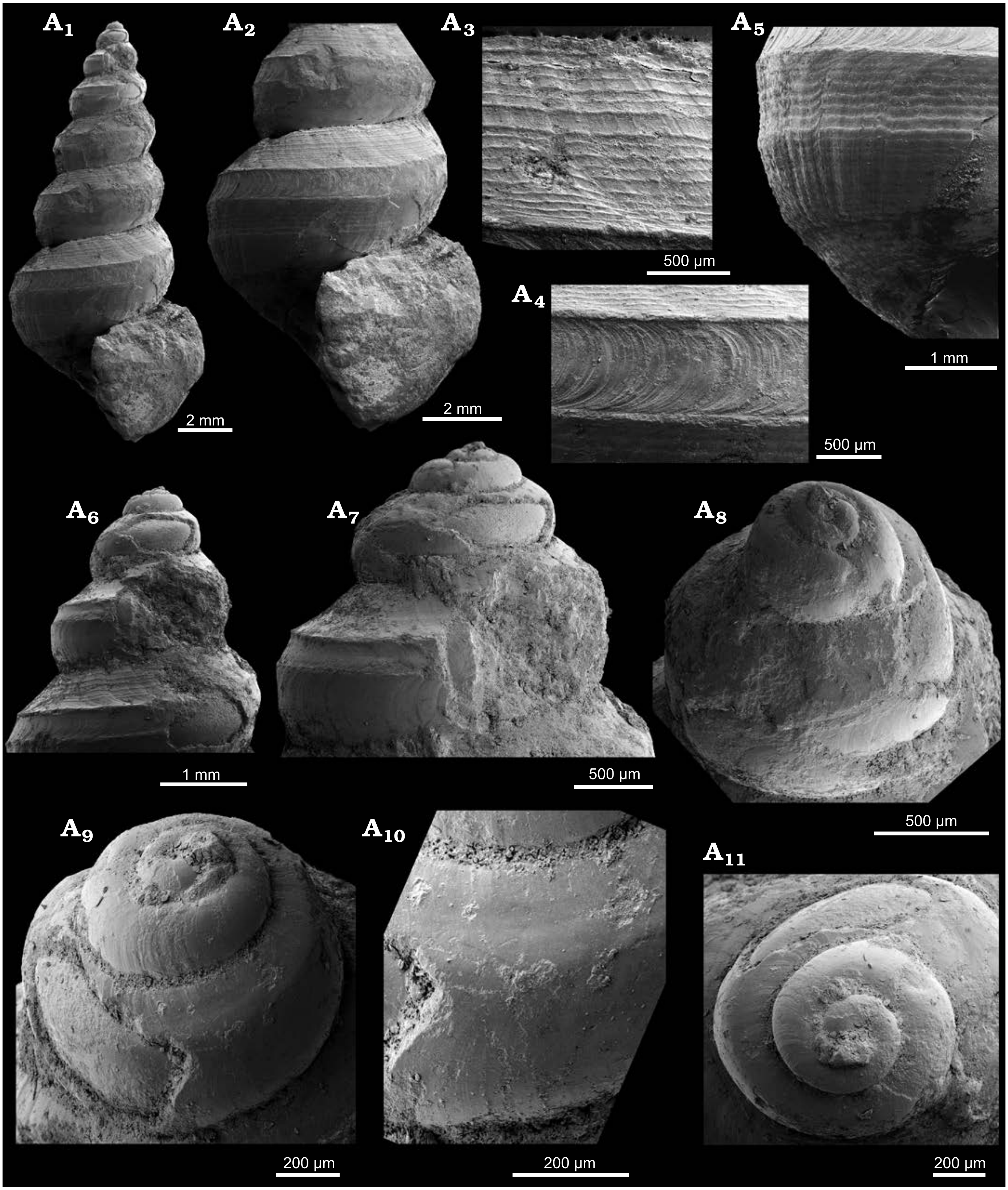


Fig. 1. Goniasmatid caenogastropod *Laschmaspira lirata* sp. nov., Carnian, Feuerkogel, Austria. **A**. NHMW 2023/0080/0001, holotype, in lateral view (A_1), detail of last whorls in lateral view (A_2), detail adapical whorl face with spiral lirae in lateral view (A_3), detail selenizone (slit-band) in lateral view (A_4), detail of whorl face and base of last whorl with spiral lirae in lateral view (A_5), early whorls in lateral view (A_6, A_7), early whorls in oblique lateral view (A_8, A_9), detail of early whorls in oblique lateral view showing beginning of selenizone as a sinus (A_{10}), early whorls in apical view (A_{11}).

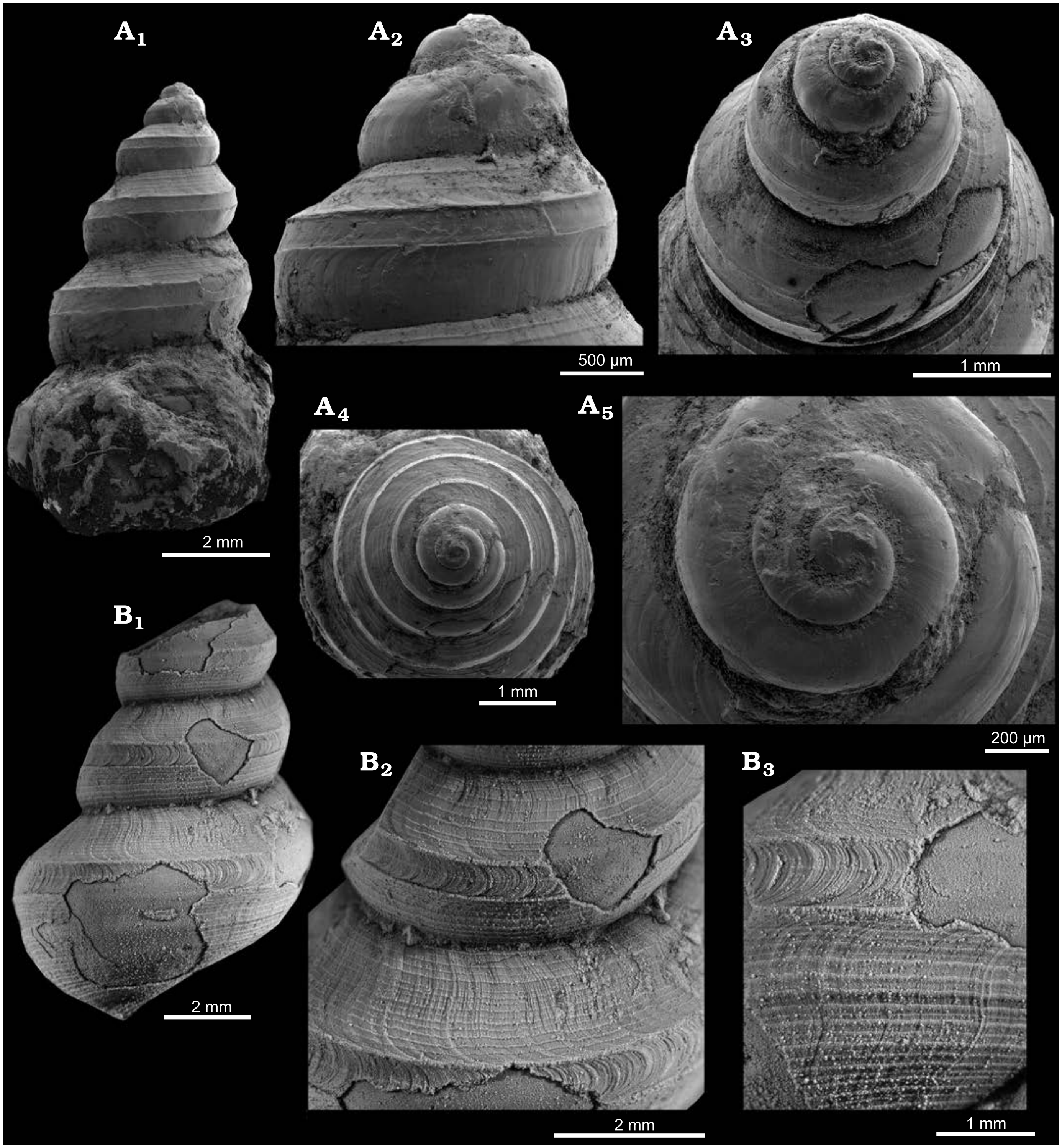


Fig. 2. Goniasmatid caenogastropod *Laschmaspira lirata* sp. nov., Carnian, Feuerkogel, Austria. **A**. NHMW 2023/0080/0002, paratype, in lateral view (A_1), early whorls in lateral (A_2), oblique lateral (A_3), and apical (A_4, A_5) views. **B**. NHMW 2023/0080/0003, paratype, in lateral view (B_1), detail of whorl face with selenizone (slit-band) and ornamentation of spiral lirae in oblique lateral (B_2) and lateral (B_3) views.

Type material: Holotype, NHMW 2023/0080/0001, well preserved shell with protoconch. Paratypes, NHMW 2023/0080/0002–0007, well preserved shells. All from the typical Hallstatt Limestone facies, calcite pseudomorphoses covered by a reddish stain of ferruginous material.

Type locality: Feuerkogel, south slope, near Röthelstein und Tellschen, near Kainisch, Steiermark, Austria.

Type horizon: Hallstatt Limestone, Carnian (Upper Triassic).

Material.—Type material only.

Description.—Shell high-spired; holotype consists of about 9 whorls, 15.4 mm high, 7.9 mm wide; first four whorls smooth, convex, dome-shaped with an apical angle of 70–80°;

initial whorl 0.33–0.36 mm wide; clear ontogenetic boundaries (embryonic/larval/teleoconch) not visible due to preservation or possibly gradual; later teleoconch with an apical angle of ca. 30°; teleoconch whorls markedly convex, angulated at borders of selenizone, with a broad ramp; selenizone forming from third whorl onwards as an increasingly deepening sinus of growth lines; selenizone on mature whorls broad, concave with lunulae of dense, distinct growth lines; late teleoconch whorls with numerous, distinct spiral lirae above and below selenizone; suture deep; base convex, anomphalous, demarcated from whorl face by an angulation, with numerous spiral threads.

Remarks.—The most similar Triassic species is *Laschmaspira euglypha* (Koken, 1896), from the same locality (Feuerkogel). However, this species lacks spiral ornament, its whorls are more angulated, and the selenizone starts after the first whorl according to Koken (1896, 1897). *Laschmaspira lirata* sp. nov. exhibits a marked ontogenetic change regarding apical angle and ornament from broad, smooth, slitless initial whorls to ornamented much more slender and slit-bearing later whorls. However, a clear indication of a larval shell of the planktotrophic type could not be found. The size of the initial whorl (>0.3 mm) is rather large and suggests non-planktotrophic larval development (see Nützel 2014). *Laschmaspira lirata* sp. nov. can be regarded as a descendant of Paleozoic Goniasmatidae. The Permian *Goniasma gerasimovi* Mazaev, 2019, resembles *Laschmaspira lirata* sp. nov. in having an ornament of numerous spiral lirae which is otherwise unusual for *Goniasma*. However, *G. gerasimovi* differs in having a submedian angulation as is typical for *Goniasma*.

Stratigraphic and geographic range.—Type horizon and locality only.

Genus *Pseudomurchisonia* Koken, 1896

Type species: *Pseudomurchisonia insueta* Koken, 1896, Austria, Norian (Upper Triassic); subsequent designation by Cossmann (1897).

