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 (Cheliotomoninae) 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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Received 14 June 2023, accepted 19 August 2023, available online 11 September 2023.

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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 Murchisionioidea (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 Pennsylvania 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, Fissurellioidea; 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, Chelatomona, 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 Staatsammlung 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 Altdamea 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. Murchisonieta Nützel, Kaim, and Grädinaru, 2018, a subjective younger synonym of Wortheniosis 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 tirata sp. nov., both from the Feuerkogel, Austria. Laschmaspira tirata sp. nov. and the type species of Laschmaspira have a spiral ornament on the teleoconch whors. 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–Upper Triassic (Carnian).

Laschmaspira tirata sp. nov.

Figs. 1, 2.


Etymology: From Latin tirata, 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 (A₁), detail of last whorls in lateral view (A₂), detail adapical whorl face with spiral lirae in lateral view (A₃), detail selenizone (slit-band) in lateral view (A₄), detail of whorl face and base of last whorl with spiral lirae in lateral view (A₅), early whorls in lateral view (A₆, A₇), early whorls in oblique lateral view (A₈, A₉), detail of early whorls in oblique lateral view showing beginning of selenizone as a sinus (A₁₀), early whorls in apical view (A₁₁).
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 Tellischen, 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 type. No larval shell has been observed. The size of the initial whorl 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’ (1860) type specimen. The Early Triassic specimen reported by Wittenburg (1908a) could either be a member of Pleurotomariida or Goniasmataeidae. 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 re-study of the types for confirmation.

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

Pseudomurchisonia? sundaiica 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.—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.? sundaiica Krumbeck, 1924, but none from the Paleozoic or 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 Goniasmataeidae. 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 deep selenizone that appears late during ontogeny. Apart from the type, 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.
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 Trias sic), Feuerkogel, Austria.

**Subfamily Cheilotomoninae nov.**


*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 whors 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 Goniasmatidae. 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-
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 species from Japan has a mammilated protoconch of the caeno-gastropod 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.
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 Middle Triassic (Anisian), Saalfelden, Salzburg, Austria: SNSB-BSPG AS XXXIV 557, holotype and original of Schnetzer (1934: pl. 1: 12), in lateral view (A₁), detail of last preserved whorl in lateral view (A₂, A₃), detail of last preserved whorl in lateral view to show growth lines and selenizone (slit-band) on crest (A₄). B. SNSB-BSPG AS XXXIV 559, paratype, in lateral view (B₁), basal view (B₂), detail of last preserved whorl in lateral view to show growth lines and selenizone (slit-band) on crest (B₃).

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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 (A₁), early whorls in lateral view (A₂), aperture with folds in lateral view (A₃). B. SNSB-BSPG 2011 XXXIX 78d, Feuerkogel, in lateral view (B₁), early whorls in lateral view (B₂). C. NHMW 1858/0047/0088, Feuerkogel, in lateral view (C₁), detail of last preserved whorl in lateral view to show growth lines and selenizone on crest (C₂), middle whorl in lateral view (C₃), detail of last preserved whorl in oblique lateral view to show growth lines and selenizone on crest (C₄).

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

*Material.*—A total of 8 specimens from the Middle Triassic (Anisian), 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.
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, distinctively convex near abapical border, forming periphery, smooth or with faint lunulæ; whorl face below selenizone narrow, concave, sharply inclining adaxially, with prosocyt growth lines; base flat, with opisthocyt 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, sur-..
Fig. 7. Goniasmatid caenogastropod *Altadema hausmannae* sp. nov., Lower Triassic, Dienerian/Smithian transition, 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 (E₁), detail (E₂). F. MUSE-PAL 8181, paratype, in lateral view. G. MUSE-PAL 8182, paratype, in lateral view (G₁), detail (G₂). H. MUSE-PAL 8183, paratype, detail to show slit-band, in oblique lateral view (H₁) and specimen in lateral view (H₂). I. MUSE-PAL 8184, paratype, in lateral view. J. MUSE-PAL 8185, paratype, in apertural (J₁) and lateral (J₂) 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-BB6-A0A705260DD

*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.

