Phylogeny, classification and palaeodiversity of slit shells (order Pleurotomariida, Gastropoda)



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Statutory declaration and statement

I hereby confirm that my thesis entitled **"Phylogeny, classification and palaeodiversity of slit shells (order Pleurotomariida, Gastropoda)"**, is the result of my own original work. Furthermore, I certify that this work contains no material which has been accepted for the award of any other degree or diploma in my name, in any university and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. In addition, I certify that no part of this work will, in the future, be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of the Ludwig-Maximilians-Universität München.

München, 02.03.2022

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Abstract

Gastropoda are one of the most diverse living animal group and show an almost steady increase in diversity since their origination in the Cambrian. However, not all gastropod groups underwent this continuous diversification. Many groups became either extinct or decreased in diversity significantly during the evolutionary history of Gastropoda. Understanding why some groups got extinct while others survived over the course of gastropod evolution and also the phylogenetic relationships of extinct and extant taxa are two major challenges in the field of gastropod research and beyond it. The gastropod order Pleurotomariida is the only living group with a fossil record that can be reliably traced back to the Cambrian–Ordovician. This important gastropod group peaked in diversity in the Middle and Late Palaeozoic and formed one of the most diverse gastropod groups in the Upper Palaeozoic assemblages. However, their diversity decreased sharply at the end-Permian mass extinction and continuously declined since then with the exception of a short Middle to Late Triassic recovery. The present thesis aims to improve the classification of Pleurotomariida, document their diversity in Earth history and to reconstruct their phylogeny with modern phylogenetic methods. The classification of Pleurotomariida is revised by studying new collections of exceptionally well-preserved specimens as well as and hitherto insufficiently known type specimens and by an extensive literature survey. The study of type material and of exceptionally well-preserved Late Palaeozoic and Triassic material facilitated the phylogenetic analyses with modern methods by increasing the number of shell characters. Finally, the diversity evolution of Pleurotomariida from an assemblage level to a global level is analyzed especially regarding the impact of the end-Permian mass extinction event.

Over the last decades, gastropod researchers found that early ontogenetic shells (especially the protoconch) are of high value for classification. However, the protoconch and early ontogenetic development of many Pleurotomariida from the Palaeozoic have not yet been well documented. In second chapter (Karapunar et al. 2022a), exceptionally well-preserved Pennsylvanian pleurotomariidan gastropods from 37 localities from the USA are studied. A total of 38 species, representing 19 genera including 10 new species, one new genus and one new subgenus are described. Early ontogeny and protoconchs of numerous taxa are documented for the first time. Early shell characters are found to be conservative above species level, implying that they might be phylogenetically informative. Two globally distributed genera, *Peruvispira* and *Platyzona*, are excluded from Pleurotomariida (Vetigastropoda) and are placed in Caenogastropoda because they have protoconchs of the planktotrophic larval development type

that is unknown in Vetigastropoda. Two studied Pennsylvanian assemblages from the Finis Shale Member and Colony Creek Shale Member of Texas indicate that Pleurotomariida were the most diverse and abundant group. However, their relative abundance depends on the sampling method and mesh size used in the analysis and they are more abundant in surface samples and coarser size fractions. Repaired shell scars were found in individuals as small as 1 mm in size, indicating the presence of considerable predatory pressure at all size ranges.

Study of new assemblages from poorly studied regions are important to decrease the geographical bias in global diversity studies. In chapter three (Ketwetsuriya et al. 2020), a new silicified gastropod assemblage from the Middle Permian Khao Khad Formation of Thailand is studied. A total of 44 gastropod species representing 30 genera including 13 new species (five Pleurotomariida) and one new pleurotomariidan genus are described. The Khao Khad assemblage is the most diverse gastropod assemblage reported from the Permian of Thailand so far. In chapter four (Karapunar et al. 2022b), the oldest gastropod collections from the Permian of Thailand are described. In contrast to the previous report of this collection, no pleurotomariid gastropod was found in the Ban Kao assemblage. It yields only two species and is dominated strongly by *Peruvispira*, a genus which is no longer regarded as Pleurotomariida due to the presence of a protoconch reflecting planktotrophic larval development that is unknown in Vetigastropoda.

The Triassic is a critical period in the evolutionary history of Pleurotomarida and of other members of the biota because it represents a relatively short period of time between two major mass extinction events. It witnessed a considerable turnover (extinction/origination) probably accentuated by the Late Triassic Carnian Pluvial Event. The Carnian St. Cassian Formation yields about a quarter of all globally known Triassic gastropod species. Nearly half of the Triassic pleurotomariidan genera are present in the St. Casssian Fm. and specimens are commonly exceptionally well preserved. In fifth chapter (Karapunar & Nützel 2021), all gastropods previously assigned to Pleurotomariida from the St. Cassian Fm were revised. Numerous type specimens including the types of several type species have been known only from their original drawings and descriptions for more than a century, which caused several erroneous attributions by subsequent authors. A total of 106 lectotypes were designated and figured, 67 species were described including 9 new genera and 8 new species. As a result of the revision, 77 pleurotomariidan species were found in the St. Cassian Fm, none of them representing Palaeozoic genera. This indicates all St. Cassian pleurotomariidan genera originated during the recovery after the end-Permian mass extinction. Additionally, the Triassic

diversity of Pleurotomariida and four gastropod subclasses were analyzed with a global Triassic gastropod species database (comprising 2177 species). Furthermore, the diversity changes of Pleurotomariida and Gastropoda through the Permian–Triassic interval was analyzed by using this global Triassic database and the Paleobiology database (for Permian data). The analyses show that the recovery of Pleurotomariida during the Triassic was sluggish compared to other gastropod groups, especially caenogastropods and they never reached the diversity they had during the Permian and thus failed to recover fully in contrast to other gastropod clades. The analysis further indicates an interruption of recovery within the Carnian, likely as a result of the Carnian Pluvial Episode.

There are only a few quantitative phylogenetic analyses of fossil gastropods. The evolutionary relationships between pleurotomariidan taxa are largely based on experts' opinions. In sixth chapter (Karapunar & Nützel, in prep.), the first comprehensive phylogenetic analyses of Pleurotomariida are presented. Parsimony and Bayesian (Fossilized Birth Death (FBD) model) analyses are performed by using 93 morphological shell characters comprising 109 pleurotomariidan species representing 80 genera ranging from the Ordovician to the Recent. Similar clades were recovered in both analyses but the relationship of clades to each other differs drastically. Since FBD method incorporates the stratigraphic information in tree reconstruction, it reconstructs more stratigraphically congruent trees than the Parsimony method. According to the Bayesian (FBD) phylogeny, Pleurotomariida split into three lineages during the Devonian and two of them survived the end-Permian mass extinction. Although Wortheniellini showed a higher diversification during the Triassic, only Pleurotomariini could persist until today. This indicates that diversification dynamics of Pleurotomariida did not play a crucial role in surviving mass extinctions. The FBD tree further indicates that the clades with fossil records only known from the Triassic originated during the Permian although they have not been reported form the Permian. Therefore, the Permian fossil record needs further examination.

Zusammenfassung

Gastropoda sind eine der artenreichsten lebenden Tiergruppen und weisen seit ihrer Entstehung im Kambrium eine fast stetige Zunahme an Diversität auf. Allerdings haben nicht alle Gastropodengruppen diese kontinuierliche Diversifizierung durchlaufen. Viele Gruppen sind während der Evolutionsgeschichte der Gastropoda entweder ausgestorben oder haben in ihrer Diversität erheblich abgenommen. Um zu verstehen, warum einige Gruppen ausgestorben sind, während andere im Laufe der Evolution der Gastropoden überlebt haben, und wie die phylogenetischen Beziehungen zwischen den ausgestorbenen und noch vorhandenen Taxa sind, sind zwei große Herausforderungen auf dem Gebiet der Gastropodenforschung und darüber hinaus. Die Gastropodenordnung Pleurotomariida ist die einzige lebende Gruppe mit einem Fossilienbestand, der zuverlässig bis ins Kambrium-Ordovizium zurückverfolgt werden kann. Diese wichtige Gastropodengruppe erreichte im Mittel- und Spätpaläozoikum den Höhepunkt ihrer Vielfalt und bildete eine der vielfältigsten Gastropodengruppen in den fossilen Ansammlungen des Oberpaläozoikums. Ihre Vielfalt nahm jedoch am Ende des Perm-Massenaussterbens stark ab und ging seitdem kontinuierlich zurück, mit Ausnahme einer kurzen Erholung in der mittleren bis späten Trias. Die Ziele der vorliegenden Dissertation sind die Verbesserung der Klassifizierung der Pleurotomariida, die Dokumentation ihrer Diversität in der Erdgeschichte und die Rekonstruktion ihrer Phylogenie mit modernen phylogenetischen Methoden. Die Klassifizierung von Pleurotomariida wird durch das Studium neuer Sammlungen von außergewöhnlich gut erhaltenen Exemplaren sowie von bisher unzureichend bekannten Typusexemplaren und durch eine umfangreiche Literaturrecherche überarbeitet. Die Untersuchung von Typusmaterial und von außergewöhnlich gut erhaltenem spätpaläozoischen und triassischen Material erleichterte die phylogenetischen Analysen mit modernen Methoden, indem die Anzahl an Gehäuseeigenschaften erhöht wurde. Abschließend wird die Evolution der Diversität von Pleurotomariida von der Ansammlungsebene bis zur globalen Ebene analysiert, insbesondere im Hinblick auf die Auswirkungen des Massenaussterbens am Ende des Perm.

In den letzten Jahrzehnten fanden Gastropodenforscher heraus, dass frühe ontogenetische Schalen (insbesondere der Protoconch) für die Klassifizierung von hohem Wert sind. Der Protoconch und die frühe ontogenetische Entwicklung vieler Pleurotomariida aus dem Paläozoikum sind jedoch noch nicht gut dokumentiert. Im zweiten Kapitel (Karapunar et al. im Druck) werden außergewöhnlich gut erhaltene Schlitzbandschnecken (Pleurotomariida) aus 37 Fundorten aus dem Pennsylvanium in den USA untersucht. Insgesamt werden 38 Arten

beschrieben, die 19 Gattungen repräsentieren, darunter 10 neue Arten, eine neue Gattung und eine neue Untergattung. Frühe Ontogenese und Protoconche zahlreicher Taxa werden erstmals dokumentiert. Es wird festgestellt, dass frühe Schalenmerkmale von mehreren Arten geteilt werden, was darauf hindeutet, dass sie phylogenetisch informativ sein könnten. Zwei weltweit verbreitete Taxa (*Peruvispira* und *Platyzona*) werden von Pleurotomariida (Vetigastropoda) ausgeschlossen und werden Caenogastropoda zugeordnet, weil sie Protoconche des planktotrophen Larvenentwicklungstyps haben, der bei Vetigastropoda unbekannt ist. Zwei untersuchte Sammlungen aus dem Pennsylvanium von Texas (Finis Shale Member und Colony Creek Shale Member) weisen darauf hin, dass Pleurotomariida die vielfältigste und am häufigsten vorkommende Gruppe waren. Ihre relative Häufigkeit hängt jedoch von der bei der Analyse verwendeten Entnahmemethode und der Maschenweite der Siebe ab – sie sind in Oberflächenproben und gröberen Größenfraktionen häufiger anzutreffen. Reparierte Gehäusenarben wurden bei Individuen ab einer Größe von nur 1 mm gefunden, was auf das Vorhandensein eines beträchtlichen räuberischen Drucks in allen Größenbereichen hinweist.

Die Untersuchung neuer fossiler Vergesellschaftungen aus wenig untersuchten Regionen ist wichtig, um die geografische Verzerrung in globalen Diversitätsstudien zu verringern. In Kapitel drei (Ketwetsuriya et al. 2020) wird eine neue verkieselte Gastropoden-Ansammlung aus der mittelpermischen Khao-Khad-Formation in Thailand untersucht. Insgesamt werden 44 Gastropodenarten aus 30 Gattungen beschrieben, darunter 13 neue Arten (fünf Pleurotomariida) und eine neue Gattung der Pleurotomariida. Die Ansammlung von Khao Khad ist die vielfältigste Ansammlung von Gastropoden, die bisher aus dem Perm von Thailand gemeldet wurde. In Kapitel vier (Karapunar et al. 2022b) werden die ältesten Schneckensammlungen aus dem Perm Thailands beschrieben. Im Gegensatz zum vorherigen Bericht dieser Sammlung wurden in der Ban-Kao-Ansammlung keine Pleurotomariida gefunden. Sie bringt nur zwei Arten hervor und wird stark von *Peruvispira* dominiert, einer Gattung, die nicht mehr als Pleurotomariida angesehen wird, da ein Protoconch vorhanden ist, der die bei Vetigastropoda unbekannte planktotrophe Larvenentwicklung aufzeigt.

Die Trias ist eine kritische Periode in der Evolutionsgeschichte der Pleurotomariida und auch der restlichen Biota, da sie einen relativ kurzen Zeitraum zwischen zwei großen Massenaussterben darstellt. Sie erlebte einen beträchtlichen Artenwechsel (Aussterben / Neuentstehung), die wahrscheinlich durch das spättriassische karnische Pluvialereignis akzentuiert wurde. Die karnische St. Cassian-Formation liefert etwa ein Viertel aller weltweit bekannten triassischen Gastropodenarten. Fast die Hälfte der triassichen Gattungen der

Pleurotomariida sind in der St. Casssian Fm vorhanden. und ihre Exemplare sind im Allgemeinen außergewöhnlich gut erhalten. Im fünften Kapitel (Karapunar & Nützel 2021) wurden alle zuvor Pleurotomariida zugeordneten Gastropoden aus der St. Cassian Fm überarbeitet. Zahlreiche Typusexemplare, einschließlich Typmaterial mehrerer Typusarten, sind seit mehr als einem Jahrhundert nur aus ihren Originalzeichnungen und -beschreibungen bekannt, was zu mehreren fehlerhaften Zuweisungen durch nachfolgende Autoren führte. Insgesamt wurden 106 Lectotypen bestimmt und abgebildet, 67 Arten wurden beschrieben, darunter neun neue Gattungen und acht neue Arten. Als Ergebnis der Überarbeitung wurden 77 Pleurotomariida-Arten in der St. Cassian Fm gefunden, von denen keine paläozoische Gattungen repräsentieren. Dies deutet darauf hin, dass alle St. Cassianer Pleurotomariida-Gattungen während der Erholung nach dem Massensterben am Ende des Perm entstanden sind. Zusätzlich wurde die Trias-Diversität der Pleurotomariida und vier Gastropoden-Unterklassen mit einer globalen Trias-Gastropoden-Artendatenbank (mit 2177 Arten) analysiert. Darüber hinaus wurden die Diversitätsänderungen der Pleurotomariida und Gastropoda während des Perm-Trias-Intervalls unter Verwendung dieser globalen Trias-Datenbank und der Paleobiology Database (für Perm-Daten) analysiert. Die Analysen zeigen, dass die Erholung von Pleurotomariida während der Trias im Vergleich zu anderen Gastropodengruppen, insbesondere Caenogastropoden, schleppend verlief und sie nie wieder die Diversität erreichten, die sie während des Perms hatten, und sich daher im Gegensatz zu anderen Gastropoden-Kladen nicht vollständig erholten. Die Analyse weist ferner auf eine Unterbrechung der Erholung innerhalb des Karnischen Meeres hin, wahrscheinlich als Ergebnis der Karnischen Pluvialepisode.

Es gibt nur wenige quantitative phylogenetische Analysen fossiler Schnecken. Die evolutionären Beziehungen zwischen Pleurotomariida-Taxa basieren weitgehend auf Expertenmeinungen. Im sechsten Kapitel (Karapunar & Nützel, in Vorbereitung) werden die ersten umfassenden phylogenetischen Analysen von Pleurotomariida vorgestellt. Parsimony- und Bayes-Analysen (Fossilized Birth Death (FBD)-Modell) werden unter Verwendung von 93 morphologischen Schalenmerkmalen durchgeführt, die 109 Pleurotomariidan-Arten umfassen, die 80 Gattungen repräsentieren, und die vom Ordovizium bis zur Neuzeit reichen. In beiden Analysen wurden ähnliche Kladen wiedergefunden, aber die Beziehung der Kladen zueinander unterscheidet sich drastisch. Da die FBD-Methode die stratigraphischen Informationen in die Baumrekonstruktion einbezieht, rekonstruiert sie mehr stratigraphisch kongruente Bäume als die Parsimony-Methode. Gemäß der Bayesianischen (FBD) Phylogenie

teilten sich Pleurotomariida während des Devon in drei Linien auf und zwei von ihnen überlebten das Massensterben am Ende des Perm. Obwohl Wortheniellini während der Trias eine höhere Diversifikation aufwiesen, konnten nur Pleurotomariini bis heute bestehen bleiben. Dies deutet darauf hin, dass die Diversifikationsdynamik der Pleurotomariida keine entscheidende Rolle beim Überleben von Massensterben spielte. Der FBD-Baum weist ferner darauf hin, dass die Kladen mit fossilen Vertretern, die nur aus der Trias bekannt sind, während des Perms entstanden sind, obwohl sie nicht aus dem Perm gemeldet wurden. Daher bedarf der Fossilienbestand des Perm einer weiteren Untersuchung.

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Chapter 1. Introduction

1.1. Introduction

Mollusca represents the second largest animal phylum (Gonzalo & Giribet 2020). Gastropoda is the most diverse class within Mollusca (MolluscaBase). Gastropods occupy a broad range of habitats both on land and in the sea (Ponder & Lindberg 2020) and represent one of the most diverse and abundant animal groups in recent marine environments (e.g., Bouchet et al. 2002). The diversity of gastropods increases almost steadily since their origination in the Cambrian (Sepkoski 1981; Fig. 1). However, this continuously increasing diversity trend does not reflect the diversity of individual gastropod groups which existed in the Phanerozoic (e.g., Erwin 1990; Fig. 5). Most gastropod groups from the early evolutionary history of the clade got extinct either in the Palaeozoic (e.g., Macluritoidea) at or shortly after the end-Permian mass extinction (e.g., Euomphaloidea, Bellerophontida; Tracey et al. 1993), the largest extinction event for animals in the Earth history (e.g., Payne & Clapham 2012). The order Pleurotomariida was one of the few, who existed in the early Palaeozoic and survived several mass extinction events, including the end-Permian event. Their diversity, however, decreased gradually after the end-Permian mass extinction. Caenogastropoda, on the other hand, experienced significant radiations from the Mesozoic onwards and represent the most diverse living gastropod group, comprising 60% of living gastropod species (Ponder & Lindberg 2020). The reason why some groups got extinct over the course of gastropod evolution while others were radiating is still not fully understood.

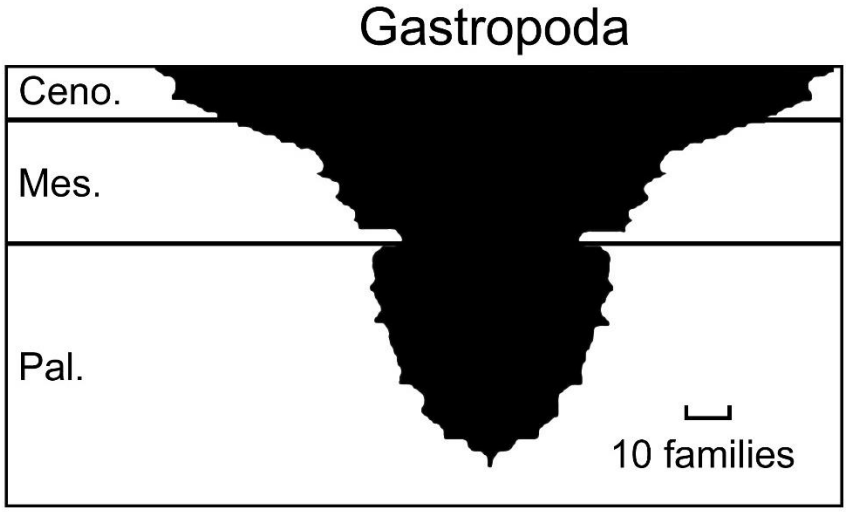

Figure 1: Family diversity of Gastropoda through the Phanerozoic (redrawn after Sepkoski 1981).

1.2. What is Pleurotomariida

Pleurotomariida (slit shells) are one of the most ancient living gastropod groups (e.g., Hickman 1984). Their shell is characterized by a deep slit in the outer lip (labrum), an inner nacreous shell layer and a protoconch (larval shell) consisting of nearly one whorl, reflecting a non-planktotrophic larval development (e.g., Bandel 1982; Nützel 2014; Fig. 2A–C). The most characteristic, name-giving part of the pleurotomariidan shell is the slit and the related selenizone, a region on the shell surface consisting crescentic growth lines or crescentic lirae (lunulae, Fig. 2D). The selenizone is formed by a gradual closure of the shell slit during the accretionary shell growth (Fig. 2E–G). Although shell slit, protoconch or original aragonitic shell layers are rarely preserved in fossil shells, the selenizone is generally preserved and is useful for the identification of Pleurotomariida, both fossil and Recent.

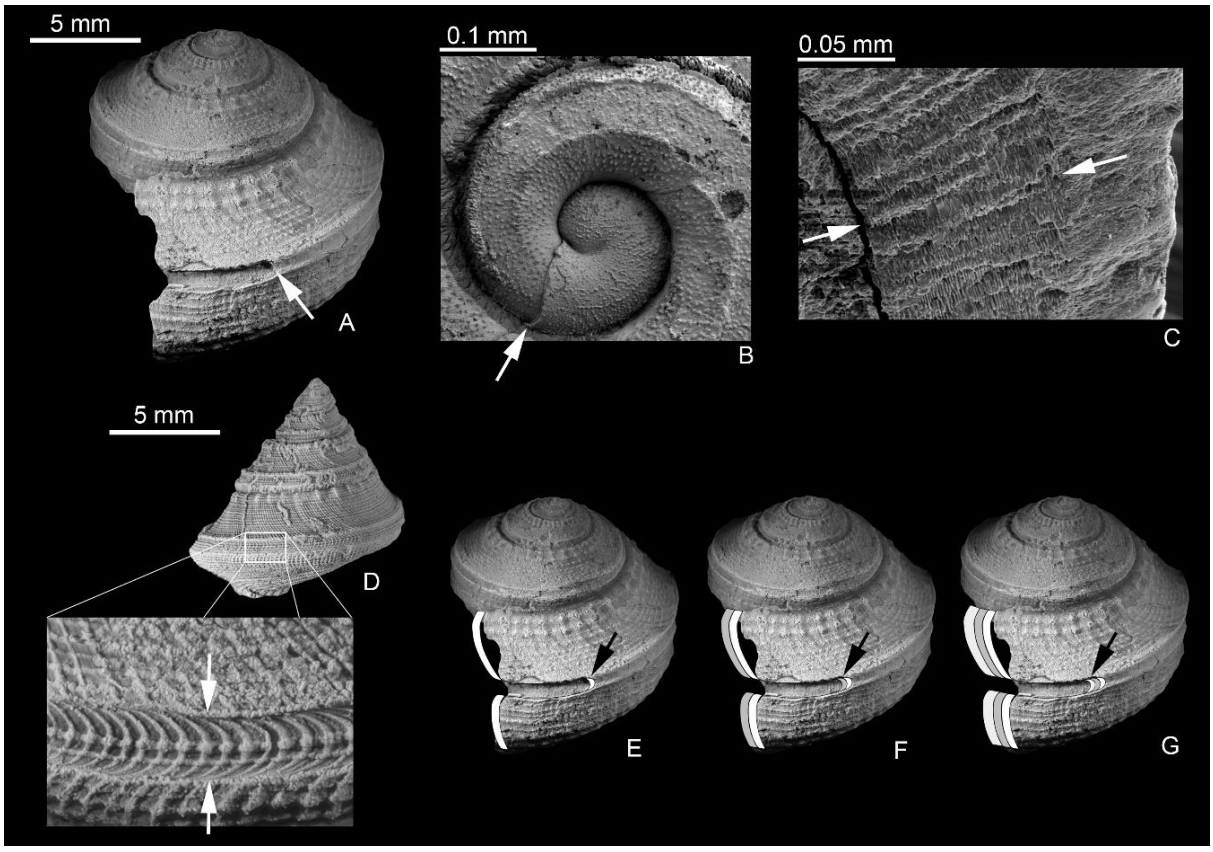

Figure 2: Characteristic shell features of Pleurotomariida. **A.** *Glabrocingulum* (*Glabrocingulum*) *grayvillense* (Norwood & Pratten), arrow indicates the proximal (posterior) end of the shell slit. **B.** *Wortheniella coralliophila* (Kittl), arrow indicates the protoconch-teleoconch boundary. **C.** *Pseudoananias subgranulata* (Münster), arrows indicate the borders of the inner nacreous shell layer. **D.** *Phymatopleura brazoensis* (Shumard), arrows indicate the borders of the selenizone. **E–G.** *Glabrocingulum* (*Glabrocingulum*) *grayvillense* (Norwood & Pratten), the formation of selenizone by gradual closure of shell slit, the arrows point newly formed shell at the proximal end of the slit.

The shell shape of pleurotomariidans varies from trochiform to wortheniform (gradate spire) and occasionally discoidal or high-spired (Knight et al. 1960). The teleoconch whorls (i.e., post larval whorls) are not always coiled in the same helicospiral direction. Some taxa start coiling planispiral and changes to dextral (e.g., Worthenielidae), some start coiling dextral and change to sinistral or planispiral (Porcelliidae) during ontogeny. The pleurotomariidan shells are rarely smooth (e.g., *Gosseletina*, *Ptychomphalus*; Fig. 3B), most taxa exhibit diverse array of ornament on their shell. For instance, the shell ornament can consist of only axial ribs (e.g., *Ptychomphalina*; Fig. 3D), only spiral cords (e.g., *Baylea*; Fig. 3C) or a meshwork of equally strong axial and spiral lirae (e.g., *Kokenella*; Fig. 3E). Some taxa might form prominent nodes (e.g., Pleurotomariidae; Fig. 3A) or long spines (e.g., Schizogoniidae) on their shells.

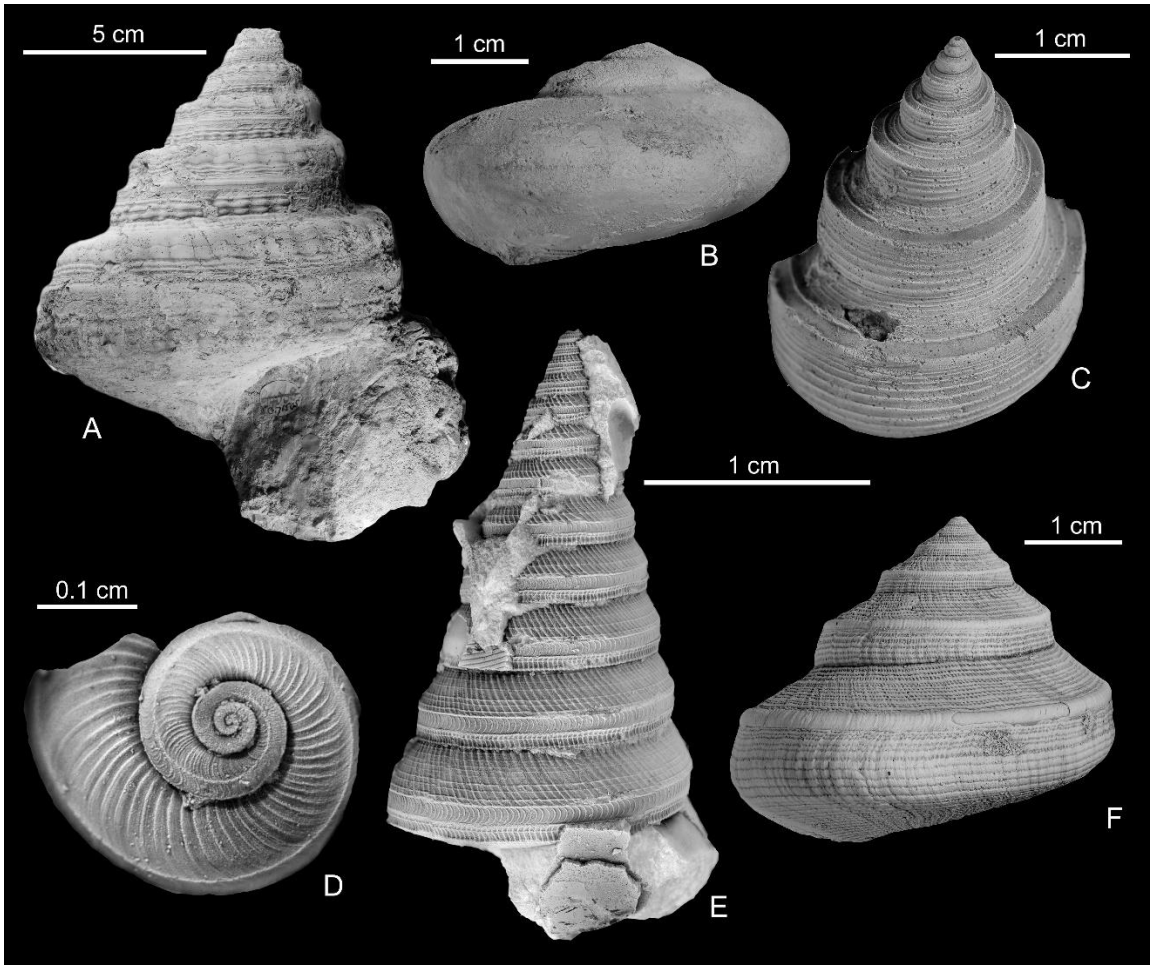

Figure 3: Pleurotomariida with different shell shape and ornament. **A.** *Pleurotomaria anglica* (J. Sowerby), with prominent nodes and gradate spire, Jurassic; **B.** *Cryptaenia heliciformis* (Eudes-Deslongchamps), lenticular shell with smooth whorl face, Jurassic; **C.** *Baylea yvanii* (Léveillé), wortheniform shell ornamented with only spiral cords, Carboniferous; **D.** *Euryzone undulata* (Phillips), ornament of only axial ribs, Carboniferous; **E.** *Eymeralla scalariformis* (Koken), high spired shell with cancellate ornament, Triassic; **F.** *Bathrotomaria reticulata* (J. Sowerby), shell with gradate spire and cancellate ornament, Jurassic.

The living Pleurotomariida have a rhipidoglossan type radula and paired mantle organs including two bipectinate gills (ctenidia), auricles, kidneys and hypobranchial glands (Yonge 1947; Harasewych 2002). The paired organs are positioned bilaterally symmetrical on either side of the shell slit and the anus is situated at the proximal end of the slit (Yonge 1947; Harasewych 2002). The function of the shell slit is to ventilate the mantle cavity and dispose the excretory products (Yonge 1947; Voltzow et al. 2004). The living animal forms a current within the mantle cavity, the inhalant current enters at the distal part of the shell slit and the exhalant current leaves at the proximal end of the shell slit (Voltzow et al. 2004).

About 44 living species representing four genera of the family Pleurotomariidae have been described and represent the few modern remainders of the group (MolluscaBase, accessed February 2022). The living members of Pleurotomariida occupy deep water (> 200m), unlike their extinct relatives, which inhabited largely shallow water environments (Harasewych 2002). The recent pleurotomariids are carnivorous grazers feeding on sponges (Harasewych 2002).

1.3. Classification

Early classifications within Pleurotomariida were published by Koken (1889), Koken & Perner (1925), Thiele (1929–1931) and Wenz (1938–1944). Knight et al. (1960) published the last comprehensive classification of Pleurotomariida on the generic level. In earlier works, Pleurotomariida was considered as a basal group within Gastropoda and within former Archaeogastropoda (Thiele 1929–1931; Wenz 1938–1944; Yonge 1947). Accordingly, the presence of paired organs and their symmetrical arrangement within the mantle were regarded as ancestral characters in gastropods (e.g., Yonge 1947). This view was criticized by Haszprunar (1988) and Ponder & Lindberg (1997), who conducted phylogenetic analyses of Gastropoda and recovered Pleurotomariida within Vetigastropoda (corresponds largely to Archaeogastropoda). However, the position of Pleurotomariida within Vetigastropoda is still a matter of discussion. In the phylogenetic analyses using morphological data (anatomy and few shell characters), the living Pleurotomariidae were recovered as a derived clade within Vetigastropoda (Ponder & Lindberg 1997; Sasaki 1998). However, in molecular phylogenies Pleurotomariida is reconstructed in a more basal position within Gastropoda and Vetigastropoda (Harasewych et al. 1997; Geiger & Thacker 2005; Yoon & Kim 2005; Williams

& Ozawa 2006; Zapata et al. 2014; Cunha et al. 2021), which is more consistent with the fossil record that indicates a high geological age for the group. Thus, molecular phylogenies corroborate the earlier suggestion that Pleurotomariida are a basal clade (early offshoot) within Gastropoda. The classification of Pleurotomariida and other gastropod groups by Knight et al. (1960) was later modified by Tracey et al. (1993) and Bouchet et al. (2005, 2017). Bouchet et al. (2017) published the last comprehensive classification of Pleurotomariida on the family level and represents the last consensus view on the systematic of the group.

Bandel & Geldmacher (1996) introduced the name Selenimorpha for slit-bearing Vetigastropoda and provided a hypothetical phylogenetic tree (without a quantitative analysis), in which major vetigastropod lineages extend back to the Ordovician and form a polytomy. Wagner (2002) conducted a comprehensive phylogenetic analysis of Late Cambrian to Silurian anisostrophically coiled gastropods based on 143 shell characters. Wagner's (2002) analysis suggests that the compositions of the pleurotomariidan families from these periods are polyphyletic and that the slit-band gastropods (Pleurotomaariida) as classified by Knight et al. (1960) belong to the clades "Euomphalinaes" and "Murchisoniinaes". To date, no phylogenetic analysis of Pleurotomariida encompassing Devonian and younger species has been attempted. Bandel (2009) revised the nacreous slit-band gastropods from the highly diverse St. Cassian Formation and reported 12 families, including five new families. Bandel (2009) used shell morphology and early ontogenetic shell characters in diagnoses of the new families but did not compare these new families with the Palaeozoic ones in detail.

Pleurotomariidae is the only extant family within Pleurotomariida, which first appeared during the Middle Triassic and has become the only family representing the group since the Jurassic (e.g., Tracey et al. 1993). Therefore, the family Pleurotomariidae is the most studied group among Pleurotomariida (e.g., Monari & Gatto 2013, 2014). Harasewych & Kiel (2007) provided an overview regarding the geological ranges of pleurotomariid genera and the most important shell characters of the family Pleurotomariidae including four living genera. Harasewych et al. (1997) published the first molecular phylogeny of living members of the family Pleurotomariidae.

1.4. Diversity

Pleurotomariida first appeared in the fossil record during the Late Cambrian–Early Ordovician (e.g., Knight et al. 1960; Tracey et al. 1993; Wagner 2002). Frýda & Rohr (2004) showed that

the diversity of slit-shells rose significantly during the Ordovician radiation. This radiation continued (Hickmann 1984, Fig. 4) and Pleurotomariida became the most diversified gastropod group in the Middle and Late Palaeozoic (Erwin 1990, Fig. 5). According to Erwin's (1990) study of gastropod diversity from the late Palaeozoic to early Mesozoic, taxonomic affinity, clade history, generic age and gross morphology did not determine the survival of a clade. Erwin (1990) showed that Pleurotomariida diversified during the Early Permian, their diversity declined drastically during the end-Permian extinction but rebounded thereafter (Fig. 4). After their peak in diversity during the middle to late Palaeozoic their diversity continuously decreased especially after several major mass extinction events, and only four genera belonging to the family Pleurotomariidae survived until today (Hickman 1984, Harasewych 2002; Fig. 4).

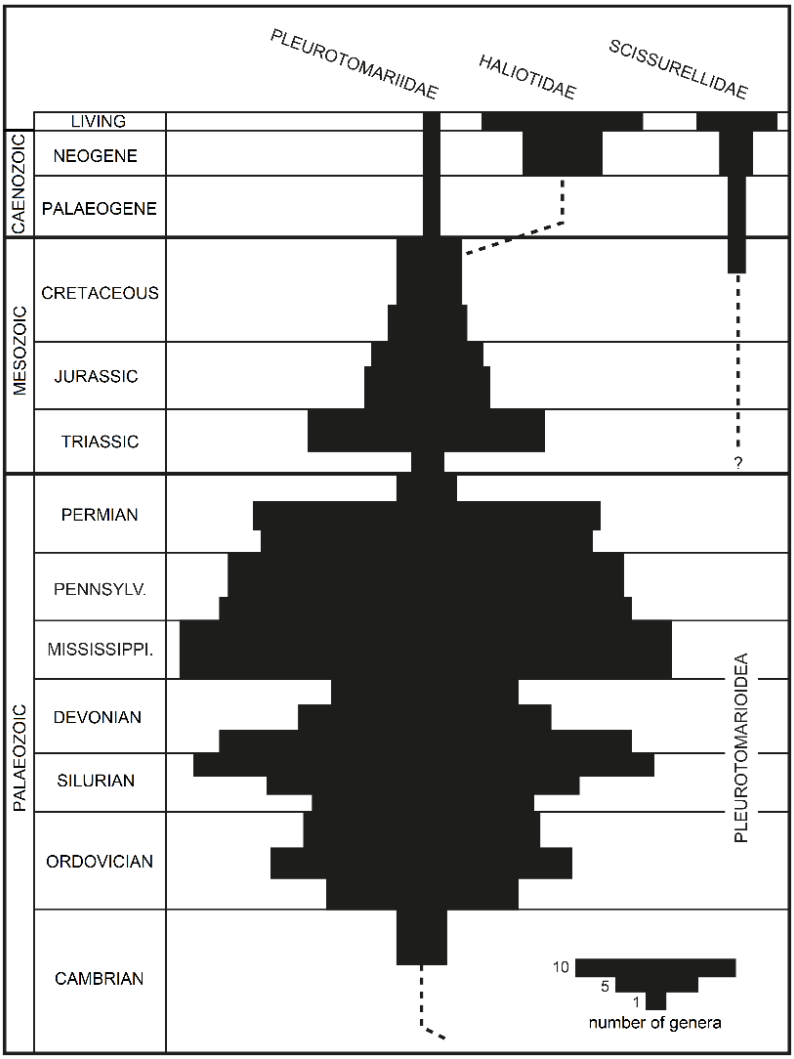

Figure 4: Spindle diagram showing the generic diversity of Pleurotomariida based on the classification by Knight et al. (1960) (redrawn after Hickman 1984).

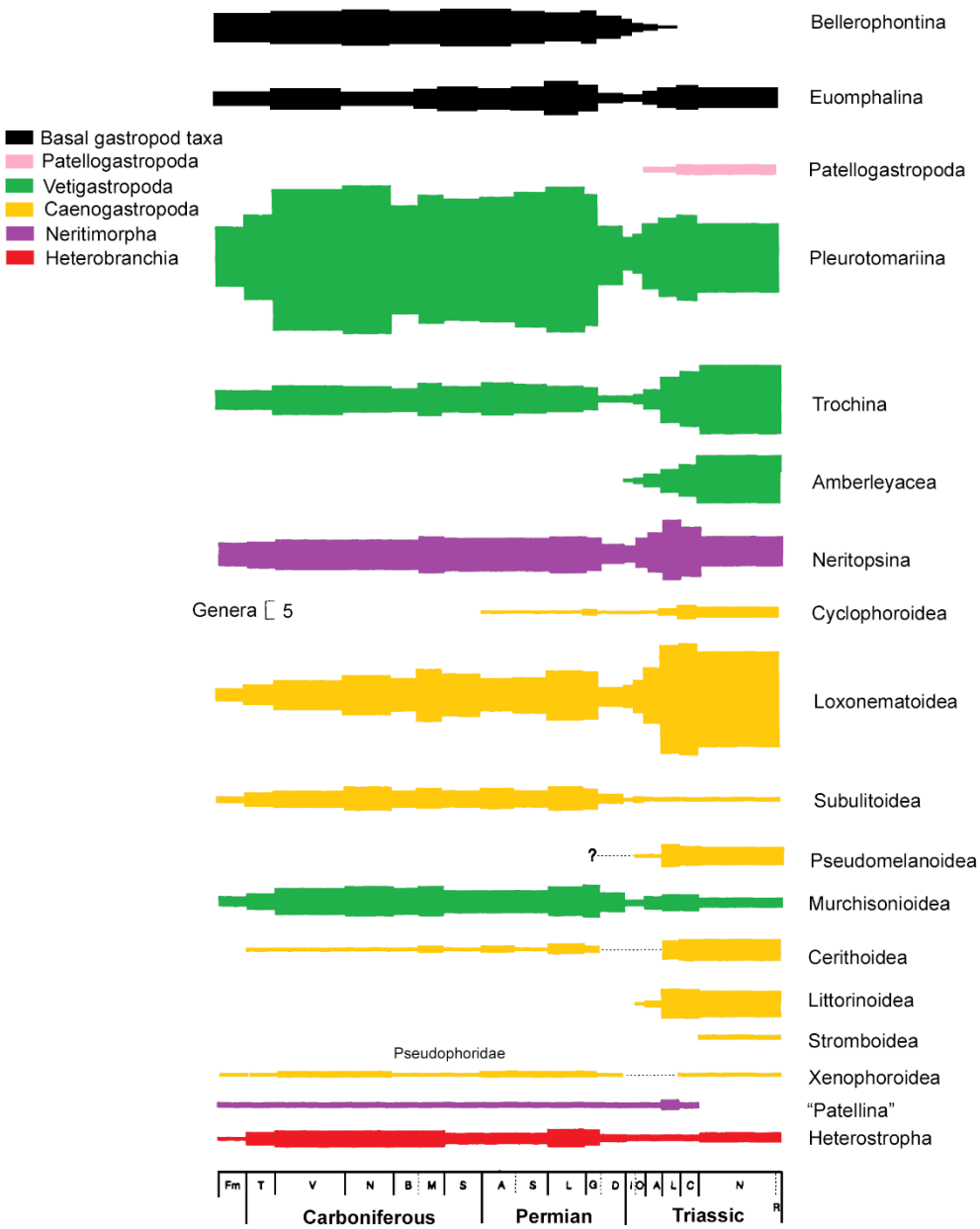

Figure 5: Spindle diagram showing the generic diversity of all gastropod groups from the Famennian (Devonian, Middle Palaeozoic) to the Rhaetian (Triassic, Early Mesozoic) (modified after Erwin 1990). Each spindle is colored according to the subclass identity of the gastropod groups.

The diversity of modern Pleurotomariida is in sharp contrast with the general expansion of Gastropoda (Fig. 1) and with the diversity of Pleurotomariida in the fossil record, which has its acme during the middle and late Palaeozoic but was also relatively high during the Triassic (Fig. 5). Bandel's (2009) study of Pleurotomariida from the Late Triassic St. Cassian Formation

indicates that the diversity of slit-band gastropods was still high compared to their diversity in any modern fauna which is corroborated herein.

Although the extinct Pleurotomariida were occupying shallow marine environments, the recent representatives of the group are restricted to deep water from the Cretaceous onwards (Harasewych 2002). Harasewych (2002) explained the shift in depth range of the group through time by "onshore-innovation, offshore-archaic" model of Jablonski et al. (1983) and suggested that the diversity decline of the family was due to the "Mesozoic Marine Revolution" (Vermeij 1977). Harasewych (2002) also discussed survival ability of the recent Pleurotomariidae from high incidence of predation inferred by multiple repaired shell breaks, and their ability to secrete large quantity of repellent against predators. Studies of shell repair frequencies in Palaeozoic and Jurassic Pleurotomariida suggest an increase in predation density through time and increasing rate of survival (Lindström 2003; Lindström & Peel 2005, 2010).

Unlike the general trend of fast recovery after extinctions in gastropods, Pleurotomariida were consistently downsized by the end-Permian, end-Triassic and end-Cretaceous mass extinctions. Pleurotomariida thus represent a group with a great evolutionary history but with very few modern representatives.