Remarks.—*Pseudomurchisonia* was tentatively placed in Purpurinidae (Caenogastropoda) by Wenz (1939: 526) who erroneously considered *P. woehrmanni* Koken, 1896, to be the type species. Thus, the genus was not included in the Treatise (Knight et al. 1960) which covered only few caenogastropods. Both originally included species, *Pseudomurchisonia insueta* Koken, 1896, and *P. woehrmanni* Koken, 1896, come from the Carnian (Upper Triassic) of the Feuerkogel in Austria. Both are moderately high-spired and have a broad selenizone that appears late during ontogeny. Apart from the two originally included species, two Early Triassic species were placed in *Pseudomurchisonia*: *P. extracta* (Berger, 1860) and *P.*? *sundaica* Krumbeck, 1924, but none from the Paleozoic and the post-Triassic.

The type species *Pseudomurchisonia insueta* (see below) differs from *Goniasma* in lacking an angulation, but resembles this genus in having a selenizone low on the whorls and lacking strong ornament. We therefore place this genus tentatively in Goniasmatidae. More knowledge about the early ontogeny of *Pseudomurchisonia insueta* is needed for a better substantiated systematic placement of this genus.

Pseudomurchisonia extracta (Berger, 1860) (originally placed in *Natica*) is based on an obviously poorly preserved specimen (probably a steinkern) from the Schaumkalk, a lithological unit of the Muschelkalk in the German Basin. The type is therefore of Anisian age. It shows a markedly gradate spire with a ramp bordered by an edge high on the whorls. This species has been placed in *Pseudomurchisonia* by Wittenburg (1908a: 284, pl. 5: 7) who illustrated a specimen with evenly rounded whorls and a median selenizone from the Werfen Formation of the Valsugana, Italy. Wittenburg's (1908a) specimen is certainly not conspecific with Bergers's (1860) type specimen. The Early Triassic specimen reported by Wittenburg (1908a) could either be a member of Pleurotomariida or Goniasmatidae. Baumgarte and Schulz (1986) and Kramm (2004) placed *Pseudomurchisoni extracta* in *Angularia*; their illustration of specimens from Hessen indicates that this assignment is more correct. *Pseudomurchisonia extracta* is probably a nomen dubium but its type specimens must be studied.

Pleurotomaria triadica Benecke, 1868, and *Pleurotomaria euomphala* Benecke, 1868, from the Lower Triassic of Mount Zacon at Borgo Valsugana (Italy) were placed in *Pseudomurchisonia* by Wittenburg (1908b), but need restudy of the types for confirmation.

Pseudomurchisonia schmidti Wittenburg, 1908b, is a nomen nudum.

Pseudomurchisonia? *sundaica* Krumbeck, 1924, from the Lower Triassic is actually close to the type species *Pseudomurchisonia insueta* Koken, 1896, and could be congeneric.

Stratigraphic and geographic range.—Lower Triassic, Timor and Carnian (Upper Triassic), Austria.

Pseudomurchisonia insueta Koken, 1896

Fig. 3.

1896 *Pseudomurchisonia insueta* Koken; Koken 1896: 86, fig. 12.
1897 *Pseudomurchisonia insueta* Koken; Koken 1897: 106, fig. 31.
2021 *Pseudomurchisonia insinueta* [sic!] Koken; Karapunar and Nützel 2021: 52.

Material.—Teleoconch fragment, NHMW 1926/0002/0461, Carnian (Upper Triassic), Feuerkogel, Austria.

Remarks.—We illustrate a single specimen (teleoconch fragment) from the Carnian of the Feuerkogel, Austria, representing the type species *Pseudomurchisonia insueta,* housed at the NHMW. The spire whorls are convex with an edge low on the whorls that is reduced later on. The earliest preserved whorl has neither a sinus nor a selenizone but straight, slightly opisthocyrt growth lines. Then a sinus and eventually a selenizone develops distinctly below mid-whorl. The selenizone is flush with the whorl face and smooth with sinuous growth lines. The whorls are smooth except of comarginal furrows in some whorls. The base is strongly convex and anomphalous. The transition from whorl face to base is evenly rounded.

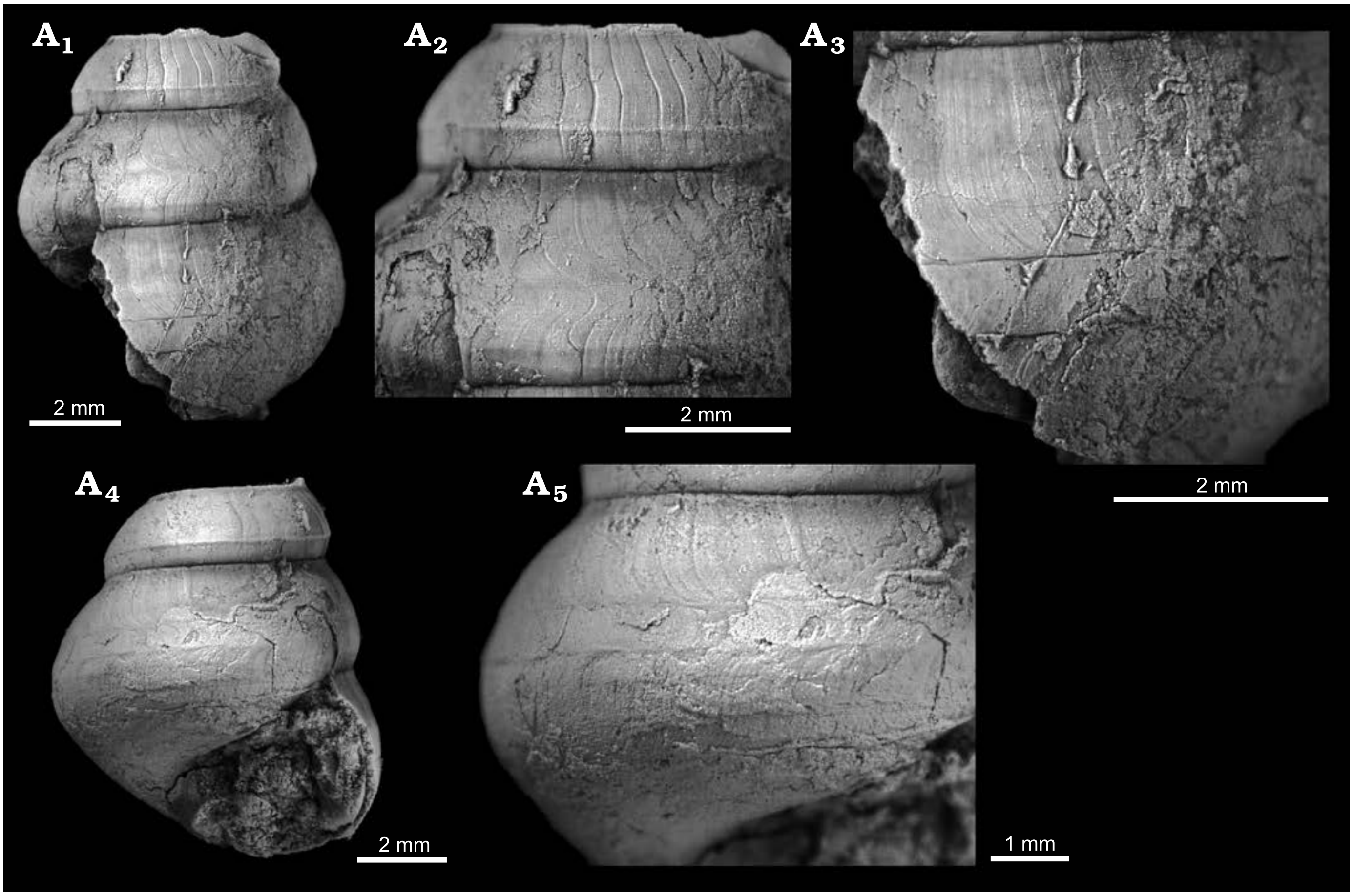


Fig. 3. Goniasmatid caenogastropod *Pseudomurchisonia insueta* Koken, 1896, Carnian, Feuerkogel, Austria. **A**. NHMW 1926/0002/0461, in lateral view (A_1), detail of spire whorls in lateral view showing lack of selenizone in adapical whorl, and beginning of selenizone in abapical whorl (A_2), detail of last part of last preserved whorl with fully developed selenizone (slit-band) in lateral (A_3) and apertural lateral (A_4) views, detail of last preserved whorl in lateral view (A_5).

The present specimen agrees well with the description and illustrations of *Pseudomurchisonia insueta* as given by Koken (1896, 1897). The apical whorls including the protoconch and the shell microstructure are unknown. Hence the higher classification of *Pseudomurchisonia* is doubtful. As already noted by Karapunar and Nützel (2021) and as discussed below, *Acutitomaria woehrmanni* (the other species originally included in *Pseudomurchisonia* by Koken 1896) clearly does not represent the *Pseudomurchisonia*.

Stratigraphic and geographic range.—Carnian (Upper Triassic), Feuerkogel, Austria.

Subfamily Cheilotomoninae nov.

Zoobank LCID: urn:lsid:zoobank.org:act:D1C49498-95D9-45A5-AF5D-12762FA25B99

Included genera: *Cheilotomona* Strand, 1928, *Trypanocochlea* Tomlin, 1931, *Vistilia* Koken, 1896.

Type genus: *Cheilotomona* Strand, 1928.

Diagnosis.—High-spired shells with slit band and a median whorl angulation; early teleoconch whorls have three spiral cords, which in later whorls become subsutural cord, whorl angulation and basal cord; nodes on whorl angulation before development of selenizone; selenizone develops late in ontogeny (4th–7th whorl); the lower border of selenizone or the selenizone itself situated at whorl angulation.

Remarks.—We place the subfamily Cheilotomoninae in Goniasmatidae due to their high-spired shell with a median selenizone. Species with a multi-whorled protoconch of the planktotrophic type with sinusigera or a paucispiral protoconch with sinusigera (characteristic of goniasmatids) have not been documented in the members of Cheilotomoninae. *Cheilotomona* has smooth early whorls with fluent transition to the teleoconch and a large initial indicating non-planktotrophic early ontogeny (Karapunar and Nützel 2021, and see below).