*Zoobank 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 prosocyrte 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 sparite, 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

[= *Murchisoniella* 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-
wards projection above mid-whorl of mature whorls forming
a shallow sinus. The same pseudo-selenizone has been re-
ported for the Anisian genus *Murchisonietta* Nützel, Kaim,
and Grădinaru, 2018 (Fig. 11) and therefore we consider
*Wortheniopsis* and *Murchisonietta* to represent synonyms.
Similar to *Altadena 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 Pleuroto-
maridiidae and Lophospirinae. Knight et al. (1960) placed
relatively high-spired taxa (but not as high as murchi-
soniids) including *Wortheniopsis* in the murchisoni-
oid family Plethospiridae, which composes taxa ranging
from the Ordovician to lower Carboniferous (for instance
*Platyzona*, formerly included in Plethospiridae is regarded

Fig. 8. Goniasmatid caenogastropod *Altadena kokeni* (Wittenburg, 1908a) and others, Lower Triassic, Dienerian/Smithian transition, Werfen Formation, Gastropod Oolite Member, Italy. A. Crack surface of Gastropod Oolite, near Borgo, Valsugana, Italy, ("Monte Zaccon" locality of Wittenburg 1908b); gastropods (*Altadena 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. *Altadena kokeni* (Wittenburg, 1908a), GPIT-PV-108710, holotype, and original of Wittenburg (1908a: pl. 5: 9, 10), Col di Rodella, Italy, Lower Triassic, Werfen Formation, in lateral view, not covered by ammonium chloride to show reddish color (B₁), detail of last whorl in lateral view to show adapical sinus of growth lines (B₂), in lateral view (B₃). C. Original drawing of *Altadena kokeni* from Wittenburg (1908a).
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 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?) eukaiensis Reed, 1927, was placed into Platyzona by Nützel and Nakazawa (2012). Wortheniopsis? [sic!] depressa Beede, 1907, is a lenticular shell and was later placed in Cyclites by Knight (1940). Wortheniopsis [sic!] sp. by Beede (1907) is a doubtful record and probably does not represent Wortheniopsis.

The Permian Wortheniopsis [sic!] bicornata Branson, 1930, is herein placed tentatively in Glabrocingulum (Anacias).

The following Permian species have a strongly angulated whorls face and a smooth selenizone. Hence, they are tentatively placed in Baylea Koninek, 1883, herein: Wortheniopsis dejactinensis Jakowlew, 1899, Wortheniopsis kyschetianaeformis Jakowlew, 1899, Wortheniopsis grandicarinata Jakowlew, 1899, Wortheniopsis 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).

**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 prosocyt growth lines and wide, faint spiral bands; transition to base rounded; base anomphalous, ornamented with wide imbricated spiral bands.

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**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 (**A1**), detail of last preserved whorl in lateral view (**A2**). **B.** NHMW 1969/1102/0000/2, original of Koken (1899: pl. 1: 15), in lateral view (**B1**), detail of last preserved whorl in lateral view (**B2**). **C.** NHMW 2019/0177/0020, juvenile specimen, in lateral (**C1**) and oblique lateral (**C2**) views.
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 trochosorial; 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
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, Alladema, and Wortheniopsis (alias Murchisonietta) (Table 1). Trypanocochlea, Wannerispira, Laschmaspira, and Alladema 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.
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 transition 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 reduction of shell slits in caenogastropods 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.

### Acknowledgements

We thank Stefano Monari (Università di Padova, Italy) and Mariel Ferrari (Instituto Patagónico de Geología y Paleoentología CCT CONICET-CENPAT, Puerto Madryn, Argentina) for their thoughtful reviews. Ingrid Werneburg (University of Tübingen, Germany) and Irene Zorn (GBA) are acknowledged for giving access to palaeontological collections under their care. Alexander Lukeneder, Andreas Kroh, and Thomas Nichertl (all NHMW) are acknowledged for providing working space, accommodation and access to the NHMW collections. The Deutsche Forschungsgemeinschaft (DFG) is acknowledged for the financial support (DFG NU 96/14-1, DFG NU 96/14-2). This research received support from the SYNTHESYS Project (http://www.syntheses.info/), which is financed by a European Community Research Infrastructure Action under the FP7 “Capacities” Program (AT TAF-1797) and provided a grant to AN for a collection visit to NHMW and GBA.

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

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<th>Name</th>
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<th>Triassic</th>
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