1.5. Aims and scope of this dissertation

The aims of this thesis are to describe the diversity of Pleurotomariida in the Earth history, improving their classification, reconstructing their phylogeny with modern quantitative methods and analyzing the decline of Pleurotomariida over time which is in sharp contrast with the general expansion of Gastropoda. The special attention is given to the Late Palaeozoic–Early Mesozoic history of the group, which is seemingly the most significant time interval in shaping the evolutionary fate of the group.

The early ontogeny (especially protoconch) gained importance in classification in the last decades (e.g., Frýda et al. 2008). However, the early ontogeny and protoconch of many pleurotomariidan taxa have been unknown. Many new pleurotomariidan genera and families have been reported from the Triassic during the last decades (e.g., Bandel 2009). However, the type specimens of these taxa (type species and type genera) have not been re-studied with modern methods since their first description over a century ago. The aim of the present work is to document the specimens from the Carboniferous to Triassic with modern imaging techniques (macro photography, SEM) in great detail including their early ontogeny,

improving the descriptions, diagnoses and the classification of taxa with a consistent descriptive terminology. Based on this, the taxonomy and classification of the group is revised.

Previous estimates of pleurotomariidan diversity are based on old compilations, given on generic level and in lower stratigraphical resolution (e.g., Hickman 1984; Fig. 4). The goal of the present work is to analyze the diversity change of the group on the species and assemblage level based on a new classification and phylogeny.

Relative abundance data on assemblage level is important to understand whether a group is ecologically important component within a fauna. Relative abundance data of Pleurotomariida within quantitatively collected samples are available only from few studies (e.g., Kues & Batten 2001). One aim is to assess if the diversity of the group in the fossil record was mirrored by their abundance in fossil assemblages and if the diversity is biased by sampling methods.

The evolutionary relationships between pleurotomariidan taxa are largely based on taxonomic studies and experts' opinions. A comprehensive phylogenetic analysis has never been conducted with taxa ranging from the Palaeozoic to Recent. Another aim of the present thesis is to reconstruct the phylogeny of the group with modern methods, which forms the basis for future studies that could include more taxa and also integrate results from molecular data.

1.6. Overview of manuscripts

In chapter two (Karapunar et al. 2022a), Carboniferous Pleurotomariida from several Pennsylvanian marine shale units of the North American midcontinent are studied. A total of 38 species, representing 19 genera including 10 new species, one new genus and one new subgenus are described. Early ontogenetic shells of the following globally distributed Upper Plalaeozoic taxa were documented: *Glabrocingulum* (*Glabrocingulum*), *Glabrocingulum* (*Ananias*), *Worthenia*, *Paragoniozona*, *Phymatopleura*, *Peruvispira*, *Baylea*, *Shansiella*, *Spiroscala*, *Platyzona*. Planktotrophic protoconchs were found in *Peruvispira* and *Platyzona*, hence they were excluded from Pleurotomariida (Vetigastropoda) and placed in Caenogastropoda. In this study, both surface and bulk collection methods are used as quantitative sampling methods and a total of 6,300 specimens larger than 0.5 mm in size are analyzed. In the samples, Pleurotomariida represent the most diverse and abundant group at two different localities, suggesting that they were ecologically dominant in the Carboniferous shallow water habitats. However, their relative abundance depends significantly on the sampling method. Pleurotomariida are more abundant in surface samples than bulk samples

and in larger size fractions in bulk samples. Repaired shell scars are found in individuals as small as 1 mm in size, further indicates the predatory pressure was present beginning from the benthic settlement.

In chapter three (Ketwetsuriya et al. 2020), a new gastropod fauna from the Middle Permian Khao Khad Formation of Thailand is studied. A total of 44 gastropod species representing 30 genera including 13 new species (five Pleurotomariida) and one new pleurotomariidan genus are described. Although the collection contained only 221 specimens, it appeared to be the most diverse gastropod assemblage reported from the Permian of Thailand so far. Vetigastropoda was the largest component of the gastropod fauna, with Pleurotomariida being the most diverse group within Vetigastropoda.

Chapter four (Karapunar et al. 2022b) presents the study on the oldest gastropod collection from the Permian of Thailand, which was briefly mentioned in one work on the brachiopod fauna of that sample (Grant 1976) but had never been described. Previously, the collection was reported to be dominated by Pleurotomariida. However, the systematic investigation reveals only two taxa. The assemblage is strongly dominated (almost monospecific) by *Peruvispira*, a genus which is no longer regarded as Pleurotomariida due to the presence of a protoconch reflecting planktotrophic larval development.

Chapter five (Karapunar & Nützel 2021) presents the results of an extensive taxonomic study of species from the Upper Triassic St. Cassian Formation that were previously identified as Pleurotomariida. The St. Cassian Formation yields nearly half of the known Triassic pleurotomariidan genera including the type genera of the Triassic families Kittlidiscidae, Zygitidae, Schizogoniidae, Lancedellidae, Stuorellidae, Wortheniellidae, Rhaphistomellidae, Temnotropidae. Type specimens scattered over European natural history collections. The majority of the types have never been studied after their original descriptions more than a century ago. A total of 106 lectotypes are designated and figured, 67 species are described including 9 new genera and 8 new species. As a result of the revision, 77 pleurotomariidan species are identified in the St. Cassian Fm., none belonging to genera that were present in the Palaeozoic. The description of all taxa and diagnoses are improved and the composition of genera and families is revised. The Triassic diversity of Pleurotomariida and four gastropod subclasses are analyzed with a global Triassic gastropod species database (comprising 2,177 species). Furthermore, the diversity changes of Pleurotomariida and Gastropoda through the Permian–Triassic interval is analyzed by using this global Triassic database and the Paleobiology database (for Permian data). The analyses indicate that the recovery of

Pleurotomariida during the Triassic was sluggish compared to other gastropod groups, especially caenogastropods and they never recovered fully (i.e., reached the diversity they had before the end-Permian mass extinction event). The analysis further indicates an interruption of recovery within the Carnian, likely during the Carnian Pluvial Episode.

Chapter six (Karapunar & Nützel in prep.) presents the first comprehensive phylogenetic analyses of Pleurotomariida with Parsimony and Bayesian (Fossilized Birth Death (FBD) model) methods. The analyses are performed with a character matrix of 93 morphological shell characters and of 109 pleurotomariidan species representing 80 genera ranging from the Early Ordovician to the Recent. Both methods reconstruct similar within-clade relationship, but the relationship of clades to each other changes drastically among the Bayesian and parsimonious trees. Since FBD method incorporates the stratigraphic information in tree reconstruction, it reconstructs trees that are more congruent with stratigraphy than the trees reconstructed with the Parsimony method. According to the Bayesian (FBD) phylogeny, Pleurotomariida split into three lineages during the Devonian and two lineages survived the end-Permian mass extinction (Wortheniellini and Pleurotomariini). Although Wortheniellini showed a higher proliferation during the Triassic, only Pleurotomariini could survive until today. This indicates that diversification dynamics of Pleurotomariida did not play an important role in resilience to mass extinctions. FBD phylogeny further suggests that the lineages with only Triassic fossil record evolved during the Permian.

Author contributions

Chapter 2

Karapunar, B., Nützel, A., Seuss, B., & Mapes, R. H. (2022a). Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA. *Papers in Palaeontology*, 8(2), 1–95 (e1417), https://doi.org/10.1002/spp2.1417.

BK and AN conceptualized the study. AN, BS and MRH collected the material. **BK** sorted, identified and described the specimens, drafted the manuscript, prepared the figures, made the diversity analyses. **BK**, AN and BS revised the manuscript. MRH revised the introduction, locality information and discussion. AN and BS acquired the funding.

Contribution percentage: **BK 70%,** AN 20%, BS 5%, MRH 5%.

Chapter 3

Ketwetsuriya, C., **Karapunar, B.**, Charoentitirat, T., & Nützel, A. (2020). Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa*, 4766(1), 1–47, https://doi.org/10.11646/zootaxa.4766.1.1.

CK and AN conceptualized the study. CK collected, sorted, identified and described the specimens, drafted the manuscript, conducted the analyses and prepared the figures. **BK** identified and described the vetigastropods (including Pleurotomariida). TC identified the fusulinids for age determination. CK, **BK** and AN revised the whole manuscript. AN acquired the funding for the field work.

Contribution percentage: CK 70%, **BK 15%**, TC 5%, AN 10%.

Chapter 4

Karapunar, B., Ketwetsuriya, C., & Nützel, A. (2022b). A low-diversity *Peruvispira*-dominated gastropod assemblage from the Permian Ratburi Group of Central Thailand. *Alcheringa*, 1–9, https://doi.org/10.1080/03115518.2022.2050814

BK conceptualized the study, identified and described the specimens, drafted the manuscript. AN arranged the loan of the specimens. CK contributed writing of the introduction and geological setting chapters, prepared the figures and measured the specimens. **BK**, CK and AN revised the manuscript. AN acquired the funding.

Contribution percentage: **BK 85%**, CK 10%, AN 5%.

Chapter 5

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

BK and AN conceptualized the study, conducted museum work, took photographs. **BK** identified and described the specimens, drafted the manuscript, prepared the figures, made the diversity analyses, processed the samples. AN compiled the global Triassic species database, wrote some passages. **BK** made higher classification of the genera in the database for the analysis. **BK** and AN revised the manuscript. AN acquired the funding, arranged the museum visits and the field trip.

Contribution percentage: **BK 80%,** AN 20%.

Chapter 6

Karapunar, B., & Nützel, A. (in prep.) Estimation of phylogeny of Pleurotomariida (Gastropoda) by using Parsimony and Bayesian methods.

BK conceptualized the study, drafted the manuscript, made the analyses, prepared the figures. **BK** and AN revised the manuscript. AN acquired the funding.

Contribution percentage: **BK 95%,** AN 5%.

1.7. References

Bandel, K. (1982). Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies, 7*, 1–198.

Bandel, K., & Geldmacher, W. (1996). The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda. *Freiberger Forschungshefte, C, 464*, 1–71.

Bouchet, P., Frýda, J., Hausdorf, B., Ponder, W. F., Valdés, Á., & Warén, A. (2005). Working classification of the Gastropoda. In: P. Bouchet, P. & J.–P. Rocroi (eds.). Classification and nomenclator of gastropod families. *Malacologia, 47*, 1–397.

Bouchet, P., Lozouet, P., Maestrati, P., & Heros, V. (2002). Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society, 75*, 421–436.

Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M., & Strong, E. E. (2017). Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia, 61*(1–2), 1–526.

Cunha, T. J., Reimer, J. D., & Giribet, G. (2021). Investigating sources of conflict in deep phylogenomics of vetigastropod snails. *Systematic Biology*, 1–14.

Erwin, D. H. (1990). Carboniferous-Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. *Paleobiology, 16*, 187–203.

Frýda, J., Nützel, A., & Wagner, P. J. (2008). Paleozoic Gastropoda. In W. F. Ponder & D. R. Lindberg (Eds.), *Phylogeny and Evolution of the Mollusca* (Vol. 309, pp. 239–270). California: University of California Press.

Frýda, J., & Rohr, D. M. (2004). Gastropods. In B. D. Webby & M. L. Droser (Eds.), *The great Ordovician biodiversification event* (pp. 184–195). New York: Columbia University Press.

Geiger, D. L., & Thacker, C. E. (2005). Molecular phylogeny of Vetigastropoda reveals non-monophyletic Scissurellidae, Trochoidea, and Fissurelloidea. *Molluscan Research, 25*(1), 47–55.

Giribet, G., & Edgecombe, G. D. (2020). *The invertebrate tree of life*: Princeton University Press.

Grant, R. E. (1976). Permian brachiopods from southern Thailand. *The Paleontological Society Memoir, 50*(S9), 1–269.

Harasewych, M., Adamkewicz, S. L., Blake, J. A., Saudek, D., Spriggs, T., & Bult, C. J. (1997). Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome c oxidase I sequences. *Molecular Marine Biology and Biotechnology, 6*, 1–20.

Harasewych, M. G. (2002). Pleurotomarioidean gastropods. *Advances in Marine Biology, 42*, 237–294.

Harasewych, M. G., & Kiel, S. (2007). Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagascar. *The Nautilus, 121*, 76–89.

Haszprunar, G. (1988). On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies, 54*, 367–441.

Hickman, C. S. (1984). *Pleurotomaria*: Pedigreed perseverance? In N. Eldredge, Stanley, S. M. (Ed.), *Living Fossils* (pp. 225–231). New York, Berlin, Heidelberg, Tokyo: Springer.

Jablonski, D., Sepkoski, J. J., Bottjer, D. J., & Sheehan, P. M. (1983). Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science, 222*(4628), 1123–1125.

Knight, J. B., Cox, L. R., Keen, A. M., Batten, R. L., Yochelson, E. L., & Robertson, R. (1960). Systematic descriptions. In R. C. Moore (Ed.), *Treatise on Invertebrate Paleontology, Part 1, Mollusca 1* (pp. I169–I310). Kansas: Geological Society of America and University of Kansas Press.

Koken, E. (1889). Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband, 6*, 440–463.

Koken, E., & Perner, J. (1925). Die Gastropoden des Baltischen Untersilurs. *Mémoires de L'Ácadémie des Sciences de Russie, 37, No. 1*, 1–186.

Kues, B. S., & Batten, R. L. (2001). Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico. *Journal of Paleontology, 75, Supplement to No 1*, 1–95.

Lindström, A. (2003). Shell breakage in two pleurotomarioid gastropods from the Upper Carboniferous of Texas, and its relation to shell morphology. *GFF, 125*(1), 39–46. doi:10.1080/11035890301251039

Lindström, A., & Peel, J. S. (2005). Repaired injuries and shell form in some Palaeozoic pleurotomarioid gastropods. *Bulletin of Geosciences, 85*, 541–550.

Lindström, A., & Peel, J. S. (2010). Shell repair and shell form in Jurassic pleurotomarioid gastropods from England. *Bulletin of Geosciences, 85(4)*, 541–550.

MolluscaBase (2022). https://www.molluscabase.org.

Monari, S., & Gatto, R. (2013). *Pleurotomaria* Defrance, 1826 (Gastropoda, Mollusca) from the lower Bajocian (Middle Jurassic) sediments of Luxembourg, with considerations on its systematics, evolution and palaeobiogeographical history. *Palaentology, 56*, 751–781.

Monari, S., & Gatto, R. (2014). The genus *Leptomaria* E. Eudes-Deslongchamps, 1864 (Gastropoda, Pleurotomariidae) from the Early Bajocian of Luxembourg: systematics and paleobiogeography. *Historical Biology, 26*, 810–826.

Nützel, A. (2014). Larval ecology and morphology in fossil gastropods. *Palaeontology, 57*, 479–503.

Payne, J. L., & Clapham, M. E. (2012). End-Permian Mass Extinction in the Oceans: An Ancient Analog for the Twenty-First Century? *Annual Review of Earth and Planetary Sciences, 40*(1), 89–111. doi:10.1146/annurev-earth-042711-105329

Ponder, W. F., & Lindberg, D. R. (1997). Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society, 119*, 83–265.

Ponder, W. F., Lindberg, D. R., & Ponder, J. M. (2020). *Biology and Evolution of the Mollusca. Vol. 1–2*. Boca Raton: CRC Press.

Sepkoski, J. J. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleozoic, 7*, 36–53.

Thiele, J. H. (1929-1931). *Handbuch der systematischen Weichtierkunde*. Jena: Gustav Fischer.

Tracey, S., Todd, J. A., & Erwin, D. H. (1993). Mollusca: Gastropoda. In M. J. Benton (Ed.), *The Fossil Record 2* (pp. 131–167). Cambridge: Chapman & Hall.

Vermeij, G. J. (1977). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology, 3*, 245–258.

Voltzow, J., Morris, P. J., & Linsley, R. M. (2004). Anatomy of and patterns of water currents through the mantle cavities of pleurotomariid gastropods. *Journal of Morphology, 262*(2), 659–666.

Wagner, P. J. (2002). Phylogenetic relationships of the earliest anisostrophically coiled gastropods. *Smithsonian Contributions to Paleobiology, 88*, 1–152.

Wenz, W. (1938–1944). Gastropoda. Teil I: Allgemeiner Teil und Prosobranchia *Handbuch der Paläozoologie* (pp. xii + 1639). Berlin: Gebrüder Borntraeger.

Williams, S., & Ozawa, T. (2006). Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics and Evolution, 39*(1), 33–51.

Yonge, C. M. (1947). The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 232*(591), 443–518.

Yoon, S. H., & Kim, W. (2005). Phylogenetic relationships among six vetigastropod subgroups (Mollusca, Gastropoda) based on 18S rDNA sequences. *Molecules and Cells, 19*(2), 283–288.

Zapata, F., Wilson, N. G., Howison, M., Andrade, S. C., Jörger, K. M., Schrödl, M., Goetz, F. E., Giribet, G. & Dunn, C. W. (2014). Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. *Proceedings of the Royal Society B: Biological Sciences, 281*(1794), 20141739.

CHAPTER 2

Karapunar, B., Nützel, A., Seuss, B., & Mapes, R. H. (in press). Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA. *Papers in Palaeontology*, 8(2), 1–95 (e1417), https://doi.org/10.1002/spp2.1417.

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Taxonomy and diversity of slit-band gastropods (Order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA

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Abstract: Pleurotomariida have the longest fossil record among living gastropods and are diverse and abundant in the middle and upper Palaeozoic. Its traditional classification is based on adult shell characters. The early shell morphology has been largely unknown. We describe exceptionally well-preserved Pleurotomariida from the Pennsylvanian marine shales of Texas, Oklahoma, Kansas and Ohio. In total, 38 species representing 19 genera are described, including 10 new species, one new genus and one new subgenus: *Eirlysella buckhornensis* gen. et sp. nov., *Shansiella* (*Oklahomaella*) *globilineata* subgen. et sp. nov., *Phymatopleura girtyi*, *Phymatopleura conica*, *Worthenia* (*Yochelsonospira*) *kuesi*, *Dictyotomaria turrisbabel*, *Paragoniozona yanceyi*, *Spiroscala shwedagoniformis*, *Peruvispira oklahomaensis*, *Baylea tenera*. Replacement names are *Paragoniozona ornata* nom. nov. (for *Pleurotomaria aspera* Girty), *Spiroscala quasipulchra* nom. nov. (for *Euconospira pulchra* Batten). The early ontogenetic shells including protoconchs and early teleoconchs are reported in detail for the first time for most taxa. Most species have a protoconch of one whorl as that of living Vetigastropoda. Planktotrophic protoconchs (multi-whorled larval shells with sinusigera) are reported for *Platyzona* and *Peruvispira*; they are therefore placed in the family Goniasmatidae (Caenogastropoda). Repaired shell scars were found in juvenile Pleurotomariida specimens (*c.* 1 mm), suggesting exposure to predation from an early stage of ontogeny. Pleurotomariida are strongly dominant in surface samples of the Finis Shale (Texas) but in bulk samples using fine mesh-sizes, dominance is much less pronounced, indicating a change in clade proportion depending on sampling method. The taxonomic richness and abundance of Pleurotomariida seen in these Carboniferous shales have not been reported from post-Triassic formations.

Key words: Vetigastropoda, Caenogastropoda, Carboniferous, Pennsylvanian, diversity, predation.

THIS contribution presents descriptions and illustrations of exceptionally well-preserved Pennsylvanian Pleurotomariida (Gastropoda) from the USA. Several new taxa are proposed and others are documented showing details not known before. Special emphasis is put on the morphology of early ontogenetic shells that has rarely been documented hitherto. This manuscript increases the number of known shell characters and thus improves taxonomic and systematic assignments. Moreover, the study facilitates future phylogenetic analyses of the Pleurotomariida that played a pivotal role in gastropod evolution. Based on the original illustrations and descriptions, we propose additional new generic assignments for several species (Appendix 1).

Due to an almost steady increase in diversity and a resistance to extinction pressure (Erwin & Signor 1990) gastropods became one of the most diverse animal clades during the Phanerozoic. However, this overall evolutionary success (manifested as diversity increase) masks major shifts within the mollusc class Gastropoda. Once highly diverse and dominant groups are either extinct (e.g. bellerophontids) or have only few living representatives; the latter is the case for the order Pleurotomariida. According to the fossil record, Pleurotomariida first appeared during the late Cambrian, became the dominant and most diversified gastropod group in the middle and late Palaeozoic and dominated shallow water communities during that time (Hickman 1984). However,

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Pleurotomariida are represented by only four genera and *c.* 40 species in Recent seas (WoRMS; https://www.marinespecies.org/; accessed 20 February 2021) and none of those occurs in a shallow marine environment (Harasewych 2002).

The pleurotomariid shell is characterized by the presence of a deep sinus or a slit in the outer lip (labrum). The shells are commonly trochiform to turbiniform and occasionally planispiral or high-spired. As other members of Vetigastropoda, they have non-planktotrophic larval development with a protoconch consisting of approximately one whorl; the so-called trochoid condition (e.g. Bandel 1982; Haszprunar 1993; Kaim 2004; Geiger *et al.* 2008; Nützel 2014*a*). However, there are some reports of Palaeozoic slit-bearing gastropods having multi-whorled larval shells reflecting planktotrophic larval development (for a review and discussion see: Nützel & Pan 2005; Nützel 2014*a*). Pleurotomariida have an inner nacreous shell layer (Batten 1972*a*; Bandel 1991; Bandel & Geldmacher 1996) as is also the case in several other vetigastropods (Geiger *et al.* 2008). Protoconchs and shell microstructures have been reported for only a few Palaeozoic Pleurotomariida and new data are added by the present contribution.

Anatomically, the few living pleurotomarioids have a rhipidoglossan type radula (shared with most other vetigastropods and neritimorphs) and paired mantle organs including two bipectinate gills, osphradia and hypobranchial glands (e.g. Yonge 1947; Hickman 1984; Haszprunar 1988). The paired organs are arranged bilaterally symmetrical on either side of the shell slit (or selenizone) and anal opening which corresponds to the sagittal plane (e.g. Harasewych 2002). This organization has been considered ancestral in Gastropoda for a long time but has been questioned by Haszprunar (1988) and Ponder & Lindberg (1997). The study of living Pleurotomariida revealed that these animals comprise a mosaic of primitive and highly derived characters as is usually the case in 'living fossils' (Harasewych 2002).

The shell slit of Pleurotomariida facilitates the ventilation of the mantle cavity. It expels water (exhalant current) and carries out faeces (Yonge 1947). It has long been assumed that the water inflow into the mantle cavity is through the aperture. However, Voltzow *et al.* (2004) showed that both inhalant and exhalant currents pass through the slit in living pleurotomariids (Yonge (1947) did not study living individuals). The inhalant current passes through the adapertural portion of the slit and the exhalant current through its abapertural portion. Whether this is the case in all Pleurotomariida including fossil ones remains an open question. During shell growth the slit is progressively closed by crescent-shaped growth increments forming the so-called selenizone (slit-band). In recent and many fossil pleurotomariids, the selenizone is situated more or less at the middle of the labrum which would be congruent with the symmetrical organization of the mantle cavity. This position of the slit also suggests paired, symmetrical organs in the mantle cavity in the majority of the fossil Pleurotomariida. However, in quite a number of fossil genera, the position of selenizone deviates from the middle position (e.g. close to the adapical or abapical suture) suggesting that not all of them had this condition (Hickman 1998). Instead, such taxa may have had a much more asymmetrical arrangement of the mantel cavity and its organs.

Early classifications within Pleurotomariida were presented by Koken (1889), Koken & Perner (1925), Thiele (1929–1931), Wenz (1938–1944) and Knight *et al.* (1960). Traditionally, Pleurotomariida is seen as a basal group (early offshoot) within Gastropoda and within the former Archaeogastropoda (Thiele 1929–1931; Wenz 1938–1944; Yonge 1947). More recent phylogenetic analyses and classifications place Pleurotomariida within Vetigastropoda (the bulk of the former Archaeogastropoda) which is the most diverse clade of basal gastropods (Haszprunar 1988; Ponder & Lindberg 1997; Bouchet *et al.* 2005, 2017). However, the position of Pleurotomariida within Vetigastropoda is still a matter of discussion. In phylogenetic analyses using morphological data (anatomy and few shell characters), Pleurotomarioidea are suggested to be derived within Vetigastropoda (Poder & Lindberg 1997; Sasaki 1998). However, molecular studies on living vetigastropods find a more basal position within Gastropoda and Vetigastropoda (Harasewych *et al.* 1997; Geiger & Thacker 2005; Yoon & Kim 2005; Williams & Ozawa 2006; Zapata *et al.* 2014; Cunha *et al.* 2021), which is more consistent with the fossil record that indicates a greater geological age for the group. Aktipis & Giribet (2012) also found Pleurotomarioidea in a basal position but outside the Vetigastropoda. Thus, molecular phylogenies corroborate earlier suggestions that Pleurotomariida are a basal clade of Gastropoda. The classification of Pleurotomarioidea and other groups by Knight *et al.* (1960) was modified by Tracey *et al.* (1993) and Bouchet *et al.* (2005, 2017). Bandel & Geldmacher (1996) introduced the name Selenimorpha for slit-bearing Vetigastropoda and presented a phylogenetic tree displaying a polytomy of nearly all major vetigastropods dating back to the Ordovician. Frýda & Rohr (2004) described the diversity rise of slit-shells as part of the Ordovician radiation. Wagner (2002) provided a comprehensive phylogenetic analysis of Late Cambrian to Silurian anisostrophically coiled gastropods based on 143 shell characters. This analysis suggested polyphyly of the slit-band gastropods from these periods previously assigned to Pleurotomarioidea by Knight *et al.* (1960). Wagner (2002) suggested that the studied slit-band gastropods were among the clades 'Euomphalinaes' and

'Murchisoniinaes'. To date, no encompassing phylogenetic analysis of Pleurotomariida including Devonian and younger species has been attempted. Bandel (2009) revised the nacreous slit-band gastropods from the highly diverse St Cassian Formation from which he recognized the presence of 12 families, five of them defined as new. The author used size, shape and characters of the early ontogenetic shell to recognize new families but comparisons with Palaeozoic slit-band gastropods was not a focus of this work. Karapunar & Nützel (2021) revised all St Cassian species previously assigned to Pleurotomariida and reported that none of the Palaeozoic genera were present in the Triassic St Cassian Formation.

Slit- or notch-bearing gastropods can also be found among other vetigastropods such as in the orders Seguenziida and Lepetellida as well as in the extant superfamilies Fissurelloidea and Scissurelloidea (little slit shells) (e.g. Knight *et al.* 1960). However, according to the current state of knowledge, Scissurelloidea are not closely related to Pleurotomariida (Geiger 2012, fig. 5) and thus the presence of a shell slit would be either paraphyletic or polyphyletic.

Pleurotomariida encompasses most gastropods with a slit in the outer lip of the shell and the group consists of 30 families, which are all extinct with the exception of the family Pleurotomariidae (Bouchet *et al.* 2017).

Pleurotomariida have the most extended fossil record among the living gastropod groups with their oldest occurrences in the Cambrian (e.g. *Taeniospira*; Knight *et al.* 1960; Batten 1967; see also Wagner 2002) and Ordovician (e.g. *Clathrospira*; Horný 1997; Wagner 2002). Pleurotomariida were the most diversified gastropod group in the middle and late Palaeozoic and commonly the dominant gastropod group in shallow water communities during that time (e.g. Hickman 1984; Erwin 1990; Batten 1995; Kues & Batten 2001). The group reached its peak generic standing diversity in the Carboniferous based on the systematic scheme proposed by Knight *et al.* (1960) (Hickman 1984). They declined after their middle to late Palaeozoic acme, and suffered heavily in the end-Permian mass extinction. Today they are represented by only four genera belonging to the family Pleurotomariidae and are restricted to deep water (>200 m) (e.g. Harasewych 2002). The marginal diversity of modern Pleurotomariida is in sharp contrast to the high fossil diversity particularly during the middle and late Palaeozoic, as reflected by a high number of genera and species during the Devonian and Permian periods (Hickman 1984; Harasewych 2002). Their diversity remained relatively high during the Triassic (Karapunar & Nützel 2021). The diversity of Pleurotomariida has diminished markedly several times: during the end-Devonian, end-Permian, end-Triassic and end-Cretaceous mass extinctions. Although the amount of the decline of Pleurotomariida is known and standing generic diversity has been presented at the period scale (Hickman 1984; Harasewych 2002), a finer resolution is desirable and required; also these data have largely been uncritically extracted from the literature (mostly the *Treatise on Invertebrate Palaeontology*) and are not based on a consistent taxonomic phylogenetic approach. According to Erwin's (1990) study of gastropod diversity at the end-Permian extinction event, in general, taxonomic affinity, previous clade history, generic age and gross morphology did not determine survival probability. He showed that Pleurotomariida diversified during the early Permian but were heavily hit by the following extinction. Erwin (1993) noted that Pleurotomariida declined drastically during the extinction but rebounded quickly thereafter. Karapunar & Nützel (2021) showed that the recovery of the group was slower compared to other gastropod groups in the Triassic. As a result, their species diversity decreased from 26% during the Permian to 18% during the Triassic.

Pleurotomariidae, the only extant family within Pleurotomariida, first appeared during the Middle Triassic and has become the only family representing the group since the Jurassic (e.g. Tracey *et al.* 1993). Therefore, the family Pleurotomariidae is the most studied group among Pleurotomariida. Harasewych *et al.* (1997) published the first molecular study of phylogenetic relationships within Pleurotomariidae. Harasewych & Kiel (2007) gave an overview of the geological ranges and the most important shell characters of the family Pleurotomariidae including its four living genera. They discussed the significance of some shell characters such as umbilici, whorl outline and the position of the slit. Bose *et al.* (2021) evaluated the shell characters that were traditionally used in the classification of the Cenozoic Pleurotomariidae and provided a comprehensive list of Cenozoic pleurotomariids. Harasewych (2002) explained the shift of shallow water pleurotomariids to the deep sea from the Cretaceous onwards by the 'onshore-innovation, offshore-archaic' model of Jablonski *et al.* (1983) and suggested that the decline of the family was a phenomenon of the 'Mesozoic Marine Revolution' (Vermeij 1977). He also discussed the high predation density and the ability to survive based on multiple repaired shell breakages in recent Pleurotomariidae and their ability to secrete a large quantity of repellent against predators. Studies of shell repair in Palaeozoic and Jurassic Pleurotomariida suggest an increase in predation frequency through time and have related the survival rate to the shell form and the length of the slit (Lindström 2003; Lindström & Peel 2005, 2010). Shell slits and related selenizones are not restricted to Pleurotomariida but are also present in the bilateral symmetrical Bellerophontida and high-spired Murchisoniida; some species included in the latter represent Caenogastropoda because they lack nacre and have a larval shell of the planktotrophic type (e.g. Nützel & Pan 2005). Both groups are largely restricted to the Palaeozoic. This could indicate that that selective pressure acted not only and foremost against

Pleurotomariida but against the character 'shell-slit' in general and its underlying soft body organization.

Pleurotomariida are diverse and abundant in several Pennsylvanian marine shale units of the American midcontinent and north central Texas. These deposits, poorly lithified marls, have yielded very well-preserved gastropod specimens including protoconch preservation and other fine morphological details. In some cases, shell microstructures and original aragonite are preserved but even the usual calcite pseudomorphs commonly display a superb fossil preservation. This qualifies units such as the Finis Shale of north central Texas, where many of the studied specimens come from, as a liberation Lagerstätte: a fossil occurrence from poorly lithified sediments from which fossils weather or can be extracted easily by washing and sieving (Roden *et al.* 2020).

Pennsylvanian fossiliferous shales were deposited in epicontinental shallow marine seas under a regime of glacio-eustatic cycles and some of the shale units are considered to be pro-deltaic deposits (e.g. Schindel 1982; Boardman & Heckel 1989; Forcino *et al.* 2010). The benthic fauna found with the pleurotomariid gastropods consists of other gastropods, brachiopods, bivalves and other groups. Pleurotomariid gastropods such as *Glabrocingulum* and *Worthenia* belong to the most abundant molluscan taxa in some of these fossil assemblages (pers. obs.) According to the marly, clayey lithology, this fauna consisted of soft-bottom dwellers.

Shell characters used traditionally for the classification of Pleurotomariida include shell shape, whorl outline (profile), position and curvature (concave, flush or convex) of the selenizone, surface ornament and presence/absence of an umbilicus. In recent decades, researchers who study fossil gastropods have increasingly considered the early ontogeny and especially the protoconch (e.g. Bandel *et al.* 2002), which is found to be informative in higher classification (e.g. Frýda *et al.* 2008). However, the early ontogeny of many pleurotomariid taxa, particularly those from the Palaeozoic, is unknown except for a few examples (e.g. Yoo 1994; Frýda & Blodgett 2004; Peel 2016; Mazaev 2017) because of the generally poor preservation of the Palaeozoic fossils. The excellent preservation in a few Palaeozoic formations such as the Pennsylvanian Boggy Formation from Buckhorn Asphalt Quarry and the Pennsylvanian Finis Shale, which are called impregnation Lagerstätte and liberation Lagerstätte respectively (Seuss *et al.* 2009; Roden *et al.* 2020), provide an opportunity to extract more information on the early ontogeny including the protoconch. The aim of the present study is thus to describe the pleurotomariid taxa of newly gathered collections from various Pennsylvanian outcrops in Texas, Oklahoma, Kansas and Ohio, to document the early ontogeny of the pleurotomariid taxa, which has been neglected in most previous studies, and to discuss taxonomic affinity and higher classification of the taxa in the light of new information. As outlined above this improves the taxonomy of the group and represents an important step towards future phylogenetic and diversity analysis.

MATERIAL AND METHOD

The specimens studied have been collected from the surface at several localities in Texas, Oklahoma, Kansas and Ohio (Fig. 1, Appendix 2). Quantitative surface samples were collected from the Finis Shale Member at localities TXV–200 and TXV–56 (both Texas), and from the Colony Creek Shale Member at locality TXV–46 (Texas). Additionally, bulk samples have been taken from the Finis Shale Member at localities TXV–200 and TXV–56 (both Texas) and from the Boggy Formation at the Buckhorn Asphalt Quarry (Oklahoma). The bulk samples from the Finis Shale were processed by drying, followed by immersion in an organic solvent (Stoddard solvent or mineral spirits), decanting the solvent for reuse, immersion in water which caused the sample to disaggregate into mud that was then washed through multiple sieves to extract the fossils (see Mapes & Mapes 1982). Some shale samples were disaggregated using 3% hydrogen peroxide (H_2O_2) for 1 day and wet sieved with 0.5 mm mesh size. Some samples were soaked solely in water and wet sieved with 0.2 mm mesh size. The samples from the Buckhorn Asphalt Quarry were treated by dissolving the asphalt matrix with carbon tetrachloride (CCl_4) or methylene chloride (CH_2Cl_2) in a Soxhlet extractor (Bandel *et al.* 2002; Seuss *et al.* 2009). The residue was sieved and picked. Both the bulk samples and the surface samples were picked or collected quantitatively by the authors. A few of the studied specimens were collected by Myron Thomas Sturgeon. A total of *c.* 6300 specimens (*c.* 3000 from the surface collections, *c.* 3300 from the bulk collections) have been studied. Full details of all localities mentioned in the Systematic Palaeontology section are listed in Appendix 2. The studied material is reposited in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG) in Munich.

Most of the material is calcite replacement. The studied Pleurotomariida might have an outer calcitic layer (Cox & Knight 1960), but this has not been checked. The material from the Buckhorn Asphalt deposits are partly original aragonitic preservations, having an inner layer of columellar nacre and outer complex crossed lamellar layer.

The specimens were coated with ammonium chloride (NH_4Cl) before macrophotography if not stated otherwise. All measurements (Fig. 2) were taken with a digital vernier caliper in millimetres. If a specimen was broken, the measurements are given in brackets and represent exact measurements.



FIG. 1. Conterminous map of the USA (excluding Hawaii and Alaska) showing borders of the states. The studied material was collected from the four states indicated with grey shading (Texas, Oklahoma, Kansas and Ohio).

Measurements & ratios used. **H**, height of shell; **Hlw**, height of last whorl; **Nn**, number of nodes on last whorl; **PA**, pleural angle; **RSwh**, ratio of selenizone width to whorl height (= WS/Hlw); **RSwf**, ratio of selenizone width to whorl face width (= WS/Wwf); **W**, width of shell; **Wwf**, width of whorl face (of last whorl), the shortest distance along whorl face from adapical suture to imaginary extension of suture in a spiral direction (defined as 'point X' by Cox 1960*a*, p. I116, fig. 64), some taxa develop an angulation and have an upper whorl face ('a' in Fig. 2) and a lateral or lower whorl face ('b' in Fig. 2); **Wfw**, width of first whorl; **WS**, width of selenizone (last whorl), the shortest distance along whorl face between the upper and lower boundary of selenizone.

Synoptic classification

The Systematic Palaeontology section follows the classification scheme proposed by Bouchet *et al.* (2017) and is as follows:

Subclass VETIGASTROPODA Salvini-Plawen, 1980
Order PLEUROTOMARIIDA Cox & Knight, 1960
Superfamily EOTOMARIOIDEA Wenz, 1938
Family EOTOMARIIDAE Wenz, 1938
Subfamily LIOSPIRINAE Knight, 1956
Genus *Trepospira* Ulrich *in* Ulrich & Scofield, 1897
Subfamily EOTOMARIINAE Wenz, 1938
Genus *Baylea* de Koninck, 1883
Genus *Glabrocingulum* Thomas, 1940*a*
Subgenus *Glabrocingulum* Thomas, 1940*a*

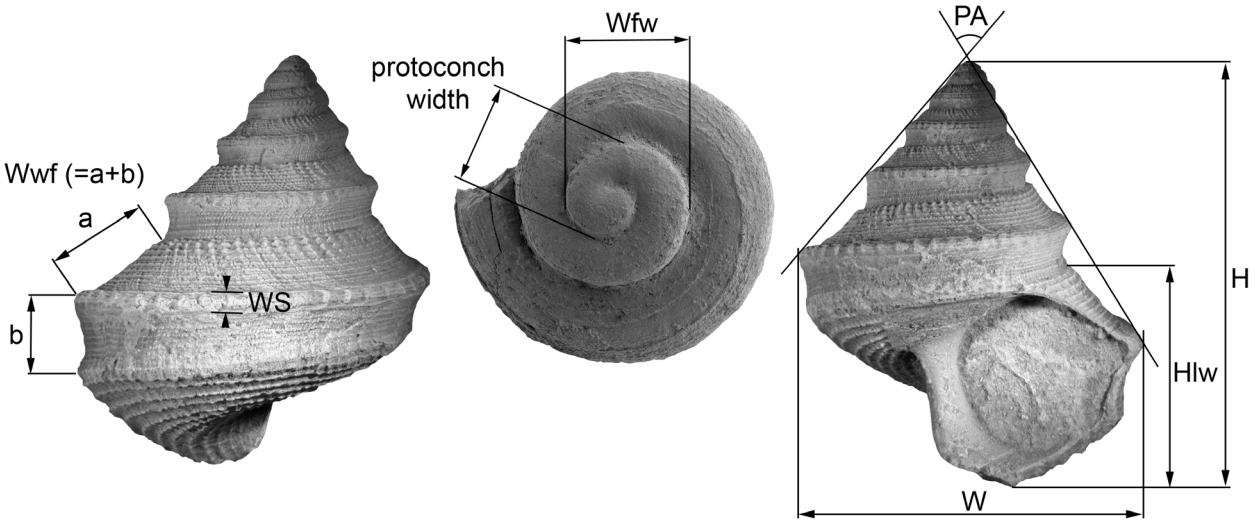

FIG. 2. Measurements used in this study. H, height of shell; Hlw, height of last whorl; PA, pleural angle; W, width of shell; Wfw, width of first whorl; WS, width of selenizone; Wwf, width of whorl face.

Subgenus *Ananias* Knight, 1945
Genus *Spiroscala* Knight, 1945
Genus *Euconospira* Ulrich *in* Ulrich & Scofield, 1897
Family LUCIELLIDAE Knight, 1956
Genus *Eotrochus* Whitfield, 1882
Genus *Eirlysella* nov.
Superfamily PLEUROTOMARIOIDEA Swainson, 1840
Family PHYMATOPLEURIDAE Batten, 1956
Genus *Phymatopleura* Girty, 1939
Genus *Paragoniozona* Nelson, 1947
Genus *Worthenia* de Koninck, 1883
Subgenus *Worthenia* de Koninck, 1883
Subgenus *Yochelsonospira* Thein & Nitecki, 1974
Genus *Borestus* Thomas, 1940*a*
Genus *Glyptotomaria* Knight, 1945
Genus *Dictyotomaria* Knight, 1945
Family PORTLOCKIELLIDAE Batten, 1956
Genus *Shansiella* Yin, 1932
Subgenus *Shansiella* Yin, 1932
Subgenus *Oklahomaella* nov.
Subclass CAENOGASTROPODA Cox, 1960*b*
Superfamily ORTHONEMATOIDEA Nützel & Bandel, 2000
Family GONIASMATIDAE Nützel & Bandel, 2000
Genus *Peruvispira* Chronic, 1949
Genus *Platyzona* Knight, 1945

SYSTEMATIC PALAEONTOLOGY

By Baran Karapunar *and* Alexander Nützel

Subclass VETIGASTROPODA Salvini-Plawen, 1980
Order PLEUROTOMARIIDA Cox & Knight, 1960
Superfamily EOTOMARIOIDEA Wenz, 1938
Family EOTOMARIIDAE Wenz, 1938

Original diagnosis. 'Gehäuse vorwiegend ziemlich flach kegelförmig bis kreiselförmig oder linsenförmig; Gewinde wenig erhoben; Umgänge meist kantig, oben mehr oder weniger abgeflacht, seltener gerundet, ohne kräftigere Skulptur, gelegentlich mit Spiralstreifen; Schlitzband mäßig breit bis breit, flach oder schwach konkav, auf der Kante oder darüber am Rande der Oberseite; Endwindung groß, genabelt; Mündung rundlich, viereckig; Außenrand mit tiefem Sinus, oft schlitzartig verlängert, aber meist ohne deutlich abgegrenzten Schlitz' (Wenz 1938, p. 137).

Translation. Shell mainly flatly conical to turbiniform or lens-shaped; spire slightly raised; whorls mostly angular, adapical portion more or less flattened, more rarely rounded, without pronounced sculpture, occasionally with spiral striae; slit band moderately wide to wide, flat or slightly concave, at the edge of the whorls or above it; body whorl large, phaneromphalous; aperture rounded, quadrangular; outer lip with deep sinus, often elongated slit-like, but mostly without a clearly defined slit.

Emended diagnosis. 'Shell turbiniform to trochiform; labral slit invariably present, generating concave selenizone bordered by threads at approximately mid-height of whorl. U. Cam.–L. Jur. (Lias.)' (Knight *et al.* 1960, p. I202).

Remarks. At present, more than 90 genera, ranging from the early Palaeozoic to the Mesozoic, have been assigned to the family Eotomariidae. This family has been subdivided into various subfamilies and tribes (Knight *et al.* 1960; Gordon & Yochelson 1987). In a work on Mississippian gastropods, Gordon & Yochelson (1987) discussed the complex systematics of the group and noted that Eotomariidae in the *Treatise* (Knight *et al.* 1960) is probably not monophyletic. They also noted that the *Treatise* arrangement was largely based on the whorl shape and they correctly proposed that other characters must also be considered for an improved systematic arrangement. The relationship of the Ordovician *Eotomaria*, the type genus of the family, to late Palaeozoic taxa such as *Glabrocingulum* is still unclear. Here, we keep the genera *Glabrocingulum* (*Glabrocingulum*), *Glabrocingulum* (*Ananias*), *Spiroscala* and *Euconospira* in Eotomariidae and we place the genera *Trepospira, Baylea*, and the subfamily Liospirinae in Eotomariidae (based on Wagner's (2002) analysis which placed *Liospira* in Eotomariidae). Based on the present finding of a caenogastropod larval shell in *Peruvispira oklahomaensis* and *Peruvispira* sp., *Peruvispira* is now removed from Neilsoniinae and placed in Goniasmatidae (Caenogastropoda) (see below).