Cheilotomona, *Trypanocochlea*, and *Vistilia* were previously placed in Murchisoniidae but *Murchisonia* lacks a prominent whorl crest on which the selenizone is situated, and this brings these genera close to *Goniasma* and thus they are placed in Gonismatidae. The protoconch of *Trypanocochlea cerithioides* is unknown and therefore, the possibility that *Trypanocochlea* belongs to Pleurotomariida and not to the caenogastropod family Goniasmatidae cannot be excluded. On the other hand, general whorl morphology, surface orna-

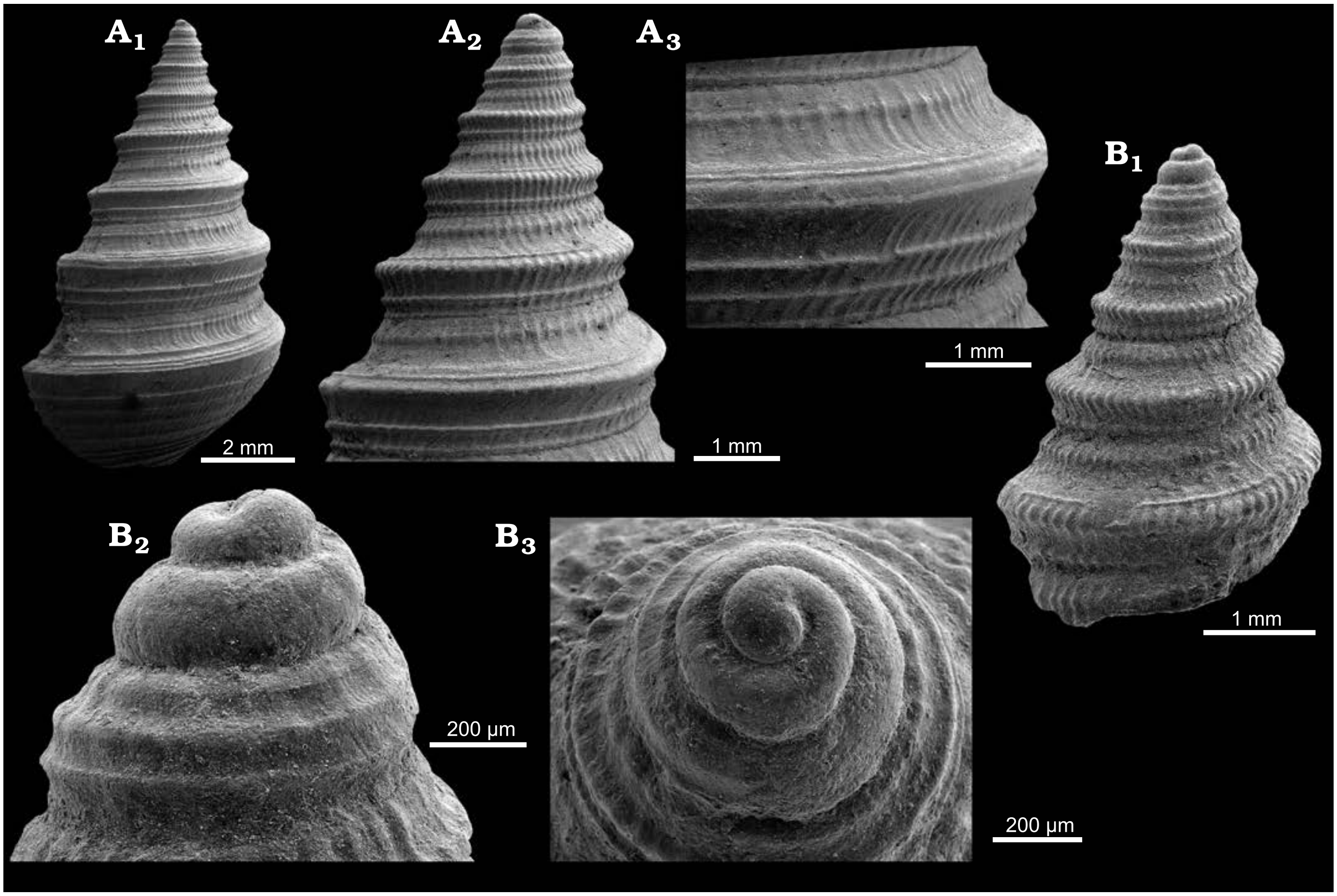


Fig. 4. Goniasmatid caenogastropod *Cheilotomona blumi* (Wissmann in Münster, 1841), Carnian, St. Cassian Formation, Italy. **A**. MB.Ga.4307.2, in lateral view (A_1), early whorls in lateral view (A_2), detail of whorl face with selenizone (slit-band) on crest in lateral view (A_3). **B**. MB.Ga.4304.1, in lateral view (B_1), early whorls including smooth protoconch in lateral view (B_2), early whorls including smooth protoconch in oblique lateral view (B_3).

ment (subsutural cord and strong axial ribs), and early ontogenetic shell development (nodular periphery, subsutural cord) supports its close association to *Cheilotomona*. Nützel and Nakazawa (2012) showed that a Permian *Trypanocochlea s*pecies from Japan has a mammilated protoconch of the caenogastropod type supporting a placement in Goniasmatidae.

Genus *Cheilotomona* Strand, 1928

Type species: *Pleurotoma blumi* Wissmann in Münster, 1841, Carnian (Upper Triassic), St. Cassian Formation, South Tyrol, Italy; subsequent designation by Diener (1926).

Remarks.—Replacement name for *Cheilotoma* Koken, 1889, a junior homonym (see also Karapunar and Nützel 2021).

Stratigraphic and geographic range.—Anisian (Middle Triassic)–Carnian (Upper Triassic), Italy, Austria, Romania, Poland, Hungary, China.

Cheilotomona blumi (Wissmann in Münster, 1841)

Fig. 4.

1841 *Pleurotoma blumi* Wissmann n. sp., Wissmann in Münster: 123, pl. 13: 47a–c

For exhaustive synonymy an chresonymy see Karapunar and Nützel (2021)

Remarks.—A detailed description of this abundant and variable species and other three *Cheilotomona* species from the St. Cassian Formation was given by Karapunar and Nützel (2021). *Cheilotomona blumi* has about two smooth initial whorls with an indistinct transition to the teleoconch and a diameter of the first whorl of about 0.3 mm indicating an early ontogeny without planktotrophic larval development. The selenizone develops very late. Mature whorls have an angulated periphery at which the selenizone is situated.

Bandel (2006: 92) stated that “if *Cheilotomona blumi* was found in Paleozoic deposits, it could be placed with the genus *Goniasma*” and that “*Cheilotomona* represents the last known member of the Orthonematidae” (he considered Goniasmatidae and Orthonematidae to be synonymous, but see Nützel and Pan 2005 for a different opinion). *Goniasma* might be related to but is certainly not synonymous with *Cheilotomona* which has a strong axial ornament on early teleoconch whorls that is absent in *Goniasma*. Karapunar and Nützel (2021) placed *Cheilotomona* in the family Goniasmatidae Nützel and Bandel, 2000 (superfamily Orthonematoidea Nützel and Bandel, 2000).

Stratigraphic and geographic range.—Only known from the St. Cassian Formation, Carnian (Upper Triassic), N Italy.

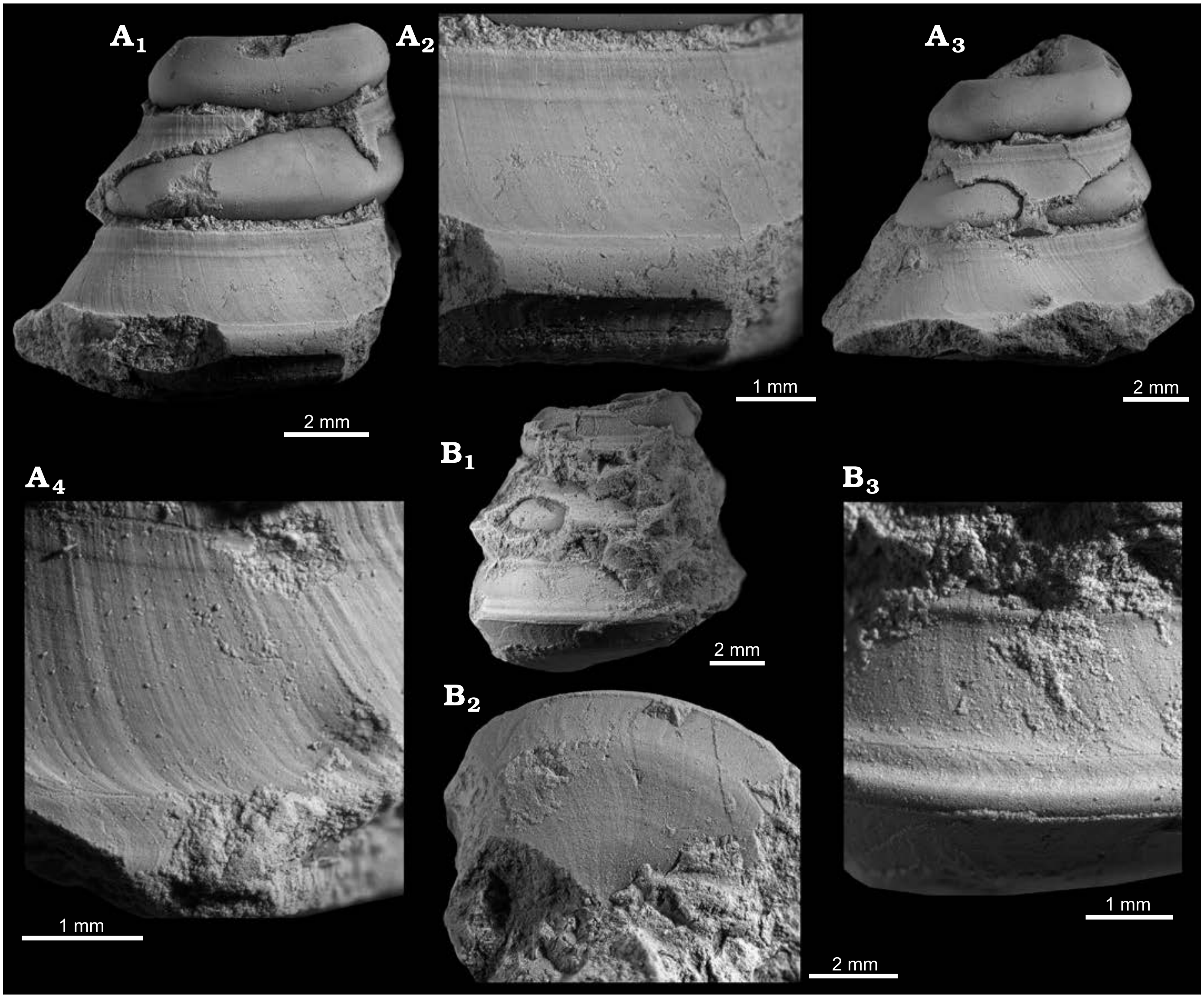


Fig. 5. Goniasmatid caenogastropod *Vistilia salisburgensis* (Schnetzer, 1934), Anisian, Saalfelden, Salzburg, Austria. **A**. SNSB-BSPG AS XXXIV 557, holotype and original of Schnetzer (1934: pl. 1: 12), in lateral view (A_1), detail of last preserved whorl in lateral view (A_2, A_3), detail of last preserved whorl in lateral view to show growth lines and selenizone (slit-band) on crest (A_4). **B**. SNSB-BSPG AS XXXIV 559, paratype, in lateral view (B_1), basal view (B_2), detail of last preserved whorl in lateral view to show growth lines and selenizone (slit-band) on crest (B_3).

Genus *Vistilia* Koken, 1896

Type species: *Vistilia klipsteini* Koken, 1896, Austria, Carnian (Upper Triassic); subsequent designation by Cossmann (1897).

Stratigraphic and geographic range.—Anisian (Middle Triassic)–Norian (Upper Triassic), Austria, Italy, Turkey.

Vistilia salisburgensis (Schnetzer, 1934)

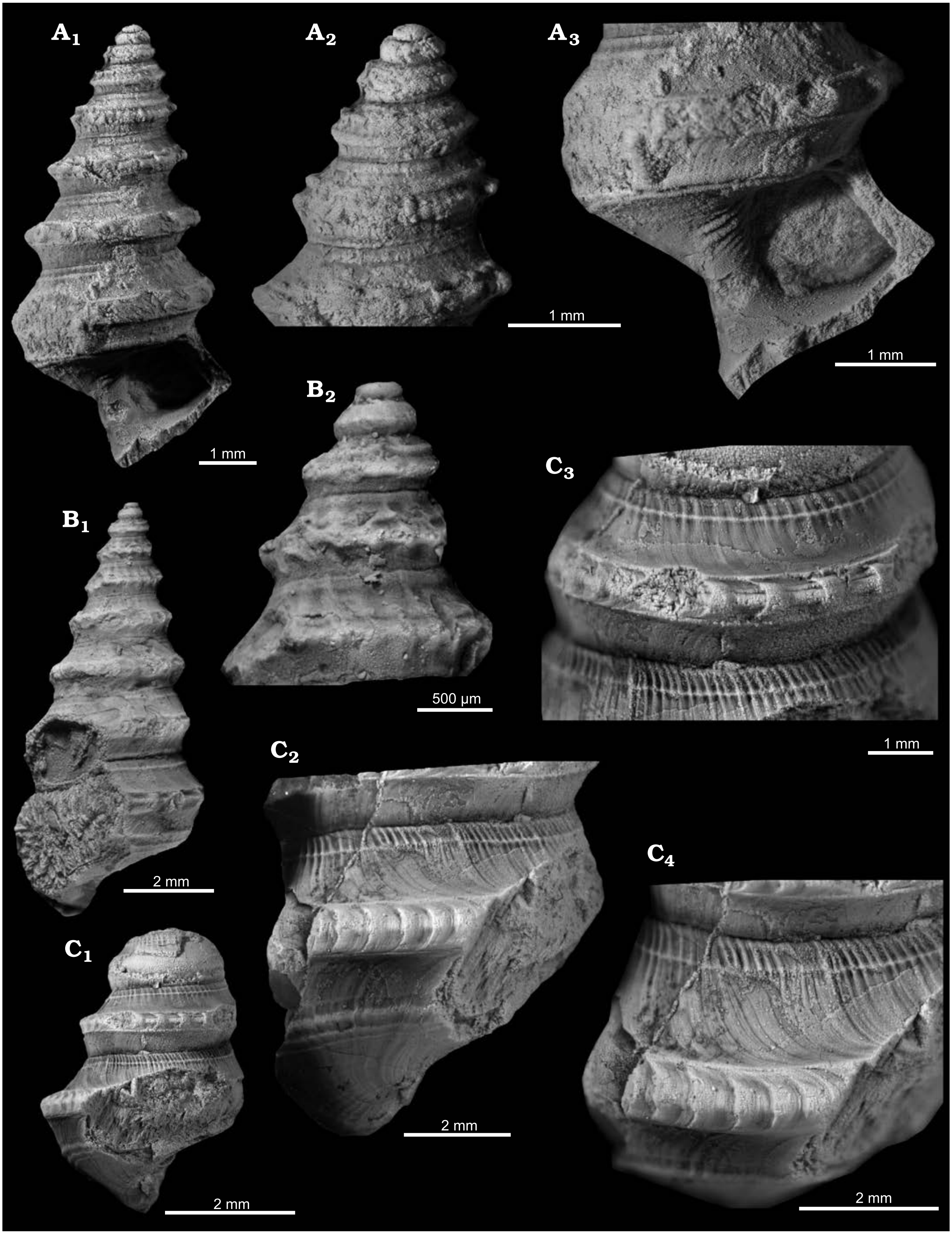
Fig. 5.

1934 *Stuorella salisburgensis* n. sp.; Schnetzer 1934: 35, pl. 1: 12, 13.

2021 *Vistilia salisburgensis* (Schnetzer, 1934); Karapunar and Nützel 2021: 6, 60.

Material.—A total of 8 specimens from the Anisian (Middle Triassic), Saalfelden, Salzburg, Austria: SNSB-BSPG AS XXXIV 557, holotype, original of Schnetzer 1934: pl. 1: 12, teleoconch fragment of ca. three whorls, parts of shell preserved; paratypes: SNSB-BSPG AS XXXIV 558 (original of Schnetzer 1934: pl. 1: 12), SNSB-BSPG AS XXXIV 559 (five specimens), SNSB-BSPG AS XXXIV 560.

Fig. 6. Goniasmatid caenogastropod *Trypanocochlea cerithioides* (Koken, 1896), Carnian, Austria. **A**. SNSB-BSPG, lectotype, 1878 XI B 478 and original of Koken (1896: text-fig. 11) and Koken (1897: text-fig. 29), Röthelstein, Aussee, in lateral view (A_1), early whorls in lateral view (A_2), aperture with folds in lateral view (A_3). **B**. SNSB-BSPG 2011 XXXIX 78d, Feuerkogel, in lateral view (B_1), early whorls in lateral view (B_2). **C**. NHMW 1858/0047/0088, Feuerkogel, in lateral view (C_1), detail of last preserved whorl in lateral view to show growth lines and selenizone on crest (C_2), middle whorl in lateral view (C_3), detail of last preserved whorl in oblique lateral view to show growth lines and selenizone on crest (C_4). →


A1
A2
A3
1 mm
1 mm
1 mm
B1
B2
500 µm
2 mm
C1
C2
C3
C4
1 mm
2 mm
2 mm
2 mm

Description.—Fragments of a high-spired shell; whorls low with strong angulation above abapical suture; adapical whorl face steeply sloping, slightly concave, largely smooth with fine prosocline growth lines, faint spiral striation, and distinct spiral cord below adapical suture; selenizone concave at adapical border, distinctly convex near abapical border, forming periphery, smooth or with faint lunulae; whorl face below selenizone narrow, concave, sharply inclining adaxially, with prosocyrt growth lines; base flat, with opisthocyrt growth lines, only partly preserved.

Remarks.—As previously stated by Karapunar and Nützel (2021), Schnetzer's (1934) original assignment to *Stuorella* cannot be maintained because this genus does not have a whorl angulation with a convex selenizone. Instead, *Stuorella* has a selenizone on flat whorl face somewhat above basal edge of the whorls. *Vistilia salisburgensis* has the characteristic teleoconch morphology of *Vistilia* with low whorls. However, protoconch and early teleoconch of *Vistilia salisburgensis* are unknown. *Vistilia salisburgensis* closely resembles *Cheilotomona tristriata* (Münster, 1841) from the lower Carnian St. Cassian Formation (Karapunar and Nützel 2021: fig. 86) in general whorl morphology, surface ornament and in having a pronounced subsutural spiral cord. The presence of a single subsutural cord is a feature also shared by *Cheilotomona* (Fig. 4) and *Trypanocochlea* (Fig. 6). *Vistilia salisburgensis* is the oldest known Triassic species of this genus. *Vistilia* last appeared in the Carnian (Koken 1896).

Stratigraphic and geographic range.—Known from the type locality only, see above.

Genus *Trypanocochlea* Tomlin, 1931

Type species: *Verania cerithioides* Koken, 1896, Carnian (Upper Triassic), Austria; original designation.

Remarks.—*Trypanocochlea* is a replacement for *Verania* Koken, 1896.

Stratigraphic and geographic range.—Middle Permian, Japan–Norian (Upper Triassic), Austria.

Trypanocochlea cerithioides (Koken, 1896)

Fig. 6.

1896 *Verania cerithioides* Koken; Koken 1896: 86, text-fig. 11.
1897 *Verania cerithioides* Koken; Koken 1897: 105, text-fig. 29.

Material.—Lectotype, herein designated, SNSB-BSPG 1878 XI B 478 (original of Koken 1896: text-fig. 11; original of Koken 1897: text-fig. 29), Carnian (Upper Triassic), Röthelstein, Aussee, Austria. NHMW 1858/0047/0088, SNSB-BSPG 2011 XXXIX 78d, Carnian (Upper Triassic), Feuerkogel, Austria.

Description.—Shell high-spired, apical angle ca. 45°; type specimen consists of ca. 8 whorls, 7.8 mm high, 3.4 wide; earliest preserved whorls rounded, smooth, developing an angulation low on whorl face after one-two whorls; whorl face strongly angulated slightly below middle of whorl face; selenizone broad, situated on angulation, forming periphery; selenizone forms late (after the second preserved whorl), ornamented with pronounced node-forming lunulae, and a median spiral cord; lunulae closely spaced in early whorls, widely spaced in later whorls; selenizone bordered by outward bending shell forming sharp edges (spiral cords); whorl face steeply sloping above selenizone, ornamented with strengthened growth lines and spiral thread in subsutural zone; whorl face below selenizone sharply inclined adaxially; transition from whorl face to conical, convex base demarcated by spiral cord, accompanied by one or few spiral threads; aperture trapezoidal; inner lip convex with about 12 spiral lirae (folds).

Remarks.—*Trypanocochlea cerithioides*, type species of *Trypanocochlea*, is a murchisonimorph gastropod with a strongly ornamented, convex selenizone. Its inner lip has spiral lirae (folds) unlike any other members of Goniasmatidae. A middle Permian representative of *Trypanocochlea*, has been reported by Nützel and Nakazawa (2012) but that species seemingly lacks folds on the inner lip (maybe due to preservation). Similar gastropods (also lacking folds on the inner lip) have also been reported from the Pennsylvanian/lower Permian of the USA: *Taosia crenulata* (Girty, 1939) (Kues 1991, 2004a, b). *Taosia crenulata* differs much from the type species of *Taosia*, and at first glance this late Paleozoic species resembles *Trypanocochlea*. However, while the selenizone of *Taosia crenulata* is situated on upper whorl face above the nodular periphery, the selenizone of *Trypanocochlea cerithioides* is situated on the angular periphery and the nodes are formed within the selenizone. *Cheilotomona subgranulata* (Klipstein, 1844) from the St. Cassian Formation develops similar nodular selenizone on whorl periphery, but species of *Cheilotomona* lack the folds on inner lip. The only other report of *Trypanocochlea* (an unnamed species) is from the ?upper Norian/Rhaetian (Upper Triassic) of Peru by Haas (1953), who reported absence of folds in the Peruvian species. Due to the unclear age if this probably last occurrence of *Trypanocochlea*, the exact timing of the exticntion of this genus is unknown.

Stratigraphic and geographic range.—Known from the type locality area only, see above.

Subfamily uncertain

Genus *Altadema* Kues, 2002

Type species: *Altadema convexa* Kues, 2002, Pennsylvanian, USA.

Remarks.—The type species of *Altadema* has a small, moderately high-spired largely smooth shell with strongly convex whorls; its selenizone is situated high on whorl. So far, four Pennsylvanian species have been assigned to this genus (Kues 2002; Mazaev 2003). Herein, we place the Early Triassic species *Altadema kokeni* (Wittenburg, 1908a) and *Altadema hausmannae* sp. nov. in *Altadema*. *Altadema hausmannae* has a broad slit-band above the periphery in mature whorls whereas *Altadema kokeni* (Wittenburg, 1908a) has a sinus or selenizone high on the whorls.