Subfamily LIOSPIRINAE Knight, 1956

Remarks. The subfamily Liospirinae was assigned to Raphistomatidae by Knight *et al.* (1960). As a result of a phylogenetic analysis of early Palaeozoic gastropods, Wagner (2002) placed Raphistomatidae in Euomphalida (a finding that needs confirmation) and *Liospira* in Eotomariidae. Based on this, the subfamily Liospirinae was listed as synonym of Eotomariini by Bouchet *et al.* (2005, 2017). Here, we keep Liospirinae and assign it to Eotomariidae following the results of Wagner (2002) and keep the assignment of *Trepospira* to Liospirinae as suggested by Knight *et al.* (1960). This arrangement needs testing by a comprehensive phylogenetic analysis including early and late Palaeozoic representatives.

Genus TREPOSPIRA Ulrich *in* Ulrich & Scofield, 1897

Type species. Pleurotomaria sphaerulata Conrad, 1842 from the Carboniferous of Illinois, USA; original designation.

Remarks. Knight *et al.* (1960) treated *Trepospira* and *Angyomphalus* as subgenera of *Trepospira*. Later, both taxa were used

at the genus level (Shikama & Nishida 1968; Blodgett & Johnson 1992; Peel 2016). *Trepospira* differs from *Angyomphalus* by having an umbilical callus. Both taxa share a similar shape and an ornament of subsutural nodes. *Angyomphalus* differs from *Trepospira* by having a circumumbilical funicle. A well preserved early ontogenetic shell of a Mississippian *Angyomphalus* species from the Imo Formation, Arkansas was documented by Geiger *et al.* (2008, fig. 12.4E). It has a depressed initial whorl followed by low-spired, evenly convex, smooth early whorls.

Trepospira sphaerulata (Conrad, 1842)
Figure 3

* 1842 *Pleurotomaria sphaerulata* Conrad, p. 272, pl. 16 fig. 12.
1967 *Trepospira* (*Trepospira*) *sphaerulata* (Conrad); Yochelson & Saunders, p. 237 (for further synonymy).

Material. A total of 28 specimens. 25 from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 22–23, and a further 23 specimens (SNSB-BSPG 2020 LVIII). 2 from the Virgilian of Kansas (Lawrence Formation, KSV–05): SNSB-BSPG 2020 LXVI 2–3. 1 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 38.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh	Nn
2020 LVIII 22	17.9	26.4	104°	–	12.7	9.9	1.9	0.19	0.15	23
2020 LVIII 23	13.6	20.7	108°	[0.3]	10.1	7.9	1.4	0.18	0.14	21
2020 XCI 38	14.2	21.3	106	–	10.1	8.7	1.4	0.16	0.14	21
2020 LXVI 2	6.2	11.5	119	–	5.0	4.7	0.8	0.17	0.17	15
2020 LXVI 3	8.4	12.4	117	0.22	6.7	5.1	0.9	0.17	0.13	16

Description. Shell moderate sized, lenticular, low-spired, the largest specimen with about 6–7 whorls; suture incised, situated at abapical edge of selenizone; spiral angle about 100–120°; whorls angulated at crest-like periphery at lower edge of selenizone; early whorl face flat to convex, smooth; later whorl face flatly convex, ornamented with pronounced subsutural nodose bulge starting at the fourth whorl; number of nodes per whorl increasing during ontogeny, 21–23 on last whorl; selenizone flat, oblique, flush with whorl face; abapical border of selenizone forming peripheral crest; faint line forms adapical border of selenizone; selenizone, only visible on last whorl, covered by succeeding whorls in previous whorls; growth lines faint, oblique prosocyrt on whorl face, strongly prosocyrt on base; whorl face and base meet at an angle of about 80–90°; base slightly convex, smooth; aperture lenticular, outer lip, basal lip and columellar lip flat; circumumbilical area closed by callus; base anomphalous.

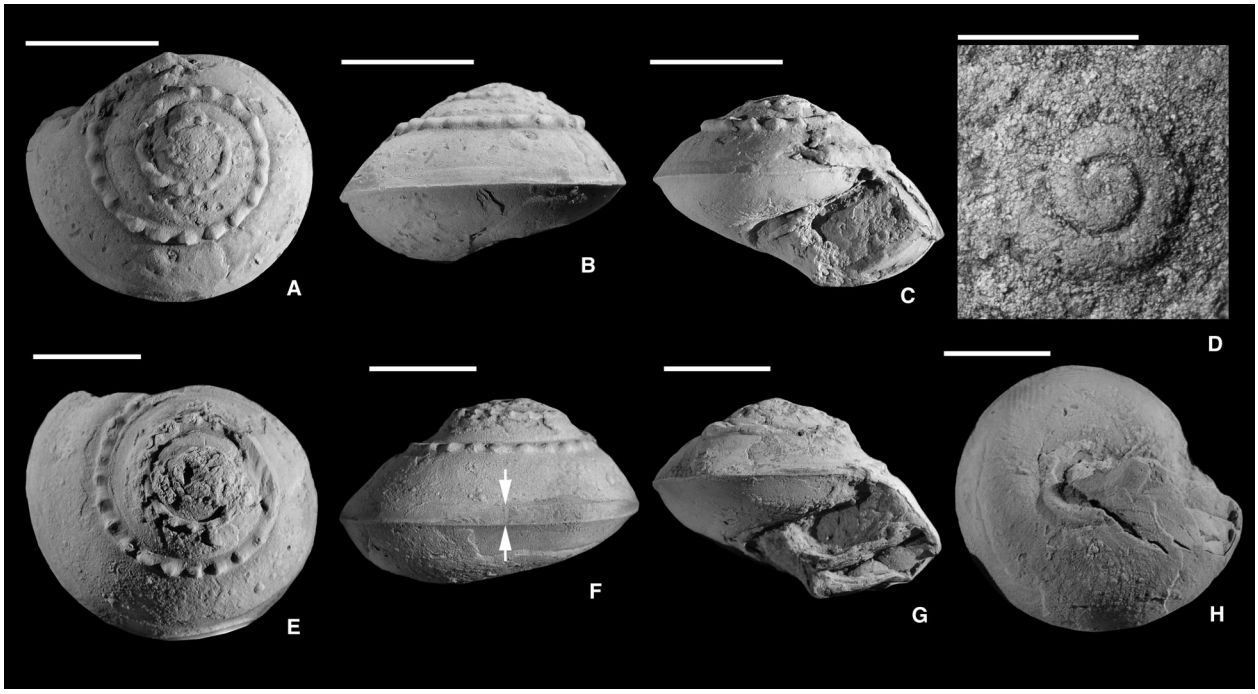

FIG. 3. *Trepospira sphaerulata* (Conrad, 1842) from the Gene Autry Shale (Morrowan, Oklahoma). A–D, SNSB-BSPG 2020 LVIII 23; D, apical view, detail of early whorls. E–H, SNSB-BSPG 2020 LVIII 22; F, arrows indicate selenizone margins. Scale bars represent: 10 mm (A–C, E–H); 1 mm (D).

Trepospira cf. *illinoiensis* (Worthen, 1884)
Figure 4

?	1857	*Pleurotomaria depressa* Cox, p. 569, pl. 8 figs 10, 10a [non *Pleurotomaria depressa* Phillips, 1836].
cf. *	1884	*Pleurotomaria illinoiensis* Worthen, p. 4.
?	1889	*Pleurotomaria kentuckiensis* Miller, p. 421 [replacement name for *Pleurotomaria depressa* Cox, 1857].
	1915	*Trepospira depressa* Cox; Girty, p. 158, pl. 21 figs 6–11c (see for discussion on the synonymy).
	1922	*Trepospira depressa*; Plummer & Moore, pl. 14 fig. 21; pl. 22 figs 20–22; pl. 24 fig. 19.
?	1961	*Trepospira minima* Hoare, p. 150, pl. 20 figs 14, 16, 18.
	1964*a*	*Trepospira* (*Trepospira*) cf. *Trepospira* (*Trepospira*) *illinoiensis* (Worthen); Sturgeon, p. 203, pl. 34 figs 7–15; pl. 36 fig. 6.
cf.	1964*b*	*Trepospira* (*Trepospira*) *illinoiensis* (Worthen); Sturgeon, p. 742, pl. 121 figs 10–14.
cf.	1967	*Trepospira* (*Trepospira*) *illinoisensis* (Worthen); Yochelson & Saunders, p. 236 (for further synonymy).
	1972*a*	*Trepospira illinoisensis*; Batten, fig. 27.
	2001	*Trepospira* (*Trepospira*) *illinoisensis* (Worthen); Kues & Batten, p. 21, figs 5.1–5.3.

Material. A total of 748 specimens. 1 from the Desmoinesian of Oklahoma (Wetumka Formation, OKD–13): SNSB-BSPG 2020 LIX 2. 2 from the Desmoinesian of Oklahoma (Wetumka Formation, OKD–14): SNSB-BSPG 2020 LX 2–3. 191 from the Desmoinesian of Oklahoma (Wewoka Formation, OKD–11): SNSB-BSPG 2020 LXII. 4 from the Desmoinesian of Oklahoma (Holdenville Formation, OKD–01): SNSB-BSPG 2020 LXIII. 2 from the Missourian of Oklahoma (Barnsdall Formation, Eudora Shale Member, OKM–02): SNSB-BSPG 2020 LXIV. 1 from the Missourian of Oklahoma (Coffeyville Formation, Mound City Shale Member, OKM–25): SNSB-BSPG 2020 LXV. 2 from the Virgilian of Kansas (Lawrence Formation, KSV–06): SNSB-BSPG 2020 LXVII 1–2. 10 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 20, and a further 9 specimens (SNSB-BSPG 2009 XXII). 284 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 8, 32, 36–38, and a further 279 specimens (64 from the surface sample, 215 from the bulk sample; SNSB-BSPG 2020 XCI). 222 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 6, 10, and a further 220 specimens (36 from the surface sample, 184 from the bulk sample; SNSB-BSPG 2020 LXXX). 5 from the Virgilian of Texas (Finis Shale Member, TXV–29): SNSB-BSPG 2020 LXXIV. 12 from the Virgilian of Texas (Finis Shale Member, TXV–36): SNSB-BSPG 2020 LXXVI. 11 from the Virgilian of Texas (Finis Shale Member, TXV–120): SNSB-BSPG 2020 LXXXII. 1 from the Virgilian of Texas (Finis Shale Member, TXV–69): SNSB-BSPG 2020 LXXXIII.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh	Nn
2020 LIX 2	11.7	21.8	126	–	9.5	8.0	1.6	0.20	0.17	21
2020 LX 2	13.3	22.7	120	–	9.5	8.15	1.6	0.20	0.17	24
2020 LX 3	14.0	24.2	128	–	11.3	8.5	1.8	0.21	0.16	23
2009 XXII 20	7.6	11.7	134	–	5.9	4.4	0.7	0.16	0.12	16
2020 XCI 8	11.3	22.2	134	0.2	9.1	8.2	1.5	0.18	0.16	16
2020 XCI 32	6.4	12.8	136	–	5.7	4.9	1.0	0.21	0.18	13
2020 LXXX 6	14.0	28.6	135	–	11.7	10.3	1.7	0.17	0.15	21
2020 LXXX 10	16.2	31.8	122	–	13.4	11.87	2.2	0.19	0.17	30

Description. Shell of moderate size, lenticular, low-spired; largest specimen with about 7–8 whorls; suture incised, situated at abapical edge of selenizone; spiral angle about 125–135°; whorls angulated at crest-like periphery; early whorl face flat to slightly convex, smooth; later whorl face flatly convex, ornamented with subsutural nodose bulge starting at fourth whorl; number of nodes per whorl increasing during ontogeny, between 17 and 30 on last whorl; selenizone flat, smooth, flush with whorl face; abapical border of selenizone formed by peripheral crest; adapical border of selenizone marked by faint line; selenizone only visible on last whorl, covered by subsutural nodose bulge of succeeding whorls in spire whorls; growth lines faint, oblique prosocyrt on whorl face, prosocyrt on base; whorl face and base meet at an angle of about 65–70°; base slightly convex, smooth; aperture lenticular, outer lip, basal lip and columellar lip flat; circumumbilical area closed by callus; base anomphalous.

Remarks. The relatively large specimens at hand comprise seven whorls and have about 17–20 nodes on the last whorl. A single large specimen from the Finis Shale Member of Texas (SNSB-BSPG 2020 LXXX 10) appears to have 7.5 whorls, with 30 nodes on the last whorl.

Sturgeon (1964*a*, *b*) pointed out the complicated taxonomy of Pennsylvanian *Trepospira* species from the USA. The *Trepospira* species *Pleurotomaria depressa* Cox, 1857 (non Phillips 1836, p. 227) was replaced by *Pleurotomaria kentuckiensis* Miller, 1889. The illustrations and description given by Cox (1857) are insufficient and the type specimen needs to be studied to clarify its identity. Worthen (1884) erected *Trepospira illinoiensis* and differentiated it from *T. depressa* by having 'more flattened volutions, the impressed band on the lower volution, and its smaller and less conspicuous nodes'. Ulrich (*in* Ulrich & Scofield 1897) erected the genus *Trepospira* and included *Pleurotomaria depressa* and *Pleurotomaria illinoiensis* as two separate members of the genus. Girty (1915) synonymized many species with *Trepospira depressa* including *T. illinoiensis*. Further discussion of synonyms prior to 1915 can be found in Girty (1915) and a comprehensive chresonymy and synonymy list prior to 1967 can be found in Yochelson & Saunders (1967).

Sturgeon (1964*b*) figured the original material of Worthen (1884) and designated a lectotype for *T. illinoiensis*. This specimen has much weaker subsutural nodes and the periphery is not as acute as in the specimens at hand. Our specimens seem to be conspecific with Girty's (1915) specimens, which he called

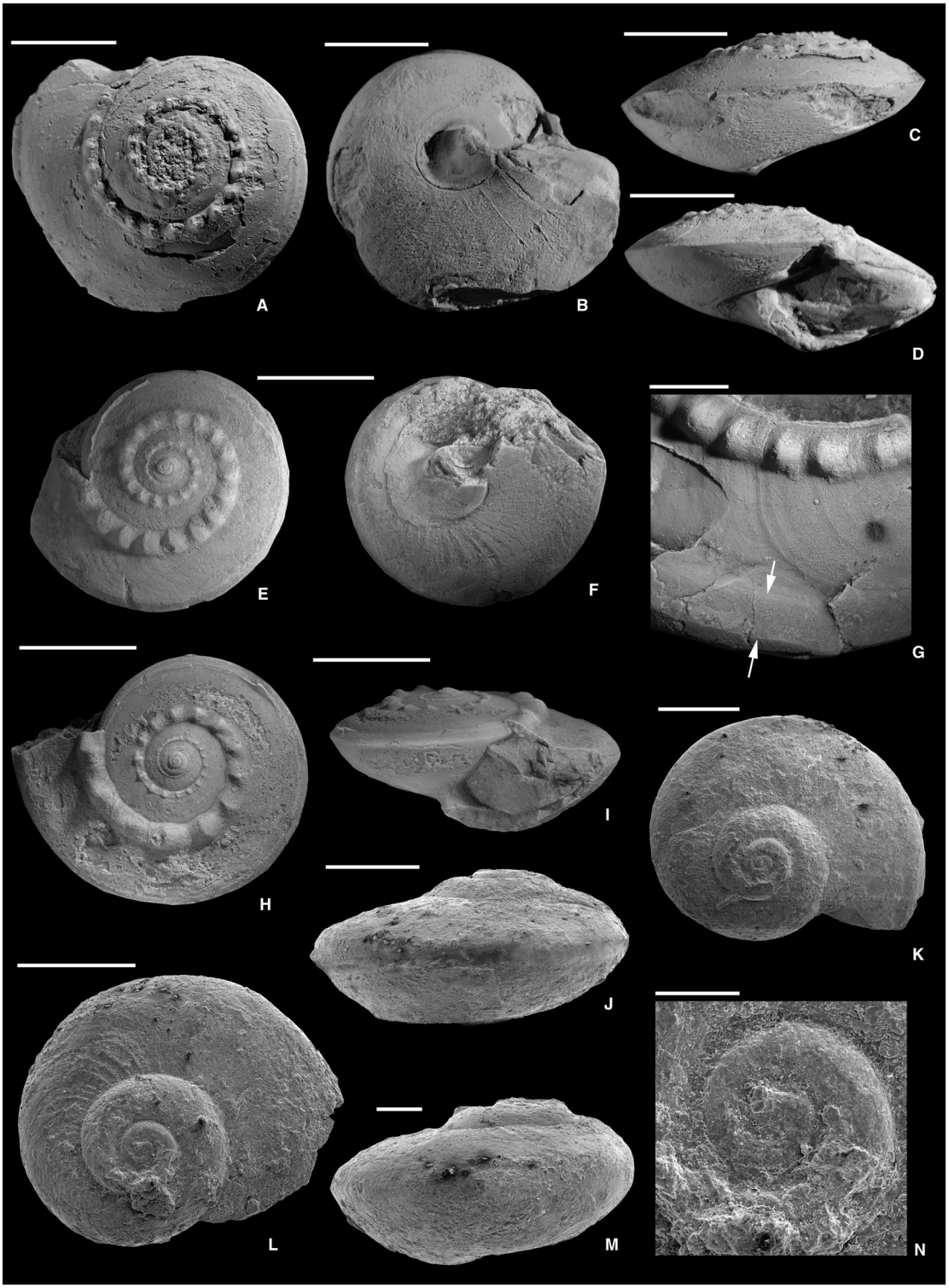

FIG. 4. *Trepospira* cf. *illinoiensis* (Worthen, 1884). A–D, SNSB-BSPG 2020 LXXX 6, from the Finis Shale Member (Virgilian, Texas). E–F, SNSB-BSPG 2009 XXII 20, from the Colony Creek Shale (Virgilian, Texas). G, SNSB-BSPG 2020 LXVII 1, from the Dickerson Shale (Desmoinesian, Texas), apical view, detail of growth lines, arrows indicate selenizone margins. H–I, SNSB-BSPG 2020 XCI 32, from the Finis Shale Member (Virgilian, Texas). J–K, SNSB-BSPG 2020 XCI 36, juvenile specimen from the Finis Shale Member (Virgilian, Texas). L–N, SNSB-BSPG 2020 XCI 37, juvenile specimen from the Finis Shale Member (Virgilian, Texas); N, apical view, detail of early whorls. Scale bars represent: 10 mm (A–D); 5 mm (E–F, H–I); 2 mm (G); 0.5 mm (J–L); 0.2 mm (M); 0.1 mm (N). J–N, SEM images.

Trepospira depressa (Cox). *Trepospira depressa* and many other species have long been considered synonyms of *T. illinoiensis* (e.g. Girty 1915; Yochelson & Saunders 1967; Kues & Batten 2001). It is also possible that the *T. depressa* and *T. illinoiensis* are not conspecific. As Sturgeon (1964*b*) stated, 'a comprehensive study of all available low-spired specimens of *Trepospira* will be necessary to solve this nomenclatural problem'; this is still so.

Hoare (1961) erected a new species, *T. minima*, and differentiated it from *T. illinoiensis* in having a lower spiral angle. Yochelson & Saunders (1967) and Kues & Batten (2001) treated *T. minima* as a distinct species, but we are in doubt whether it represents a synonym of *T. illinoiensis*.

Trepospira discoidalis Newell, 1935 differs from *T. illinoiensis* by having a concave whorl face, while *T. sphaerulata* differs in having a higher spire. The Mississippian species *T. baconi* Gordon & Yochelson, 1987 has a rounded periphery rather than a sharp whorl angulation. The Mississippian species *T. diadema* Gordon & Yochelson, 1987 can be differentiated from *T. illinoiensis* by the presence of fewer nodes on the last whorl (14–17 nodes) according to Gordon & Yochelson (1987). However, the number of nodes is within the range of variation for *T. illinoiensis* as given by Kues & Batten (2001; 11 to 24 on last whorl).

As is discussed below, small *Trepospira* specimens (*c.* 1 mm) show frequently repaired scars, suggesting durophagous predation on juveniles.

Subfamily EOTOMARIINAE Wenz, 1938

Genus BAYLEA de Koninck, 1883

Type species. Trochus yvanii Léveillé, 1835 from the Carboniferous of Belgium; subsequent designation by Wenz (1938).

Emended diagnosis. Turbiniform; spire gradate; whorl face angulated at abapical border of selenizone; angulation separating ramp and vertical outer whorl face; initial whorl planispiral or depressed; early teleoconch whorls evenly rounded, smooth or weakly ornamented by spiral threads; whorl angulation, selenizone and strong spiral cords appearing at about fourth whorl; selenizone facing in adapical direction, inclined, concave to almost flush, smooth or with lunulae; mature teleoconch whorls ornamented with spiral cords and occasionally with weaker axial threads or ribs; inner shell layer nacreous.

Remarks. Thanks to the well-preserved specimens at hand representing two *Baylea* species and those reported by Mazaev (2015, 2016) from the Permian, we are able to give a sharper diagnosis of this genus, especially regarding its early whorls. Mazaev (2015) also reported the smooth convex early whorls including a planispiral initial whorl in Permian *Baylea* species from Russia that are also present in both Pennsylvanian species treated herein. The type material of *Ba. yvanii*, type species of *Baylea*, has also smooth, evenly rounded whorls so this character can be used in the diagnosis. In his diagnosis of *Baylea* Mazaev (2015) interpreted these early whorls as a protoconch of about two whorls; thus it would be not of the vetigastropod type. However, we find that the early whorls consist of a vetigastropod-type, smooth protoconch of about one whorl followed by smooth early teleoconch (e.g. see Fig. 8J, M below). Because both are smooth, the protoconch/teleoconch border is not or hardly visible in less well-preserved specimens. In very well-preserved specimens from the Buckhorn Asphalt deposit, the transition from the smooth early whorls to the ornamented later ones is fast but not abrupt and this also suggests that the early smooth whorls (except of the first one) do not belong to the protoconch but to the early teleoconch. As will be shown, the Carboniferous species *Ba. giffordi* (Worthen, 1884) and *Ba. tenera* from the Buckhorn Asphalt deposit have an inner nacreous layer; in gastropods, nacre is restricted to Vetigastropoda. A nacreous vetigastropod with more than one protoconch whorl has never been reported.

Baylea (alias *Yvania* Fischer, 1885) was placed in Gosseletininae by Wenz (1938) and in the family Raphistomatidae, subfamily Omospirinae by Knight *et al.* (1960). The Ordovician type genus of Omospirinae, *Omospira* differs considerably from *Baylea* in being rather high-spired and in having a broader sinus. Wagner (2002) placed *Omospira* in Loxonematidae and based on this, Omospirinae was listed as a synonym of Loxonematidae in Bouchet *et al.* (2005, 2017). The Ordovician *Omospira* has rather high-spired shell with a broad sinus high on the whorls. It has no selenizone produced by a parallel sided slit and lacks lunulae or any ornament and is hence certainly not closely related to *Baylea*. We note that the proposed placement of *Omospira* in Loxonematidae is unlikely, as is the synonymization of Omospirinae with Loxonematidae. *Baylea* was placed in Phymatopleuridae by Mazaev (2015, 2016) without discussion. We argue that the formation of the selenizone between two spiral cords high on whorl face suggests an eotomariid affinity. The characteristic growth line pattern of *Baylea* is quite similar to that of *Gosseletina*. Growth lines in *Gosseletina* are opisthocyrt then prosocyrt above the selenizone and strongly prosocyrt below the selenizone (e.g. Batten 1966). Hence, *Baylea* might belong to Gosseletinidae as proposed by Wenz (1938). The composition of Gosseletinidae by Knight *et al.* (1960) is mainly based on the position of selenizone and the family in this composition is probably polyphyletic. Here we tentatively place *Baylea* within Eotomariidae until a comprehensive phylogenetic analysis is conducted. As stated by Ketwetsuriya *et al.* (2020*a*), *Biarmeaspira* Mazaev, 2006 is probably derived from *Baylea* and therefore both genera should be considered when changing the family assignment of either of them.

The specimen identified as *Worthenia* cf. *schirjaevensis* by Batten (1972*b*) resembles *Baylea*, *Biarmeaspira* Mazaev, 2006, and *Pseudobaylea* Dickins, 1963 more than it resembles *Worthenia*. In the discussion of *Worthenia* cf. *schirjaevensis*, Batten (1972*b*) described a group of species ranging from the Permian to the Triassic with an angulated selenizone without nodes on it. These species probably represent *Biarmeaspira* and *Sisenna*.

The Permian genus *Guizhouspira* Wang *in* Wang & Xi 1980 has a short subsutural shoulder and horizontally lying selenizone of which the lower edge represents the whorl periphery. These

characters are shared by *Baylea* and hence *Guizhouspira* represents junior synonym of *Baylea* without doubt.

Pleurotomaria bilineata Sayre, 1930 (p 132, pl. 13 fig. 13) from the Pennsylvanian Drum Limestone of Kansas can be assigned to *Baylea* due to the whorl shape, position of selenizone and dominant spiral ornaments.

Baylea giffordi (Worthen, 1884)
Figure 5

* 1884 *Pleurotomaria giffordi* Worthen, p. 5.
1890 *Pleurotomaria giffordi* Worthen; Worthen, pp 135–136, pl. 23 figs 8–8a.
1929 *Yvania giffordi* (Worthen); Weller, pp 36–38, pl. 2 figs 6–8b; pl. 3 figs 5, 11.
1964*a* *Baylea* cf. *B. giffordi* (Worthen); Sturgeon, p. 204, pl. 33 figs 11–12.
1967 *Baylea giffordi* (Worthen); Yochelson & Saunders, p. 35.
2001 *Baylea kuesi* Batten; Kues & Batten, p. 21, figs 5.4–5.6.

Material. A total of 13 specimens. 8 from the Desmoinesian of Texas (Lazy Bend Formation, TXD–03): SNSB-BSPG 2020 LXIX 5–6, and a further 6 specimens (SNSB-BSPG 2020 LXIX). 5 from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 83, 259, and a further 3 specimens (SNSB-BSPG 2011 X).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXIX 5	7.1	4.8	70	0.24	3.8	2.8	0.5	0.16	0.12
2020 LXIX 6	9.3	[5.77]	73	–	4.9	3.1	0.6	0.20	0.13
2011 X 83	7.1	6.2	76	0.21	3.7	2.9	0.5	0.19	0.15

Description. Shell very small, trochiform, higher than wide, the largest specimen with six whorls; spire gradate, moderately high; suture moderately deep, situated slightly below abapical angulation (basal edge) of preceding whorl; first whorl planispirally coiled, 0.21 mm wide; approximately the first three whorls smooth, convex; spiral cords appear on whorl face within the fourth whorl; later whorl face with subsutural angulation, mid-angulation and abapical angulation; subsutural angulation forming a short concave area lying horizontally (perpendicular to axis); whorl face between subsutural angulation and mid-angulation concave, steeply inclining; lateral whorl face slightly concave, lying parallel to axis; whorl face between adapical suture and mid-angulation ornamented with one cord on subsutural angulation and maximum of three spiral cords below; lateral whorl face ornamented with maximum of four spiral cords; selenizone flat, wide, slightly concave, situated just above the mid-angulation, almost horizontal to slightly oblique; selenizone onset within fourth whorl, formed between uppermost second and third spiral cords high on whorl face; selenizone in later whorl face bordered adaxially by a cord and abaxially by mid-angulation, ornamented with regularly spaced lunulae; lunulae not symmetrical, zenith point situated adaxial half of the selenizone; growth lines opisthocline from adapical suture to subsutural angulation, prosocline between subsutural angulation and adaxial (adapical) edge of the selenizone; growth lines at lateral whorl face sinuous: oblique prosocyrt from mid-angulation to lowermost cord, oblique opisthocline between lowermost cord and abapical angulation; growth lines forming axially elongated nodes or weakly globular nodes where they intersect with spiral cord on subsutural angulation and occasionally on abapical angulation; base convex, with angular basal edge, ornamented with 13–14 equally prominent spiral cords; basal growth lines prosocline near edge turning into opisthocyrt; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip straight; base anomphalous.

Remarks. In contrast to the original description of *Baylea giffordi* by Worthen (1884, p. 5), there are no revolving lirae on the selenizone of the studied specimens. Worthen did not mention a nodose spiral ornament in the original description, but Weller (1929) (who also had access to the holotype) described *Ba. giffordi* with subsutural nodes that are 'associated with growth markings'. *Baylea kuesi* Batten, 1995 lacks subsutural nodes and has only two spiral cords above the selenizone. The specimens identified as *Ba. kuesi* by Kues & Batten (2001) possess 'subsutural interference nodes' and have 4–5 spiral cords above the selenizone, which matches our material. The specimens reported by Kues & Batten (2001), by Sturgeon (1964*a*) and the studied specimens are conspecific and differ from the type material of *Ba. giffordi* in having a higher pleural angle (45–55° vs 55–65°). This difference was pointed out by Sturgeon (1964*a*) together with 'the presence of faint nodes on the ventrolateral angulation' (= abapical angulation). Nevertheless, the studied specimens and the specimens mentioned above are placed herein into *Ba. giffordi* due to the identical ornamentation on the whorl face. The difference in pleural angle (spire height) is regarded as intraspecific variation. According to Weller (1929), *Ba. giffordi* has subsutural nodes but the strength of the nodes varies within the species. *Baylea kuesi* Batten, 1995 differs from *Ba. giffordi* in having a lower number of spiral cords and an absence of nodes at intersections of spiral cords and axial threads.

The growth line pattern of our material is the same as that reported by Weller (1929, pl. 3, fig. 1) for *Ba. giffordi* and Kues & Batten (2001, p. 23) for *Ba. kuesi*.

Baylea gurleyi (Meek, 1871)
Figure 6

* 1871 *Pleurotomaria gurleyi* Meek p. 177.
1873 *Pleurotomaria gurleyi*; Meek & Worthen, pl. 30 figs 6a, b.
1929 *Yvania gurleyi* (Meek); Weller, p. 20, pl. 3 figs 1a–d, 7.
1967 *Baylea gurleyi* (Meek); Yochelson & Saunders, p. 35.

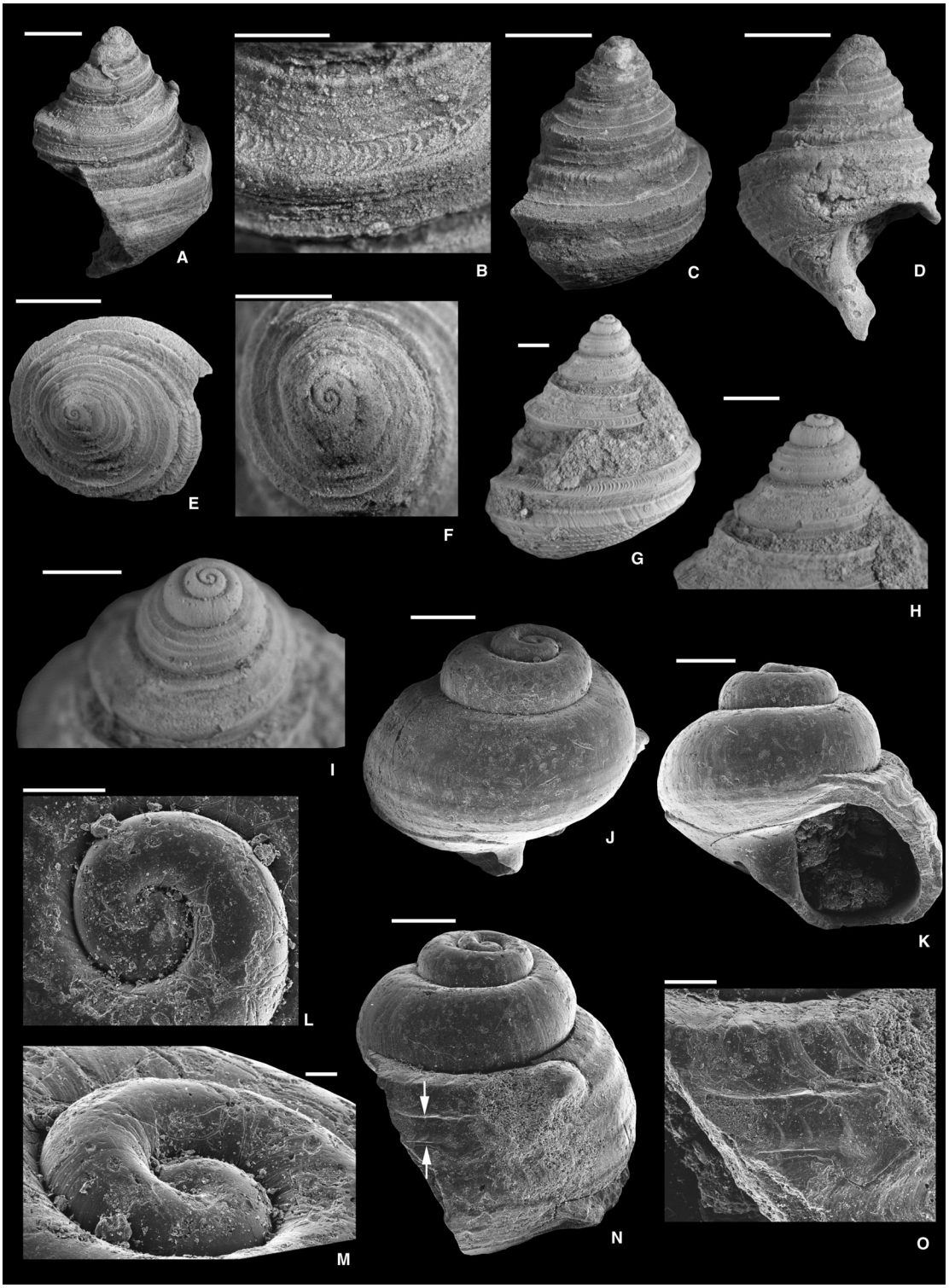

FIG. 5. *Baylea giffordi* (Worthen, 1884). A–B, SNSB-BSPG 2020 LXIX 6, from the Lazy Bend Formation (Desmoinesian, Texas); B, oblique apical view, detail of surface ornament and lunulae. C–F, SNSB-BSPG 2020 LXIX 5, from the Lazy Bend Formation (Desmoinesian, Texas); F, apical view, detail of early whorls. G–I, SNSB-BSPG 2011 X 83, from the Buckhorn Asphalt (Desmoinesian, Oklahoma); I, oblique apical view, detail of early whorls. J–O, SNSB-BSPG 2011 X 259, juvenile specimen from the Buckhorn Asphalt (Desmoinesian, Oklahoma); L, apical view, detail of early whorls; M, oblique apical view, detail of early whorls with planispiral coiling; N, oblique lateral view, arrows indicate selenizone margins; O, detail of N showing surface ornament and newly formed selenizone. Scale bars represent: 2 mm (A, C–E); 1 mm (B, F–I); 0.3 mm (J–K, N); 0.1 mm (L, O); 0.03 mm (M). J–O, SEM images.

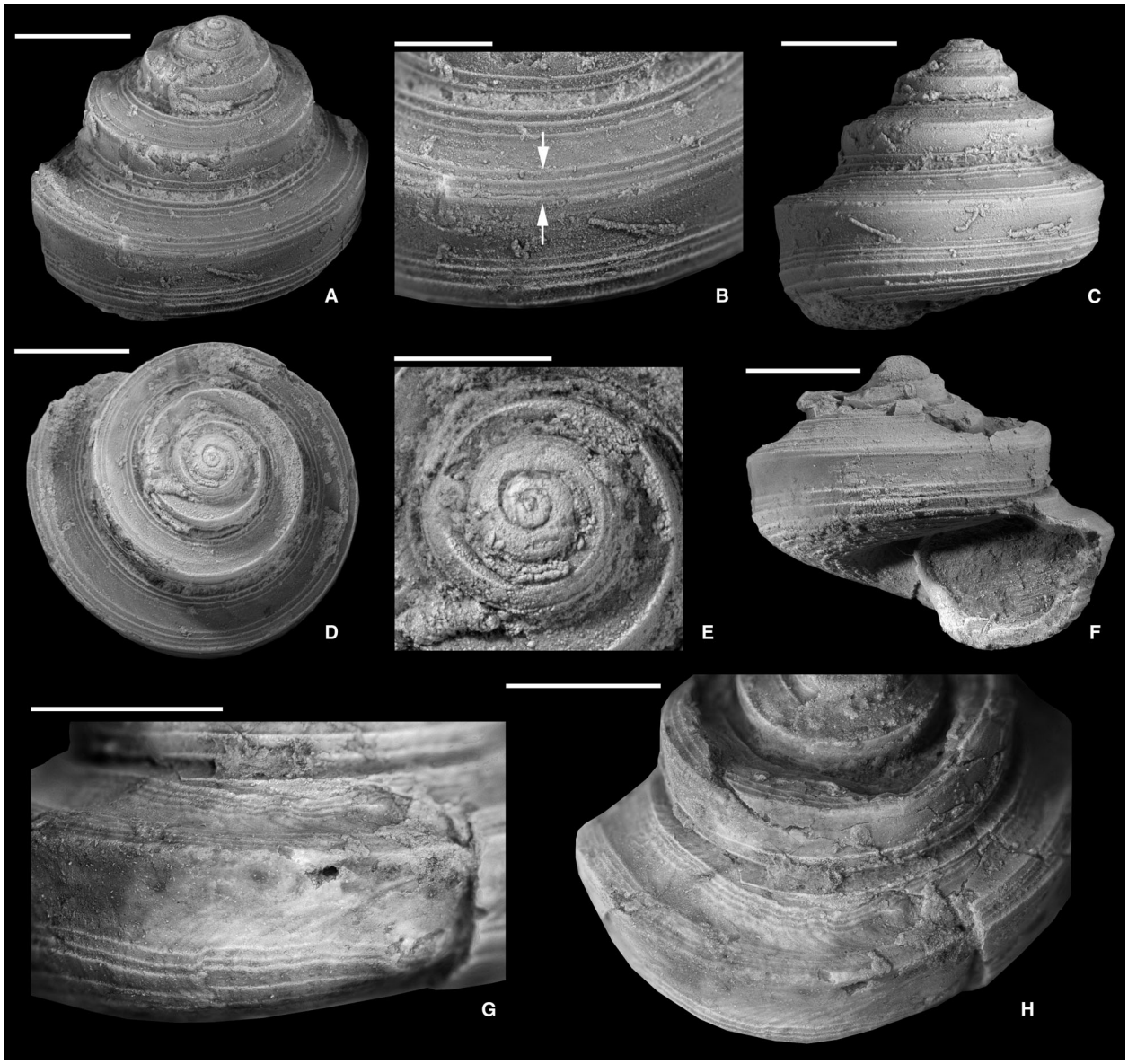

FIG. 6. *Baylea gurleyi* (Meek, 1871). A–E, SNSB-BSPG 2020 LXXIV 2, from the Finis Shale Member (Virgilian, Texas); B, oblique apical view, detail surface ornamentation, arrows indicate selenizone margins; E, apical view, detail of early whorls. F–H, SNSB-BSPG 2020 LXXX 5, from the Finis Shale (Virgilian, Texas); F, adapertural view; G, abapertural view, detail of growth lines on lateral whorl face; H, oblique apical view, detail of surface ornaments and repaired shell injury. Scale bars represent: 2 mm (A, C, D, F–H); 1 mm (B, E).

Material. A total of 3 specimens. 1 crushed specimen from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII. 1 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 5. 1 from the Virgilian of Texas (Finis Shale Member, TXV–29): SNSB-BSPG 2020 LXXIV 2.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXX 5	[5.33]	6.5	79	–	2.8	2.7	0.3	0.12	0.12
2020 LXXIV 2	5.5	5.8	83	0.25	[2.66]	2.7	0.4	0.13	0.14

Description. Shell very small, trochiform, slightly wider than high, largest specimen with six whorls; spire gradate; suture moderately deep, situated at abapical angulation (basal edge) of preceding whorl; first whorl planispirally coiled, convex, without a visible ornament, with diameter of 0.2 mm; early whorl face convex, ornamented with spiral threads; later whorl face with subsutural angulation, mid-angulation and abapical (basal) angulation; subsutural angulation forming narrow channel lying perpendicular to axis; whorl face between subsutural angulation and mid-angulation slightly concave, inclining gently at 60° towards axis; lateral whorl face slightly concave, lying parallel to shell axis; whorl face between suture and mid-angulation

ornamented with one spiral cord on subsutural angulation and maximum of 3–4 spiral cords just below it, smooth at abapical half; lateral whorl face ornamented with maximum of four spiral cords on abapical half, adapical half smooth except one cord just below mid-angulation; selenizone flat, situated at upper whorl face, bordered adaxially (adapically) and abaxially (abapically) by spiral cords, abaxial edge of the selenizone situated at mid-angulation; selenizone ornamented with up to 2–3 spiral cords; lunulae weak, barely visible; growth lines from suture to subsutural angulation opisthocline, between subsutural angulation and adaxial edge of the selenizone asymmetrically prosocyrt with zenith point at adaxial half, growth lines at lateral whorl face asymmetrically prosocyrt with zenith point at abapical half; base flatly convex, with angular basal edge, ornamented with 13–14 equally prominent spiral cords; basal cords more prominent than the ones on whorl face; aperture subovate, wider than high; outer lip angular, basal lip convex, columellar lip convex; base narrowly phaneromphalous.

Remarks. The present specimens closely resemble those figured by Meek & Worthen (1873) and Weller (1929). Although details of the ornamentation are not clearly visible in these publications, Weller (1929) provided a very detailed description of *Ba. gurleyi* that agrees well with the specimens at hand. The ornamentation on the early whorl face is poorly preserved and barely visible. Therefore, the presence of six spiral lirae on the early whorls as described by Meek (1871) and Weller (1929) could not be observed. The spiral cords on the early whorl face of this species can be used to differentiate *Ba. gurleyi* from *Ba. inclinata* (Weller, 1929).

Baylea inclinata (Weller, 1929)
Figure 7

*	1929	*Yvania inclinata* Weller, p. 15, pl. 1 fig. 1; pl. 2 fig. 9; pl. 3 figs 2–3b, 6.
	1967	*Baylea inclinata* (J. Weller); Yochelson & Saunders, p. 36.
	2001	*Baylea*? *inclinata* (Weller); Kues & Batten, p. 23, figs 5.7–5.11.
?	2019*a*	*Baylea gurleyi* (Meek); Mazaev, p. 1292, fig. 44.

Material. 4 specimens from the Desmoinesian of Texas (Lazy Bend Formation, TXD–03): SNSB-BSPG 2020 LXIX 7–8, and a further 2 specimens (SNSB-BSPG 2020 LXIX).