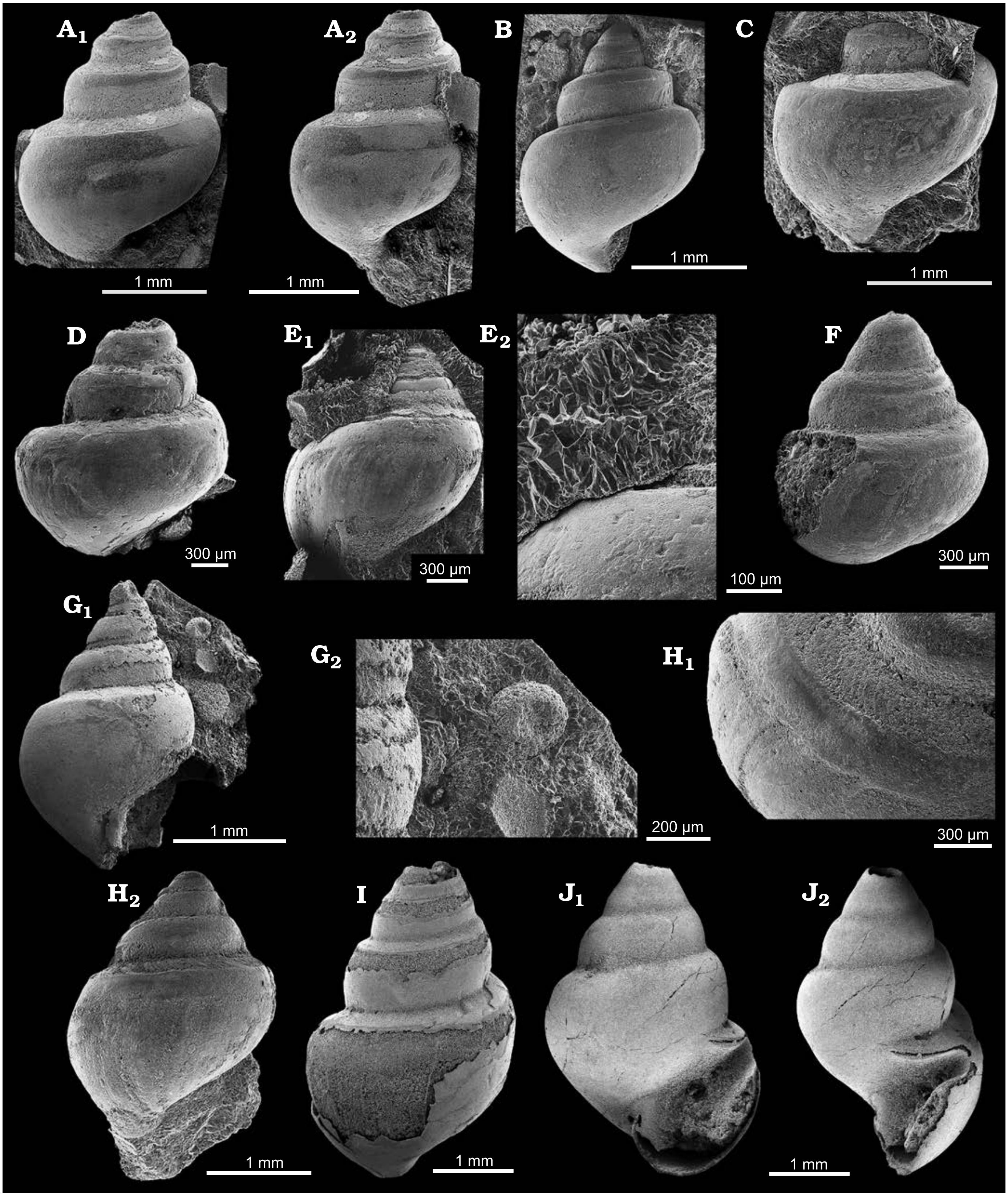


Fig. 7. Goniasmatid caenogastropod *Altadema hausmannae* sp. nov., Dienerian/Smithian transition, Lower Triassic, Werfen Formation, Gastropod Oolite Member, Italy. **A**. MUSE-PAL 8176, holotype, lateral view. **B**. MUSE-PAL 8177, paratype, lateral view. **C**. MUSE-PAL 8178, paratype, in lateral view. **D**. MUSE-PAL 8179, paratype, in lateral view. **E**. MUSE-PAL 8180, paratype, in lateral view (E_1), detail (E_2). **F**. MUSE-PAL 8181, paratype, in lateral view. **G**. MUSE-PAL 8182, paratype, in lateral view (G_1), detail (G_2). **H**. MUSE-PAL 8183, paratype, detail to show slit-band, in oblique lateral view (H_1) and specimen in lateral view (H_2). **I**. MUSE-PAL 8184, paratype, in lateral view. **J**. MUSE-PAL 8185, paratype, in apertural (J_1) and lateral (J_2) views.

The Triassic species *Wannerispira shangganensis* Kaim and Nützel in Kaim et al. 2010, closely resembles *Altadema* but has a more pronounced selenizone situated lower on the whorls.

Stratigraphic and geographic range.—Upper Carboniferous, USA and Russia–Lower Triassic, Italy.

Altadema hausmannae sp. nov.

Fig. 7.

2005 *Pseudomurchisonia kokeni* Wittenburg, 1908; Nützel and Schulbert 2005: 497, fig. 16.

Zoobank LCID: urn:lsid:zoobank.org:act:CA52C5A2-AF63-458F-BBB6-AD0A705260DD

Etymology: Dedicated to Imelda M. Hausmann for her work on Triassic marine biota.

Type material: Holotype, MUSE-PAL 8176, specimen of ca. four whorls lacking apex, with attached rock matrix. Paratypes, nine specimens: MUSE-PAL 8177–8185.

Type locality: 750 m south of Cimirlo, near the road from Cimirlo to Busa del Vent, where road crosses creek in a narrow curve; GPS (WGS 84): 46°03'50.5'' N, 11°10'58.0'' E; Trentino, North Italy.

Type horizon: Werfen Formation, Gastropod Oolite Member, Lower Triassic, probably Dienerian/Smithian transition (Hofmann et al. 2015).

Material.—Type material; in addition numerous specimens in rock-forming quantities.

Description.—Largest specimen comprises ca. six whorls (apex missing), 4.9 mm high, 3.0 mm wide, turbiniform with variable apical angle of ca. 60–80°; whorls markedly convex, separated by distinct sutures; whorls with more or less pronounced subsutural shelf so that spire is gradate in most specimens; shell smooth (but studied specimens covered by a reddish crust of iron oxides or hydroxides that may obscure ornament if ornament was present); ramp demarcated by the adapical edge of broad selenizone; transition from ramp to lateral whorl face may be angular; selenizone situated high on the whorls; base convex with an umbilical chink; transition from whorl face to base evenly rounded.

Remarks.—*Altadema hausmannae* sp. nov. occurs in rock-forming quantities at its type locality (Nützel and Schulbert 2005). Nützel and Schulbert (2005) identified this species as *Pseudomurchisonia kokeni* Wittenburg, 1908a (also from the Lower Triassic Werfen Formation) but a closer examination of the holotype of *P. kokeni* reveals that they are not conspecific (see below). *Altadema kokeni* has only a slight sinus, not a selenizone. Otherwise both species resemble each other closely. *Altadema hausmannae* differs widely from the type species *Pseudomurchisonia insueta* in whorl morphology and position of selenizone. The other species of *Altadema* (*A. convexa* Kues, 2002, *A. cryptocarina* Mazaev, 2003, *A. altadema* Mazaev, 2003, *A. cryptocarina* Mazaev, 2003, and *A. lira* Mazaev, 2003, all Pennsylvanian) are more slender and the spire is less gradate (having a larger angle between sutural shelf and outer whorl face).

Stratigraphic and geographic range.—Known from the type locality only, see above.

Altadema kokeni (Wittenburg, 1908a) comb. nov.

Fig. 8.

1908a *Pseudomurchisonia kokeni* n. sp.; Wittenburg 1908a: 16, text-fig. 1; pl. 2: 1.

non 2005 *Pseudomurchisonia kokeni* Wittenburg, 1908; Nützel and Schulbert 2005: 497, fig. 16.

Material.—The holotype, GPIT-PV-108710 (original of Wittenburg 1908a: pl. 5: 9, 10). Wittenburg (1908a) reported it from the Campiler Schichten (upper Werfen Formation, Lower Triassic) at the Col di Rodella, near the Sella Pass in the Dolomites, North Italy.

Description.—The holotype comprises about four whorls, is 4.8 mm high and 3.5 mm wide. It is turbiniform with an apical angle of ca. 65°. The whorls are markedly convex and separated by deep sutures. The shell is smooth and shiny except for fine growth lines. The growth lines are oblique prosocline below the adapical suture, form a shallow sinus above the periphery and almost orthocline prosocyrt between periphery and abapical suture.

Remarks.—The preservation is good when compared with the otherwise mostly poor preservation of the Werfen gastropods. The shell is replaced by a sparitic, slightly reddish calcite. The specimen is embedded in a hard calcareous rock. It is therefore likely that it comes from the gastropod oolite because other fossiliferous rocks of the Werfen Formation are usually more marly. It resembles *Altadema hausmannae* sp. nov. in general shape and by having a smooth shell, but it lacks a true selenizone; instead it has a sinus high on the whorls. It is possible that this specimen represents a juvenile shell and that a selenizone would develop later during ontogeny.

Stratigraphic and geographic range.—Known from the type locality only, see above.

?Family Goniasmatidae Nützel and Bandel, 2000

Genus *Wortheniopsis* Böhm, 1895

[= *Murchisonietta* Nützel, Kaim, and Grădinaru, 2018]

Type species: *Pleurotomaria margarethae* Kittl, 1894, Anisian (Middle Triassic), Marmolada Limestone, Italy; type by monotypy.

Emended diagnosis.—Shell moderately high-spired to fusiform; whorls evenly rounded or weakly angulated; whorls embracing somewhat below periphery; surface smooth or with spiral ornament; sinus or shallow slit high on whorl face, which may form a weak angulation; sinus/slit appears very late in ontogeny.

Remarks.—*Wortheniopsis* was erected by Böhm, 1895, for *Worthenia*-like shells (placed in Pleurotomariidae) lacking prominent shell angulations. The growth lines are not well-preserved or documented for the type species *W. margarethae* and hence the presence of a slit-band (selenizone) was only assumed by Kittl (1894) and Böhm (1895). We studied material from the Marmolada Limestone (Figs. 9, 10) and found that *Wortheniopsis margarethae* (Fig. 9) lacks a true selenizone (slit-band). Instead, growth lines have a back-

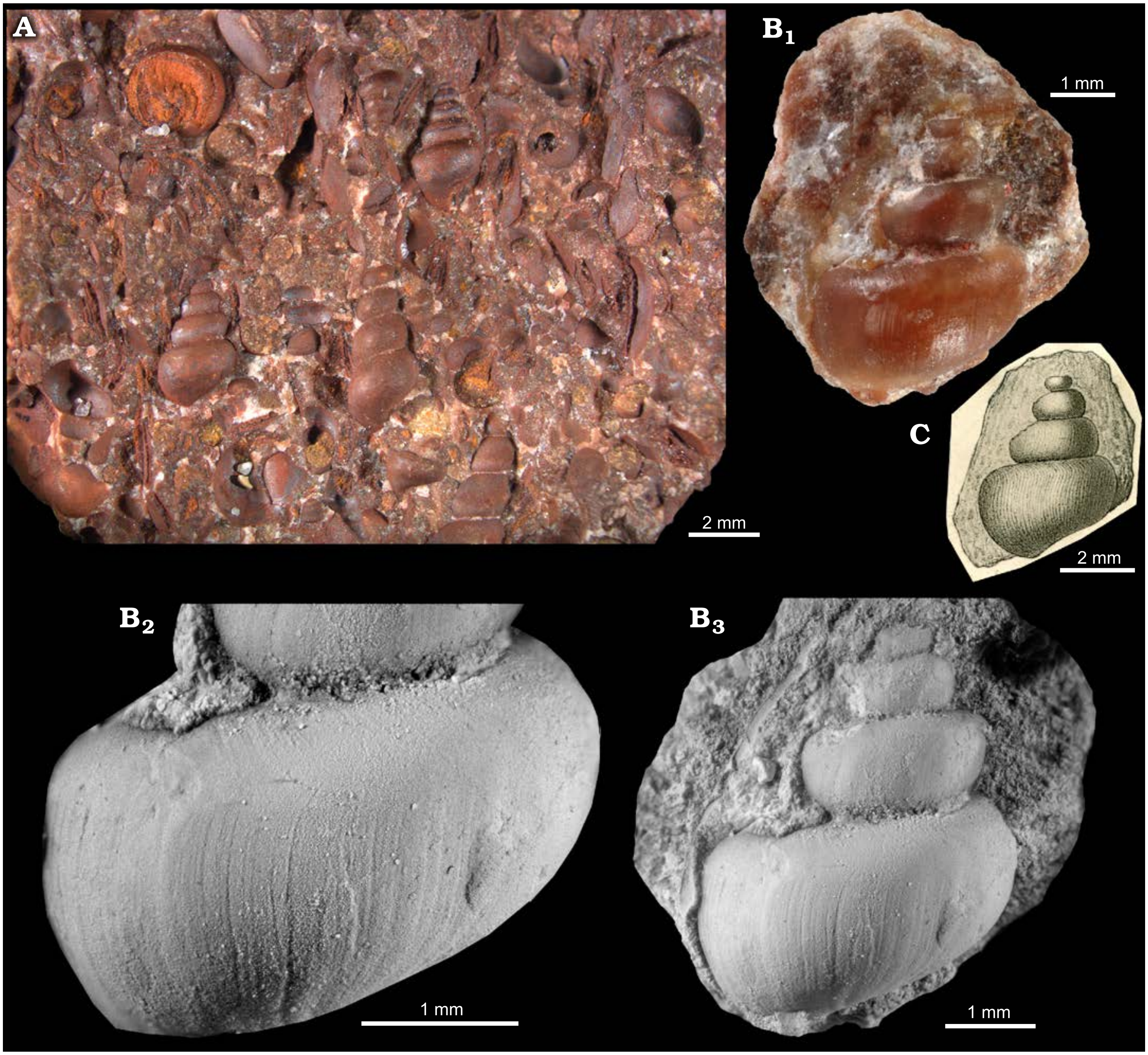


Fig. 8. Goniasmatid caenogastropod *Altadema kokeni* (Wittenburg, 1908a) and others, Dienerian/Smithian transition, Lower Triassic, Werfen Formation, Gastropod Oolite Member, Italy. **A**. Crack surface of Gastropod Oolite, near Borgo, Valsugana, Italy, ("Monte Zaccon" locality of Wittenburg 1908b); gastropods (*Altadema kokeni* and "*Polygyrina gracilior*") as well as other clasts covered with iron oxide; Wittenburg's (1908a, b) material, collection of University of Tübingen (Nützel and Schulbert 2005: fig. 15). **B**. *Altdema kokeni* (Wittenburg, 1908a), GPIT-PV-108710, holotype, and original of Wittenburg (1908a: pl. 5: 9, 10), Col di Rodella, in lateral view, not covered by ammonium chloride to show reddish color (B_1), detail of last whorl in lateral view to show adapical sinus of growth lines (B_2), in lateral view (B_3). **C**. Original drawing of *Altdema kokeni* from Wittenburg (1908a).

wards projection above mid-whorl of mature whorls forming a shallow sinus. The same pseudo-selenizone has been reported for the Anisian genus *Murchisonietta* Nützel, Kaim, and Grădinaru, 2018 (Fig. 11) and therefore we consider *Wortheniopsis* and *Murchisonietta* to represent synonyms. Similar to *Altadema kokeni*, *Wortheniopsis* also develops a sinus high on the whorls in late ontogeny. At this point, the higher classification of *Wortheniopsis* is unclear because it lacks a true selenizone, its shell microstructure and early whorls including protoconch are unknown.

Wenz (1938: 128) included *Wortheniopsis* in Pleurotomariidae and Lophospirinae. Knight et al. (1960) placed relatively high-spired taxa (but not as high as murchisoniids) including *Wortheniopsis* in the murchisonioid family Plethospiridae, which composes taxa ranging from the Ordovician to lower Carboniferous (for instance *Platyzona*, formerly included in Plethospiridae is regarded as Goniasmatidae, see Karapunar et al. 2022) and is likely a not monophyletic group in its current composition. Nützel et al. (2018) placed the Middle Triassic *Murchisonietta* (which

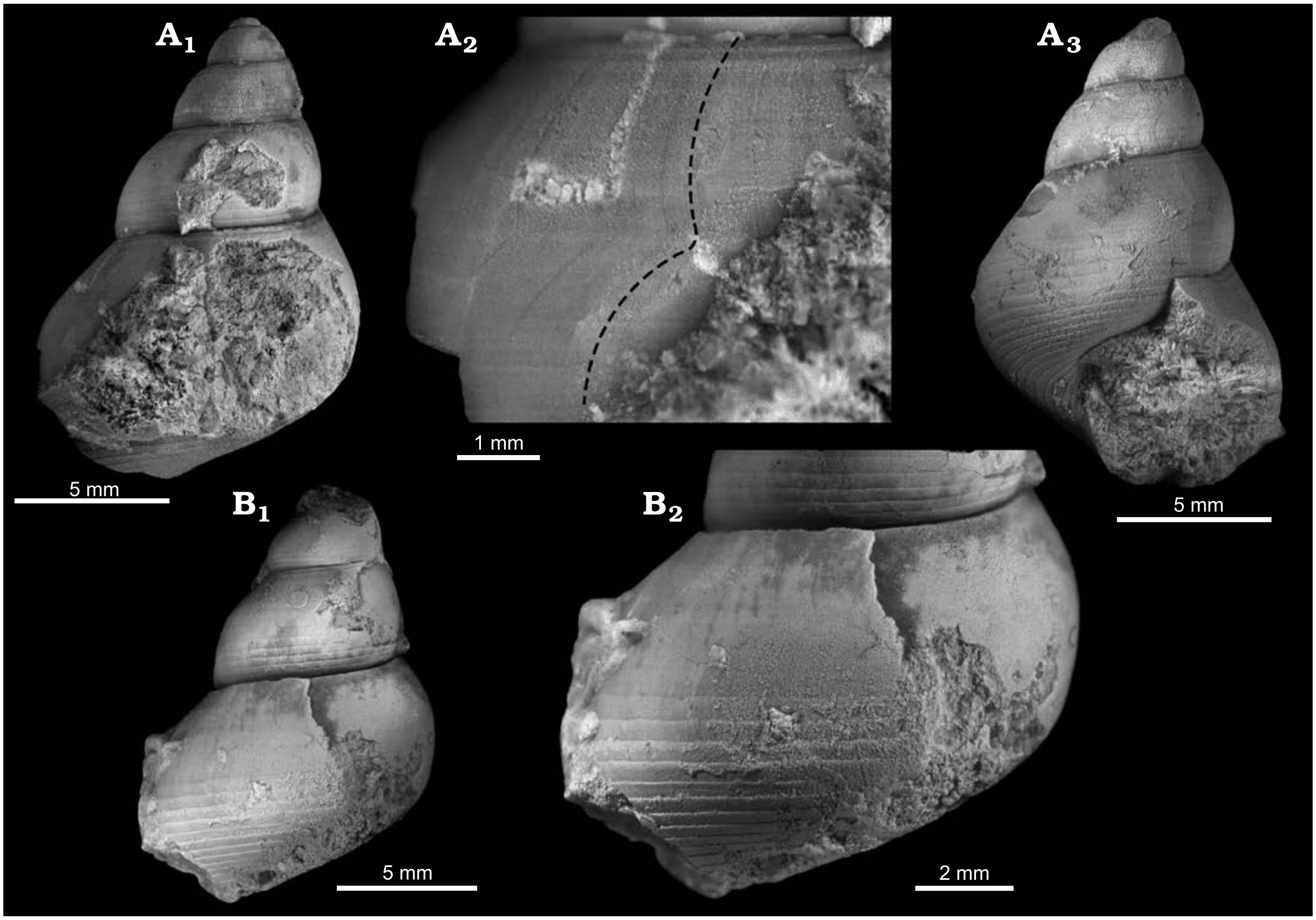


Fig. 9. Goniasmatid? caenogastropod *Wortheniopsis margarethae* (Kittl, 1894), Ladinian, Marmolada Limestone, Italy. **A**. NHMW 1884/0006/0872/1, in lateral (A_1) and apertural (A_3) views, detail of last preserved whorl in lateral view (A_2) to show growth lines (course indicated with dashed line). **B**. NHMW 1884/0006/0872/2, in lateral view (B_1), detail of last preserved whorl in lateral view (B_2).

is considered a junior synonym of *Wortheniopsis* herein) tentatively in Goniasmatidae and at present, we maintain this arrangement. We consider *Wortheniopsis* to represent Caenogastropoda, close to Goniasmatidae, but more evidence for that placement is needed, especially from early ontogenetic shell morphology.

There are many erroneous attributions of Permian and Jurassic species to *Wortheniopsis*.

The species attributed to *Wortheniopsis* by Szabó (2008) were later correctly removed from that genus and placed in *Kericserispira* Szabó, 2018 [replacement name for the pre-occupied *Faveolaria* Szabó, 2016]. Unlike *Wortheniopsis*, the following two Jurassic species have a clearly developed selenizone and therefore they are removed from *Wortheniopsis* and placed in *Kericserispira* Szabó, 2018: *Wortheniopsis bakonyensis* Szabó, 2016 [*Kericserispira bakonyensis* (Szabó, 2016) comb. nov.]; *Wortheniopsis rakusi* Szabó, 2016 [*Kericserispira rakusi* (Szabó, 2016) comb. nov.]

Branson (1948) listed many Permian species that were assigned to *Wortheniopsis* and some have been assigned to other genera since then. *Wortheniopsis netschajewi* Jakowlew, 1899 and *Wortheniopsis burtasorum* (Golowkinsky, 1868) were placed in *Biarmeaspira* by Mazaev (2015). Specimens previously identified by Licharew (1967) as *Pleurotomaria* (*Wortheniopsis*) *sequens* Waagen, 1880, were placed in *Baylea* by Mazaev (2016, 2018). *Pleurotomaria* (*Wortheniopsis*?) *eulkaiensis* Reed, 1927, was placed into *Platyzona* by Nützel and Nakazawa (2012). *Worthenopsis*? [sic!] *depressa* Beede, 1907, is a lenticular shell and was later placed in *Cyclites* by Knight (1940). *Worthenopsis* [sic!] sp. by Beede (1907) is a doubtful record and probably does not represent *Wortheniopsis*.

The Permian *Worthenopsis* [sic!] *bicarinata* Branson, 1930, is herein placed tentatively in *Glabrocingulum* (*Ananias*).

The following Permian species have a strongly angulated whorls face and a smooth selenizone. Hence, they are tentatively placed in *Baylea* Koninck, 1883, herein: *Worthenopsis dejactinensis* Jakowlew, 1899, *Worthenopsis kyschertianaeformis* Jakowlew, 1899, *Worthenopsis grandicarinata* Jakowlew, 1899, *Worthenopsis denjatinensis* Jakowlew, 1899. The placement of the following species in *Wortheniopsis* are

doubtful; they probably represent *Ananias* Knight, 1945, or *Baylea* Koninck, 1883:
Wortheniopsis sequens (Waagen, 1880)
Wortheniopsis orientalis (Krotow, 1885)
Wortheniopsis kyschertiana (Stuckenberg, 1898)
Wortheniopsis permiana (Stuckenberg, 1898)
Wortheniopsis jakovlewi Stuckenberg, 1905
Wortheniopsis pachti Stuckenberg, 1905
Wortheniopsis volgensis Stuckenberg, 1905
Wortheniopsis sysranicus Stuckenberg, 1905

The Triassic *Wortheniopsis* sp. reported by Sha (1995) and *Wortheniopsis budensis* Kutassy, 1927, are doubtful records. At present, there are only three accepted species of *Wortheniopsis* (from the Anisian and Ladinian): *Wortheniopsis margarethae* (Kittl, 1894), *Wortheniopsis quirini* (Stoppani, 1860), and *Wortheniopsis acuta* (Nützel, Kaim, and Grădinaru, 2018) (Fig. 11).

Stratigraphic and geographic range.—Anisian (Middle Triassic)–Norian (Upper Triassic), Italy, Romania, Hungary.