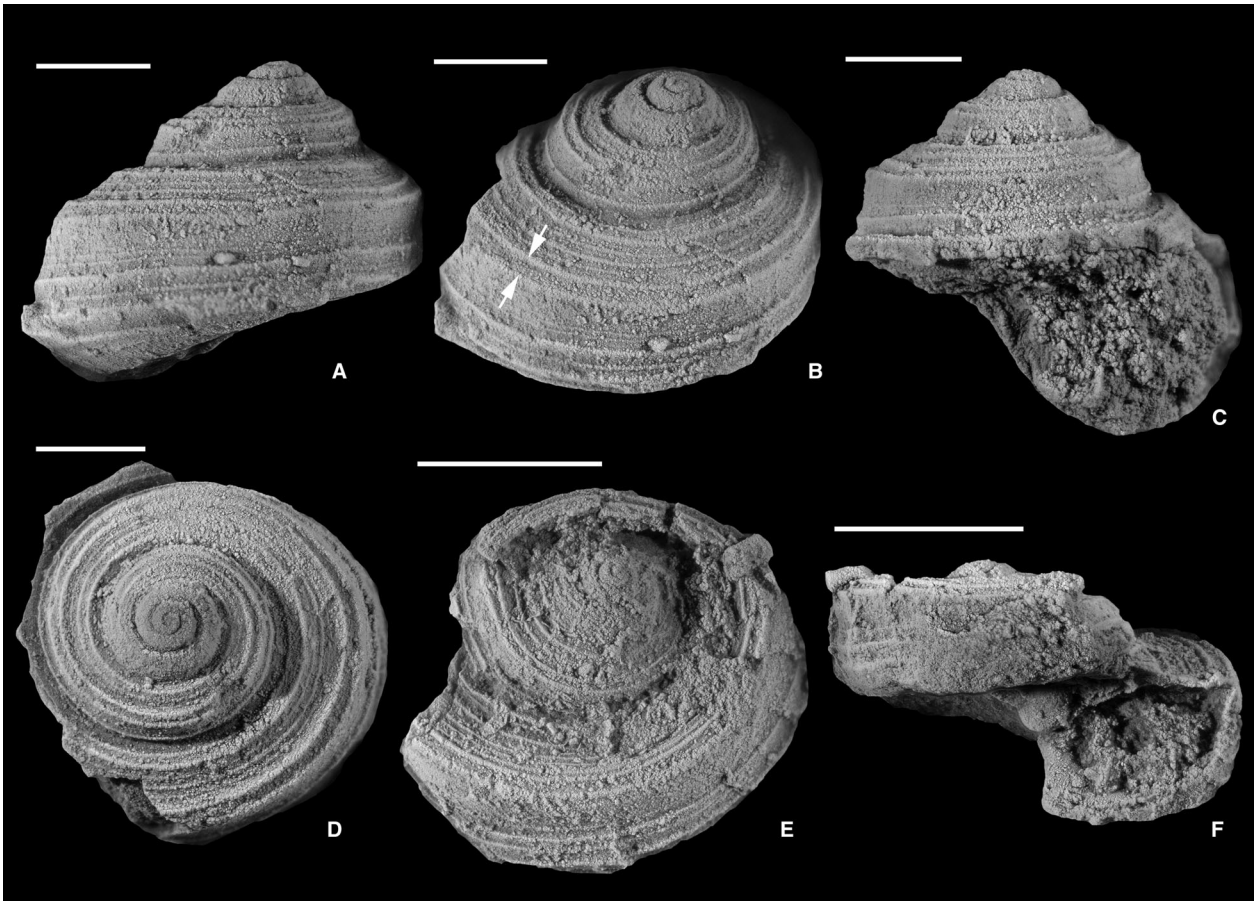

FIG. 7. *Baylea inclinata* (Weller, 1929), from the Lazy Bend Formation (Desmoinesian, Texas). A–D, SNSB-BSPG 2020 LXIX 7; B, arrows indicate selenizone margins. E–F, SNSB-BSPG 2020 LXIX 8. Scale bars represent: 1 mm (A–D); 2 mm (E, F).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXIX 7	3.0	3.2	99	0.25	1.9	1.7	0.2	0.14	0.12
2020 LXIX 8	–	4.3	–	–	1.8	2.0	0.2	0.08	0.09

Description. Shell very small, trochiform, broad, wider than high, largest specimen with five whorls; spire gradate; suture deep, situated at abapical angulation; first whorl planispirally coiled, smooth, 0.2 mm in diameter; first three whorls with convex, smooth whorl face; later whorl face with subsutural angulation, mid-angulation and abapical angulation; subsutural angulation forming channel lying perpendicular to axis; whorl face between subsutural angulation and mid-angulation concave, gently inclining at an angle of 60° with shell axis; lateral whorl face slightly concave, lying parallel to shell axis; whorl face between suture and mid-angulation ornamented with up to seven spiral cords; lateral whorl face ornamented with up to 5–6 spiral cords, most of which cluster in abapical half, obscure on adapical half; cords on lateral whorl face vary in prominence, two of which as strong as basal cords, lowermost strong spiral cord situated on basal edge; selenizone concave, narrow, gently inclining, situated at upper whorl face, bordered adaxially and abaxially by spiral cords, abaxial edge of the selenizone situated on mid-angulation; base convex, with angular basal edge, ornamented with 12–13 equally prominent spiral cords; basal cords more prominent than the ones on whorl face; aperture subovate, wider than high; outer lip angular, basal lip convex, columellar lip convex; base anomphalous.

Remarks. Baylea gurleyi (Meek, 1871) differs from *Ba. inclinata* (Weller, 1929) in having a stronger and more spiral cords and in lacking a smooth area on the upper whorl face. These differences might be intraspecific and both taxa could be synonyms, as pointed out by Kues & Batten (2001) but a formal synonymization needs further study of the type specimens. Mazaev (2019*a*) synonymized *Ba. gurleyi*, *Ba. inclinata* and *Ba. pusilla* Weller, 1929 and used the name *Ba. gurleyi* according to the rule of priority. The specimens figured by Mazaev (2019*a*) have sharp spiral cords all over the whorl face and hence are assigned to *Ba. inclinata* herein.

Kues & Batten (2001, p. 23) interpreted the absence of a spiral ornament on the selenizone as variation within *Ba. inclinata*. We could not find any spiral ornament on the narrow selenizone of the specimens at hand.

Baylea tenera sp. nov.
Figures 8, 9

2002 *Salterospira*? sp.; Bandel *et al.*, p. 643, pl. 1 figs 1–8.

LSID. urn:lsid:zoobank.org:act:F39C1003-059F-4A5F-842E-509691185EDC

Derivation of name. Latin *tenera* meaning delicate.

Holotype. SNSB-BSPG 2011 X 238

Paratypes. SNSB-BSPG 2011 X 242, 243

Type location & age. The Boggy Formation outcrop at the Buckhorn Asphalt Quarry (34°26′44″N; 96°57′41″W), Desmoinesian.

Material. A total of *c.* 308 specimens from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 238–245, and a further *c.* 300 juvenile specimens: SNSB-BSPG 2011 X.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 238	4.2	4.2	87	0.25	2.0	2.0	0.3	0.15	0.15

Description. Shell small, trochiform; largest specimen comprises five whorls; early whorls evenly rounded convex, with weak angulations at the borders of selenizone developing on latest preserved whorls; protoconch smooth, consisting of slightly less than one whorl, diameter *c.* 0.16 mm; first whorl 0.2 mm in diameter; first two whorls planispiral; spiral cords appear at about third whorl; whorl face between primary spiral cords concave; adult whorl face (fourth whorl onwards) ornamented with 4–5 prominent spiral cords: subsutural cord forms narrow shoulder, two cords delimit selenizone, 1–2 cords situated on lateral whorl face; lowermost cord represents basal edge at suture; adult whorl face ornamented with additional secondary spiral cords (weaker than the primary spiral cords) and growth lines; growth lines opisthocline on subsutural shoulder, oblique prosocyrt between subsutural cord and adapical edge of selenizone, prosocyrt between abapical edge of selenizone and fourth primary cord, opisthocyrt between fourth and fifth primary cords; selenizone develops from U-shaped sinus within the fourth whorl, concave, inclined at 45° with axis, bordered by two primary spiral cord; lower cord represents the whorl periphery; selenizone ornamented with prominent lunulae; base convex, ornamented with secondary spiral cords and slightly sinuous growth lines, prosocyrt near basal edge, then opisthocyrt; aperture subcircular; base minutely phaneromphalous.

Remarks. The studied specimens are juveniles; the early ontogeny of the species is well documented but the variation in adult shell characters remains to be studied in more detail when larger specimens are found. One specimen (SNSB-BSPG 2011 X 241) has equally strong spiral cords on the whorl face and strengthened growth lines, together forming a reticulate pattern (Fig. 8G). This specimen also bears a spiral cord on the selenizone.

This species was previously attributed to *Salterospira* by Bandel *et al.* (2002) in open nomenclature. *Salterospira* Batten, 1966 is a phymatopleurid genus with the selenizone positioned at the centre of the lateral whorl face similar to *Borestus* Thomas, 1940*a* but differs from the latter by its wide umbilicus and planispirally coiled early whorls. The position of the selenizone, the early ontogeny and other shell characters (shape of growth

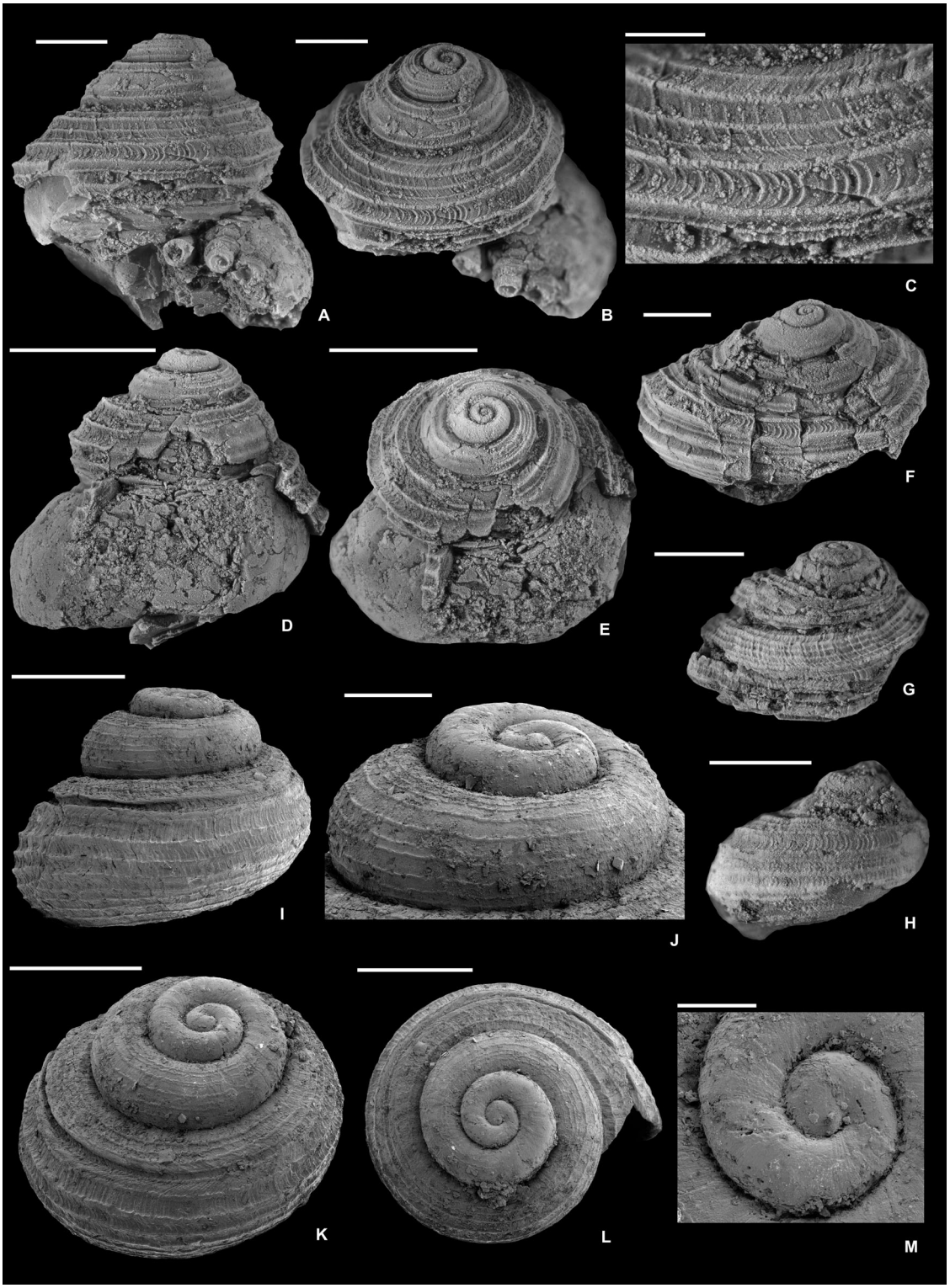

FIG. 8. *Baylea tenera* sp. nov. from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–E, SNSB-BSPG 2011 X 238, holotype; C, detail of ornamentation of ramp and lunulae. F, SNSB-BSPG 2011 X 239. G, SNSB-BSPG 2011 X 241. H, SNSB-BSPG 2011 X 240. I–M, SNSB-BSPG 2011 X 243, paratype, juvenile specimen; J, oblique lateral view, detail of growth lines and ornament on early whorls; M, detail of first whorl. Scale bars represent: 1 mm (A, B, F–H); 0.5 mm (C, I, K, L); 2 mm (D, E); 0.2 mm (J); 0.1 mm (M). I–M, SEM images.

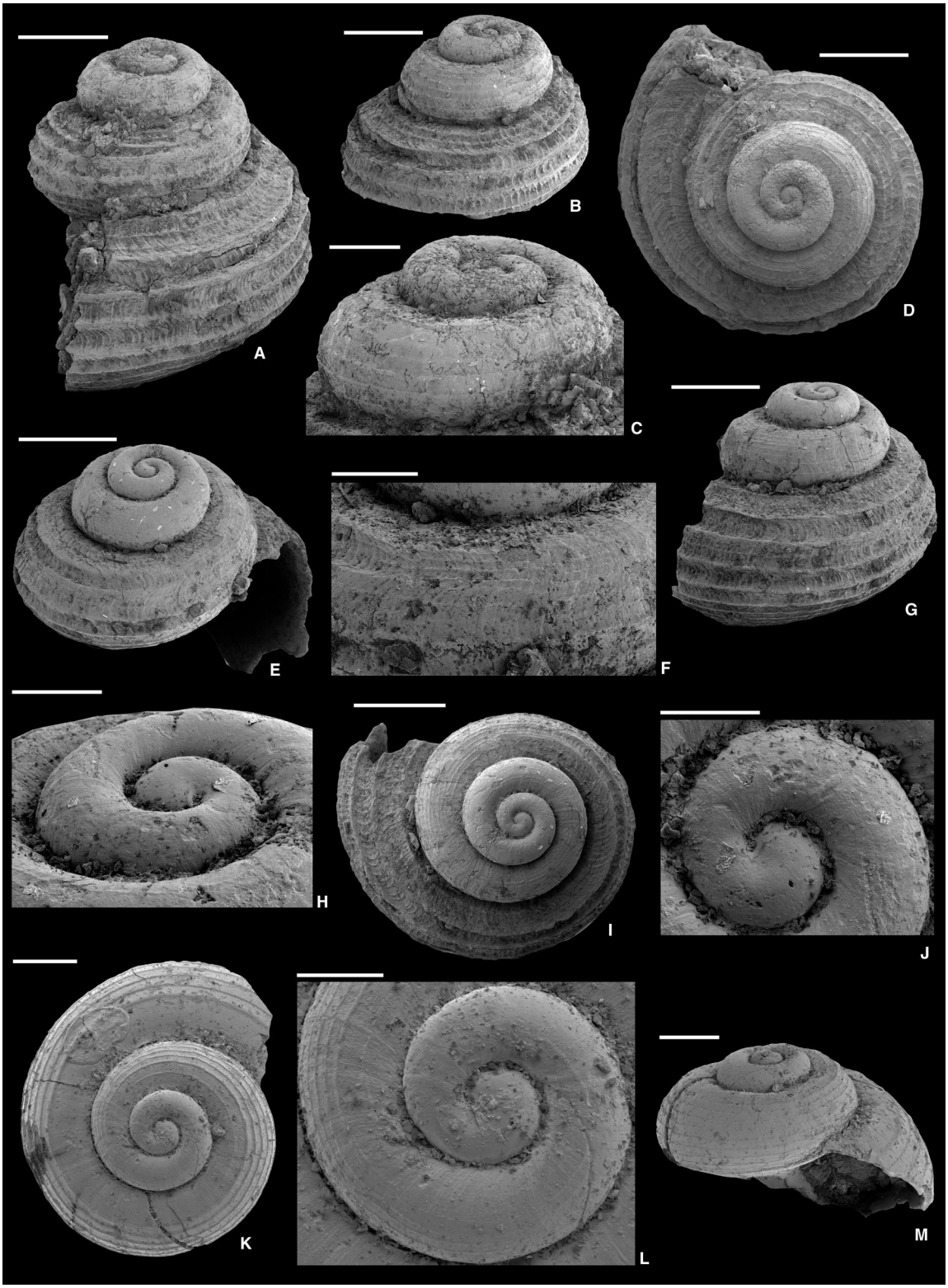

FIG. 9. *Baylea tenera* sp. nov. juveniles from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–D, SNSB-BSPG 2011 X 242, paratype; C, oblique lateral view, detail of early whorls with bioerosion. E–J, SNSB-BSPG 2011 X 244, F, close up showing the development of selenizone from concave sinus; H, oblique lateral view, detail of smooth early whorls; J, apical view, detail of first whorl. K–M, SNSB-BSPG 2011 X 245; L, apical view, detail of first two whorls, showing gradual formation of spiral thread. Scale bars represent: 0.5 mm (A, B, D, E, G, I); 0.2 mm (C, F, K, M); 0.1 mm (H, J, L). All SEM images.

lines, prominent spiral cords) suggest that this species belongs to *Baylea*.

Most *Baylea* species, including the type species *Ba. yvanii*, have a gradate spire with a distinctly angulated whorl face. *Baylea tenera* differs from most of *Baylea* species in having a basically convex whorl profile and only slight angulations in the latest preserved whorls. There are other *Baylea* species that have a convex whorl profile; *Ba. capertoni* Beede, 1907 (= ?*Ba. texana* Girty, 1908; see Knight 1940) closely resembles *Ba. tenera* in ornamentation but is more high-spired and has trochospiral early whorls (Knight 1940). The Permian species *Ba. subpenea* (Netchaev, 1894) as documented by Mazaev (2015) and *Ba. nemdaensis* Mazaev, 2015 from Russia are similar in whorl profile but differ in having much stronger spiral cords and in being more high-spired.

Isaji & Okura (2020) reported a Pleurotomariida species from the Carboniferous of Fukuji, Japan that is similar to *Ba. tenera* in whorl profile and ornamentation. The specimen figured by these authors is probably a juvenile and this species might belong to *Baylea*. It differs from *Ba. tenera* in having more strongly developed and fewer spiral cords on the third whorl.

Genus GLABROCINGULUM Thomas, 1940*a*

Emended diagnosis. Turbiniform with conical (subgenus *Glabrocingulum*) or gradate (subgenus *Ananias*) spire; selenizone at whorl angulation at about mid-whorl or above; whorls embrace just below selenizone (*Glabrocingulum*) or distantly below selenizone (*Ananias*); selenizone concave, smooth with lunulate growth lines only; early whorls smooth, occasionally with fine spiral threads, evenly convex with first whorl planispiral; ornament of collabral axial ribs or threads and spiral lirae or cords appearing on third or fourth whorl along with formation of selenizone and whorl angulation; ornament forming reticulate pattern with nodular intersections; commonly with subsutural nodes or riblets.

Remarks. Glabrocingulum is a cosmopolitan, diverse genus ranging at least from the Mississippian to the Triassic. The well-preserved specimens at hand show the early ontogeny in great detail. In principle, the well-preserved juvenile specimens representing *G. parvum* Foster *et al.*, 2017 from the Early Triassic of Svalbard have the same type of early ontogenetic shell (although with a fine spiral striation) as the species reported herein. *Glabrocingulum parvum* has a weak ornamentation on the later teleoconch whorls but is otherwise clearly a representative of *Glabrocingulum* witnessing the survival of this genus at the end-Permian mass extinction.

Subgenus GLABROCINGULUM Thomas, 1940*a*

Type species. Glabrocingulum beggi Thomas, 1940*a* from the Carboniferous of Scotland; original designation.

Remarks. In the literature there are several erroneous taxonomic attributions either of *Glabrocingulum* specimens to other genera or of specimens representing other genera to *Glabrocingulum*. In these remarks we will try to clarify these problematic assignments.

Gosseletina nodosa Hoare *et al.*, 1997 does not belong to *Gosseletina*, which has a slightly convex selenizone that is flush to the whorl surface. However, *Gosseletina nodosa* has a concave selenizone, which is bordered by projecting shell edges and it has a nodose ornament on its base which is characteristic of many Carboniferous *Glabrocingulum* species. *Gosseletina nodosa* Hoare *et al.*, 1997 represents a junior synonym of *Glabrocingulum* (*Glabrocingulum*) *beedei* (Mark, 1912) (see Sturgeon 1964*b*, pl. 121 figs 1–5, and Kues 2004, figs 8.6–8.13, for illustrations of this species). The specimen assigned to *Gosseletina spironema* (Meek & Worthen, 1866*a*) by Sturgeon (1964*a*, pl. 32 fig. 11) was included in the synonymy of *Gosseletina nodosa* (= *Glabrocingulum* (*Glabrocingulum*) *beedei*) by Hoare *et al.* (1997). Sturgeon's (1964*a*) specimen agrees well with the specimens assigned to *Gosseletina spironema* by Kues & Batten (2001, figs 7.2–7.4) and therefore Sturgeon's (1964*a*) initial assignment is correct.

Bandel (2009) erected *Campbellospira missouriensis* from the Pennsylvanian Henrietta Shale from Missouri, USA. In our opinion the three specimens figured by Bandel (2009) belong to two different taxa, neither of which represents *Campbellospira*. The holotype (Bandel 2009, pl. 5 fig. 63) differs from *Campbellospira* in having more pronounced spiral cords and is ornamented with denser and stronger axial ribs starting from the second whorl, forming a reticulate pattern. The other two specimens (Bandel 2009, pl. 5 figs 64–65) are ornamented with widely spaced axial ribs starting from the third whorl and have a smaller protoconch (Bandel 2009 stated in the figure caption that all three specimens are 1.5 mm in width/height). In our opinion the holotype (Bandel 2009, pl. 5 fig. 63) is a juvenile phymatopleurid belonging to either *Phymatopleura* (Fig. 24) or *Paragoniozona* (Figs 28–30) and the other specimens (Bandel 2009, pl. 5 figs 64–65) represent juvenile *Glabrocingulum* (Figs 11, 14–15). Therefore, it is herein assigned to *Phymatopleura*: *Phymatopleura*? *missouriensis* (Bandel, 2009) comb. nov.

Bandel (2009) assigned three juvenile specimens from the Pennsylvanian Henrietta Shale from the Missouri, USA to *Glabrocingulum*. The specimens assigned to *Glabrocingulum* by Bandel (2009, pl. 1 figs 7–8) have a reticulate ornament as discussed above and could be assigned to *Phymatopleura* (Fig. 24) or *Paragoniozona* (Figs 28–30). The second specimen (Bandel 2009, pl. 1 fig. 8) has nodes and a median spiral cord on its selenizone, which are typical of *Phymatopleura*. The specimen assigned to *Glabrocingulum* by Bandel (2009, pl. 1 fig. 6) has prominent lunulae, which is not a feature of *Glabrocingulum*. In *Glabrocingulum* the selenizone is concave and smooth, without visible ornament. The prominent lunulae and other shell characters suggest that the specimen figured by Bandel (2009, pl. 1 fig. 6) is a phymatopleurid. It might be assigned to *Eirlysia* Batten, 1956 based on the growth lines, shell shape, position of selenizone.

Yoo (1994) erroneously assigned species from the Lower Carboniferous of Australia to *Glabrocingulum*. *Glabrocingulum obesum* Yoo, 1994 (pl. 6 figs 4–10) has a selenizone with node-like lunulae and a median spiral cord, its selenizone is situated low

on whorl face and represents the whorl periphery. In contrast, *Glabrocingulum* has a smooth selenizone and the lower edge of the selenizone represents the periphery. *Glabrocingulum obesum* represents without doubt a phymatopleurid species due to its selenizone ornamentation. Therefore, it is herein assigned to *Paragoniozona*: *Paragoniozona obesum* (Yoo, 1994) comb. nov. *Glabrocingulum pustulum* Yoo, 1994 (pl. 7, figs 1–4) likewise is herein assigned to *Paragoniozona* (*Paragoniozona) pustulum* (Yoo, 1994) comb. nov.) although its lunulae are not as prominent as in other members of *Paragonizona*. *Glabrocingulum* sp. in Yoo (1994, pl. 7 figs 1–4) should be assigned to *Rhineoderma* (see Remarks on *Paragoniozona*, below, for more discussion on *Rhineoderma*).

The specimen figured as '*Glabrocingulum tongxinensis* (Guo)' by Pan (1997, fig. 2-18–19) from the Lower Carboniferous of Ningxia, China has a convex selenizone with nodular lunulae and represents *Worthenia* (*Worthenia*).

Glabrocingulum (*Glabrocingulum*) *grayvillense* (Norwood & Pratten, 1855)
Figures 10, 11

* 1855 *Pleurotomaria grayvillensis* Norwood & Pratten, p. 75, pl. 9 figs 7a–b.
1922 *Phanerotrema grayvillense*; Plummer & Moore, pl. 22 figs 14–15.
1955 *Glabrocingulum grayvillense* (Norwood & Pratten); Sloan, p. 278, figs 109–110.
1967 *Glabrocingulum* (*Glabrocingulum*) *grayvillense* (Norwood & Pratten); Yochelson & Saunders, p. 86.
1972*a* *Glabrocingulum grayvillense*; Batten, fig. 10.
1982 *Glabrocingulum* (*Glabrocingulum*) *grayvillense*; Schindel, figs 2a, 3.1a–f.
2001 *Glabrocingulum* (*Glabrocingulum*) *grayvillense* (Norwood & Pratten); Kues & Batten, p. 27, figs 6.5–6.9.
2014*b* *Glabrocingulum grayvillense*; Nützel, fig. 1H.

Material. A total of 2303 specimens. 3 from the Desmoinesian of Oklahoma (Wetumka Formation, OKD–15): SNSB-BSPG 2020 LXI. 526 from the Desmoinesian of Oklahoma (Wewoka Formation, OKD–11): SNSB-BSPG 2020 LXII 3–5, and a further 523 specimens (SNSB-BSPG 2020 LXII). 2 from the Desmoinesian of Oklahoma (Holdenville Formation, OKD–01): SNSB-BSPG 2020 LXIII. 6 from the Missourian of Oklahoma (Barnsdall Formation, Eudora Shale Member, OKM–02): SNSB-BSPG 2020 LXIV. 1 from the Desmoinesian of Texas (Dickerson Shale, TXD–01): SNSB-BSPG 2020 LXVIII. 6 from the Missourian of Texas (Placid Shale Member, TXM–14): SNSB-BSPG 2020 LXXI. 37 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 9, and a further 36 specimens (SNSB-BSPG 2009 XXII). 767 specimens from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 7, 20, 25–27, 33–35, and a further 759 specimens (256 specimens from the surface sample, 503 specimens from the bulk sample; SNSB-BSPG 2020 XCI). 832 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 2–3, and a further 830 specimens (169 specimens from the surface sample, 661 specimens from the bulk sample; SNSB-BSPG 2020 LXXX). 4 from the Virgilian of Texas (Finis Shale Member, TXV–29): SNSB-BSPG 2020 LXXIV. 4 from the Virgilian of Texas (Finis Shale Member, TXV–34): SNSB-BSPG 2020 LXXV. 63 from the Virgilian of Texas (Finis Shale Member, TXV–36): SNSB-BSPG 2020 LXXVI. 2 from the Virgilian of Texas (Finis Shale Member, TXV–40): SNSB-BSPG 2020 LXXVII. 1 from the Virgilian of Texas (Finis Shale Member, TXV–44): SNSB-BSPG 2020 LXXVIII. 3 from the Virgilian of Texas (Finis Shale Member, TXV–60): SNSB-BSPG 2020 LXXXI. 27 from the Virgilian of Texas (Finis Shale Member, TXV–120): SNSB-BSPG 2020 LXXXII. 11 from the Virgilian of Texas (unnamed shale member, Jacksboro Airport): SNSB-BSPG 2020 LXXXIV. 6 from the Virgilian of Texas (Wayland Shale Member, TXV–10): SNSB-BSPG 2020 LXXXVII. 2 from the Virgilian of Texas (Wayland Shale Member, BB-TXV–06): SNSB-BSPG 2020 LXXXVIII.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXX 2	15.4	16.3	96	–	9.5	7.8	0.7	0.08	0.07
2009 XXII 9	7.9	7.7	100	0.22	5.4	3.1	0.4	0.14	0.08
2020 XCI 7	17.4	17.4	100	–	10.6	8.5	0.9	0.11	0.09
2020 XCI 20	9.8	10.6	107	–	6.4	5.5	0.6	0.10	0.09
2020 XCI 25	11.3	13.8	112	–	8.2	7.3	0.6	0.08	0.07
2020 XCI 26	11.2	12.7	107	–	7.2	6.8	0.6	0.08	0.08

Description. Shell of moderate size, rotelliform, with conical to slightly gradate spire; largest specimen with about six whorls; suture impressed, situated just below abapical edge of selenizone, shifting downwards in last deflected whorl; initial whorl almost planispiral with a diameter of 0.15–0.19 mm; first 3–3.5 whorls smooth, evenly convex; onset of selenizone and subsutural riblets as well as spiral cord 1 after third whorl and somewhat later spiral cord 2 appears on subsutural zone; mature whorls embracing just below selenizone; whorl face angulated with selenizone at angulation; selenizone narrow (8–10% of whorl width), bordered by angular, raised crests (projecting shell edges of the slit); surface of selenizone oblique, concave, smooth with lunulate growth lines only; abapical border of selenizone forms periphery; mature whorl face above selenizone concave near selenizone, then straight, inclined, with adapical adpressed zone; adpressed zone ornamented with two spiral cords and axial riblets with nodular intersections; these subsutural nodes and riblets much stronger and more distant to each other than on remaining upper whorl face; whorl between suture and selenizone with more than 10 densely spaced spiral threads and prosocyrt growth striae with slightly nodose intersections; mature whorl face below selenizone concave, more or less parallel to shell axis, ornamented with up to six nodose cords and prosocyrt growth lines; base convex, with blunt angulation, ornamented with *c.* 17 nodose spiral cords; basal ornamentation more prominent than on whorl face; basal growth lines opisthocyrt near basal edge, prosocyrt near umbilicus; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex, curved backwards; base phaneromphalous.

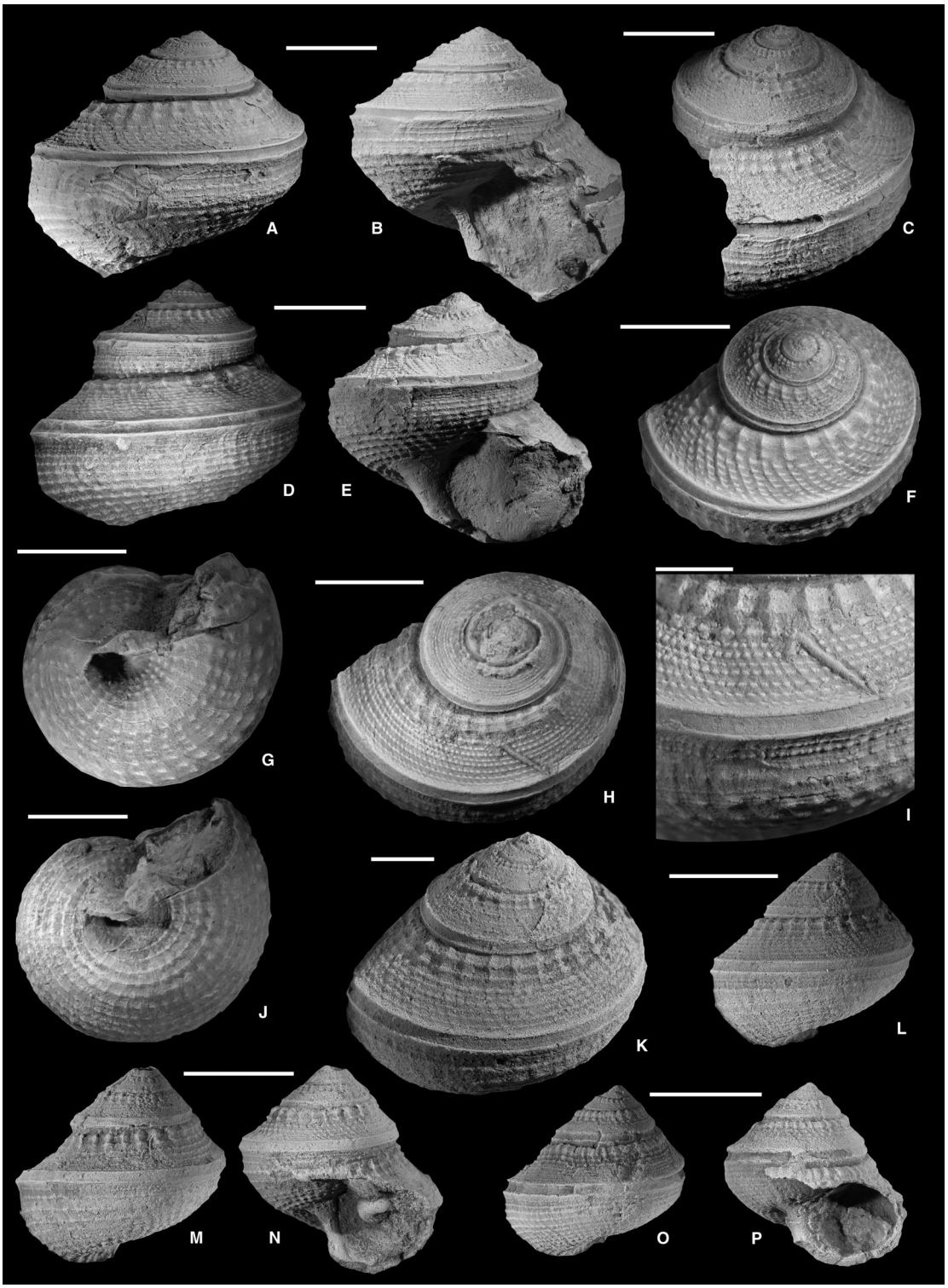

FIG. 10. *Glabrocingulum* (*Glabrocingulum*) *grayvillense* (Norwood & Pratten, 1855). A–C, SNSB-BSPG 2020 LXXX 2, from the Finis Shale Member (Virgilian, Texas). D–E, SNSB-BSPG 2020 LXXX 3, a specimen with highly deflected last whorl, from the Finis Shale Member (Virgilian, Texas). F–G, SNSB-BSPG 2020 XCI 26, from the Finis Shale Member (Virgilian, Texas). H–J, SNSB-BSPG 2020 XCI 25, from the Finis Shale Member (Virgilian, Texas); I, oblique apical view, detail of whorl face ornamentation. K–L, SNSB-BSPG 2020 LXII 3, from the Wewoka Formation (Desmoinesian, Oklahoma). M–N, SNSB-BSPG 2020 LXII 5, from the Wewoka Formation (Desmoinesian, Oklahoma). O–P, SNSB-BSPG 2020 LXII 4, from the Wewoka Formation (Desmoinesian, Oklahoma). Scale bars represent: 5 mm (A–H, J, L–P); 2 mm (I, K).

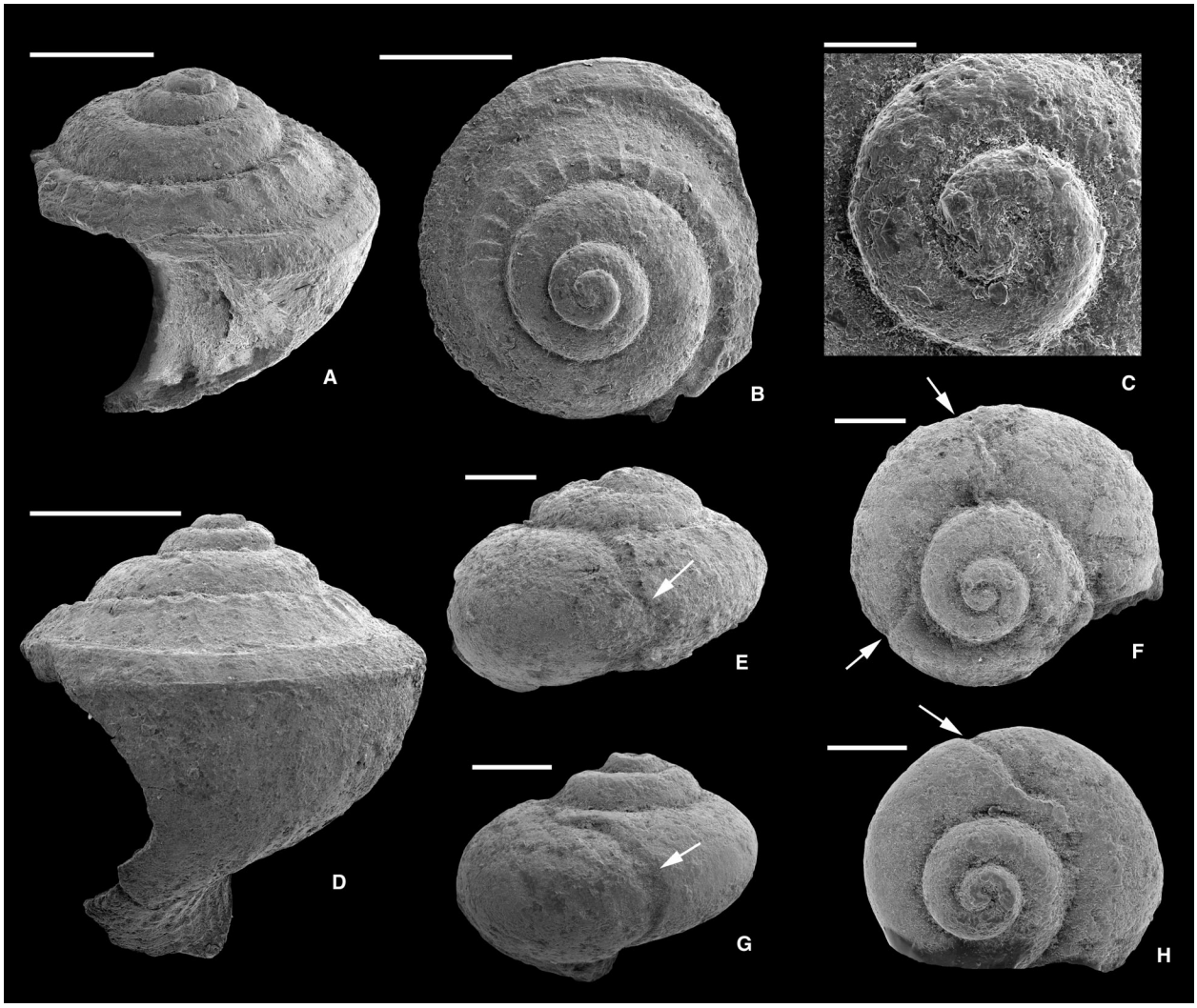

FIG. 11. *Glabrocingulum* (*Glabrocingulum*) *grayvillense* (Norwood & Pratten, 1855) juvenile specimens from the Finis Shale Member (Virgilian, Texas). A–D, SNSB-BSPG 2020 XCI 27. E–F, SNSB-BSPG 2020 XCI 34, arrows indicate repaired shell breakages. G–H, SNSB-BSPG 2020 XCI 35, arrows indicate repaired shell breakages. Scale bars represent: 0.5 mm (A, B, D); 0.1 mm (C); 0.2 mm (E–H). All SEM images.

Remarks. This is one of the most abundant Pennsylvanian gastropods of the US mid-continent. Sloan (1955) designated a neotype which agrees well with the present material. The specimen illustrated in Figure 10D–E is untypical because the last whorl shows a higher translation rate so that the suture is at the basal blunt angulation and the entire shell appears more high-spired than normal, thus becoming similar to *Ananias*. This characteristic and abundant species has been well studied and its smooth early whorls were previously documented by Schindel (1982). The small initial whorl and the fact that the first three whorls are smooth could point to the possession a larval shell of the planktotrophic type as is typical of Caenogastropoda (see Nützel 2014*a*). However, the transition to the mature, ornamented teleoconch is gradual and we did not find an indication of an abrupt change that would indicate metamorphosis. At present, we assume that the smooth second to fourth whorl section represents the early teleoconch. The shape of the early whorl and the late onset of the selenizone are similar to those of *G.* (*G.*) *parvum* Foster *et al.*, 2017 from the Lower Triassic of Svalbard. However, this species has spiral threads on the third whorl. Foster *et al.* (2017) interpreted the early whorl of *G.* (*G.*) *parvum* as a multi-whorled protoconch. However, as in our specimens, there seems to be no clear indication of that.

The specimens from the Desmoinesian Wewoka Formation of Oklahoma show considerable variability. These specimens are smaller than other studied specimens placed in *G.* (*G.*) *grayvillense* from younger horizons. Although some specimens from the Wewoka Formation have the same surface ornamentation and apical angle as the specimens from younger horizons, some of them have a higher apical angle and show an ornamentation similar to that of *G.* (*G.*) *quadrigatum*. The *Glabrocingulum* specimens from the Wewoka Formation are smaller than the specimens assigned to *G.* (*G.*) *quadrigatum* in the present study. The specimens from the Wewoka Formation might be stunted or represent a transition between the two species. They are

assigned to *G.* (*G.*) *grayvillense* tentatively and three high-spired specimens are figured herein (Fig. 10K–P).

Some of the studied juvenile *Glabrocingulum* specimens with a shell width of 1 mm show repaired scars (Fig. 11E–H) (see discussion below).

Glabrocingulum (*Glabrocingulum*) cf. *quadrigatum* Sadlick & Nielsen, 1963
Figure 12

cf. * 1963 *Glabrocingulum quadrigatum* Sadlick & Nielsen, p. 1098, pl. 150 figs 1–4, 9–12 [non figs 5–8], text-figs 5, 7.
cf. 1987 *Glabrocingulum* (*Glabrocingulum*) *quadrigatum* Sadlick & Nielsen; Gordon & Yochelson, p. 61, pl. 5 figs 10–15, pl. 6 figs 11, 16, 19.
cf. 1994 *Glabrocingulum* (*Glabrocingulum*) *quadrigatum* Sadlick & Neilsen; Jeffery *et al.*, p. 68, figs 6.22–6.27.

Material. 29 specimens from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 10–14, 24, and a further 23 specimens (SNSB-BSPG 2020 LVIII).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 10	7.4	6.8	105	0.25	5.3	3.1	0.4	0.13	0.07
2020 LVIII 11	–	11.9	99	0.24	–	–	–	–	–
2020 LVIII 12	8.6	9.6	98	–	5.0	3.8	0.4	0.10	0.08
2020 LVIII 14	12.4	12.8	94	–	8.9	7.1	0.8	0.11	0.09
2020 LVIII 24	9.2	8.8	105	0.24	5.3	3.6	0.4	0.10	0.07

Description. Shell small, with low, conical spire, largest specimen with *c.* 6 whorls; suture impressed, situated below selenizone, shifting downwards in last whorl; early whorl face before onset of selenizone convex, smooth then becoming flatly convex with onset of selenizone, ornamented with spiral cords; subsutural cord strongest, nodose, angulating whorl face somewhat; later whorl face above selenizone flat to slightly concave, ornamented with 6–9 nodose spiral cords; prominence of nodes increase towards adapical suture; later whorl face below selenizone concave, ornamented with up to four nodose cords; growth lines on whorl face prosocline above selenizone, prosocyrt below selenizone; nodes on the adapical three cords on the last whorl bridged by axial riblets; selenizone concave, oblique, visible after third whorl, bordered above and below by raised straight shell edges, situated at whorl angulation; selenizone ornamented with faint striae-like lunulae; base convex, ornamented with about 16–20 nodose spiral cords; basal ornamentation more prominent than the ones on whorl face; basal growth lines opisthocyrt near basal edge, prosocyrt near umbilicus; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex, callus-like thickened, curved backwards; base narrowly phaneromphalous.

Remarks. Gordon & Yochelson (1987) erected a new species based on the paratype of *Glabrocingulum quadrigatum* (Sadlick & Nielsen 1963, pl. 150 figs 5–8) and emendated the diagnosis of *G.* (*G.*) *quadrigatum*. The studied specimens fall within the range of variation of *G.* (*G.*) *quadrigatum* as described by Gordon & Yochelson (1987). However, the specimens reported by Gordon & Yochelson (1987) have fewer (10–15) and stronger spiral cords on the base than the specimens studied herein (which have 16–20 fine spiral cords on base). In some of the studied specimens, the suture is situated distinctly below the selenizone (as is also the case in *G.* (*Ananias*)) whereas it is close to the suture in *G.* (*Glabrocingulum*). Apart from this difference, the specimens are identical in whorl morphology and ornamentation, so this character is treated herein as intraspecific variation.

The specimens that are assigned to *G.* (*G.*) cf. *quadrigatum* herein differ from *G.* (*G.*) *grayvillense* in having more closely spaced subsutural nodes, fewer spiral cords, a thickened inner lip, and a lower spiral angle (higher spire).