Wortheniopsis margarethae (Kittl, 1894)

Fig. 9.

1894 *Pleurotomaria margarethae* Kittl n.f.; Kittl 1894: 114, pl. 6: 1–3.
1895 *Wortheniopsis margarethae* Kittl sp.; Böhm 1895: 220, text-fig. 6; pl. 14: 24.

Material.—Two specimens, NHMW 1884/0006/0872/1, 2, from the Anisian (Middle Triassic), Marmolada Limestone, Italy.

Description.—Shell moderately high-spired, acutely conical, with four preserved whorls (earlier whorls missing), 15 mm high, 10 mm wide; whorls high, with convex to slightly angulated profile and incised suture; whorls above sinus steeply sloping, with prosocline growth lines and faint subsutural spiral cords; sinus situated on faint angulation, high on whorl face; whorl face below sinus with prosocyrt growth lines and wide, faint spiral bands; transition to base rounded; base anomphalous, ornamented with wide imbricated spiral bands.

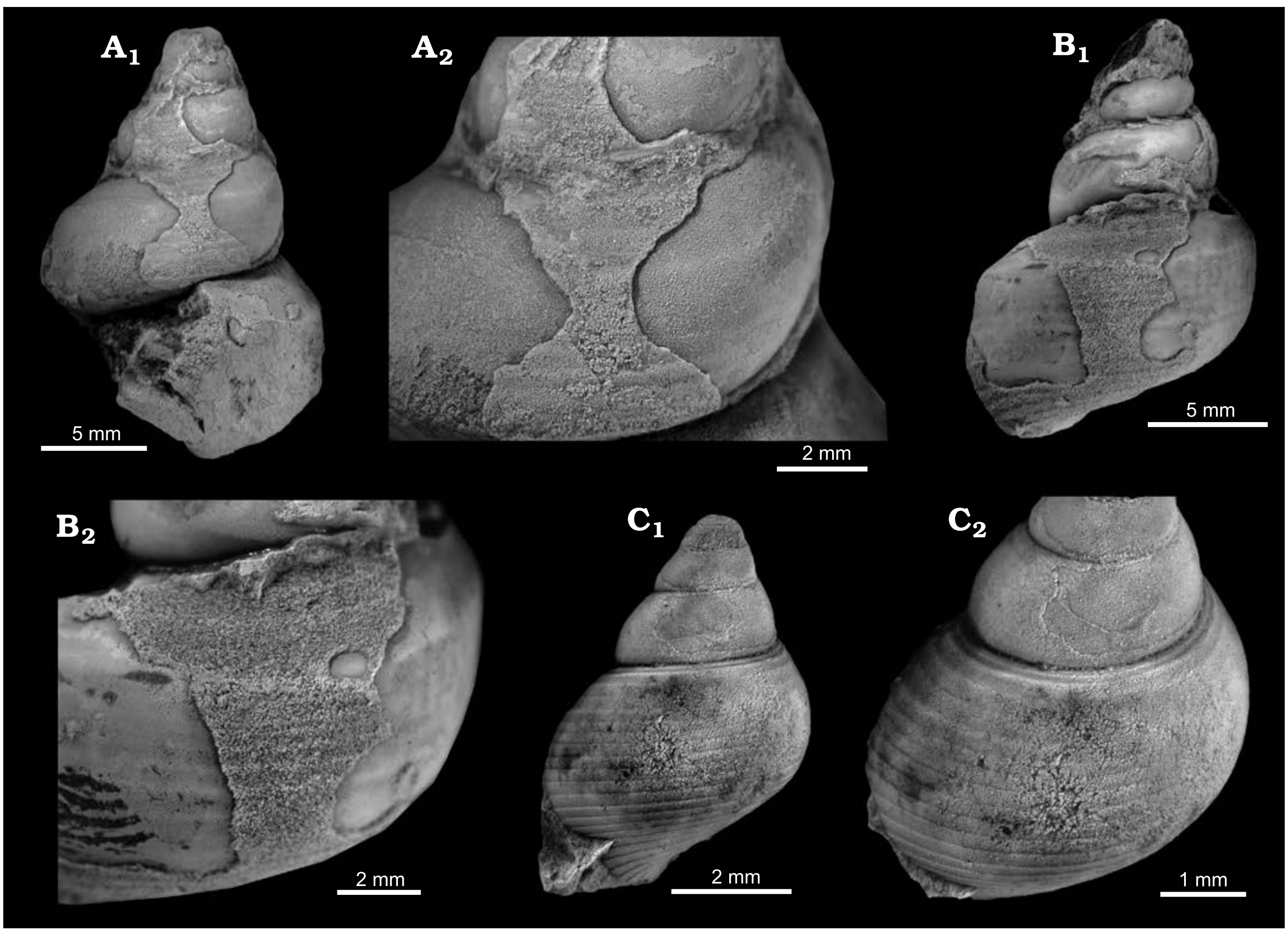


Fig. 10. Goniasmatid? caenogastropod *Wortheniopsis quirini* (Stoppani, 1860), Ladinian, Marmolada Limestone, Italy. **A**. NHMW 1969/1102/0000/1, original of Koken (1899, pl. 1: 14), in lateral view (A_1), detail of last preserved whorl in lateral view (A_2). **B**. NHMW 1969/1102/0000/2, original of Koken (1899: pl. 1: 15), in lateral view (B_1), detail of last preserved whorl in lateral view (B_2). **C**. NHMW 2019/0177/0020, juvenile specimen, in lateral (C_1) and oblique lateral (C_2) views.

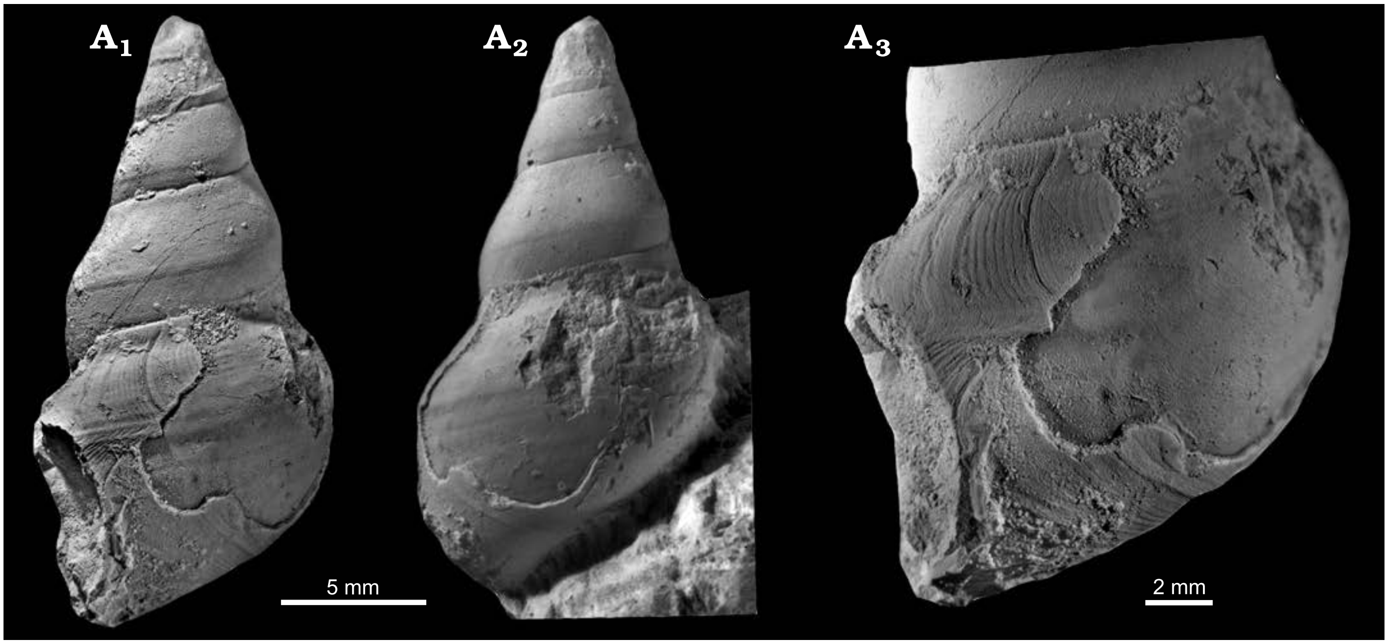


Fig. 11. Goniasmatid? caenogastropod *Wortheniopsis acuta* (Nützel, Kaim, and Gradinaru, 2018) comb. nov., Anisian, Romania. **A**. SNSB-BSPG 2015 VI 32, holotype, in lateral view (A_1,A_2), detail of last preserved whorl in lateral view (A_3).

Remarks.—The specimens placed in *Wortheniopsis quirini* (Stoppani, 1860) by Kittl (1899) are figured herein (Fig. 10). Their whorls are more angulated, and although poorly preserved, they show the characteristic imbricated spiral bands.

Stratigraphic and geographic range.—Ladinian (Middle Triassic), Marmolada, Italy.

Triassic gastropods erroneously identified as *Murchisonia*-like gastropods

Subclass Vetigastropoda Salvini-Plawen, 1980

Order Pleurotomariida Cox and Knight in Knight et al., 1960

Family Lancedelliidae Bandel, 2009

Genus *Acutitomaria* Karapunar and Nützel, 2021

Type species: *Acutitomaria kustatscherae* Karapunar and Nützel, 2021, Carnian (Upper Triassic), St. Cassian Formation, South Tyrol, Italy; original designation.

Remarks.—This genus unites exceptionally high-spired Pleurotomariida with late developing selenizone and a pronounced cancellate ornamentation (see Karapunar and Nützel 2021 for emended diagnosis of the family Lancedelliidae).

Acutitomaria woehrmanni (Koken, 1896) comb. nov.

Fig. 12.

1896 *Pseudomurchisonia woehrmanni* Koken; Koken 1896: 87, fig. 13.
1897 *Pseudomurchisonia woehrmanni* Koken; Koken 1897: 106, fig. 30, pl. 6: 3.
2021 *Pseudomurchisonia woehrmanni* Koken; Karapunar and Nützel 2021: 51.

Material.—Four fragments from the GBA, three of which were photographed and might represent Koken's (1896) illustrated type specimen that is broken (GBA 1897/003/0001). The label says "Unterer Rötelstein", in the publications (Koken 1896, 1897), the Feuerkogel is given as locality. GBA 1897/003/0001 is designated herein as lectotype.

Description.—Shell moderately high-spired, apical angle ca. 60°; early whorls not well-preserved but earliest whorls seem low trochospiral; whorls distinctly convex, ornamented with strong, densely spaced axial ribs and few spiral cords; axial ribs become knobby when crossing spiral cords in lower part of whorls; axial ribs become visible on third whorl where they are straight prosocline; selenizone appears within 4th whorl, high on whorl face, flush to slightly concave with strong lunulae; in addition, selenizone has a fine ornament of converging spiral threads (so far unknown from this species); base convex with strong spiral cords and axial ribs with small and axially elongated nodes at intersections.

Stratigraphic and geographic range.—Carnian (Upper Triassic), Austria.

Discussion

High-spired slit-band gastropods are an important component of late Paleozoic gastropod faunas. A considerable number of Permian (some of them latest Permian) species have been reported in the last decades (Winters 1963; Pan and Erwin 2002; Nützel and Nakazawa 2012; Nützel and Pan 2005; Mazaev 2006, 2015, 2018, 2019; Karapunar et al. 2022; Ketwetsuriya et al. 2016, 2020a, b, 2021). At least 27 Permian

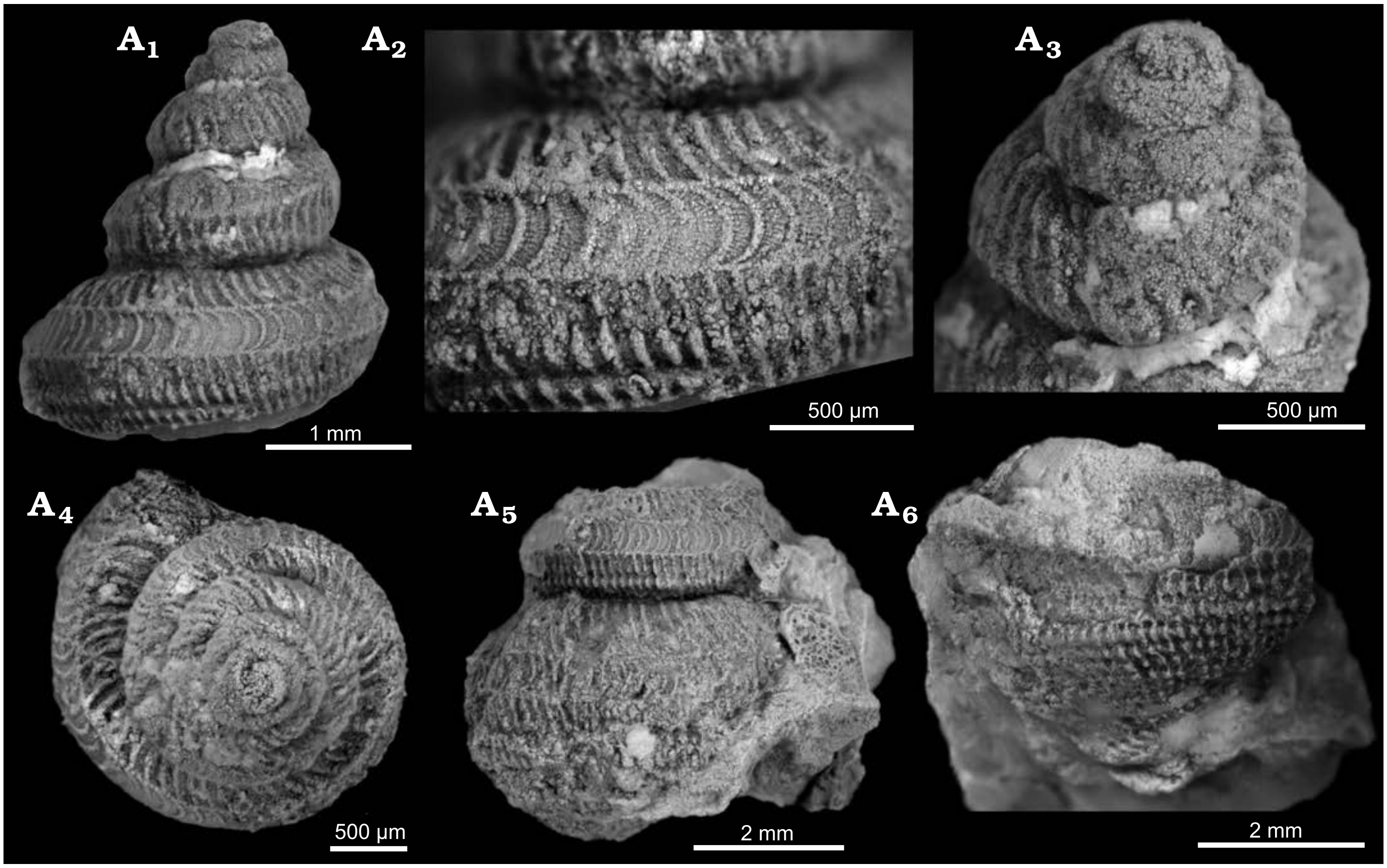


Fig. 12. Pleurotomariid vetigastropod *Acutitomaria woehrmanni* (Koken, 1896) "Unterer Rötelstein", according to Koken (1896, 1897), Feuerkogel, Austria is given as locality. **A**. GBA 1897/003/0001, fragmented lectotype, early whorls in lateral view (A_1), detail of whorl face in lateral view showing ornament, selenizone with lunulae and converging micro-ornament (A_2), early whorls in oblique lateral (A_3) and apical (A_4) views, last whorl in lateral views (A_5, A_6).

Murchisonia-like genera of the family Goniasmatidae have been reported (Table 1).

As has been elaborated in the introduction of this contribution, several of these *Murchisonia*-like gastropods proved to represent caenogastropods based on their protoconch morphology, the absence of nacre, their high-spired shape, and the presence of siphonal canals. We have shown that this group of caenogastropods apparently survived the end-Permian mass extinction event. On the other hand, high-spired Pleurotomariida were also present in that period of time (Karapunar and Nützel 2021) and *Acutitomaria* is shown as being a Late Triassic example for that.

Triassic *Murchisonia*-like gastropods are a small but heterogeneous group as our study has shown. Previously, Triassic murchisonimorph species have been attributed to the genera *Murchisonia*, *Pseudomurchisonia*, *Cheilotomona*, *Trypanocochlea*, *Wannerispira*, and *Vistilia*. We add the genera *Laschmaspira*, *Altadema*, and *Wortheniopsis* (alias *Murchisonietta*) (Table 1). *Trypanocochlea*, *Wannerispira*, *Laschmaspira*, and *Altadema* originate in the Paleozoic and persist into the Triassic. *Pseudomurchisonia*, *Wortheniopsis*, *Cheilotomona*, and *Vistilia* are restricted to the Triassic. However, the four Triassic species assigned to *Murchisonia* (*M. euglypha* Koken, 1894, *M. sera* Böhm, 1895, *M. subeuglypha* Krumbeck, 1924, and *M. timorensis* Krumbeck, 1924) likely do not represent this genus. *Murchisonia euglypha* Koken, 1894, is likely a member of the *Laschmaspira* (see above), *Murchisonia sera* Böhm, 1895, is a very slender, small form with a median slit-band and a pronounced ornament of spiral cords. It certainly does not belong in *Murchisonia*. Its generic assignment needs to be revised, it possibly represents *Stegocoelia* or an undescribed genus. *Murchisonia timorensis* also strongly deviates from the type species of *Murchisonia*, as does *M. subeuglypha* that as a strong angulation low on the whorls and additional strong spiral cords.

The Triassic *Wortheniopsis* lacks a true slit-band and have instead a more or less pronounced sinus. Therefore its assignment to Goniasmatidae is tentative; it might represent a new caenogastropod family.

Thus, at the generic level, there seems to be a considerable turnover in *Murchisonia*-like gastropods at the Paleozoic/Mesozoic transition according to the current state of knowledge. At the family level, it seems that only Goniasmatidae survived into the Triassic. *Murchisonia*-like gastropods have been reported from the Lower Triassic to the Norian but no clear Rhaetian species have been identified (species from the Carnian/Norian of Timor need a better dating; commonly only "Late Triassic" is given as age in the literature) and representatives are absent in the Jurassic. Amongst *Murchisonia*-like gastropods only *Trypanocochlea* has been considered

Table 1. Permian and Triassic *Murchisonia*-like gastropod genera (Goniasmatidae).

	Permian	Triassic
Aclisina Koninck, 1881	×	
Akasakiella Nützel in Nützel and Nakazawa, 2012	×	
Altadema Kues, 2002 (Carboniferous and Triassic)	×	×
Arribazona Kues, 1990	×	
Cerithioides Haughton, 1859	×	
Cerithiozone Nützel in Nützel and Nakazawa, 2012	×	
Cheilotomona Strand, 1928		×
Cibecuia Winters, 1956	×	
Costataenia Nützel in Nützel and Nakazawa, 2012	×	
Donaldospira Batten, 1966	×	
Erwinispira Nützel and Pan, 2005	×	
Goniasma Tomlin, 1930	×	
Helicospira Girty, 1915	×	
Hypergonia Donald, 1892	×	
Kazanella Mazaev, 2015	×	
Laschmaspira Mazaev, 2003	×	×
Loxisonia Batten, 1985	×	
Metorthonema Erwin, 1988	×	
Micheliopsis Termier and Termier in Termier et al., 1977	×	
Peruvispira Chronic, 1949	×	
Platyzona Knight, 1945	×	
?*Pseudomurchisonia* Koken, 1896		×
Stegocoelia Donald, 1889	×	
Taosia Girty, 1939	×	
Trypanocochlea Tomlin, 1931	×	×
Vebericochlis Licharew, 1967	×	
Vistilia Koken, 1896		×
Wannerispira Kaim and Nützel in Kaim et al., 2010	×	×
?*Wortheniopsis* Böhm, 1895		×

by Ferrari and Hautmann (2022) who restricted their analysis of gastropod diversity to genera from the Norian to the Pliensbachian. They found that the number of genera declined considerably at the Triassic/Jurassic boundary. The standing gastropod diversity declined considerably from the Carnian to the Rhaetian and was very low in the Rhaetian (Nützel 2005; Karapunar and Nützel 2021). *Murchisonia*-like gastropods are absent in all important Rhaetian faunas with the possible exception of *Trypanocochlea* sp. from the Pucará Group, Peru. The single specimen in question is from Lot 48, and Haas (1953: 307) indicated that this lot has an age from the "Late Norian or Early Rhaetian" to the Rhaetian, thus it is unclear whether that specimen has a Norian or Rhaetian age. Generally, there are only few species-rich Rhaetian gastropod faunas (e.g., Haas 1953; Nützel and Senowbari-Daryan 1999; Nützel et al. 2022). It is well possible that most of the *Murchisonia*-like gastropods became extinct at the mid-Carnian crisis (Carnian Pluvial Event) and were thus already extinct prior to the end-Triassic event. Slit-bearing vetigastropods (Pleurotomariida) were also selectively affected by the mid-Carnian crisis (Karapunar and Nützel 2021).

Conclusions

Murchisonia-like caenogastropods, chiefly Goniasmatidae, were diverse and abundant until the Permian, barely survived the end Permian extinction, regained a certain generic diversity within the Triassic with the evolution of several new genera but failed by far to regain their Permian generic diversity. Thus, this once successful and diverse group shares a similar fate (surviving the end-Permian extinction, a reduced Triassic diversity and extinction during Late Triassic crises) as conodonts, orthoceratids, conulariids, and others. This diversity pattern does not qualify for the "Dead Clade Walking" phenomenon i.e., the extinction shortly after a major mass extinction event (survival without recovery) as outlined by Jablonski (2002) because they have survived for ca. 30 Ma (at least until the Norian) and even produced a number of new genera. Among gastropods bellerophontids would be a typical example for "Dead Clade Walking", they survived the end-Permian extinction but eventually became extinct within the Early Triassic, at the end of the Smithian (Kaim and Nützel 2011). In both cases, bellerophontids and *Murchisonia*-like gastropods, the marginalization at end-Permian extinction event increased the vulnerability of the groups and likelihood for subsequent complete extinction. Both groups are slit-band gastropods and their dwindling that is accentuated by extinction events is part of a long-term overall decline of slit-band gastropods (see also Karapunar and Nützel 2021). Obviously, there prevailed a long-term selective trend against the character "shell-slit". It is likely that Goniasmatidae and similar forms are related to the ancient caenogastropod clade Cerithioidea (e.g., Nützel 1998; Nützel and Pan 2005) and in so far, this evolutionary lineage still persists until today but this once successful group has ceased at the genus- and family-level. The elimination of shell slits in caenogastropods probably also reflects an evolutionary change of the ventilation of the mantle cavity in these caenogastropods. The exhalant flow went in a lateral or dorsal direction in *Murchisonia*-like caenogastropods and that changed to a more ventral or posterior direction in modern Cerithioidea.

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