Subgenus ANANIAS Knight, 1945

Type species. Phanerotrema welleri Newell, 1935

Remarks. Glabrocingulum (*Ananias*) can be differentiated from *Glabrocingulum* (*Glabrocingulum*) by its more high-spired shell and in having a well-developed vertical lateral whorl face in all teleoconch whorls. In *G.* (*Glabrocingulum*) whorls embrace just below the selenizone except on the last whorl, which is progressively deflected downwards. By contrast, whorls embrace well below the selenizone in *G.* (*Ananias*) throughout its ontogeny. The early shells of the two subgenera differ: low-spired in *G.* (*Glabrocingulum*), more high-spired and acute in *G.* (*Ananias*) (compare the juvenile specimens in Fig. 11 with those in Figs 14–15). *Ananias* was used at genus level and separated from *Glabrocingulum* by Batten (1989) since 'the suture is positioned well below the lower selenizone margin even in early ontogeny'. This approach was refuted by the majority of subsequent workers but followed by some (see Pinilla 2012). We prefer to keep *Ananias* as a subgenus because it differs from *Glabrocingulum* only in the translation rate and hence the transition from the *Glabrocingulum* to *Ananias* or vice versa might have occurred multiple times (see Remarks on *G.* (*A.*) *welleri*, below). It is possible that *G.* (*Ananias*) originated multiple times from different *G.* (*Glabrocingulum*) species by increasing the whorl translation. As mentioned above, *G.* (*G.*) *quadrigatum* specimens may show the *G.* (*Ananias*) type of high-spired shells by situating the suture distantly below the selenizone.

Glabrocingulum (*Ananias*) originates in the Mississippian (Gordon & Yochelson 1983, 1987; Amler 2006) and has been reported from the Middle Triassic (Yin & Yochelson 1983). Although *Glabrocingulum* passed the Permian–Triassic boundary (Foster *et al.* 2017), it is not certain if the Middle Triassic species are true representatives of *Glabrocingulum*.

Glabrocingulum (*Ananias*) *welleri* (Newell, 1935)
Figure 13

1922 *Worthenia tabulata*; Plummer & Moore, pl. 19 fig. 25 [non pl. 22 figs 17–19].

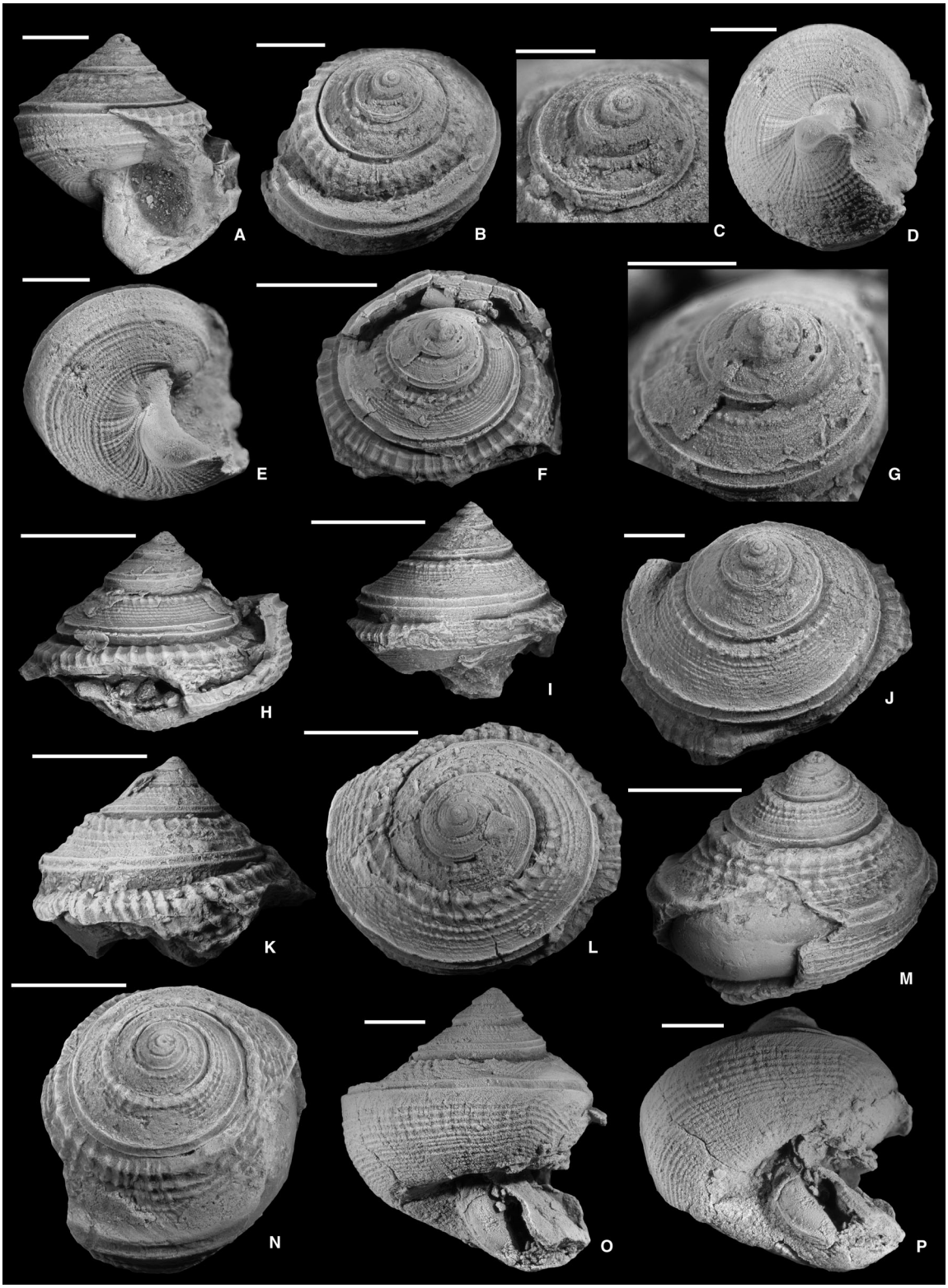

FIG. 12. *Glabrocingulum* (*Glabrocingulum*) cf. *quadrigatum* Sadlick & Nielsen, 1963 from the Gene Autry Shale (Morrowan, Oklahoma). A–E, SNSB-BSPG 2020 LVIII 10; C, oblique apical view, detail of earl whorls; D–E, oblique basal views, showing the thickened inner lip. F–H, SNSB-BSPG 2020 LVIII 11; G, oblique apical view, detail of early whorls. I–J, SNSB-BSPG 2020 LVIII 12. K–L, SNSB-BSPG 2020 LVIII 13. M–N, SNSB-BSPG 2020 LVIII 14. O–P, SNSB-BSPG 2020 LVIII 24; O, apertural view; P, oblique basal view, showing the thickened inner lip. Scale bars represent: 2 mm (A, B, D, E, G, J, O, P); 1 mm (C); 5 mm (F, H, I, K–N).

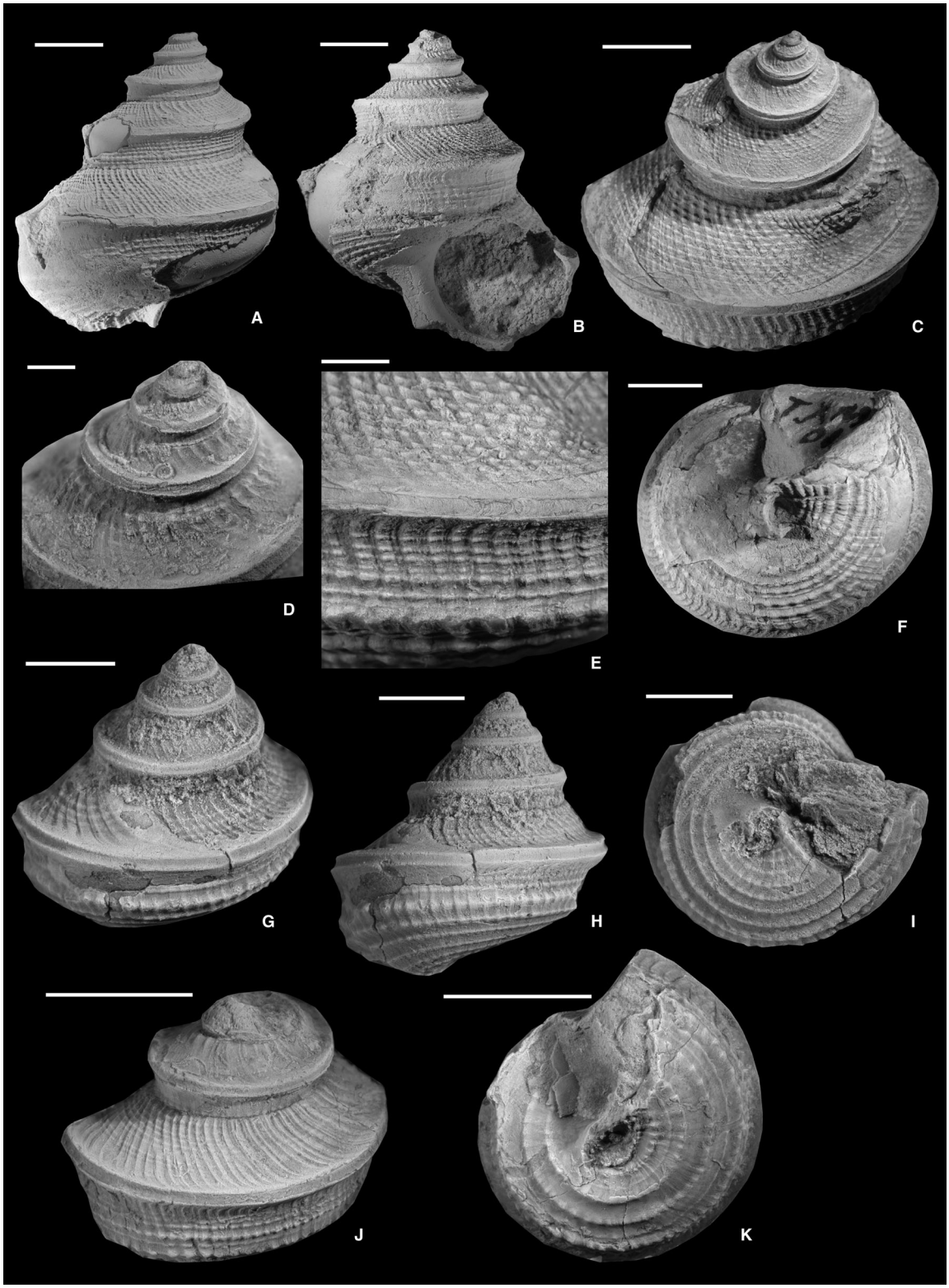

FIG. 13. *Glabrocingulum* (*Ananias*) *welleri* (Newell, 1935). A–B, SNSB-BSPG 2020 LXXXII 1, from the Finis Shale Member (Virgilian, Texas). C–F, SNSB-BSPG 2020 LXX 1, from the Wolf Mountain Shale (Missourian, Texas); D, oblique apical view, detail of early whorls; E, oblique apical view, detail of whorl face ornamentation. G–I, SNSB-BSPG 2020 LXIII 3, from the Holdenville Formation (Desmoinesian, Oklahoma). J–K, SNSB-BSPG 2020 LXVI 1, from the Lawrence Formation (Virgilian, Kansas). Scale bars represent: 5 mm (A–C, F, J–K); 1 mm (D); 2 mm (E, G–I).

* 1935 *Phanerotrema*? *welleri* Newell p. 34B, pl. 36 fig. 3a–g.
1967 *Glabrocingulum* (*Ananias*) *welleri* (Newell); Yochelson & Saunders, p. 85.
1982 *Glabrocingulum* (*Ananias*) *welleri*; Schindel, fig. 3.2d [non fig. 3.2a–c].

Material. A total of 12 specimens. 1 from the Desmoinesian of Oklahoma (Wetumka Formation, OKD–13): SNSB-BSPG 2020 LIX 1. 1 from the Desmoinesian of Oklahoma (Holdenville Formation, OKD–01): SNSB-BSPG 2020 LXIII 3. 1 from the Virgilian of Kansas (Lawrence Formation, KSV–05): SNSB-BSPG 2020 LXVI 1. 2 from the Virgilian of Kansas (Lawrence Formation, KSV–06): SNSB-BSPG 2020 LXVII. 2 from the Missourian of Texas (Wolf Mountain Shale Member, TXM–01): SNSB-BSPG 2020 LXX 1–2. 4 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 41 and a further 3 specimens (SNSB-BSPG 2020 XCI). 1 from the Virgilian of Texas (Finis Shale Member, TXV–120): SNSB-BSPG 2020 LXXXII 1.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXIII 3	6.8	6.4	80	–	3.6	3.5	0.3	0.08	0.08
2020 LIX 1	12.5	11.8	82	–	6.8	6.6	0.5	0.07	0.07
2020 LXX 1	22.1	21.2	85	–	13.1	11.9	0.5	0.05	0.04
2020 LXX 2	15.2	12.8	75	–	8.2	7.4	0.7	0.09	0.08
2020 LXXXII 1	24.1	21.6	73	–	11.5	11.4	0.7	0.06	0.06
2020 XCI 41	22.1	19.3	74	–	10.2	10.5	0.7	0.06	0.06

Description. Shell of moderate size, trochiform, higher than wide; largest specimen with about eight whorls; spire gradate; suture shallow, situated at basal edge; early whorl face after the onset of selenizone angulated, ornamented with prosocline axial ribs which form subsutural nodes near adapical suture and disappear near selenizone; later whorl face ornamented with fine spiral cords and axial ribs with nodular intersections; nodes commonly spirally elongated; later whorl face concave above selenizone, ornamented with up to 14 spiral cords and oblique prosocline axial ribs; later whorl face concave below selenizone, lying subparallel to shell axis, facing slightly abapically, ornamented with up to six spiral cords and sinuous axial ribs forming groove and ridge pattern, slightly prosocyrt below selenizone, slightly opisthocyrt above suture; selenizone elevated, flat, bordered above and below by raised, straight shell edges; lower edge somewhat more protruding forming periphery; selenizone ornamented with faint U-shaped lunulae formed by growth-lines; base convex, ornamented with up to 12 nodose spiral cords of alternating strength; basal edge angular; basal growth lines slightly opisthocyrt near basal edge, slightly prosocyrt near umbilicus; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex, curved backwards; base narrowly phaneromphalous.

Remarks. Glabrocingulum (*Ananias*) *welleri* can be differentiated from *G.* (*A.*) *tularosaensis* Kues, 2004 by its larger shell, in details of the ornamentation (that of *G.* (*A.*) *tularosaensis* is generally denser), by having a more protruding selenizone that lacks spiral lirae and by having an angular basal edge.

Schindel (1982) suggested that *G.* (*A.*) *marcouianum* (Geinitz, 1866) might be a synonym of *G.* (*A.*) *welleri* (Newell, 1935) and figured representatives of two different species under that name. Schindel (1982) proposed an evolutionary lineage from *G.* (*G.*) *grayvillense* to *G.* (*A.*) *wannense* (Newell, 1935) to *G.* (*A.*) *welleri* characterized by a transition from a low to a higher spire based on the stratigraphic occurrences of these three species. He supported his opinion with a study by Eldredge (1968) which reported a co-occurrence of *G.* (*A.*) *welleri* and *G.* (*A.*) *wannense* in the Desmoinesian of Oklahoma. Our study confirms the presence of *G.* (*A.*) *welleri* in the Desmoinesian of Oklahoma (locality OKD–13).

Glabrocingulum (*Ananias*) *tularosaensis* Kues, 2004
Figures 14, 15

? 1866 *Pleurotomaria marcouiana* Geinitz, p. 10, table 1, fig. 10.
? 1967 *Glabrocingulum* (*Ananias*) *marcouianum* (Geinitz); Yochelson & Saunders, p. 85.
1982 *Glabrocingulum* (*Ananias*) *welleri*; Schindel, figs 2b, 3.2a–c [non fig. 3.2d].
* 2004 *Glabrocingulum* (*Ananias*) *tularosaensis* Kues, figs 8.14–8.23.
2014*b* *Ananias* sp.; Nützel, fig. 1H.

Material. A total of 2013 specimens. 1 from the Missourian of Oklahoma (Barnsdall Formation, Eudora Shale Member, OKM–02): SNSB-BSPG 2020 LXIV. 387 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 7, 18, and a further 385 pecimens (SNSB-BSPG 2009 XXII). 840 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 28–31, and a further 836 specimens (14 from the surface sample, 822 from the bulk sample; SNSB-BSPG 2020 XCI). 750 specimens (8 from the surface sample, 742 from the bulk sample) from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX. 11 from the Virgilian of Texas (Finis Shale Member, TXV–29): SNSB-BSPG 2020 LXXIV. 4 from the Virgilian of Texas (Finis Shale Member, TXV–36): SNSB-BSPG 2020 LXXVI. 4 from the Virgilian of Texas (un-named shale member, Jacksboro Airport): SNSB-BSPG 2020 LXXXIV. 2 from the Virgilian of Texas (Wayland Shale Member, BB-TXV–06): SNSB-BSPG 2020 LXXXVIII.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 7	8.9	8.4	87	0.23	4.7	3.9	0.3	0.09	0.07
2009 XXII 18	8.9	7.8	88	–	4.6	3.8	0.4	0.10	0.08
2020 XCI 28	6.2	6.1	82	0.20	3.3	2.8	0.3	0.11	0.09

Description. Shell small, trochiform, higher than wide; largest specimen with about seven whorls; suture shallow, situated at basal edge; first whorl almost planispiral, with a diameter of 0.15 mm; first 3.5 whorls smooth; early whorl face before the onset of selenizone convex, smooth; early whorl face angulated

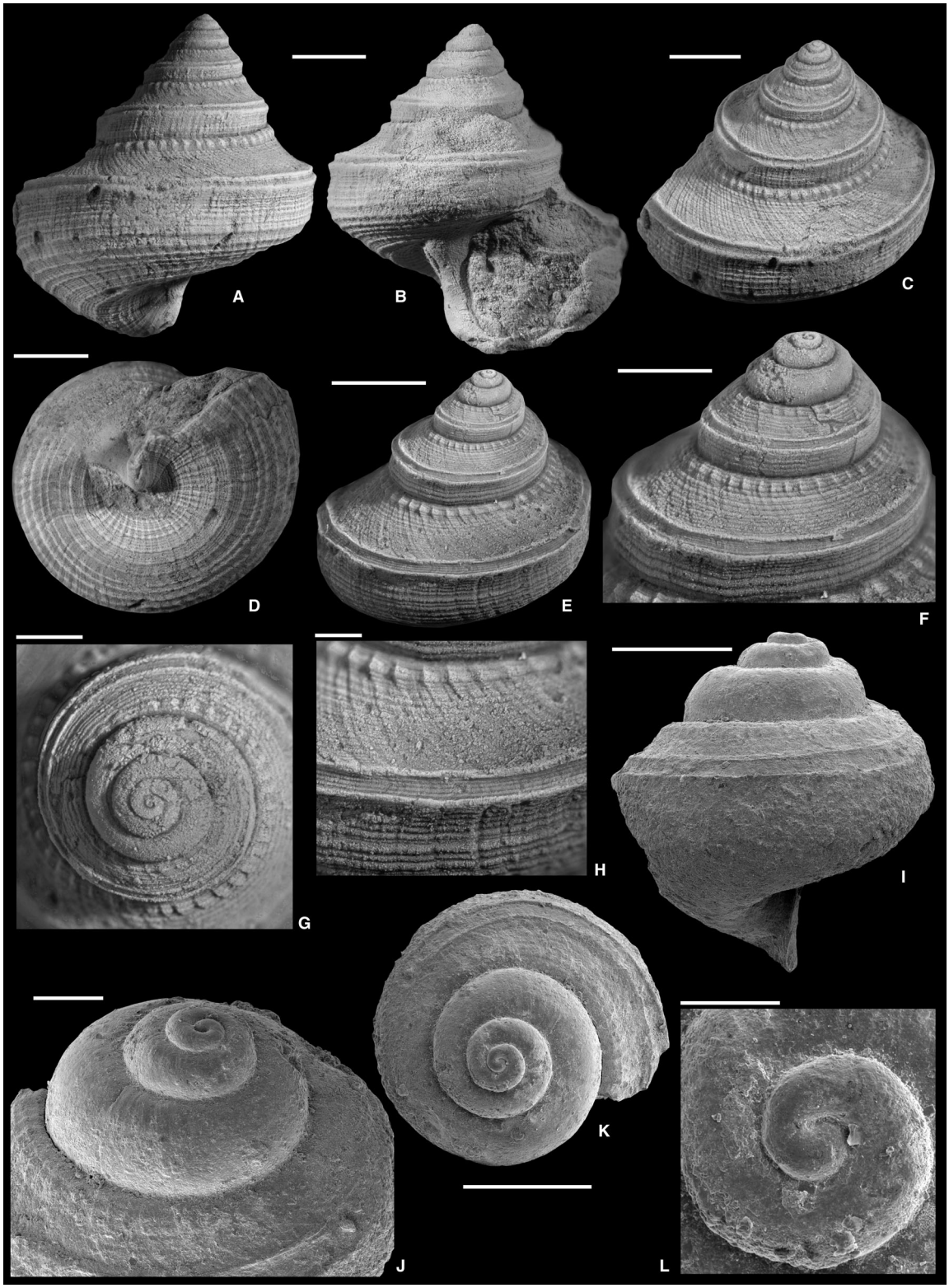

FIG. 14. *Glabrocingulum* (*Ananias*) *tularosaensis* Kues, 2004. A–D, SNSB-BSPG 2009 XXII 18, from the Colony Creek Shale (Virgilian, Texas). E–H, SNSB-BSPG 2020 XCI 28, from the Finis Shale Member (Virgilian, Texas); F, oblique apical view, detail of early whorls and ornament; G, apical view, detail of early whorls; H, oblique apical view, detail of whorl face ornamentation. I–L, SNSB-BSPG 2020 XCI 29, juvenile specimen from the Finis Shale Member (Virgilian, Texas); L, apical view, detail of first whorl. Scale bars represent: 2 mm (A–E); 1 mm (F); 0.5 mm (G–I, K); 0.2 mm (J); 0.1 mm (L). I–L, SEM images.

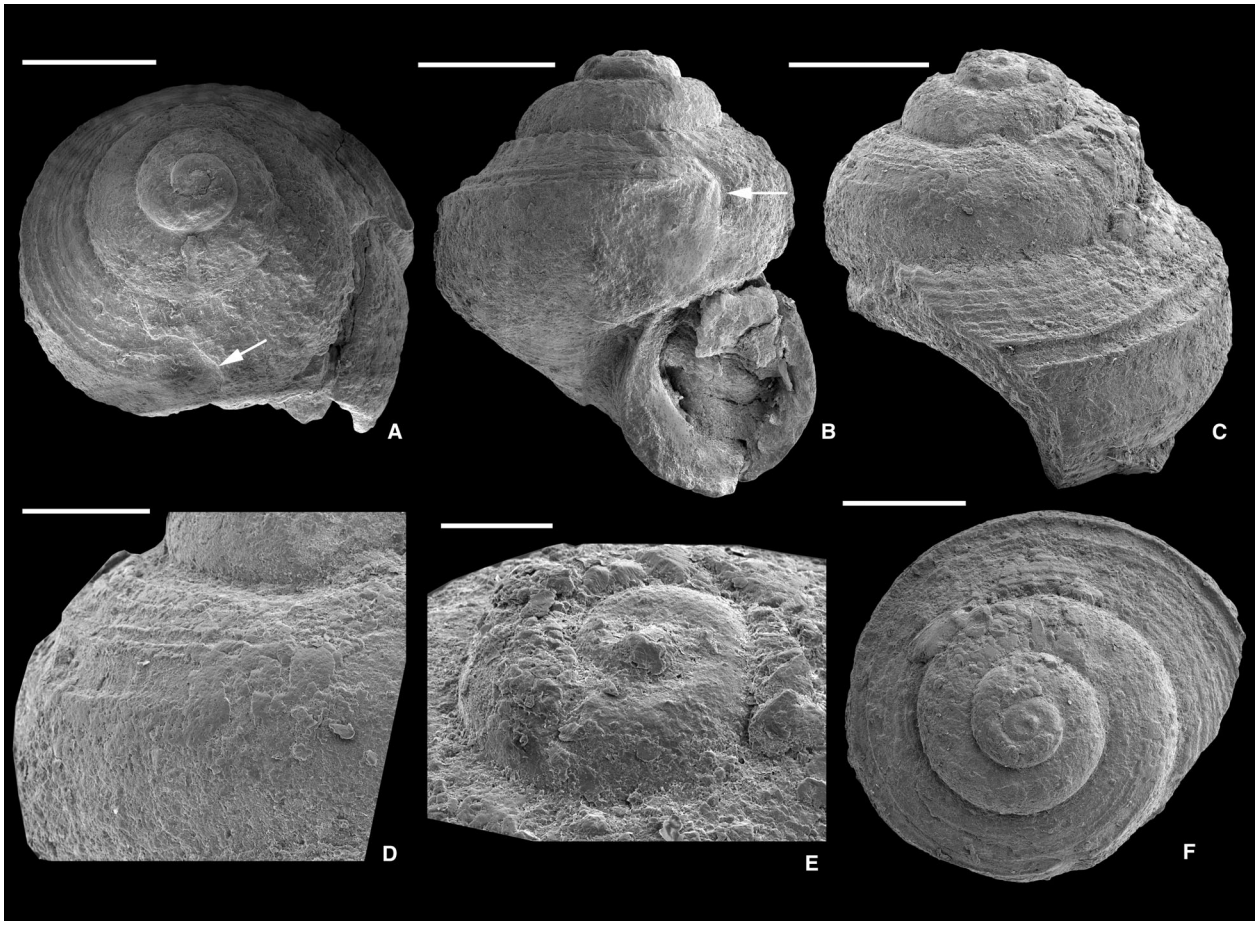

FIG. 15. *Glabrocingulum* (*Ananias*) *tularosaensis* Kues, 2004, juvenile specimens from the Finis Shale Member (Virgilian, Texas). A–B, SNSB-BSPG 2020 XCI 30, arrows indicate repaired shell breakages. C–F, SNSB-BSPG 2020 XCI 31; E, oblique apical view, detail of first whorl. Scale bars represent: 0.5 mm (A–C, F); 0.2 mm (D); 0.1 mm (E). All SEM images.

after the onset of selenizone and ornamented with subsutural nodes and spiral striae; later whorl face angulated at both borders of selenizone with abapical border forming periphery; whorl face concave above selenizone, ornamented with fine, densely spaced spiral cords or lirae and oblique prosocyrt growth striae; whorls adpressed at subsutural zone with distinct, slightly axially elongated nodes; selenizone concave, oblique, starting after the third whorl, bordered above and below by raised straight shell edges, situated at median angulation; selenizone ornamented with spiral threads and faint, striae-like lunulae; later whorl face below selenizone concave just below selenizone then flatly convex, ornamented with fine, densely spaced spiral striae and cords and prosocyrt growth striae; spiral cords of variable strength with the strongest ones low on whorl face, some of which much broader than interspaces; spiral striae/cords on whorl face, selenizone and base are somewhat trembling/wavy; basal edge rounded; base convex, ornamented with striae and occasionally 12–14 spiral cords; basal growth lines opisthocyrt near basal edge, prosocyrt near umbilicus; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex, curved backwards; base narrowly phaneromphalous.

Remarks. The early ontogeny of *G.* (*A.*) *tularosaensis* resembles that of *G.* (*G.*) *grayvillense* as discussed above including the small size of the initial whorl and the first 3.5 whorls being smooth and rounded. As discussed for *G.* (*G.*) *grayvillense*, we do not interpret this as a caenogastropod-type larval shell because a clear boundary indicating metamorphosis is lacking. Instead, we interpret the early smooth whorl as representing the juvenile teleoconch.

Kues (2004) discussed the differences between *G.* (*A.*) *tularosaensis* and other *G.* (*Ananias*) species and the possible relation of *G.* (*A.*) *tularosaensis* to *G.* (*A.*) *marcouianum* (Geinitz, 1866). Geinitz (1866, p. 10) mentioned the spiral striation of variable strength in *G.* (*A.*) *marcouianum* that is also present in our material. However, the figure provided by Geinitz (1866, fig. 10) does not show the subsutural nodes or riblets which are distinct in our material as well as in the type material figured by Kues (2004) for *G.* (*A.*) *tularosaensis*. The type material of *G.* (*A.*) *marcouianum*, which is housed at Harvard University's Museum of Comparative Zoology (Gordon & Yochelson 1987, p. 75), has not been well documented yet; therefore, the possibility that the two species are conspecific cannot be ruled out with certainty.

Glabrocingulum (Ananias) cf. *talpaensis* Kues & Batten, 2001
Figure 16

cf. * 2001 *Glabrocingulum* (*Ananias*) *talpaensis* Kues & Batten, p. 29, figs 6.14–6.15.

Material. A total of 3 specimens. 2 from the Missourian of Oklahoma (Coffeyville Formation, Mound City Shale Member, OKM–25): SNSB-BSPG 2020 LXV 1–2. 1 from the Desmoinesian of Texas (Lazy Bend Formation, TXD–03): SNSB-BSPG 2020 LXIX.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXV 1	3.5	3.1	79	0.18	2.0	1.2	0.2	0.13	0.08
2020 LXV 2	4.8	4.1	65	0.19	2.2	1.7	0.2	0.09	0.07

Description. Shell very small, trochiform, higher than wide, the largest specimen with about seven whorls; spire gradate; suture shallow, situated at basal edge; first whorl 0.17 mm in diameter, without visible ornament; early whorl face before the onset of selenizone rounded convex, ornamented with spiral cords; later whorl face above selenizone concave, ornamented with three spiral cords and oblique prosocyrt, axial ribs and nodes where axial ribs and spiral cords intersect; axial ribs cover adapical two-thirds of upper whorl face; later whorl face below selenizone starts concave just below selenizone, then turns convex, ornamented with two spiral cords; upper and lateral whorl face equally wide; lower third of upper whorl face and upper third of lateral whorl face without ornament; selenizone concave, starting after 3.5 whorls, bordered above and below by raised straight shell edges, situated at median angulation; base convex, ornamented with about 12 strong spiral cords; basal edge rounded, representing periphery; aperture not seen.

Remarks. Glabrocingulum (*A.*) cf. *talpaensis* differs from other *Glabrocingulum* species studied here in having spiral cords on its early teleoconch and in being very small. Peel (2016, fig. 9Q) figured the juvenile whorls of *G.* (*G.*) *armstrongi* Thomas, 1940*a*, which is ornamented with spiral lirae on its early teleoconch

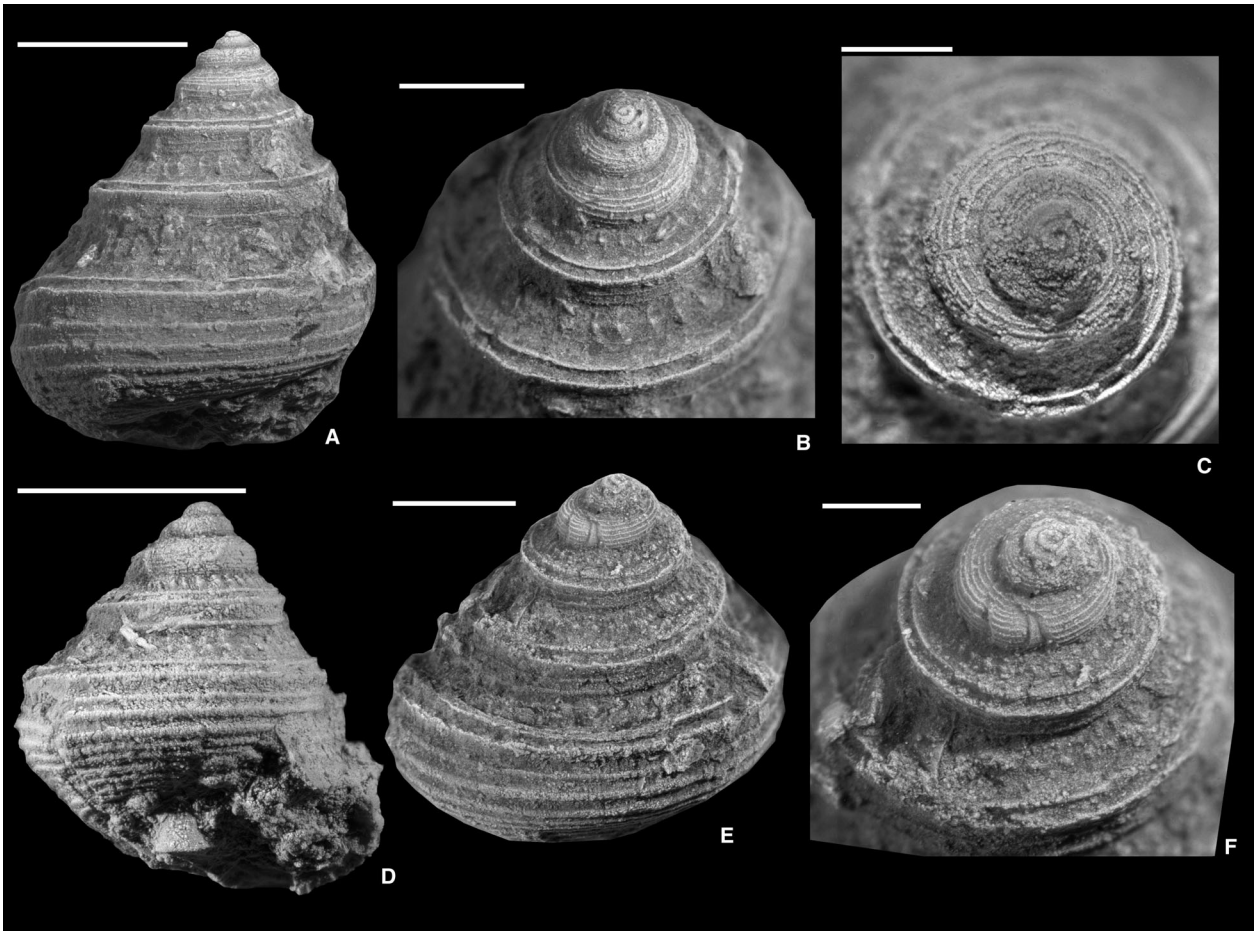

FIG. 16. *Glabrocingulum* (*Ananias*) cf. *talpaensis* Kues & Batten, 2001 from the Mound City Shale (Missourian, Oklahoma). A–C, SNSB-BSPG 2020 LXV 2; B, oblique apical view, detail of early whorls; C, apical view, detail of first four whorls before the onset of selenizone and the fifth whorl with selenizone. D–F, SNSB-BSPG 2020 LXV 1; F, oblique apical view, detail of early whorls. Scale bars represent: 2 mm (A, D); 1 mm (B, E); 0.5 mm (C, F).

similar to the studied specimens. The studied specimens are smaller than the type specimens of *G.* (*A.*) *talpaensis*, which are up to 12 mm in height (Kues & Batten 2001, p. 30) and differ slightly in ornamentation.

Genus SPIROSCALA Knight, 1945

Type species. Spiroscala pagoda Knight, 1945 from the Carboniferous of Texas, USA; original designation.

Remarks. Spiroscala unites species with a conical shell having the selenizone low on the spire whorls (close to the abapical suture). The morphology of the early whorls of *Spiroscala* specimens documented herein (Fig. 17C, F) and elsewhere (e.g. *Spiroscala costata* [= *Borestus costatus*] in Yoo 1988, fig. 27; *Spiroscala* sp. in Jeffery *et al.* 1994, figs 7–20, 21) shows a protoconch of the trochoid condition and a selenizone formation similar to that of other eotomariid taxa; in the early teleoconch it is higher on the whorl face and moves downward later on. It is bordered by two spiral edges, the lower one representing the periphery. Based on these characters, *Spiroscala* is kept within Eotomariidae. The whorl face of mature whorls of *Spiroscala* species is angulated at the adapical border of the selenizone which is situated low on the whorl face.

The selenizone of *Spiroscala* is not only bordered by spiral ridges but also develops vertical plate-like extensions (Batten 1958) between the prominent spiral ridges; the selenizone is bordered by these plates. This morphological character is also shared with the eotomariid genera *Oehlertia* Perner, 1907 (e.g. Knight 1941, pl. 35 fig. 2), *Shwedagonia* Batten, 1956 (see Batten 1958 for examples), *Quadricarina* Blodgett & Johnson, 1992 (e.g. Frýda 2012, fig. 12H) and *Paraoehlertia* Frýda, 1998. These five genera also share axial ribs as dominant ornament. Axial ribs represent the dominant type of ornamentation in many Palaeozoic eotomariid taxa such as *Mourlonia* de Koninck, 1883, *Ptychomphalina* Fischer, 1885, *Lunulazona* Sadlick & Nielsen, 1963, *Tropidostropha* Longstaff, 1912 and *Euconospira* Ulrich *in* Ulrich & Scofield, 1897.

The presence of vertical plate-like extensions bordering the selenizone and the ornamentation pattern (dominance of prosocline axial ribs and weaker spiral threads) suggest an affinity of *Borestus costatus* Yoo, 1988 from the Early Carboniferous of Australia to *Spiroscala*. *Borestus costatus* has orthocline threads on the vertical plates bordering the selenizone as is also the case in *Spiroscala shwedagoniformis* as described below. However, the spiral ridge on the ramp and the slightly wider selenizone compared to other *Spiroscala* species prevent us from assigning *Bo. costatus* to *Spiroscala* with confidence; therefore, it is herein assigned as *Spiroscala*? *costata* (Yoo, 1988) comb. nov. Yoo (1994) assigned an additional specimen to *Bo. costatus* (Yoo 1994, pl. 10 figs 4–5). This specimen does not represent *Spiroscala*? *costata* because it differs in ornamentation (absence of prominent spiral ridge on ramp), has a higher position of the selenizone on the whorl face and in that the lower edge of the selenizone represents the whorl periphery. This specimen probably represents a *Glabrocingulum* species. *Borestus* sp. in Jeffery *et al.* (1994, figs 7–20, 21) from the Mississippian of Arkansas, USA can be assigned to *Spiroscala*.

The vertical plates bordering the selenizone are not developed in the type species of *Euconospira* as reported by Knight (1941, pl. 35 fig. 1) and are also absent in its subjective synonym *Trechmannia* Longstaff, 1912 (Knight 1941, pl. 35, fig. 3). However, the species assigned to *Euconospira* by Batten, 1958, *Eu. pulchra* and *Eu. varizona* have vertical plates bordering the selenizone and hence, the selenizone is narrower than in typical *Euconospira* species. They also have a distinctly convex ramp rather than a flat one and a more convex base so that the selenizone of these species is situated slightly higher on the whorls than in *Euconospira*. *Euconospira pulchra* and *Eu. varizona* are closer to *Spiroscala* than to *Euconospira*. The specimen assigned to *Eu. pulchra* by Batten (1958, pl. 40 figs 7–8) is not conspecific with the holotype and other figured *Eu. pulchra* specimens (Batten 1958, figs 1–6) and represents a true *Euconospira* due to the above discussed characters. *Euconospira varizona* specimens figured by Batten (1958, pl. 40 figs 10–11) come from the same formation as *Eu. pulchra* and more closely resemble *Spiroscala*. Other *Eu. varizona* specimens figured by Batten (1958, pl. 39 figs 18–23) seem to represent *Euconospira*. Herein, we place *Eu. pulchra* into *Spiroscala*. Since *Spiroscala pulchra* is occupied by Batten (1958), we replace *Euconospira pulchra* Batten, 1958, with *Spiroscala quasipulchra* nom. nov. Further study with the type material of Batten (1958) is needed to clarify whether *Eu. varizona* represents *Spiroscala* or not. Batten (1966, pl. 4 figs 2–4) erected *Spiroscala intricata* from the Lower Carboniferous of England that is quite similar to the species that Batten (1958) previously assigned to *Euconospira*. He also documented the vertical plates at the borders of the selenizone of *Sp. intricata*.

Spiroscala closely resembles *Shwedagonia* Batten, 1956 in shape and in position and morphology of the selenizone. Mazaev (2019*a*) discussed the genus *Shwedagonia* and placed species with or without umbilicus in *Shwedagonia*. We think that the very wide umbilicus of *Shwedagonia* and hence the smaller size of the aperture in comparison to the shell size are important characters. Moreover, the whorl portion below the selenizone and the base are much more prominent in the type species of *Shwedagonia*, *Shw. elegans* Batten, 1956, so that the selenizone is situated well above the mid-height of the last whorl. In contrast, the selenizone is situated at mid-height in *Spiroscala pagoda* Knight, 1945. The position of the selenizone and the prominence of the base suggest an important difference in the proportion of soft tissues above and below the selenizone between *Spiroscala* and *Shwedagonia*. In the classification proposed by Mazaev (2019*a*), all the above-mentioned characters are lumped into *Shwedagonia* and the depth of slit becomes the only criterion to differentiate the two genera. Mazaev (2019*a*) used the presence of vertical plates in the selenizone as a diagnostic character for *Shwedagonia* but they are also present in the selenizone of the type species of *Spiroscala*; therefore, the selenizone character complex cannot be used for a separation of *Shwedagonia* from *Spiroscala* but might indicate a close phylogenetic relationship. *Spiroscala* and *Shwedagonia* are probably closely related but a phylogenetic analysis is needed to show this.

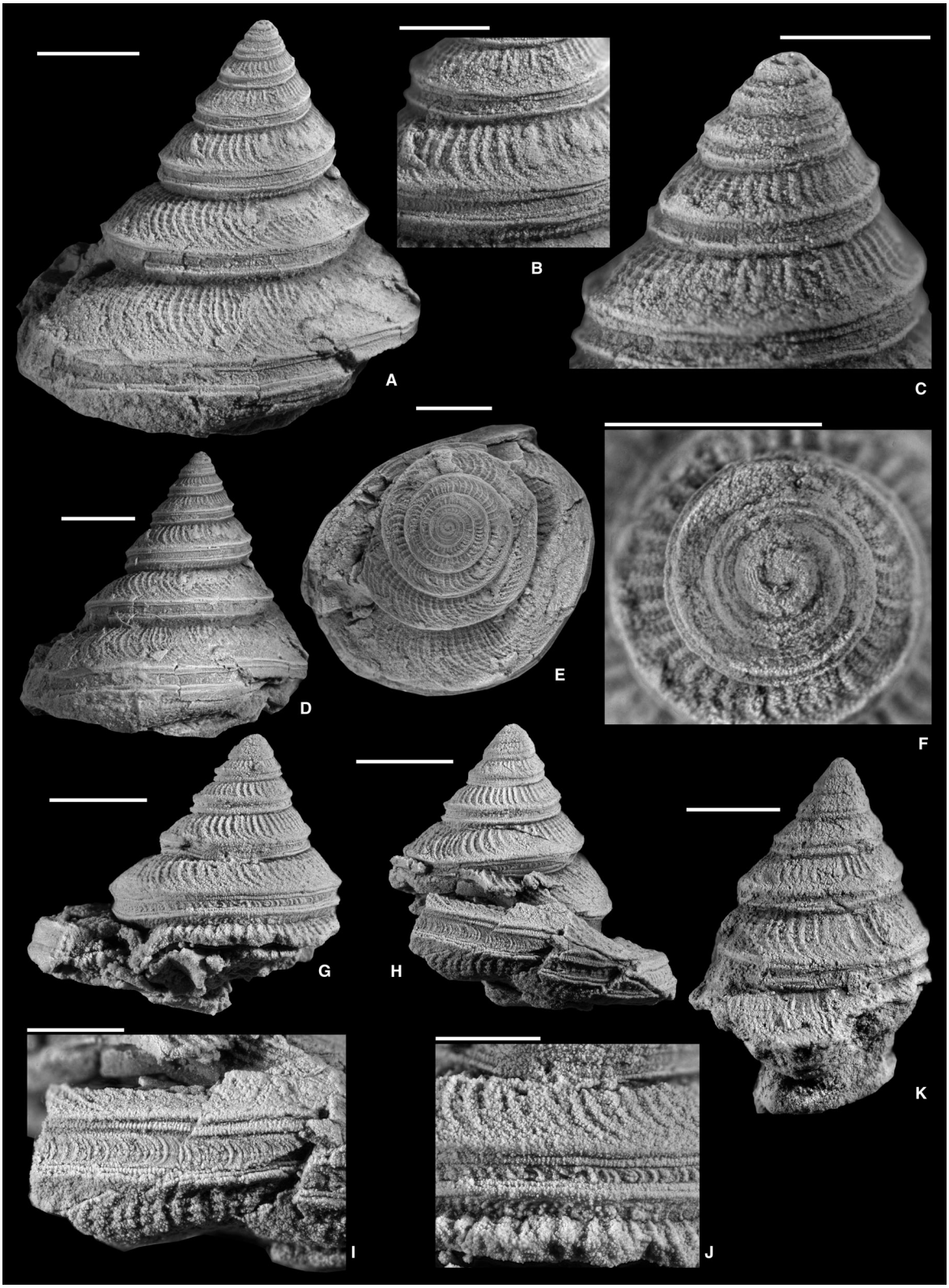

FIG. 17. *Spiroscala shwedagoniformis* sp. nov. from the Gene Autry Shale (Morrowan, Oklahoma). A–F, SNSB-BSPG 2020 LVIII 15, holotype; B, detail of whorl face ornament on two whorls; C, lateral view, detail of early whorls; F, apical view, detail of early whorls. G–J, SNSB-BSPG 2020 LVIII 16, paratype; I–J, lateral view, detail of selenizone and selenizone borders. K, SNSB-BSPG 2020 LVIII 17, paratype. Scale bars represent: 2 mm (A, D, E, G, H, K); 1 mm (B, C, F, I, J).

Spiroscala shwedagoniformis sp. nov.
Figure 17

LSID. urn:lsid:zoobank.org:act:DE457B7B-9099-4679-B9D8-09F92BB08B44

Derivation of name. Referring to its resemblance to *Shwedagonia* Batten, 1956 and thus to Shwedagon Pagoda in Myanmar.

Holotype. SNSB-BSPG 2020 LVIII 15

Paratypes. SNSB-BSPG 2020 LVIII 16, 17

Type location & age. Morrowan, Gene Autry Formation exposed in gullies on east side of unnamed tributary of Sycamore Creek on the Daube Ranch, NW¼, NW¼, SW¼, sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7½′ Quadrangle, Oklahoma (AMNH locality 5270; 34°14′13.76″N, 96°52′42.02″W).

Material. 3 specimens from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 15–17.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 15	7.3	7.9	71	0.38	3.1	2.8	0.5	0.18	0.16
2020 LVIII 16	5.6	6.0	80	0.35	1.7	1.4	0.3	0.22	0.18

Description. Shell small, conical, higher than wide, largest specimen with seven whorls; suture incised, shallow; protoconch consists of less than one whorl, without visible ornament, diameter 0.33 mm; first whorl diameter 0.42 mm; first teleoconch whorl convex, with fine spiral lirae; later teleoconch whorls low, angulated well below mid-whorl of spire whorls at a pronounced keel above selenizone and second keel somewhat above abapical suture and below selenizone forming periphery; whorl face above upper keel forming wide, convex ramp; ramp ornamented with numerous sharp, regularly spaced prosocline/prosocyrt axial ribs and up to eight spiral threads; whorl face below abapical keel concave, incised then turning into convex basal edge, ornamented with prosocyrt growth lines; selenizone starts after the 1.5 whorls at mid-whorl face; selenizone flat, depressed, parallel to shell axis, situated at lower half of whorl face, between keels but not bordered by them; selenizone bordered by spiral vertical plates that are situated between two spiral keels; vertical plates are ornamented with axial orthocline threads; selenizone ornamented with prominent, densely spaced lunulae; basal features not seen.

Remarks. Spiroscala conula (Hall, 1858) is more slender according to the original description and the illustration provided by Whitfield (1882, pl. 9 fig. 17). Moreover, *Spiroscala shwedagoniformis* has a wider selenizone, a more gently inclined upper whorl face and more rapidly enlarging whorls similar to those found in *Shwedagonia* species, and has spiral threads on the upper whorl face. *Mourlonia solida* Hyde, 1953 is herein placed into *Spiroscala* due to its high spire and whorl profile. *Spiroscala? solida* (Hyde, 1953) comb. nov. differs from *Spiroscala shwedagoniformis* in being higher spired, having a lower whorl expansion rate and a spiral carination on the whorl face. *Spiroscala pagoda* Knight, 1945 is similar but differs in having a concave upper whorl face and a narrower selenizone. *Pleurotomaria conoides* Meek & Worthen, 1866*a* from the Pennsylvanian of Illinois was previously assigned to *Spiroscala* by Knight (1945) but is herein placed in *Euconospira*. *Euconospira conoides* (Meek & Worthen, 1866*a*) comb. nov. has a non-gradate shell profile with an almost flat whorl face and contrasts with *Spiroscala* species, which have convexo-concave or strongly convex ramp. *Spiroscala rockymontana* (Girty, 1934) from the Pennsylvanian of Colorado is more high-spired and has lower whorls and a lower whorl expansion rate.

Spiroscala? cf. *georgiannae* Kues & Batten, 2001
Figure 18

cf. * 2001 *Spiroscala georgiannae* Kues & Batten, p. 26, figs 6.1–6.3.

Material. 1 specimen from the Missourian of Texas (Placid Shale Member, TXM–14): SNSB-BSPG 2020 LXXI 1.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXI 1	8.3	6.6	60	–	2.6	2.5	0.6	0.22	0.21

Description. Shell small, conical, relatively high-spired; slightly coeloconoid; suture incised, situated below carina; whorl face angulated at periphery at rounded carina; later whorl face somewhat adpressed with subsutural bulge; concave between selenizone and subsutural bulge; ornamented with oblique prosocyrt axial riblets; whorl face concave below selenizone then turn into convex bulge at periphery, ornamented with prosocyrt axial riblets; selenizone flat to slightly convex, situated at lower half of the whorl face, bordered above and below by shell edges; selenizone ornamented with prominent lunulae; lunulae not symmetrical, zenith point situated on adapical half of selenizone; base flat; aperture subrectangular, wider than high; outer lip concave, basal lip flat, columellar lip flat, thickened; base anomphalous.

Remarks. The studied specimen has a slightly lower spiral angle than *Spiroscala georgiannae* (45° vs 50–60°) and lacks spiral cords but is similar in 'having a relatively wide, flat to convex selenizone bordered by sharp lirae' (Kues & Batten 2001). The holotype of *Sp. georgiannae* has finer and more densely spaced axial ribs. *Spiroscala georgiannae* has a wide, convex and oblique selenizone bordered by shell edges. This kind of selenizone is unlike the typical selenizone of *Spiroscala*, which is narrow, depressed and bordered by vertical plates that are situated between two prominent spiral cords or carinae. Therefore, we are not sure about the generic assignment of *Sp. georgiannae*.

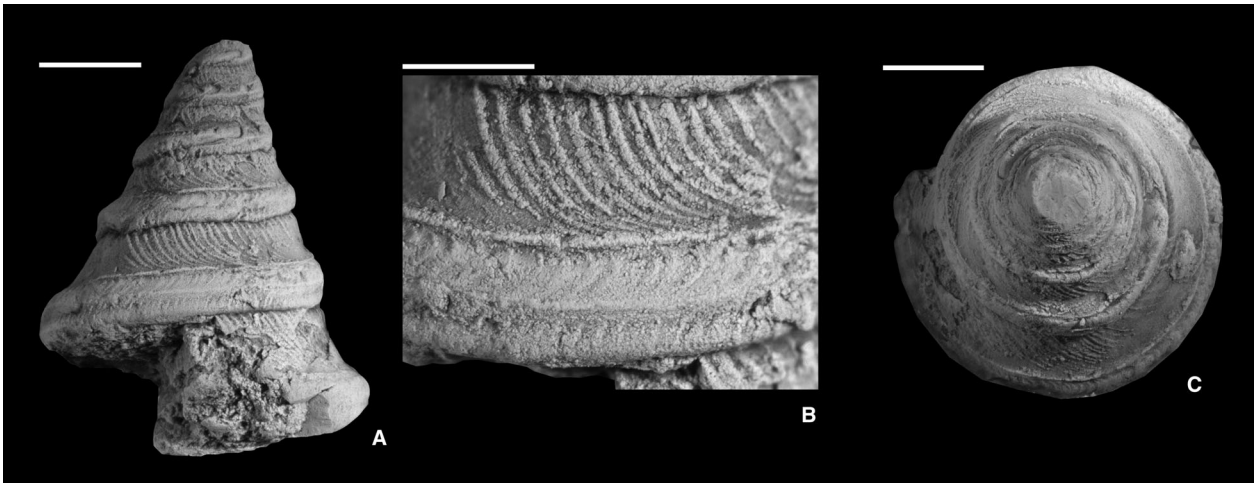

FIG. 18. *Spiroscala*? cf. *georgiannae* Kues & Batten, 2001. A–C, SNSB-BSPG 2020 LXXI 1 from the Placid Shale (Missourian, Texas); B, oblique apical view, detail of ornament. Scale bars represent: 2 mm (A, C); 1 mm (B).

Genus EUCONOSPIRA Ulrich *in* Ulrich & Scofield, 1897

Type species. Pleurotomaria turbiniformis Meek & Worthen, 1861, from the Carboniferous of Illinois, USA; subsequent designation by Knight (1937).

Euconospira sp.
Figure 19

Material. 2 specimens from the Buckhorn Asphalt deposit (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 252, 253.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 252	[12.08]	[9.36]	60	–	3.3	3.4	0.5	0.15	0.16
2011 X 253	9.6	9.9	63	–	4.3	3.9	–	–	–

Description. Shell conical, with a pleural angle of 60°; suture slightly incised; early whorls not preserved; largest specimen with four whorls; whorl profile with weak angulation at adapical edge of selenizone; sutural ramp steeply inclining, almost straight to slightly convex, slightly concave near selenizone; ornament abraded, consisting of oblique prosocline ribs faintly visible below adapical suture, at angle of 45° with suture; selenizone situated low on the whorl face, concave, bordered by spiral cords, covering *c.* 12% of the width of whorl face at third visible whorl; lunulae abraded, faintly visible; whorl face below selenizone narrower than selenizone, parallel to shell axis, with axial ribs; transition to base at whorl angulation; base flatly convex, ornamented with numerous sinuous axial threads and weaker spiral threads; aperture oblique, subovate; anomphalous.

Remarks. Two specimens from the Buckhorn Asphalt deposit are present. The overall characters suggest that the specimens at hand belong to *Euconospira*. The whorl face of both specimens is abraded; the selenizone is faintly visible in one specimen which shows the principal ornament in detail on one spot (Fig. 19C) and the other specimen (Fig. 19D–F) has a better-preserved aperture. The ornament pattern of oblique axial ribs is very conservative among the species of *Euconospira*. Only *Eu. nodosa* Cook *et al.*, 2003 from the Upper Devonian of Australia shows a nodose ornament with strong spiral cords. It is unclear whether the selenizone of *Eu. nodosa* is concave or has nodular lunulae. The surface ornamentation suggests a phymatopleurid affinity for *Eu. nodosa*. If *Eu. nodosa* has nodular lunulae then it might represent *Paragoniozona*. The studied specimens resemble *Eu. planibasalis* Ulrich, 1897 and *Eu. conoides* (Meek & Worthen, 1866*a*). *Euconospira planibasalis* Ulrich, 1897 seems to have the same whorl profile and a similar basal ornamentation, but a narrower selenizone according to the original drawing. *Euconospira conoides* (Meek & Worthen, 1866*a*) has the same pleural angle and selenizone width according to the illustration provided by Meek & Worthen (1873); however, it has a rhombic quadrangular aperture according to the original description.

Family LUCIELLIDAE Knight, 1956

Remarks. This family unites trochiform shells, commonly with a marginal frill and a selenizone below that frill situated at the transition to the base (see Knight *et al.* 1960); the selenizone seems not to be produced by the closure of a deep shell slit but rather of a deep sinus. The family was included in Pleurotomarioidea by Knight *et al.* (1960) and later placed in Eotomarioidea by Wagner (2002). We place the genus *Eotrochus* in Luciellidae because we think it is possible that, in contrast to previous reports, this genus has a selenizone (see below). Moreover, we include *Eirlysella* gen. nov. in Luciellidae; it lacks a frill but is otherwise similar to the type species of *Luciella* and has a selenizone in the same position: at the transition to the base.

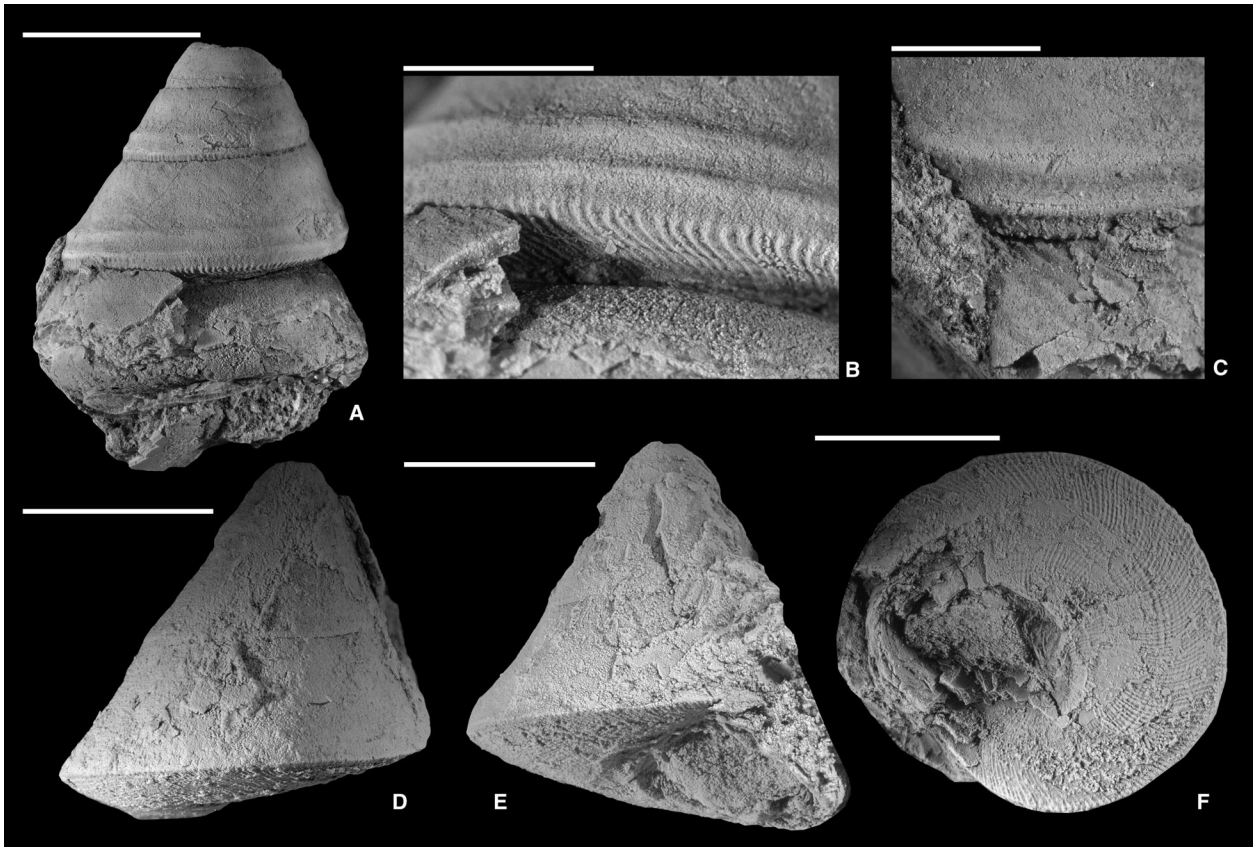

FIG. 19. *Euconospira* sp. from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–C, SNSB-BSPG 2011 X 252; B, oblique basal view, detail of ornamentation on the base of preceding whorl; C, oblique lateral view showing faint lunulae and axial ornament on subsutural region. D–F, SNSB-BSPG 2011 X 253. Scale bars represent: 5 mm (A, D–F); 2 mm (B–C).

Some Carboniferous species that are similar to the luciellid genera *Luciella* de Koninck, 1883 and *Eirlysella* have been erroneously attributed to the Triassic genus *Luciellina* Kittl, 1900 (not *Luciella*!) by Batten (1966), Amler (1987, 2006) and Kues & Batten (2001). We studied *L. contracta* Kittl, 1900, the type species of *Luciellina*, and *L. striatissima* Kittl, 1900 from the Triassic of Hungary. The type specimens of both species are housed in the Naturhistorisches Museum Wien (NHMW) and possess a convex selenizone situated at or above the periphery. In *L. contracta* the selenizone is situated at the whorl periphery. In *L. contracta* Kittl, 1900 the abapical edge of the selenizone represents the whorl periphery. In contrast, the Carboniferous species attributed to *Luciellina* by Batten (1966) and Amler (1987) have a selenizone below the periphery and the adapical edge of both species represents the whorl periphery. Batten's and Amler's species resemble *Luciella* and *Eirlysella* regarding the position of selenizone, but have a more prominent (or protruding) base and a narrower selenizone. They probably represent an undescribed new genus, but it is not certain if that genus belongs within Luciellidae. It might be closely related to *Catazona* Gordon & Yochelson, 1983 and thus represent Portlockiellidae. *Luciellina ocultabanda* Kues & Batten, 2001 has a selenizone below the shell periphery; therefore, it does not belong to *Luciellina* and is placed herein in *Eirlysella* because it has the characteristic features of that genus (i.e. growth lines, shell morphology, position of selenizone, flat base). Kues & Batten (2001) suggested that the two taxa classified as *Euconospira* sp. indet. 1 and *Euconospira* sp. indet. 2 by Thein & Nitecki (1974) should be placed within *Luciellina*. We agree with Kues & Batten (2001) that the original classification made by Thein & Nitecki (1974) is doubtful concerning the two taxa, but they do not represent *Luciellina*. They can be placed in *Eirlysella*.

Luciella infrasinuata Koken, 1896 from the Upper Triassic (Norian) Hallstatt Limestone (Koken 1897, pl. 5 fig. 11) does not represent the genus *Luciella*. It resembles *Phymatopleura conica* in whorl profile and ornament but we refrain assigning it to *Phymatopleura* since the early ontogeny of *L. infrasinuata* is unknown and the youngest known occurrence of *Phymatopleura* is in the Permian. Among the Triassic genera, *Luciella infrasinuata* resembles *Kittlidiscus* in whorl ornamentation and position of selenizone. When Kittl (1900) erected the genus *Luciellina*, he erected two new *Luciellina* species but did not designate a type species. *Luciella infrasinuata* Koken, 1896 was erroneously cited as the type species of *Luciellina* Kittl by Cossmann (1901). However, when Kittl erected *Luciellina*, he included only two new species without umbilicus. Kittl (1900) kept *Luciella infrasinuata* separate because it has a wide umbilicus. Therefore, Cossmann's (1901) act of selecting a type species that was not originally

included in *Luciellina* cannot be regarded as typification. The type species of *Luciellina* Kittl was designated later by Diener (1926) as *Luciellina contracta* Kittl, 1900.

Pleurotomaria catherinae Gemmellaro, 1889 from the Permian of Sicily was erroneously attributed to *Luciella* by Greco (1937) and Termier & Termier (*in* Termier *et al.* 1977, p. 66). In *Luciella*, the selenizone is situated at the base, below the frill. However, the selenizone is situated on sutural ramp well above the frill in *Pleurotomaria catherinae*. *Pleurotomaria catherinae* Gemmellaro, 1889 resembles *Lamellospira spinosa* Batten, 1989 from the Permian of the USA in the position of the selenizone, in whorl profile and in having a frill. Hence, *Pleurotomaria catherinae* is herein assigned to *Lamellospira* Batten, 1958: *Lamellospira catherinae* (Gemmellaro, 1889) comb. nov.

The members of Pseudophoridae resemble members of Luciellidae in gross morphology and in developing a suprasutural frill. Pseudophoridae was regarded as Archaeogastropoda (Vetigastropoda) by Knight *et al.* 1960 and as Euomphalina by Wagner (2002). Recently, Bouchet *et al.* 2017 included Pseudophoridae in the order Pleurotomariida but to our knowledge, a selenizone is not present in the genera previously included in Pseudophoridae (e.g. Knight 1941; Yochelson 1956; Knight *et al.* 1960) apart from in *Eotrochus*. It is possible that Pseudophoridae (Silurian–Permian; Knight *et al.* 1960) had been derived from the selenizone-bearing family Luciellidae (Ordovician–Carboniferous; Knight *et al.* 1960). Such an evolutionary loss of the selenizone has also been proposed for Cirroidea (Bandel 1991).

Genus EOTROCHUS Whitfield, 1882

Type species. *Pleurotomaria tenuimarginata* Hall *in* Miller, 1877 (nom. nov. pro *Pleurotomaria concava* Hall, 1858 non *Pleurotomaria concava* Deshayes, 1832), Mississippian, Indiana, USA; original designation.

Remarks. *Eotrochus* was placed in Pseudophoridae, a family that resembles Luciellidae but its species lack a selenizone. Knight (1941) illustrated and described the type material of the type species *Pleurotomaria tenuimarginata* form the Mississippian Salem Limestone (Indiana, USA) and stated that it is 'seemingly without sinus or slit'. However, judging the basal view (Knight 1941, pl. 58 fig. 3b) it displays a peripheral band that might represent a selenizone obscured by preservation.

Due to the presence of a selenizone or pseudoselenizone (see Knight 1941, pp 16–17 for terminology) that is shown here for *Eotrochus* cf. *tenuimarginatus* (Hall *in* Miller, 1877), *Eotrochus* is removed from Pseudophoridae and is assigned tentatively to Luciellidae herein. Characters of the base also suggest a placement in Luciellidae. The growth lines on the base of *Eotrochus* are prosocyrt as is also the case in luciellid genera. By contrast, in Pseudophoridae the growth lines on the base are opisthocyrt and do not develop a selenizone or pseudoselenizone (e.g. Knight 1941; Yochelson 1956; Knight *et al.* 1960). The presence of a projecting lamella in the umbilical region was reported for the type species *Eotrochus tenuimarginata* (Hall *in* Miller, 1877) by Knight (1941). This feature is also present in *Luciella* and *Eirlysella*, further suggesting a close relationship.

Eotrochus cf. *tenuimarginatus* (Hall *in* Miller, 1877)

Figure 20

cf.	1858	*Pleurotomaria concava* Hall, p. 24 [non *Pleurotomaria concava* Deshayes, 1832].
cf. *	1877	*Pleurotomaria tenuimarginatus* Hall *in* Miller, p. 245.
cf.	1882	*Eotrochus concavus*; Whitfield, p. 78, pl. 9 figs 21–23.
cf.	1906	*Eotrochus concavus* (Hall); Cumings, p. 1347, pl. 26 figs 21–23.
cf.	1941	*Eotrochus tenuimarginatus* (Miller); Knight, pp 113–114, fig. 7, pl. 58 fig. 3a–b.

Material. 1 specimen from the Virgilian of Texas (Finis Shale Member, TXV–54): SNSB-BSPG 2020 LXXIX 1.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXIX 1	[14.5]	36.9	84	–	9.5	13.9	1.7	0.12	0.18

Description. Shell relatively large, conical, with three whorls preserved; pleural angle 85°; whorl profile straight; whorl faces flush to each other; peripheral frill covers adapical portion of whorl face; whorl face straight, inclined at an angle of 45°–60°, ornamented with strongly prosocyrt growth lines and minute antimarginal, irregular spiral grooves crossing growth lines and forming tuberculate micro-ornament; growth lines prosocyrt, strongly inclined, making an angle of 30° with adapical suture; frill short, elongated towards abapical direction; pseudoselenizone/selenizone wide, with closely spaced lunulae and occasionally with spiral cords, bordered by peripheral frill and spiral thread, slightly sunken in basal surface; base flat, becoming convex at umbilical region, with wide pseudo-umbilicus; base ornamented with numerous spiral threads and sinuous growth lines; growth lines prosocyrt near selenizone, opisthocyrt near umbilical region; whorls subquadrate in cross-section.

Remarks. The present specimen from the Pennsylvanian of Texas closely resembles *Eotrochus tenuimarginatus* (Hall *in* Miller, 1877) (nom. nov. pro *Pleurotomaria concava* Hall non *Pleurotomaria concava* Deshayes) from the Mississippian of Indiana and Illinois. However, the specimen at hand is larger and has finer and more spiral threads on the base. As outlined above, a selenizone or pseudoselenizone has not been reported previously on the base of *Eo. tenuimarginatus* but this could be due to preservation. The illustrations given by Whitfield (1882), Cumings (1906) and Knight (1941) show *Eo. tenuimarginatus* with a widely phaneromphalous base including a projected lamella in the umbilical region, and the preceding whorls could be seen in umbilical view. However, the umbilicus of the present specimen is plugged with projecting lamella so that the preceding whorls cannot be seen in umbilical view. Similar projecting lamella is also present in *Luciella* and *Eirlysella*. The cross section of the *Eo. tenuimarginatus* as described and drawn by Knight (1941, p. 114, fig. 7) resembles the cross section of *Eirlysella*

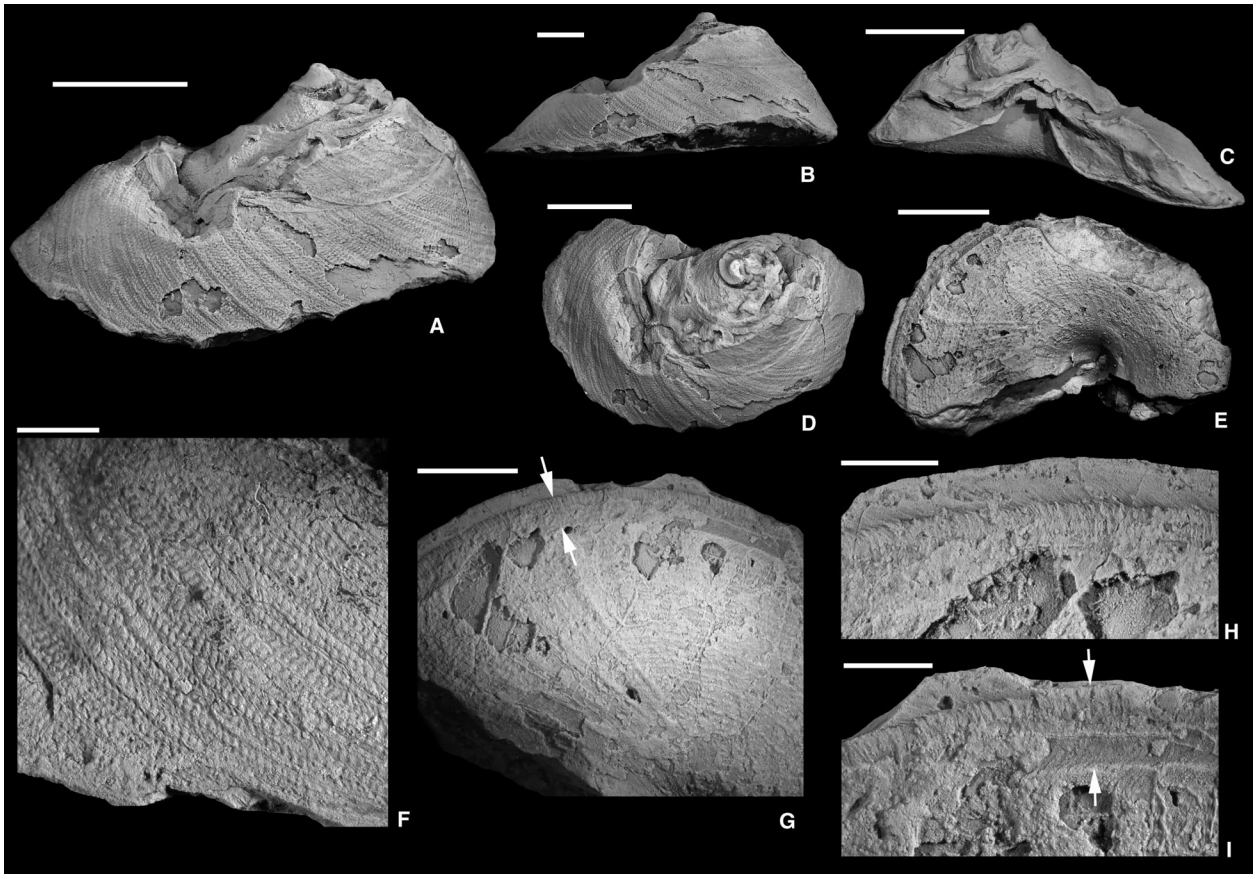

FIG. 20. *Eotrochus* cf. *tenuimarginatus* (Hall *in* Miller, 1877). A–I, SNSB-BSPG 2020 LXXIX 1, Finis Shale Member (Virgilian, Texas); G–I, basal view, detail of selenizone, arrows indicate selenizone margins. Scale bars represent: 10 mm (A, C–E); 5 mm (B, G); 2 mm (F, H–I).

hissingeriana (de Koninck, 1843) (Thomas 1940*b*, pl. 7 fig. 6). The umbilical region is smooth in both genera.

The Permian species *Eotrochus*? *liratus* Chronic, 1952 has a frill and seems to lack a selenizone; none was described and the illustrations are insufficient. It was assigned to *Sallya* Yochelson, 1956 by Yochelson (1956). The only other known species belonging to *Eotrochus* is *Eo. marigoldensis* Thein & Nitecki, 1974 from the Mississippian Salem Limestone, where the type material of *Eo. tenuimarginatus* was found. According to Thein & Nitecki (1974), *Eo. marigoldensis* differs from *Eo. tenuimarginatus* (= *Eo. concavus*) in having a lower pleural angle and more prominent spiral striae. However, the two taxa are very similar and are probably synonymous.

Genus EIRLYSELLA nov.

LSID. urn:lsid:zoobank.org:act:42043DD7-4CEE-49AF-AFCD-E88DF713ADD0

Type species. Eirlysella buckhornensis from the Desmoinesian of Oklahoma, USA.

Derivation of name. After British palaeontologist Eirlys Grey Thomas, who recognized the genus for the first time in her PhD thesis on the Carboniferous Pleurotomariidae.

Diagnosis. Trochiform, without a frill on basal angulation; selenizone wide, situated on base, below basal whorl angulation, covered by preceding whorl in spire whorls or just emerging at suture; selenizone with crowded lunulae; surface ornamented with spiral and/or antimarginal cords or threads; suture incised; base anomphalous.

Remarks. The marginal (basal) position of the selenizone that has more the character of a shallow sinus rather than a deep slit makes it questionable whether this structure is homologous to a 'real' selenizone that represents the closure of a more or less central shell slit as for instance found in Pleurotomariidae, Eotomariidae and Phymatopleuridae. Therefore, it is uncertain whether *Eirlysella* and hence Luciellidae belong to Pleurotomariida or rather to trochoid vetigastropods (e.g. *Keeneia* Etheridge). Regarding the situation of the selenizone low on the whorls and at or below the suture, *Eirlysella* resembles *Portlockiella* Knight, 1945 but this genus has a turbiniform shell with a much stronger spiral ornament. Some members of *Rhineoderma* (e.g.

Rhineoderma gemmullifera (Phillips, 1836)) converge to *Eirlysella* in whorl shape and position of selenizone.

Eirlysella differs from *Luciella* and *Eotrochus* in being more high-spired, having a narrower umbilicus and in lacking a frill at the basal periphery. *Luciella* is widely phaneromphalous and its preceding whorls can be seen in umbilical view. *Eotrochus* has a 'revolving lamella projecting inward and upward from the umbilical sides' (Knight 1941) so that the preceding whorls of *Eotrochus* cannot be seen in umbilical view. *Eirlysella* is closer to *Eotrochus* regarding this character.

Thomas (1940*b*) proposed a new genus *Brookesella* (type species *Trochus hissingerianus* de Koninck, 1843) in her PhD thesis. Since this thesis has not been published, *Brookesella* is not a valid name. Here, we include *Trochus hissingerianus* in *Eirlysella*. The specimens assigned by Thein & Nitecki (1974) to *Euconospira* sp. indet. 1 and *Euconospira* sp. indet. 2 can be referred to *Eirlysella*.

Included species. Eirlysella buckhornensis, *Trochus hissingerianus* de Koninck, 1843 [= *Eirlysella hissingeriana* (de Koninck) comb. nov.], *Pleurotomaria squamula* Phillips, 1836 [= *Eirlysella squamula* (Phillips) comb. nov.] and *Luciellina ocultabanda* Kues & Batten, 2001 [= *Eirlysella ocultabanda* (Kues & Batten) comb. nov.]

Eirlysella buckhornensis sp. nov.
Figure 21

LSID. urn:lsid:zoobank.org:act:C9323D76-78E2-49E0-867C-5576236A9D9D

Derivation of name. Referring to the Buckhorn Asphalt Quarry, Oklahoma, where the studied specimens were found.

Holotype. SNSB-BSPG 2011 X 79

Paratypes. SNSB-BSPG 2011 X 235, 236, 237

Type location & age. The Boggy Formation outcrop at the Buckhorn Asphalt Quarry (34°26′44″N; 96°57′41″W), Desmoinesian.

Material. 12 specimens from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 78, 79, 235, 236, 246, 247, and a further 6 specimens (SNSB-BSPG 2011 X).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 79	5.2	7.0	77	–	2.8	2.7	0.5	0.17	0.17
2011 X 235	6.0	7.0	73	–	2.9	2.6	0.5	0.21	0.19
2011 X 236	5.9	8.2	77	–	3.0	3.2	0.6	0.19	0.20
2011 X 237	6.6	8.1	79	–	3.2	3.1	0.5	0.16	0.15

Description. Shell small, trochiform; largest specimen with 6–7 whorls; apical angle 74°; first whorl 0.18 mm in diameter; first two whorls nearly planispirally coiled, whorl face convex, without visible ornament; from third whorl onwards whorl face flatter and ornamented with spiral cords and prosocyrt growth lines; later whorl face slightly convex to flat, with narrow subsutural shoulder, ornamented with oblique prosocline/prosocyrt growth lines and distinct spiral cords with interspaces narrower than cords; mature whorls also with antimarginal roof tile-like ornament, aligned regularly in adapical half of whorl face and forming spiral cords but irregularly aligned in abapical region and producing rough surface in abapical half of whorl face; suture incised, situated at abaxial border of selenizone; selenizone concave, situated basally between base and abapical edge of whorl face, slightly depressed below surface, ornamented with closely spaced lunulae and occasionally with spiral cords; base flat, ornamented with growth lines and occasionally with spiral cords; basal growth lines prosocyrt near selenizone, orthocline or slightly prosocyrt near umbilical region; base anomphalous with smooth, callous columellar region; aperture subquadrate.

Remarks. We have not studied the type material of *Eirlysella hissingerianus* (de Koninck, 1843). However, we studied a specimen from the Isle of Man deposited in the Natural History Museum, London (NHMUK) that fits the description and illustration given by Thomas (1940*b*) of an *E. hissingerianus* specimen from the Isle of Man. *Eirlysella hissingerianus* seems to be coeloconoid and more tightly coiled, and its suture is situated on the selenizone.

Eirlysella ocultabanda (Kues & Batten, 2001) is larger (20 mm high) with a slightly adpressed whorl face just below the suture, where the axial growth lines are slightly more prominent; it has weaker and fewer spiral cords (10–12). *Eirlysella squamula* (Phillips, 1836) has very strong antimarginal (straight opisthocline) axial ribs on the whorl face.

Superfamily PLEUROTOMARIOIDEA Swainson, 1840
Family PHYMATOPLEURIDAE Batten, 1956

Original diagnosis. 'Discoid to moderately high spired, highly ornamented pleurotomarians with a selenizone located at or slightly above the periphery; the outer whorl face vertical or sloping and may be narrow compared to upper whorl surface; selenizone convex to concave and usually strongly bordered; there may be basal sinuses; ornament in the parietal lip resorbed' (Batten 1956, p. 42).

Emended diagnosis. 'Shell highly ornamented; moderately deep slit and selenizone somewhat below mid-whorl, selenizone slightly depressed below surface; parietal ornament partly or wholly resorbed on many species. L. Carb. (Miss.)–Trias.' (Knight *et al.* 1960, p. I214).

Remarks. Early ontogenetic shells of Pennsylvanian phymatopleurids were documented by Bandel *et al.* (2002; identified as *Paragoniozona nodolirata*), Geiger *et al.* (2008, fig. 12.4A, B) and Nützel (2014*a*, fig. 3B, C). They show that this family has the vetigastropod-type protoconch of approximately one whorl, matching the trochoid condition; the early teleoconch whorls are

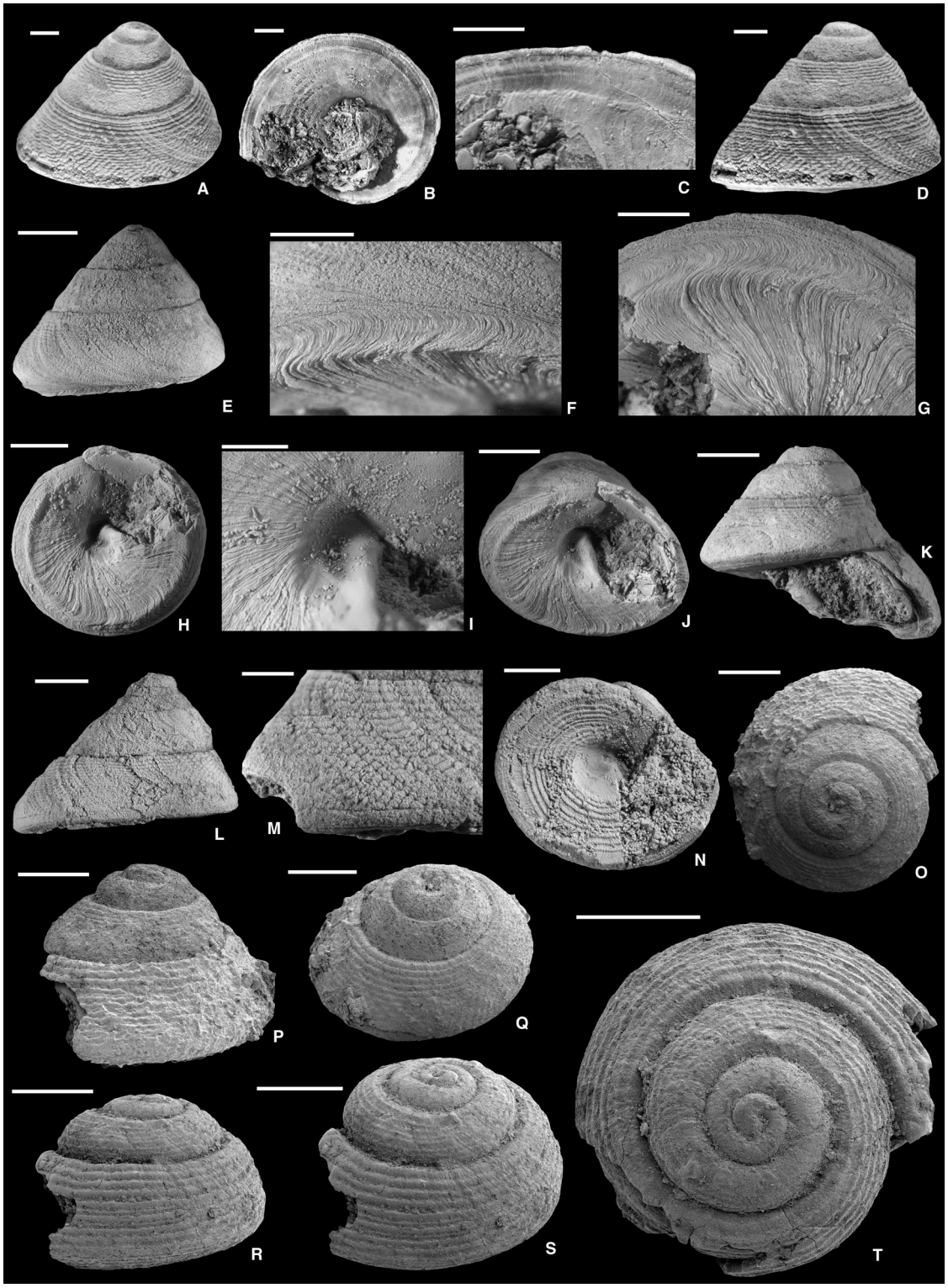

FIG. 21. *Eirlysella buckhornensis* gen. et sp. nov. from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–D, SNSB-BSPG 2011 X 79, holotype; C, basal view, detail of selenizone. E–J, SNSB-BSPG 2011 X 235, paratype; F, oblique basal view, detail of selenizone; G, basal view, detail of selenizone; I, basal view, detail of umbilical region. K, SNSB-BSPG 2011 X 237, paratype. L–N, SNSB-BSPG 2011 X 236, paratype. O–Q, SNSB-BSPG 2011 X 247, juvenile specimen. R–T, SNSB-BSPG 2011 X 246. Scale bars represent: 1 mm (A–D, F, G, I, M, O–Q); 2 mm (E, H, J–L, N); 0.5 mm (R–T). O–T, SEM images.

convex and commonly ornamented with spiral cords. The selenizone develops on the third whorl.

Recently, Mazaev (2019*b*) erected a new phymatopleurid genus *Termihabena*. Among the late Palaeozoic Pleurotomariida, *Termihabena* most closely resembles *Catazona* Gordon & Yochelson, 1983 and differs from *Catazona* in the absence of a lateral whorl face below the selenizone. Mazaev (2019*b*) included the species *Paragoniozona asiatica* Licharew, 1967 [= *Rhineoderma asiatica* (Licharew, 1967) comb. nov.] and *Rhineoderma nikitowkensis* Yakowlew, 1899 from the Permian of Russia also in *Termihabena*. Both species are herein assigned to *Rhineoderma* (see Knight 1941, p. 301, pl. 30 fig. 4, for the type species *Rhineoderma radula* (de Koninck, 1843)) because of the nodular reticulate ornamentation on surface, basally situated selenizone, nodular lunulae and soft (unornamented) columellar region.

Tapinotomaria Batten, 1956 was placed in Portlockiellidae by Batten (1956) due to the low position of selenizone on whorl face. *Tapinotomaria* closely resembles other phymatopleurid genera in whorl face and selenizone ornamentation and position of selenizone as also discussed by Batten (1958, p. 114); therefore, *Tapinotomaria* is herein included in Phymatopleuridae.

Eirlysia Batten, 1956 closely resembles *Dictyotomaria* regarding characters of the selenizone complex. Therefore, *Eirlysia* is included in the Phymatopleuridae as previously proposed by Mazaev (2015).

Genus PHYMATOPLEURA Girty, 1939
[nom. nov. pro *Orestes* Girty, 1912 non *Orestes* Blackiston & Pryer, 1880 (Aves)]

Type species. *Orestes nodosus* Girty, 1912 from the Carboniferous of Oklahoma, USA; original designation.

Phymatopleura nodosa (Girty, 1912)
Figure 22

* 1912 *Orestes nodosus* Girty, p. 137.
1915 *Orestes nodosus* Girty; Girty, p. 156, pl. 22 figs 8–10 (non fig. 7).
1941 *Phymatopleura nodosus* (Girty); Knight, p. 244, pl. 30 fig. 5a, b.
1964*a* *Phymatopleura nodosus* (Girty); Sturgeon, p. 215, pl. 33 figs 23–26. pl. 36 fig. 11.
1967 *Phymatopleura nodosus* (Girty); Yochelson & Saunders, p. 165.
1972*a* *Phymatopleura nodosa*; Batten, fig. 26.
1997 *Glyptotomaria* (*Dictyotomaria*) *faceta* Hoare *et al.*, p. 1033, figs 4.20–4.23.
2001 *Phymatopleura nodosa* (Girty); Kues & Batten, p. 39, figs 7.11–7.13.

Material. A total of 27 specimens. 22 from the Desmoinesian of Oklahoma (Wewoka Formation, OKD–11): SNSB-BSPG 2020 LXII 1–2, and a further 20 specimens (SNSB-BSPG 2020 LXII). 1 from the Desmoinesian of Texas (Dickerson Shale, TXD–01): SNSB-BSPG 2020 LXVIII 1. 4 from the Desmoinesian of Oklahoma (Holdenville Formation, OKD–01): SNSB-BSPG 2020 LXIII 1, and a further 3 specimens (SNSB-BSPG 2020 LXIII).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXII 1	9.0	8.1	73	–	4.1	3.4	0.7	0.22	0.18
2020 LXII 2	7.0	7.0	86	–	3.7	3.3	0.7	0.20	0.18
2020 LXIII 1	5.2	5.4	81	0.36	2.7	2.5	0.5	0.22	0.19
2020 LXVIII 1	5.3	6.0	100	0.31	2.7	2.6	0.7	0.26	0.25

Description. Shell small, trochiform, almost as high as wide, the largest specimen with five whorls; spire gradate; suture shallow; first three whorls evenly convex lacking angulations; first whorl low-spired, without visible ornament (but re-crystallized), diameter 0.36 mm; spiral cords appear from second whorl onward; initially seven narrowly spaced spiral cords; subsequently distance between spiral cords increases so that it exceeds width of cords distinctly; axial ribs become visible from third whorl onward; axial ribs numerous, sharp, thread-like; axial ribs of equal strength as, or weaker than spiral cords; intersections of axial ribs and spiral cords nodular; median angulation of whorl face starts to develop at fourth whorl at or slightly below mid-whorl; additional angulation of whorl face in subsutural position at adapical spiral cord from fourth whorl onward; mature whorl face between suture and subsutural angulation forming very short, flat shoulder, whorl face between subsutural and median angulation flat to slightly concave, whorl face below median angulation subparallel to axis; mature whorl face ornamented with orthocline threads between suture and subsutural angulation, with spiral cords and straight prosocline axial ribs below subsutural angulation; spiral cords increase up to eight in last whorl; axial and spiral cords form rhomboid pattern and nodes; subsutural angulation ornamented with prominent tubercles; tubercles vary in number and reach up to 32 per whorl; selenizone wide (18–25% of whorl face width), flat, slightly depressed, begins after second whorl, situated between median and abapical carinae but not bordered by carinations, low on spire whorls, about median in body whorl; selenizone bordered above and below by spiral cords; selenizone ornamented with equally-spaced strong lunulae and one median spiral cord; base flatly convex, ornamented with opisthocyrt axial ribs and pronounced spiral cords similar to those on whorl face; basal spiral cords almost equally prominent, but cords near umbilicus slightly more prominent; aperture subquadrate, as high as wide; outer lip angular, basal lip flatly convex, columellar lip convex; base anomphalous to minutely phaneromphalous.

Remarks. Our specimens fit well the descriptions and figures of *Phymatopleura nodosa* (Girty, 1912) as given by Girty (1912) and Knight (1941). The type material is from the Pennsylvanian Wewoka Formation of Oklahoma. We studied specimens from the type locality (OKD–11) and figure them herein (Fig. 22A–D). The specimen from Texas (SNSB-BSPG 2020 LXVIII 1) differs from the Oklahoma specimens in being wider than high (Fig. 22J, K). Representing the type species of *Phymatopleura*

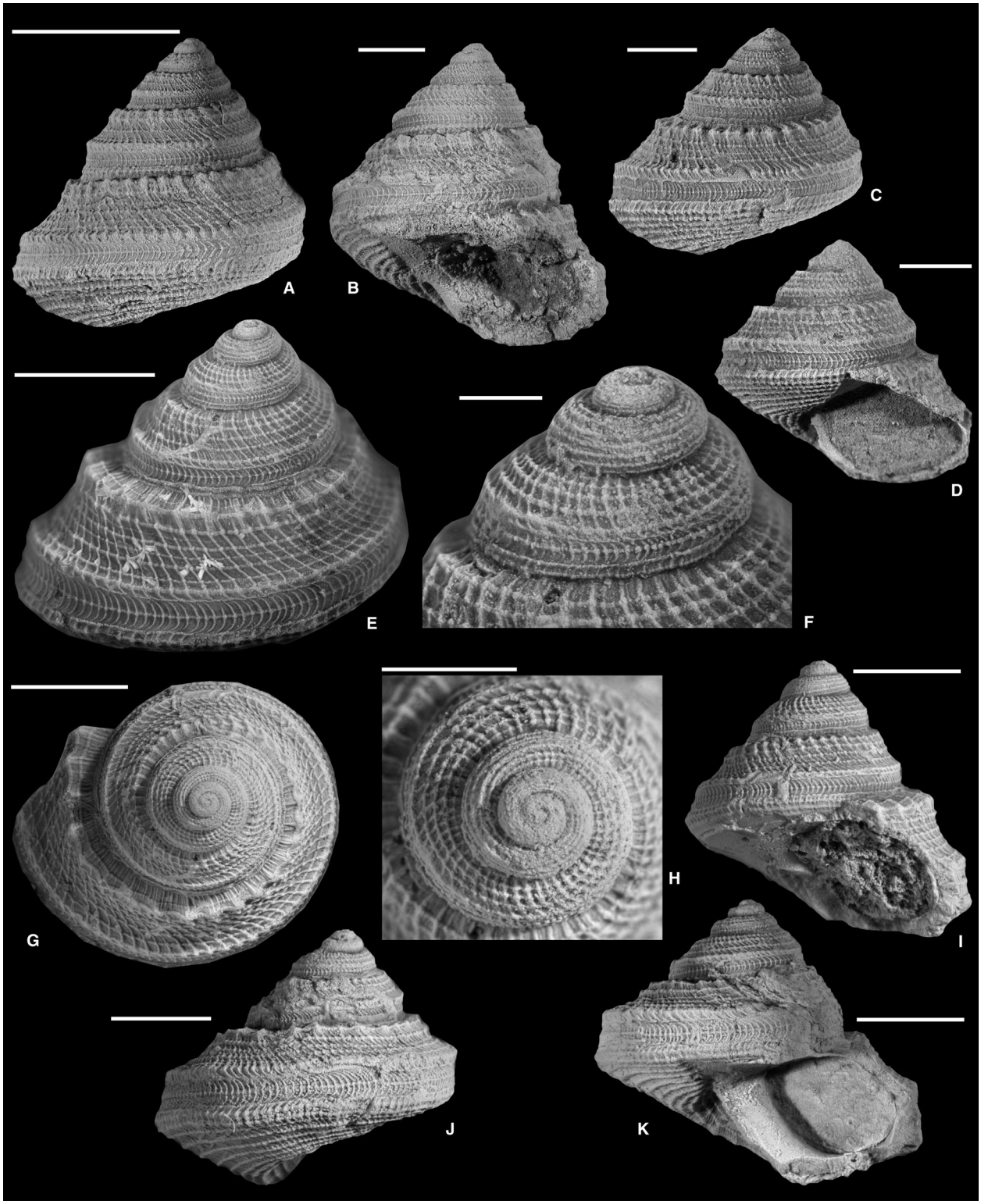

FIG. 22. *Phymatopleura nodosa* (Girty, 1912). A–B, SNSB-BSPG 2020 LXII 1, from the Wewoka Formation (Desmoinesian, Oklahoma). C–D, SNSB-BSPG 2020 LXII 2, from the Wewoka Formation (Desmoinesian, Oklahoma). E–I, SNSB-BSPG 2020 LXIII 1, from the Holdenville Formation (Desmoinesian, Oklahoma); F, oblique lateral view, detail of early whorls; H, apical view, detail of early whorls. J–K, SNSB-BSPG 2020 LXVIII 1, from the Dickerson Shale (Desmoinesian, Texas). Scale bars represent: 5 mm (A); 2 mm (B–E, G, I–K); 0.5 mm (F); 1 mm (H).

and thus Phymatopleuridae, *Ph. nodosa* is of great importance for understanding this group. Important characters are: large initial whorl; early whorls rounded without angulation; early whorls (after first whorl) with spiral cords; mature whorls with subsutural, median and basal angulation; subsutural angulation with strong nodes; whorl face forming vertical band (lateral whorl face) between median and basal angulation; selenizone developing after second whorl; selenizone situated low on spire whorls on vertical outer whorl face but not bordered by angulations; selenizone wide, with distinct lunulae and a central spiral cord.

Glyptotomaria (*Dictyotomaria*) *faceta* Hoare *et al.*, 1997 is very close and represents a subjective synonym although the spiral ornament of the early teleoconch seems to onset later. *Dictyotomaria* and *Phymatopleura* are commonly mistaken for each other in the literature. We used the presence/absence of a median cord on the selenizone to differentiate the genera. This character, together with the early shell morphology, is shared by *Worthenia*, *Phymatopleura* and *Paragoniozona*, and seems more persistent than other characters (i.e. adult shell morphology and ornamentation). Knight (1945) also noted that the vertical portion of the whorl face is much wider in *Dictyotomaria*, with the selenizone in the middle whereas *Phymatopleura* has a narrower vertical outer whorl face and whorls are angulated somewhat above selenizone.

Phymatopleura brazoensis (Shumard, 1860)
Figures 23, 24, 25

*	1860	*Pleurotomaria brazoensis* Shumard, p. 624.
?	1866	*Pleurotomaria subdecussata* Geinitz, p. 10, pl. 1 fig. 11.
	1915	*Orestes brazoensis*; Girty, p. 158.
	1922	*Orestes brazoensis*; Plummer & Moore, pl. 22 figs 16, 16a.
	1939	*Phymatopleura brazoensis* (Shumard); Girty, p. 33, figs 20–21a.
?	1958	*Phymatopleura brazoensis* (Shumard); Batten, p. 205, pl. 36 fig. 16.
	1967	*Phymatopleura brazoensis* (Shumard); Yochelson & Saunders, p. 164.
	1982	*Phymatopleura brazoensis* (Shumard); Schindel *et al.*, pl. 1 figs 6, 7.
	2014*b*	*Phymatopleura* sp.; Nützel, p. 68, fig. 1E.

Material. A total of 322 specimens. 8 from the Missourian of Texas (Placid Shale Member, TXM–14): SNSB-BSPG 2020 LXXI. 71 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 6, and a further 70 specimens (SNSB-BSPG 2009 XXII). 123 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 5, 9–15, and a further 116 specimens (42 from the surface sample, 74 from the bulk sample; SNSB-BSPG 2020 XCI). 53 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 8, and a further 52 specimens (20 from the surface sample, 32 from the bulk sample SNSB-BSPG 2020 LXXX). 21 from the Virgilian of Texas (Finis Shale Member, TXV–29): SNSB-BSPG 2020 LXXIV 1, and a further 20 specimens (SNSB-BSPG 2020 LXXIV). 3 from the Virgilian of Texas (Finis Shale Member, TXV–34): SNSB-BSPG 2020 LXXV. 22 from the Virgilian of Texas (Finis Shale Member, TXV–36): SNSB-BSPG 2020 LXXVI 1, and a further 21 specimens (SNSB-BSPG 2020 LXXVI). 3 from the Virgilian of Texas (Finis Shale Member, TXV–44): SNSB-BSPG 2020 LXXVIII 1, and a further 2 specimens (SNSB-BSPG 2020 LXXVIII). 5 from the Virgilian of Texas (Finis Shale Member, TXV–60): SNSB-BSPG 2020 LXXXI. 1 from the Virgilian of Texas (Finis Shale Member, TXV–120): SNSB-BSPG 2020 LXXXII. 3 from the Virgilian of Texas, Jacksboro (Finis Shale Member, exact location unknown): SNSB-BSPG 2020 I 43–45. 6 from the Virgilian of Texas (un-named shale member, Jacksboro Airport): SNSB-BSPG 2020 LXXXIV. 2 from the Virgilian of Texas (Wayland Shale Member, BB-TXV–06): SNSB-BSPG 2020 LXXXVIII. 1 from the Virgilian of Texas (Wayland Shale Member, TXV–61): SNSB-BSPG 2020 LXXXIX.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 6	11.0	10.9	74	0.30	5.0	3.6	0.8	0.21	0.16
2020 XCI 5	10.9	10.4	74	0.34	4.8	3.5	0.7	0.21	0.15
2020 LXXIV 1	9.3	10.4	76	–	4.2	4.0	0.8	0.19	0.18
2020 LXXVI 1	8.3	8.0	72	0.33	3.8	3.2	0.6	0.20	0.17
2020 LXXVIII 1	11.6	11.8	78	–	5.4	4.2	1.1	0.26	0.20

Description. Shell small, conical, slightly coeloconoid, slightly higher than wide, largest specimen has seven whorls; apical angle 70°; suture slightly impressed, situated just below carina; whorl face of first three whorls convex, evenly rounded; protoconch without visible ornament (but recrystallized), *c.* 0.25 mm; initial whorl diameter 0.30–0.35 mm; teleoconch whorls ornamented with 6–7 spiral cords intermediately starting after smooth protoconch and weaker prosocline/prosocyrt axial threads; later whorl face, from about third to fourth whorl onward, straight to concave; periphery formed by rounded basal angulation in suprasutural position in spire whorls; mature whorls ornamented with fine collabral axial ribs and spiral cords forming a cancellate, rhomboid pattern with nodes at intersections; axial ribs prosocline above selenizone, prosocyt below selenizone; number of spiral cords increases during ontogeny, reaching up to 22; whorl face raised below suture, ornamented with subsutural axially elongated tubercles; number of tubercles increases during ontogeny, reaching up to 36 per whorl; selenizone flat, depressed, begins within third whorl, situated just above peripheral carina, somewhat above suture; selenizone oblique, in same orientation as whorl face, bordered above by abaxially projected shell edge and below by adapically projected shell edge; selenizone ornamented with pronounced lunulae, one median spiral cord and up to three lateral spiral cords above and/or below the median cord; base flatly conical, minutely phaneromphalous, ornamented with axial and spiral cords of various strengths similar to those on whorl face and axial circumumbilical wrinkles, which give nodular appearance to adaxial spiral cords; basal axial ribs start prosocyrt just below periphery, then turning into opisthocyrt; aperture subquadrate, oblique, slightly wider than high; outer lip concave, basal lip flatly concave, columellar lip straight, oblique.

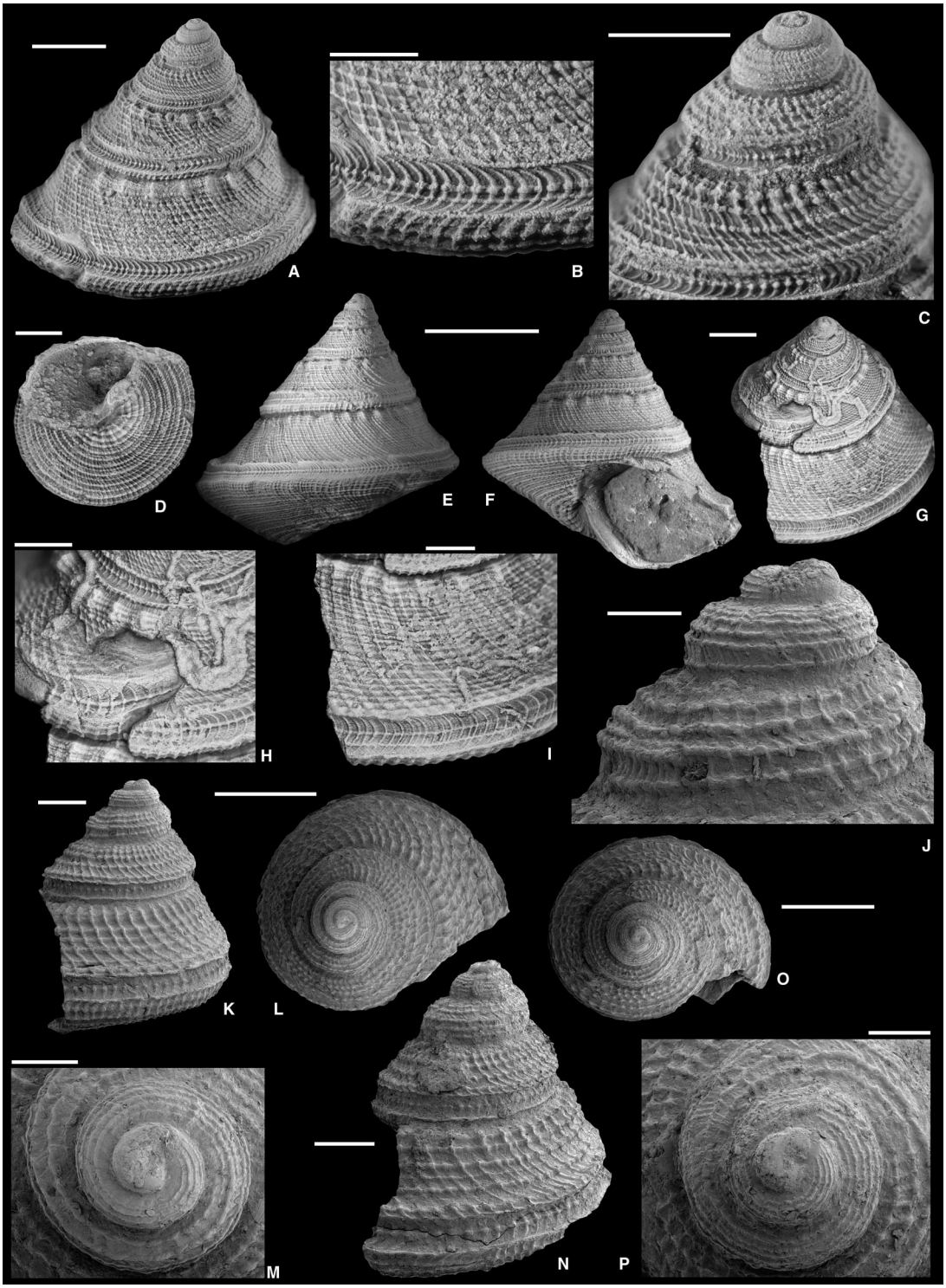

FIG. 23. *Phymatopleura brazoensis* (Shumard, 1860). A–D, SNSB-BSPG 2020 LXXVI 1, from the Finis Shale Member (Virgilian, Texas); B, oblique apical view, detail of ornament. E–F, SNSB-BSPG 2020 LXXVIII 1, from the Finis Shale Member (Virgilian, Texas). G–I, SNSB-BSPG 2020 LXXIV 1, from the Finis Shale Member (Virgilian, Texas); H, oblique apical view, detail of repaired shell scar and shift in position of selenizone during reconstruction of shell; I, oblique apical view, detail of ornament. J–M, SNSB-BSPG 2020 XCI 13, from the Finis Shale Member (Virgilian, Texas); J, lateral view, detail of early whorls showing prominent ornament; M, apical view, detail of early whorl. N–P, SNSB-BSPG 2020 XCI 15, from the Finis Shale Member (Virgilian, Texas); P, apical view, detail of early whorl. Scale bars represent: 2 mm (A, D, G); 1 mm (B, C, H, I, L, O); 5 mm (E, F); 0.2 mm (J, M, P); 0.5 mm (K, N). J–P, SEM images.

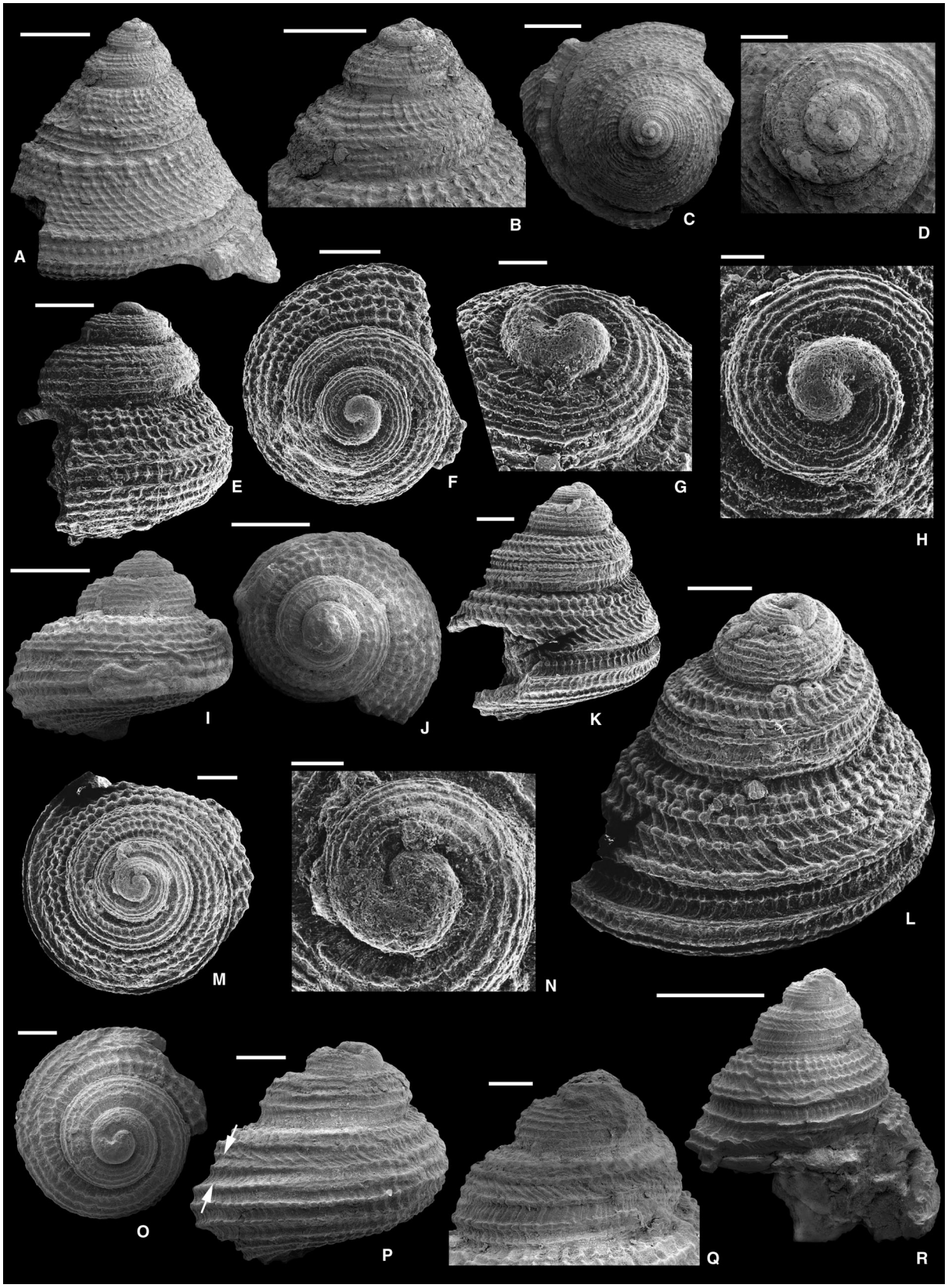
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FIG. 24. *Phymatopleura brazoensis* (Shumard, 1860). A–D, SNSB-BSPG 2020 XCI 14, from the Finis Shale Member (Virgilian, Texas); D, apical view, detail of first whorls of an adult specimen. E–H, SNSB-BSPG 2020 I 43, juvenile specimen from the Finis Shale Member (Virgilian, Texas); G, oblique apical view, detail of first two whorls; H, apical view, detail of protoconch and first whorl. I–J, SNSB-BSPG 2020 XCI 12, juvenile specimen from the Finis Shale Member (Virgilian, Texas). K–N, SNSB-BSPG 2020 I 45, juvenile specimen from the Finis Shale Member (Virgilian, Texas); N, apical view, detail of first whorl. O–P, SNSB-BSPG 2020 XCI 10, juvenile specimen showing the selenizone formation from V-shaped notch, from the Finis Shale Member (Virgilian, Texas), arrows indicate selenizone margins. Q–R, SNSB-BSPG 2020 XCI 9, from the Finis Shale Member (Virgilian, Texas). Scale bars represent: 1 mm (A, C, R); 0.5 mm (B, I, J); 0.2 mm (D, O–Q); 0.3 mm (E, F, K–M); 0.1 mm (G, H, N). All SEM images.

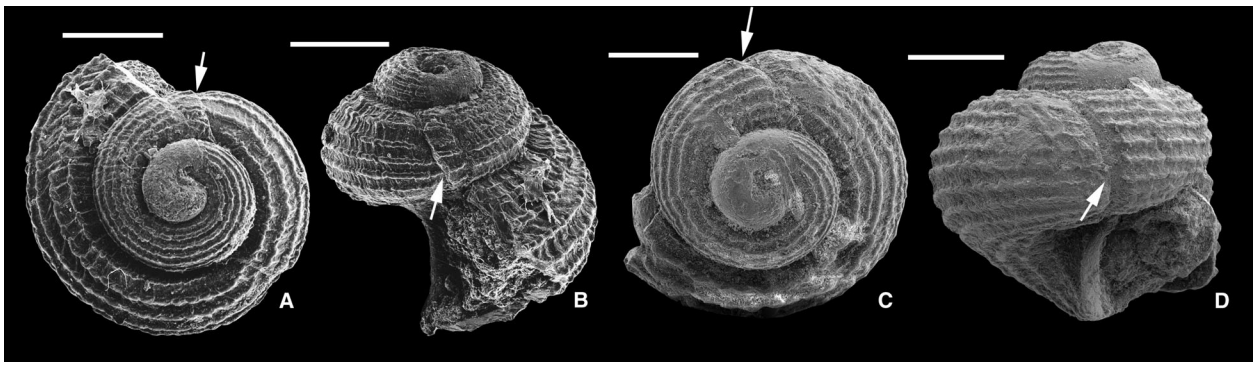

FIG. 25. *Phymatopleura brazoensis* (Shumard, 1860) juvenile specimens. A–B, SNSB-BSPG 2020 I 44, from the Finis Shale Member (Virgilian, Texas). C–D, SNSB-BSPG 2020 XCI 11, from the Finis Shale Member (Virgilian, Texas). Arrows indicate repaired shell breakages. Scale bars represent: 0.3 mm (A, B); 0.2 mm (C, D). All SEM images.

Remarks. Phymatopleura brazoensis is a characteristic species due to its intricate ornamentation and its conical shape. Its early ontogeny is very similar to that of *Ph. nodosa*. The whorl face of *Ph. brazoensis* is raised subsuturally but never forms a subsutural shoulder; angulation as *Ph. nodosa* and also lacks a median angulation. The selenizone of *Ph. brazoensis* is oblique at an angle of 35° with the axis (same as whorl face) while the selenizone of *Ph. nodosa* lies almost parallel to the shell axis. As a consequence, *Ph. brazoensis* lacks the lateral whorl face typical of other *Phymatopleura* species.

In *Phymatopleura brazoensis*, the number of subsutural tubercles is quite variable. The inner nacreous layer of the shell is thickened at the peripheral carina and the columella. Girty (1915) discussed the difference between *Ph. brazoensis* and *Ph. nodosa* but neither figured nor described *Ph. brazoensis*. Girty (1939) gave a detailed description of *Ph. brazoensis* including its intraspecific variation. Girty (1939) described the base of the shell as being anomphalous and reported 10–20 spiral cords on whorl face. By contrast, Batten (1958) counted 6–8 spiral cords on the whorl face and described its base as being phaneromphalous. Batten (1958) did not mention the presence of prominent subsutural tubercles. The discrepancies in the number of spiral cords in these reports can, at least in part, be explained by intraspecific variability and/or the presence of different ontogenetic stages. However, the lack of subsutural tubercles and of a phaneromphalous base suggests that the material illustrated and described by Batten (1958) does not represent *Ph. brazoensis*. The figured specimen (Batten 1958, pl. 36 fig. 16) has a straight flank and a low spire similar to that of *Glyptotomaria* rather than *Phymatopleura* but differs from *Glyptotomaria* in having a median cord on its selenizone.

Pleurotomaria subdecussata Geinitz, 1866 closely resembles *Ph. brazoensis* in shell morphology and ornamentation and could represent a synonym. However, the type specimen of *Ple. subdecussata* should be restudied for a formal synonymization.

Some of the studied specimens have up to three repaired shell injuries. During repair, the selenizone was reconstructed at the deepest part of the crack, distant from the pre-damage position of the selenizone (Fig. 23G, H). This indicates that the animal used the deepest part of the crack for the slit until it had recovered the shell. A similar repair pattern was documented by Schindel *et al.* (1982, pl. 1 fig. 6).

Juvenile *Phymatopleura* specimens with shell width of 1 mm show repaired scars (Fig. 25, see discussion below).

Phymatopleura girtyi sp. nov.
Figure 26

? 1915 *Orestes nodosus*; Girty, p. 320, pl. 22 figs 7–7a (non figs 8–10).

LSID. urn:lsid:zoobank.org:act:15161EEA-3133-4F0C-9BD6-043C37C782F6

Derivation of name. After George Herbert Girty (1869–1939), who contributed to our knowledge on Carboniferous invertebrates of the USA.

Holotype. SNSB-BSPG 2020 I 22

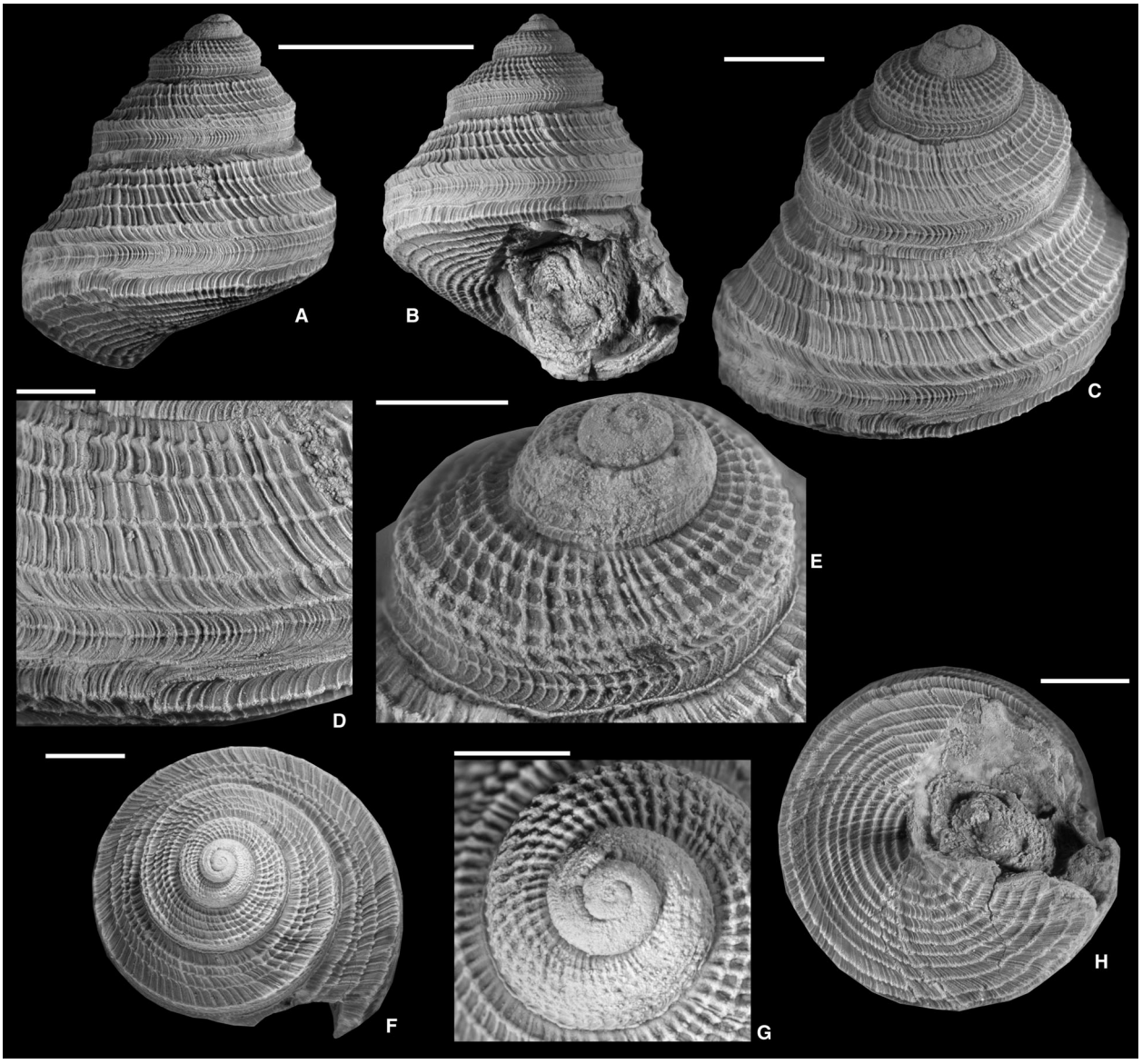

FIG. 26. *Phymatopleura girtyi* sp. nov. from the Wewoka Formation (Desmoinesian, Oklahoma). A–H, SNSB-BSPG 2020 I 22, holotype; G, (slightly oblique) apical view, detail of early whorls. Scale bars represent: 5 mm (A, B); 2 mm (C, F, H); 1 mm (D, E, G).

Type location & age. Desmoinesian Wewoka Formation, SE¼, SW¼, sec. 10, T. 13 N., R. 12 E., Okmulgee Lake 7½′ Quadrangle, Okmulgee County, Oklahoma; hillside exposure (AMNH locality 3516; 35°36′44.67″N, 96°01′30.03″W).

Material. 1 specimen from the Desmoinesian of Oklahoma (Wewoka Formation, OKD–10): SNSB-BSPG 2020 I 22.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 I 22	9.6	8.2	59	0.37	4.7	4.3	0.9	0.21	0.19

Description. Shell small, trochiform, cyrtoconoid, higher than wide, with six whorls; spire gradate; suture shallow; whorls embrace at basal angulation; initial whorl diameter 0.37 mm; first three whorls evenly convex; about first two whorls without visible ornament (but recrystallized); ornament of spiral threads and prosocline axial threads on third whorl; later whorl face flat between suture and subsutural cord, flatly concave between subsutural cord and median angulation, parallel to shell axis below median angulation (lateral whorl face); mature whorl face above selenizone ornamented with four spiral cords and straight prosocline axial threads (strengthened growth lines); adapical-most cord on whorl face forming narrow shoulder; abaxial-most cord on whorl face situated on median angulation; axial threads

curved backwards near selenizone; axial ribs more closely spaced than spiral cords; whorl face below selenizone ornamented with prosocyrt threads; slit extends along one quarter of whorl; selenizone situated at mid-whorl on last whorl, and low on whorl face of spire whorls; selenizone wide (20% of whorl face width), flat, slightly depressed, begins after second whorl, situated between median and basal angulation, bordered above and below by spiral threads; selenizone ornamented with unequally-spaced lunulae and one median spiral thread; base convex, ornamented with opisthocyrt axial threads and 11 pronounced spiral cords of same strength; abaxial-most basal cord situated on basal angulation; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex; base anomphalous.

Remarks. Phymatopleura girtyi differs from other *Phymatopleura* species studied here in having a relatively low number of spiral cords that stays constant during ontogeny, closely spaced axial threads and by its general form. The shell ornamentation of *Phymatopleura girtyi* resembles that of *Dictyotomaria quadrilineata* (Girty, 1934), but differs from it by its gradate spire and a lower apical angle, by having angulated whorls and a median thread on the selenizone. The late teleoconch morphology of *Phymatopleura girtyi* superficially resembles that of *Borestus*, but it differs from the latter by its convex rather than angular early whorls, by having a less depressed selenizone, by lacking an abaxial projection of the slit edges and by having a median spiral thread on the selenizone.

Girty (1915, p. 320) tentatively placed a single specimen in *Ph. nodosa* and proposed the name '*Orestes lineatus*' in case it proves to be a distinct species; in the figure caption it is stated: 'Side view, × 3, of a specimen included with doubt in this species. If it proves to be distinct the name *Orestes lineatus* is proposed for it.' Since Girty (1915) only gave a drawing, and no description or diagnosis, this name is a *nomen nudum*. The drawn specimen resembles our material but is broader and the median angulation is lower on the whorls.

Phymatopleura conica sp. nov.
Figure 27

LSID. urn:lsid:zoobank.org:act:578E8CDE-1CDC-411A-A9DD-9F8BB7F7AD84

Derivation of name. Latin, for the conical shape.

Holotype. SNSB-BSPG 2020 LVIII 1

Paratypes. SNSB-BSPG 2020 LVIII 2, 3

Type location & age. Morrowan, Gene Autry Formation exposed in gullies on east side of unnamed tributary of Sycamore Creek on the Daube Ranch, NW¼, NW¼, SW¼, sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7½′ Quadrangle, Oklahoma (AMNH locality 5270; 34°14′13.76″N, 96°52′42.02″W).

Material. 69 specimens from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 1–4, and a further 65 specimens (SNSB-BSPG 2020 LVIII).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 1	10.8	11.4	86	0.36	5.6	5.2	0.8	0.16	0.15
2020 LVIII 2	10.7	11.0	87	–	6.8	5.5	0.9	0.16	0.13
2020 LVIII 3	11.7	11.6	83	0.39	7.0	5.6	0.9	0.15	0.12

Description. Shell small, conical, as high as wide, comprising six whorls; suture moderately deep; whorls embrace somewhat below selenizone in early whorls and near adapical edge (almost entire selenizone covered by following whorl) to middle of selenizone in later whorls; first whorl without visible ornament; early whorl face convex, ornamented with spiral threads only, appearing on second whorl, then also with prosocyrt axial threads; narrow shoulder forming on fourth whorl by slight angulation at adapical spiral cord; later whorl face slightly concave between shoulder and median angulation, parallel to axis (vertical) below median angulation, ornamented with equally spaced spiral cords and prosocline axial ribs between suture and median angulation; spiral cords increase up to 11 on last whorl; axial ribs and spiral cords forming cancellate rhombic pattern with small nodes at intersections; nodes widely spaced and more prominent on shoulder and occasionally on median and abapical angulations; selenizone begins after second whorl, initially situated in suprasututral position, then more or less covered by subsequent whorl; selenizone in later whorls situated on peripheral lateral whorl face, between median and abapical angulation, slightly depressed bordered by spiral cords; selenizone ornamented with equally-spaced thick lunulae and one median spiral cord which forms crest with nodes at intersection with lunulae and makes selenizone slightly angulated; base flatly convex, ornamented with opisthocyrt axial threads or growth lines and nodular spiral cords; up to 14 spiral cords on base; spiral cords stronger towards umbilicus; aperture subquadrate, as wide as high; outer lip angular, basal lip oblique, convex, columellar lip convex; base anomphalous.

Remarks. Phymatopleura conica can be distinguished from the other studied species by different ornamentation and differs from all other members of the genus by embracing the selenizone so that the selenizone is obscured except the last whorl. *Phymatopleura nodosa* is similar to *Ph. conica* but *Ph. conica* is broader and *Ph. nodosa* has the selenizone higher on the spire whorls. In one specimen a '*Worthenia*-type' selenizone (see the description and figures of the selenizone of *Worthenia* (*W.*) *tabulata* below) is observed (Fig. 27I–J). This is regarded herein as result of intraspecific variation.

Genus PARAGONIOZONA Nelson, 1947

Type species. Paragoniozona nodolirata Nelson, 1947 from the Carboniferous of Texas, USA; original designation.

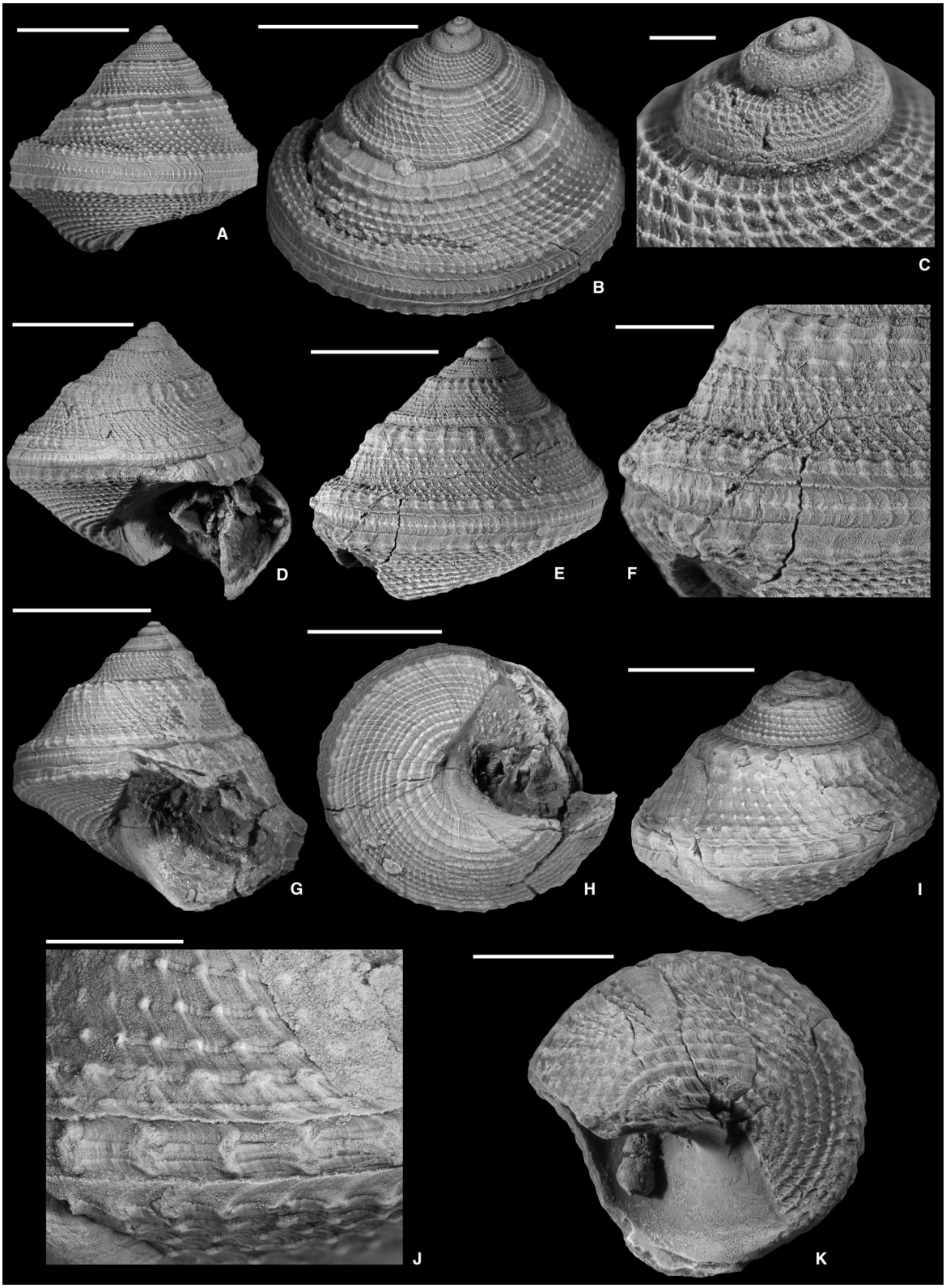

FIG. 27. *Phymatopleura conica* sp. nov. from the Gene Autry Shale (Morrowan, Oklahoma). A–C, SNSB-BSPG 2020 LVIII 1, holotype; C, oblique lateral view, detail of early whorls. D–F, SNSB-BSPG 2020 LVIII 3, paratype; F, lateral view showing the profile and detail of ornament. G–H, SNSB-BSPG 2020 LVIII 2, paratype. I–K, SNSB-BSPG 2020 LVIII 4; J, detail of '*Worthenia*-type' ornament on selenizone. Scale bars represent: 5 mm (A, B, D, E, G–I, K); 0.5 mm (C); 2 mm (F, J).

Remarks. Paragoniozona unites conical shells with a knobby ornament and highly ornamented selenizone low on the whorls, just above the suture. When Nelson (1947) erected *Paragoniozona*, he included *Pa. multilirata* Nelson, 1947 and *Pa. sarlei* Nelson, 1947 (*Pa. sarlei* was later considered to represent a probable synonym of *Pa. multilirata* by Kues & Batten (2001, p. 42)). These two species differ from all other *Paragoniozona* species in whorl ornamentation and having the selenizone well above the suture. They might represent a new genus that is more closely related to *Abylea* Sturgeon, 1964*a* (see Hoare *et al.* 1997, fig. 3, for *Abylea* species) than to *Paragoniozona*. Early ontogeny and ornamentation of whorls and selenizone suggest that *Abylea* might be closely related to *Shansiella* (family Portlockiellidae) (see Remarks on Portlockiellidae, below).

Rhinoederma hotwellsensis Batten, 1966 from the Lower Carboniferous of England does not represent *Rhineoderma* de Koninck. Unlike the type species of *Rhineoderma*, *R. radula* (de Koninck, 1843) (Knight 1941, p. 301, pl. 30 fig. 4), *R. hotwellsensis* has planispiral early whorls, a lower whorl expansion rate, a much smaller aperture and a wider umbilicus. *Rhinoederma hotwellsensis* resembles *Paragoniozona* in whorl ornamentation but differs from it in having a wide umbilicus. *Rhinoederma hotwellsensis* probably represents a new genus that is closely related to *Paragoniozona* and *Salterospira* Batten, 1966.

Mazaev (2019*b*) proposed placing *R. venustiformis* Licharew, 1967 in *Deseretospira* Gordon & Yochelson, 1987. According to the original description given by Gordon & Yochelson (1987, p. 56), the type species of *Deseretospira*, *De. monilifera* Gordon & Yochelson, 1987, has a concave selenizone without nodes and represents an eotomariid genus. In contrast, the selenizone of *R. venustiformis* Licharew, 1967 is ornamented with nodes, which suggests a placement of this species in *Paragoniozona*. Due to typical nodular reticulate ornamentation on whorl face, selenizone with nodular lunulae, convex whorl profile and median position of selenizone we herein place it in *Paragoniozona*: *Pa. venustiformis* (Licharew, 1967) comb. nov. *Deseretospira* Gordon & Yochelson, 1987, is probably younger synonym of *Wellergyi* Thein & Nitecki, 1974. This might be also true for *Hammatospira* Gordon & Yochelson, 1983. All three genera share a similar whorl profile, ornamentation on whorl face and on the selenizone, low position of the selenizone and the concave shape of the selenizone.

Paragoniozona nodolirata Nelson, 1947
Figure 28

*	1947	*Paragoniozona nodolirata* Nelson, p. 461, pl. 65 figs 2a–c.
?	1958	*Paragoniozona* cf. *P. nodolirata* Nelson; Batten, pl. 36 fig. 17.
	1967	*Paragoniozona nodolirata* Nelson; Yochelson & Saunders, p. 160.
?	2001	*Paragoniozona nodolirata* Nelson; Kues & Batten, p. 41, fig. 7.22–7.25.
	2002	*Paragoniozona nodolirata* Nelson; Bandel *et al.*, p. 643, pl. 1 figs 9–10, pl. 2 figs 11–16.

Material. 33 specimens from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 77, 260–63, 276, and a further 27 specimens: SNSB-BSPG 2011 X.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 77	[3.68]	3.8	72	-	1.8	1.5	0.4	0.24	0.20
2011 X 261	3.7	3.7	70	–	1.7	1.5	0.3	0.18	0.16
2011 X 262	3.9	4.0	65	–	2.1	1.7	0.3	0.18	0.14
2011 X 263	3.6	3.8	58	0.3	1.6	1.3	0.3	0.21	0.17

Description. Shell small, tochiform conical, higher than wide, with 5–6 whorls; whorl profile flatly convex; suture slightly impressed; first whorl smooth, well rounded, with a diameter of 0.33 mm, with growth lines towards the end of the first whorl; second whorl smooth or occasionally with eight faint spiral threads; third whorl convex, strong spiral cords (*c.* 5 in number) appear on third whorl; selenizone starts as median sinus on third whorl, that moves in abapical direction subsequently and finally appears between lowermost two cords at transition to the fourth whorl, where at the same time spiral cords form nodes and whorl face becomes flatly convex; later whorl face flat to flatly convex, ornamented with oblique prosocline/prosocyrt growth lines, four nodular spiral cords above selenizone excluding cord bordering selenizone; selenizone situated above suture, convex, ornamented with prominent nodes, bordered by two straight spiral cords; selenizone slightly protruding outward from rest of whorl face, forming periphery; base flatly convex, ornamented with opisthocyrt growth lines and *c.* 10 spiral cords; aperture subquadrate, slightly wider than high; outer, basal and columellar lips convex; base anomphalous.

Remarks. Paragoniozona nodolirata has constantly five cords throughout ontogeny according to the original description by Nelson (1947, p. 461, pl. 54 fig. 2a–c). The specimens from the Buckhorn Asphalt agree well with the description and figures of Nelson (1947), who did not describe the early ontogeny and eight spiral threads that are present on early teleoconch whorls. Batten (1958) and Kues & Batten (2001) identified specimens with 4–8 spiral cords above the selenizone as *Pa. nodolirata*, suggesting that this character is subject to considerable intraspecific variation. The specimens figured by these authors have more prominent nodes. Their assignment to *Pa. nodolirata* is therefore uncertain.

The juvenile specimens assigned to *Pa. nodolirata* by Bandel *et al.* (2002) could represent *Pa. paucinodosa*. However, these two species have the same early shell morphology and ornamentation and can only be differentiated by the adult morphology of larger specimens.

Paragoniozona paucinodosa Nelson, 1947
Figures 29, 30

*	1947	*Paragoniozona paucinodosa* Nelson, p. 461, pl. 65 figs 3a–c.
	1967	*Paragoniozona paucinodosa* Nelson; Yochelson & Saunders, p. 160.

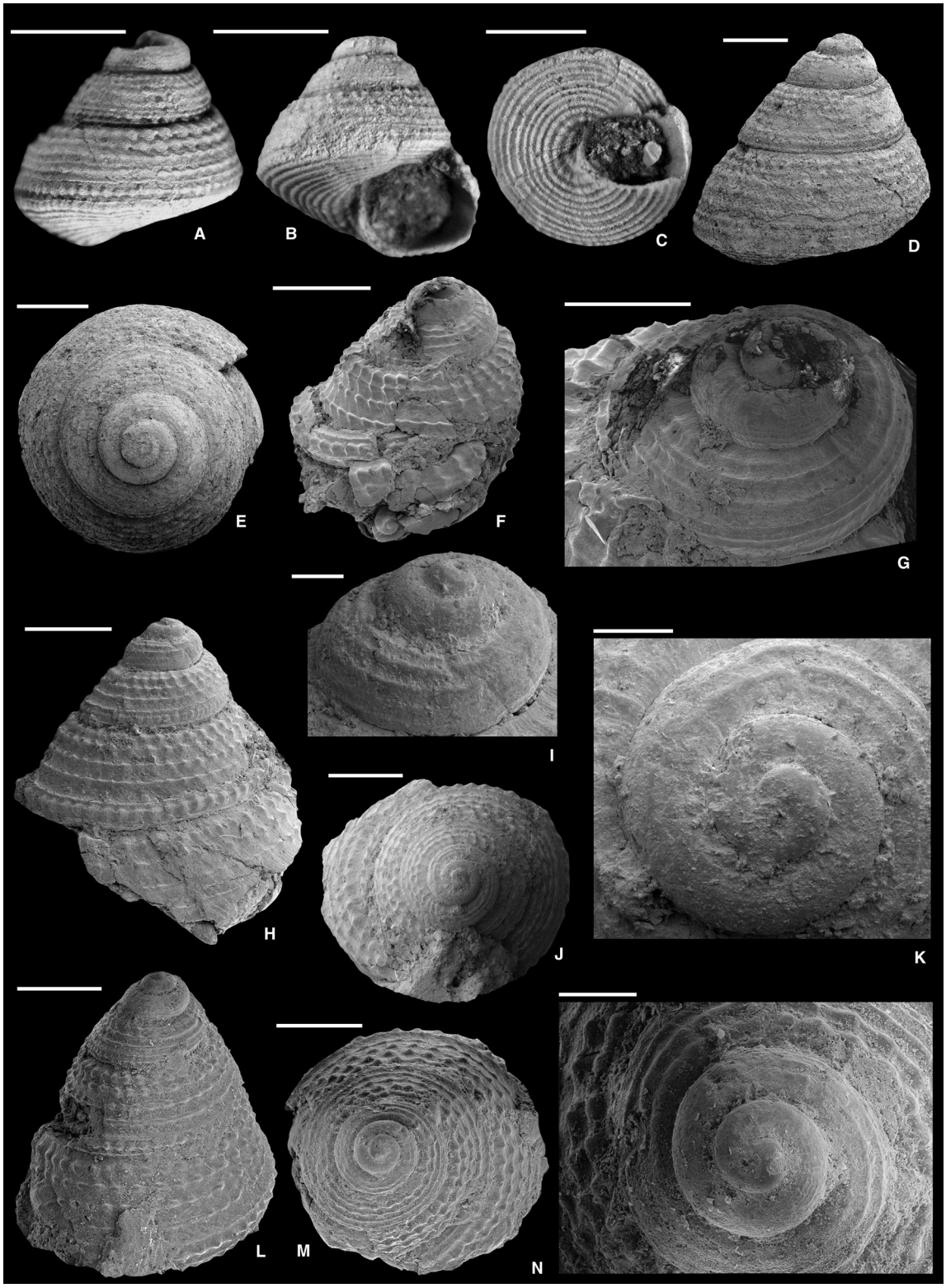

FIG. 28. *Paragoniozona nodolirata* Nelson, 1947, from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–C, SNSB-BSPG 2011 X 77. D–E, SNSB-BSPG 2011 X 262. F–G, SNSB-BSPG 2011 X 260; G, oblique apical view, detail of early whorls. H–K, SNSB-BSPG 2011 X 263; I, oblique apical view, detail of early whorls; K, apical view, detail of early whorls. L–N, SNSB-BSPG 2011 X 276; N, apical view, detail of early whorls. Scale bars represent: 2 mm (A–C); 1 mm (D–F, H, J, L, M); 0.5 mm (G); 0.2 mm (I, K); 0.3 mm (N). D–N, SEM images.

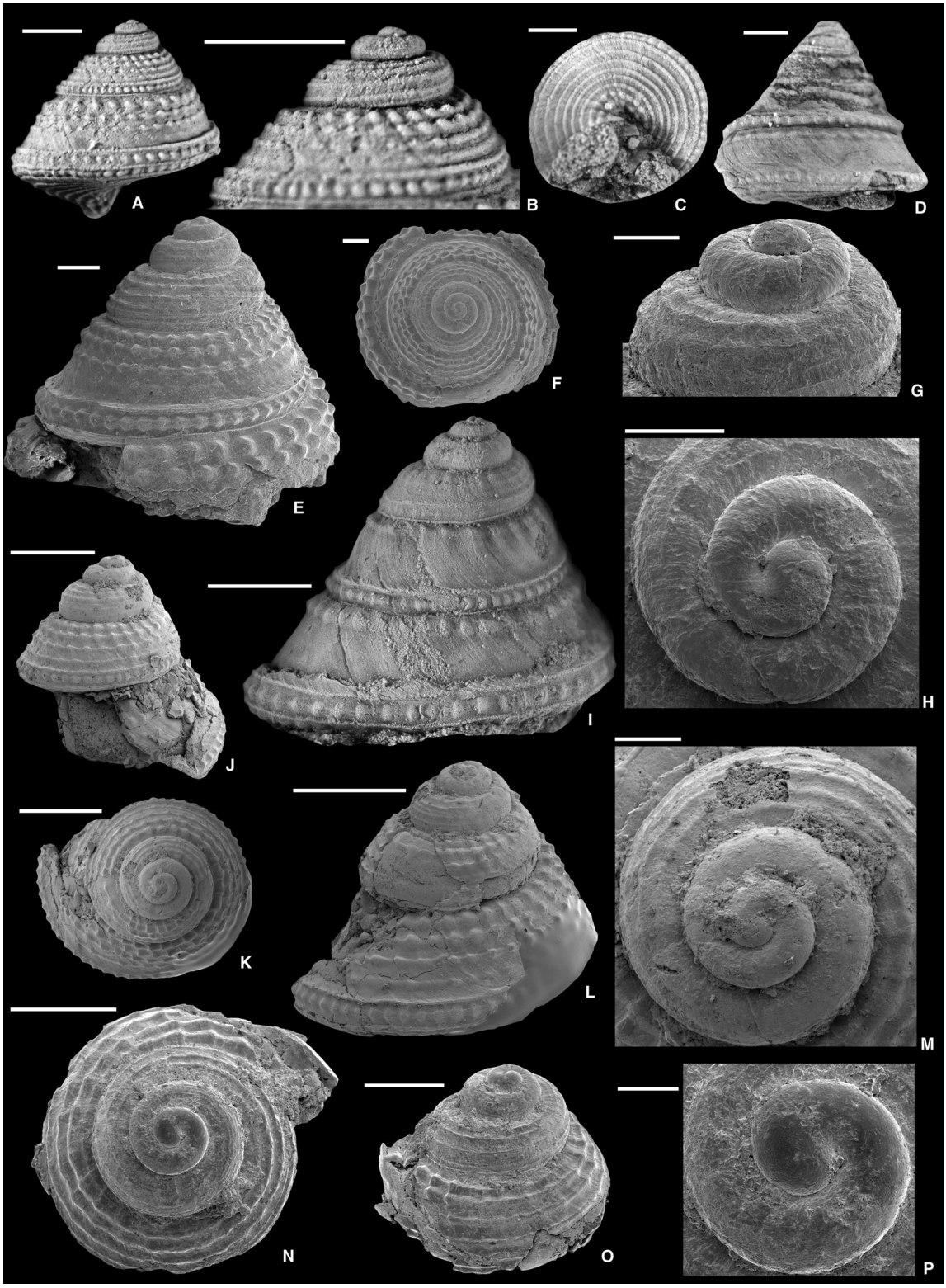

FIG. 29. *Paragoniozona paucinodosa* Nelson, 1947, from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–C, SNSB-BSPG 2011 X 81. D, SNSB-BSPG 2011 X 80. E–H, SNSB-BSPG 2011 X 265; G, oblique apical view, detail of early whorls; H, apical view, detail of early whorls. I, SNSB-BSPG 2011 X 264. J–M, SNSB-BSPG 2011 X 273, juvenile specimen; M, apical view, detail of early whorls. N–P, SNSB-BSPG 2011 X 267 juvenile specimen; P, apical view, detail of first whorl. Scale bars represent: 1 mm (A–D, I–L); 0.3 mm (E, F, G, H); 0.2 mm (M); 0.5 mm (N, O); 0.1 mm (P). E–H, J–P, SEM images.

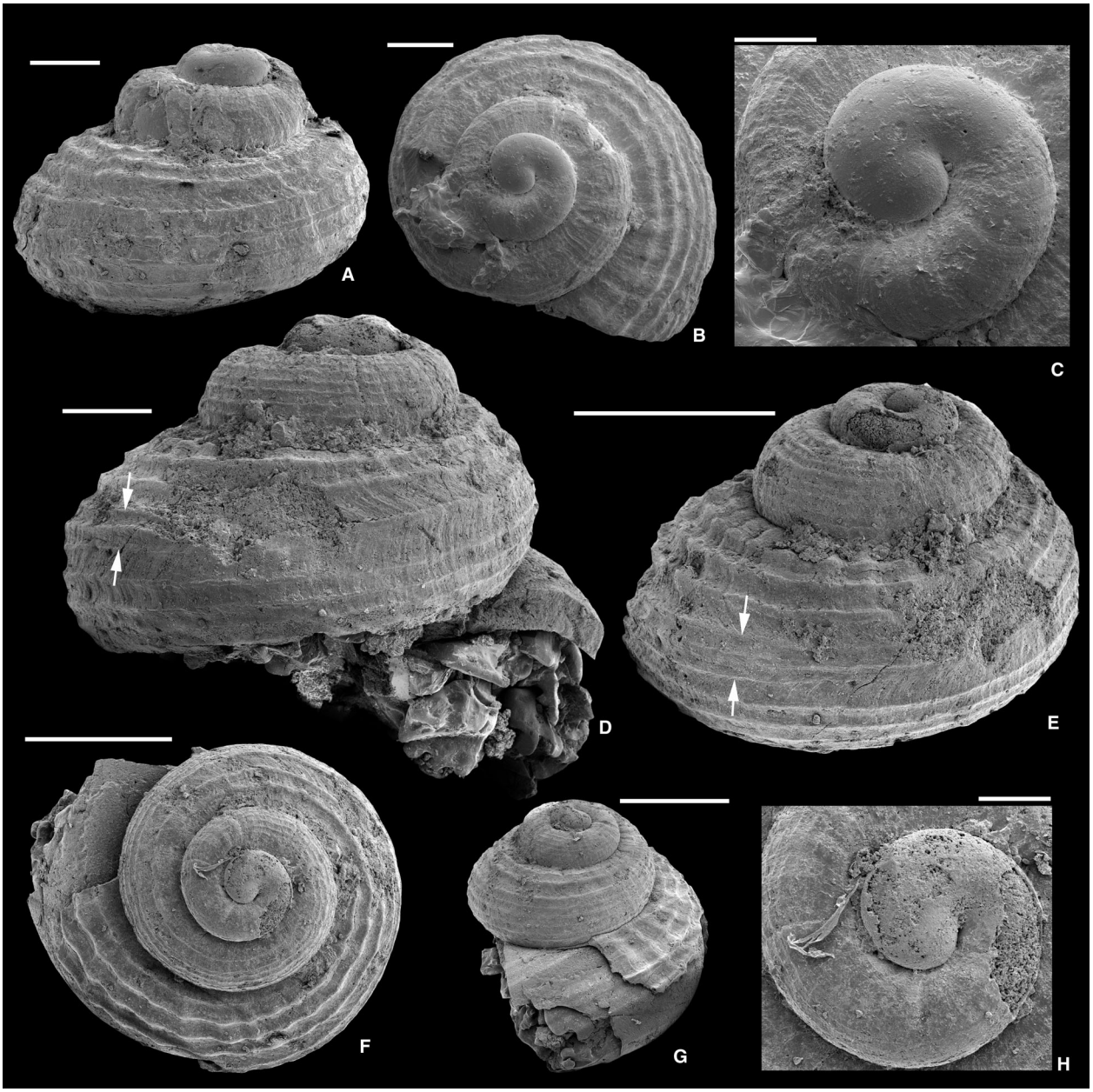

FIG. 30. *Paragoniozona paucinodosa* Nelson, 1947, from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–C, SNSB-BSPG 2011 X 271, juvenile specimen; C, apical view, detail of first whorl. D–H, juvenile specimen (missing specimen) showing the selenizone formation from V-shaped notch, arrows indicate selenizone margins; H, apical view, detail of first whorl. Scale bars represent: 0.2 mm (A, B, D); 0.1 mm (C, H); 0.5 mm (E–G). All SEM images.

Material. 45 specimens from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 80–81, 264–275, and a further 31 specimens (SNSB-BSPG 2011 X).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 80	5.2	5.2	71	0.34	2.0	1.8	0.4	0.24	0.22
2011 X 81	3.4	3.7	69	–	1.8	1.6	0.4	0.24	0.21

Measurements (mm). (Continued)

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 264	3.2	3.5	69	0.35	1.5	1.3	0.3	0.23	0.20

Remarks. Kues & Batten (2001, p. 41) mentioned that *Pa. paucinodosa* might be an interpopulation variant of *Pa. nodolirata*. *Paragoniozona paucinodosa* and *Pa. nodolirata* are found within

the same bulk samples from the Buckhorn Asphalt Quarry and show the same early shell morphology and ontogenetic development. *Paragoniozona paucinodosa* is identical to *Pa. nodolirata* in the first four whorls. Both species have four nodular spiral cords on the fourth whorl. However, while the spiral cords increase to five in number and cover whole surface in *Pa. nodolirata* from the fifth whorl onwards, the number of spiral cords decreases to three in *Pa. paucinodosa* on the fifth whorl and become restricted to the subsutural portion of the whorls. Since the nodular spiral cords cover the adapical half of the whorl face in *Pa. paucinodosa*, the lower half of the whorl face is smooth. In some specimens of *Pa. paucinodosa*, the number of spiral cords decreases from three to four on the third and fourth whorls to one in later whorls (Fig. 29D, I). If *Pa. paucinodosa* and *Pa. nodolirata* represent the same species, then the degree of variation would be extremely large compared to other *Paragoniozona* species. Therefore, we keep the specimens having spiral cords restricted to the adapical portion of the whorl face separate and assign them to *Pa. paucinodosa* as originally proposed by Nelson (1947).

The protoconch of *Pa. paucinodosa* is discernable from the teleoconch; it consists of less than one whorl and measures *c.* 0.24 mm in diameter.

The selenizone of *Pa. paucinodosa* appears within the third whorl, the slit is initially V-shaped and situated on a spiral cord on the mid whorl face (Fig. 30D, E).

Paragoniozona ornata nom. nov. [pro *Pleurotomaria aspera* Girty, 1934]
Figure 31

*	1934	*Pleurotomaria aspera* Girty, p. 259, figs 23–25 [non *Pleurotomaria aspera* J. de C. Sowerby *in* Sedgwick & Murchison, 1840].
	1947	*Pleurotomaria aspera* Girty; Nelson, p. 461.
?	1964*a*	*Paragoniozona* cf. *P. aspera* (Girty); Sturgeon, p. 214, pl. 33 figs 1–2.
	1967	*Paragoniozona aspera* (Girty); Yochelson & Saunders, p. 159.

Derivation of name. Latin, because of the pronounced, intricate axial and spiral ornamentation.

Material. 8 specimens from the Desmoinesian of Texas (Lazy Bend Formation, TXD–03): SNSB-BSPG 2020 LXIX 1–2, and a further 6 specimens (SNSB-BSPG 2020 LXIX).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXIX 1	3.9	3.2	54	0.36	1.9	1.8	0.2	0.13	0.13
2020 LXIX 2	3.9	[3.88]	56	0.31	1.9	1.7	0.3	0.20	0.18

Description. Shell small, turbiniform conical, slightly cyrtoconoid, higher than wide, largest specimen with six whorls; suture impressed, situated at abapical edge of selenizone; early whorl face rounded convex; early teleoconch whorls ornamented with spiral threads; later whorl face flatly, evenly convex with periphery low on the whorls, somewhat above selenizone; whorl face ornamented with equally-spaced spiral cords and numerous prosocline prosocyrt axial ribs; spiral cords increase to 7 on last preserved whorl; axial ribs somewhat stronger than spiral cords; axial ribs and spiral cords form reticulate pattern with prominent nodes at intersections; selenizone in suprasutural position, convex, slightly depressed, bordered by sharp shell edges; selenizone ornamented with equally-spaced thick lunulae and one median spiral cord, lunulae ornamented with nodes as in whorl face, at intersections of median spiral cord and lunulae; base flatly convex, ornamented with opisthocyrt growth lines and up to six nodular spiral cords; spiral cords become stronger towards umbilicus; aperture subovate, slightly wider than high; outer, basal and columellar lips convex; base anomphalous.

Remarks. Pleurotomaria aspera Girty, 1934 is pre-occupied by *Ple. aspera* J. de C. Sowerby *in* Sedgwick & Murchison, 1840. *Pleurotomaria aspera* J. de C. Sowerby was tentatively placed in *Phymatopleura* by Amler & Heidelberger (2003). *Pleurotomaria aspera* J. de C. Sowerby was used after 1899 as a valid name (e.g. Jukes-Browne 1912, p. 196). Here, we propose *Paragoniozona ornata* nom. nov. as a replacement name for *Pleurotomaria aspera* Girty.

Nelson (1947) erected the genus *Paragoniozona* and included *Ple. aspera* Girty (= *Pa. ornata* nom. nov.) without discussing the differences between *Ple. aspera* and other *Paragoniozona* species. Among *Paragoniozona* species, *Pa. ornata* most closely resembles *Pa. nodolirata*. *Paragoniozona ornata* differs from *Pa. nodolirata* by having 6–7 spiral cords and their number increases during ontogeny while *Pa. nodolirata* has five cords throughout ontogeny (see the Remarks on *Pa. nodolirata* above). *Paragoniozona ornata* also differs from *Pa. nodolirata* by having equally prominent axial and spiral cords. *Paragoniozona ornata* differs from the other members of *Paragoniozona* by its ornamentation (i.e. number and prominence of ribs, cords and nodes) on the whorl face and selenizone; in particular, the axial ribs are stronger than in the other species.

Paragoniozona cf. *millegranosa* (Girty, 1934)
Figure 32

cf. *	1934	*Pleurotomaria millegranosa* Girty, p. 259, figs 28–29.
cf.	1947	*Paragoniozona millegranosa* (Girty); Nelson, p. 461, pl. 65 fig. 1.
cf.	1967	*Paragoniozona millegranosa* (Girty); Yochelson & Saunders, p. 160.

Material. 1 specimen from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 5.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 5	6.8	8.4	89	0.34	3.3	3.1	0.7	0.21	0.20

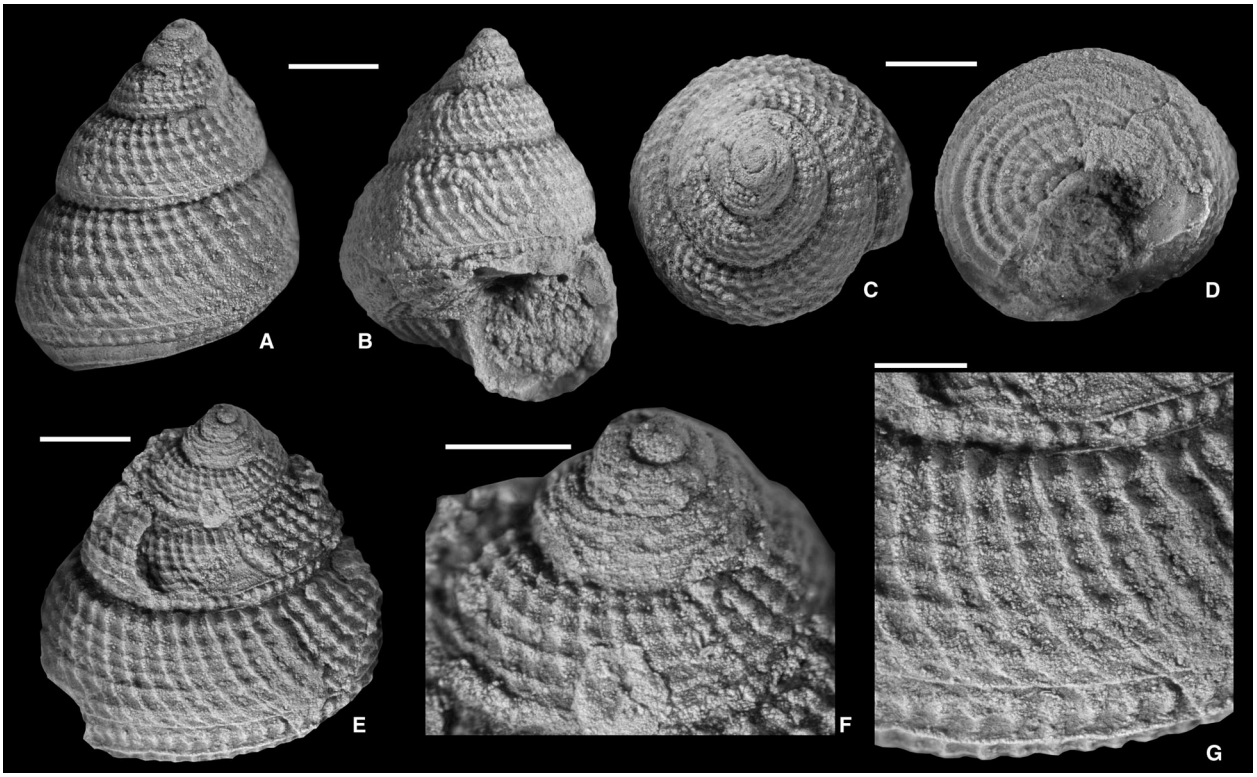

FIG. 31. *Paragoniozona ornata* nom. nov. from the Lazy Bend Formation (Desmoinesian, Texas). A–D, SNSB-BSPG 2020 LXIX 1. E–G, SNSB-BSPG 2020 LXIX 2; F, oblique apical view, detail of early whorls; G, oblique apical view, detail of ornament. Scale bars represent: 1 mm (A–E); 0.5 mm (F, G).

Description. Shell small, broadly conical, wider than high, the largest specimen with 5.5 whorls; suture incised, situated at abapical edge of selenizone; apical angle *c.* 80°–85°; early whorl face convex, ornamented with spiral threads; later whorl face convex to slightly convex, ornamented with spiral cords and prosocline to slightly prosocyrt axial ribs; four spiral cords in early whorls, increasing to six on last whorl; axial ribs and spiral cords form reticulate pattern with nodes at intersections; selenizone concave, depressed, situated near abapical edge of whorl face, bordered by sharp shell edges; selenizone ornamented with equally-spaced, strong lunulae, a median spiral cord and nodes where lunulae and median cord intersect; only peripheral portion of base is preserved; base convex near edge and ornamented with regular opisthocyrt axial ribs and spiral cords.

Remarks. The present specimen differs from *Pa. nodolirata*, the type species of *Paragoniozona*, in several aspects. *Paragoniozona nodolirata* has a conical shape, an apical angle of 65° (from illustration; 60° according to description by Nelson 1947), an almost flat to very slightly convex whorl face of mature whorls and five nodular spiral cords above the selenizone. The studied specimen has a higher apical angle (80°) and is hence lower spired, has a more convex whorl profile and differs in the number of the spiral cords (4–6 vs 5). The suture of the studied specimen is distinctly incised. The present specimen closely resembles *Pa. millegranosa* (Girty, 1934) in the whorl profile and apical angle. However, the nodes are somewhat stronger, the lunulae are pronounced and the number of spiral lirae is lower than in the holotype of *Pa. millegranosa* (Nelson 1947, pl. 65, fig. 1). Therefore, the present specimen is placed in *Pa. millegranosa* with reservation. *Paragoniozona* cf. *millegranosa* is larger than *Pa. ornata* and has a higher apical angle.

Paragoniozona yanceyi sp. nov.
Figure 33

LSID. urn:lsid:zoobank.org:act:CC803BAC-261A-4642-B517-3BE7507CEA1F

Derivation of name. After the geologist and palaeontologist Thomas E. Yancey, for his work on late Palaeozoic invertebrate faunas.

Holotype. SNSB-BSPG 2011 X 254

Paratypes. SNSB-BSPG 2011 X 255, 256, 257

Type location & age. Boggy Formation outcrop at the Buckhorn Asphalt Quarry (34°26′44″N; 96°57′41″W), Pennsylvanian, Desmoinesian.

Material. 7 specimens from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 254–258, and a further 2 specimens (SNSB-BSPG 2011 X).

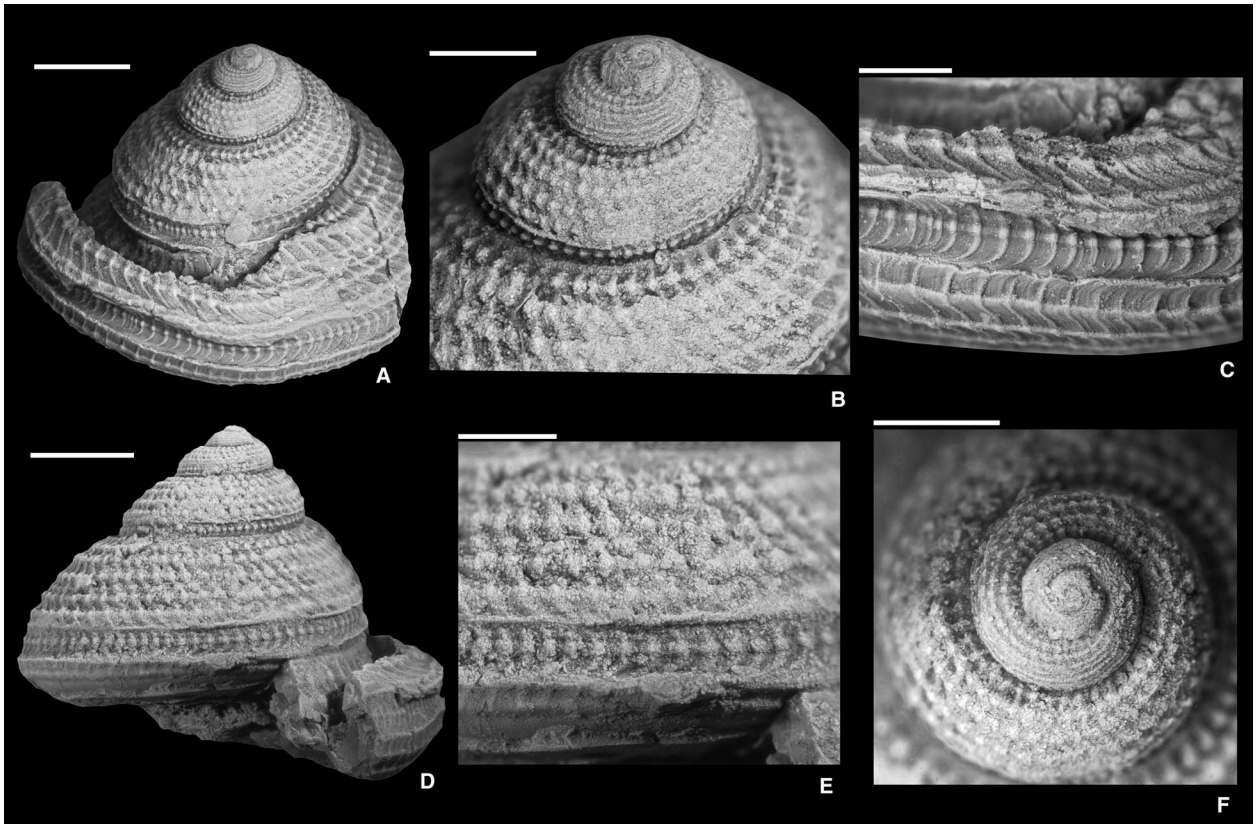

FIG. 32. *Paragoniozona* cf. *millegranosa* (Girty, 1934) from the Gene Autry Shale (Morrowan, Oklahoma). A–F, SNSB-BSPG 2020 LVIII 5; B, oblique apical view, detail of early whorls; C, lateral view, detail of selenizone and lunulae; E, lateral view, detail of ornament. Scale bars represent: 2 mm (A, D); 1 mm (B, C, E, F).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2011 X 254	4.4	5.6	95	0.31	1.9	1.9	0.4	0.20	0.20
2011 X 255	[4.72]	[5.11]	95	0.30	–	–	–	–	–
2011 X 256	[3.34]	[4.17]	90	–	1.6	1.5	0.3	0.22	0.20

Description. Shell small, low trochiform, wider than high; largest specimen with five whorls; apical angle of 90°; first whorl 0.28 mm in diameter; first two whorls convex, smooth; faint spiral cords develop within third whorl, strengthening during ontogeny; later whorl face between adapical suture and adapical border of selenizone convex, ornamented with five prominent spiral cords; nodes on intersections of spiral cords and strengthened prosocline prosocyrt growth lines; growth lines occasionally form lamellae; selenizone appears at 2.5 whorls, slightly below mid whorl face, later in suprasutural position; selenizone flatly concave, slightly sunken, delimited by straight spiral cords, ornamented with node bearing lunulae; whorl face below abapical edge of selenizone narrow; prominent spiral cord present at the transition to base; base ornamented with nodular spiral cords; other basal characters unknown.

Remarks. The specimens at hand resemble the monotypic Carboniferous genus *Hammatospira* Gordon & Yochelson, 1983 and the members of the Devonian genus *Devonorhineoderma* Frýda *in* Heidelberger, 2001, especially its type species *Dev. orbignyana* (d'Archiac & Verneuil, 1842). However, the specimens at hand are lower spired and differ in ornamentation. The early ontogeny, the morphology of the selenizone and the whorls suggest an assignment to *Paragoniozona*. *Paragoniozona yanceyi* differs from all other *Paragoniozona* species by its ornamentation pattern, which consists of five prominent nodular spiral cords, and by its lower spire. Among *Paragoniozona* species, *Pa. yanceyi* resembles *Pa. millegranosa* (Girty) most in the strength of nodes on the selenizone and whorl profile but differs in having fewer spiral node bearing cords.

Genus WORTHENIA de Koninck, 1883
Subgenus WORTHENIA de Koninck, 1883

Type species. Turbo tabulatus Conrad, 1835 from the Carboniferous of Pennsylvania, USA; original designation.

Remarks. A large number of late Palaeozoic to Triassic species with gradate spire and a selenizone situated at the angulation of the whorl face have been placed in *Worthenia*. Although several similar genera and subgenera have been proposed for a better

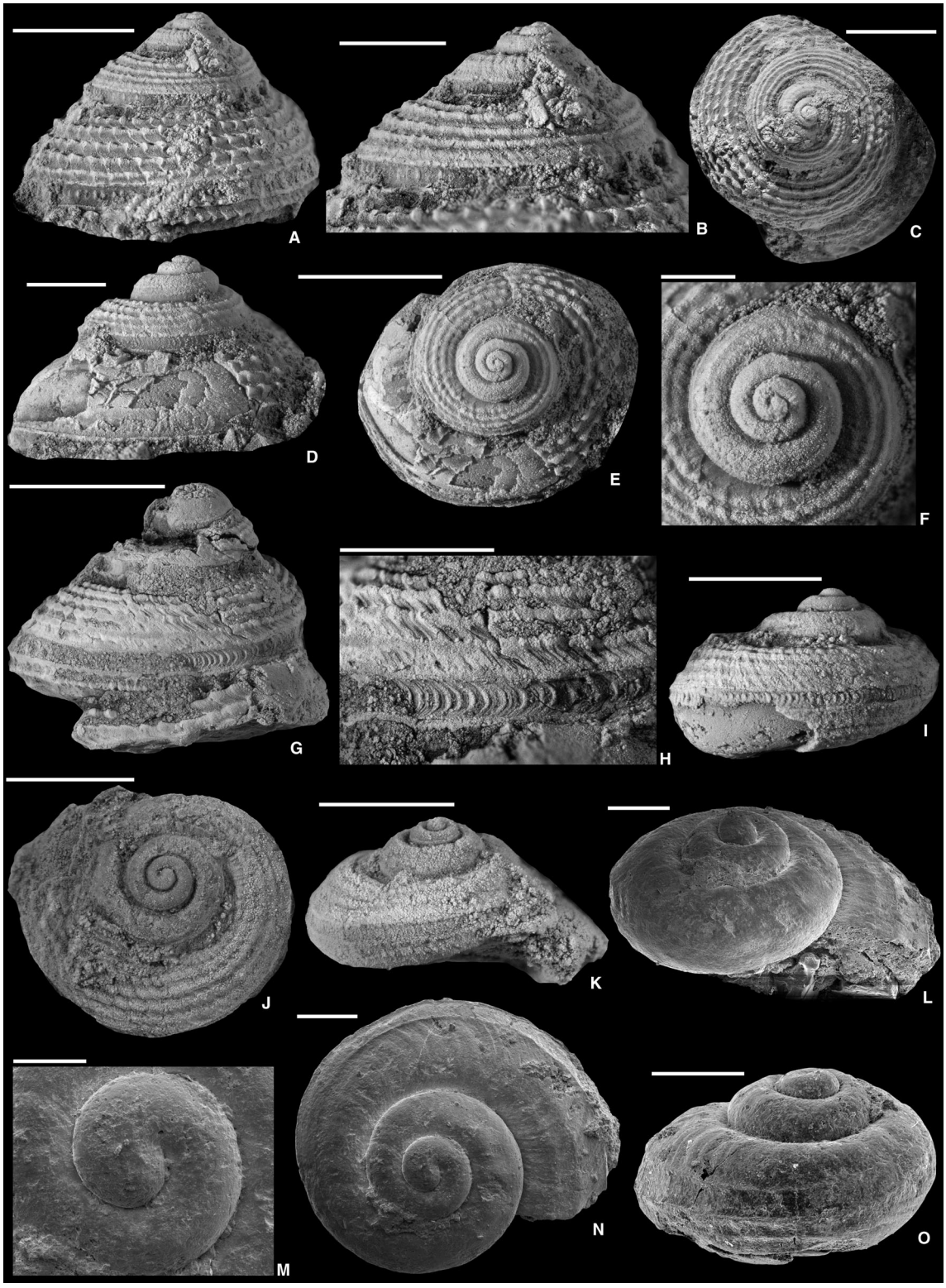

FIG. 33. *Paragoniozona yanceyi* sp. nov., from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–C, SNSB-BSPG 2011 X 254, holotype. D–F, SNSB-BSPG 2011 X 255, paratype; F, apical view, detail of early whorls. G–H, SNSB-BSPG 2011 X 256, paratype; H, lateral view, detail of ornament and lunulae. I–K, SNSB-BSPG 2011 X 257, paratype. L–O, SNSB-BSPG 2011 X 258, juvenile specimen; M, apical view, detail of first whorl. Scale bars represent: 2 mm (A, C, E, G); 1 mm (B, D, H–K); 0.5 mm (F); 0.2 mm (L, N); 0.1 mm (M); 0.3 mm (O). L–O, SEM images.

resolution, still many species are placed in *Worthenia* which was considered as a 'too large' concept by Yin & Yochelson (1983). Some of such similar genera as for instance *Platyworthenia* Chronic, 1952 and *Wortheniella* Schwardt, 1992 were primarily based on characters (especially shape) of the early ontogenetic whorls. However, the early ontogenetic shell of the type species of *Worthenia* (*W.* (*W.*) *tabulata*) has not been known in great detail and therefore the diagnostic significance of this character complex for similar genera has been unclear. Based on well-preserved specimens of *W.* (*W.*) *tabulata*, the early ontogenetic shell is reported now in great detail and this facilitates a comparison with similar taxa regarding that character complex. Many taxa classified as *Worthenia* probably do not represent this genus. It is possible that the *Worthenia*-type shell (gradate with a convex selenizone at median angulation) evolved repeatedly in Pleurotomariida.

When Girty (1911) erected the genus *Orestes* (invalid name, later replaced with the name *Phymatopleura* Girty, 1939), he proposed it as a subgenus of *Worthenia* and recognized the similarities between *Phymatopleura* and *Worthenia*. Batten (1956) established the family Phymatopleuridae but did not include *Worthenia*. The early whorls of *W. tabulata* as reported herein are similar to those of *Phymatopleura* and this could suggest a close phylogenetic relationship between the two genera, as suggested by Girty (1911). Since the type species of the genus *Worthenia* suggests this relationship, we place *Worthenia* in Phymatopleuridae.

Knight *et al.* (1960, p. I209) placed *Worthenia* and *Ruedemannia* Foerste, 1914 in the family Lophospiridae based on the position of the selenizone at the whorl angulation. However, in *Ruedemannia* the selenizone is formed on a spiral ridge from a V-shaped notch (Rollins *et al.* 1971; p. 148, fig. 9) unlike the selenizone that is developed from a U-shaped slit in *W. tabulata* (Fig. 35G, H, K), and *Ruedemannia* develops a prominent subsutural spiral ridge. Due to these two characters (subsutural ridge and the shape of whorl face where the formation of selenizone is formed), the Early Carboniferous specimens from Australia placed in *Worthenia* sp. by Yoo (1994, pl. 9 figs 9–11) and *W. crenilunula* Yoo, 1994 (p. 80, pl. 8 figs 11–14, pl. 9 figs 5–8; *Ruedemannia crenilunula* (Yoo, 1994) comb. nov.) are placed in *Ruedemannia* (= *Commozonospira* Qiao, 1983). *Worthenia*? *waterhousei* Ketwetsuriya *et al.*, 2020*b*, from the middle Permian of Thailand, can be removed from *Worthenia* because of the morphology of its early ontogenetic shell and the presence of a subsutural spiral ridge. It represents lophospirid genus *Yiningicus* Qiao, 1983 (type species *Yiningicus festivus* from the Lower Carboniferous of China): *Yiningicus waterhousei* (Ketwetsuriya *et al.*, 2020*b*) comb. nov.

Regarding their later ontogenetic shell morphology, the Ordovician–Devonian genera *Lophospira* and *Ruedemannia* converge towards *Worthenia* by developing a median and a basal carination and a selenizone situated at the median carination of the whorl face. The members of the family Lophospiridae possess a subsutural ridge/carination/shoulder which seems to be a homologous character among the members of the family. This character is also present in *Bembexia*, which differs from lophospirids in having a concave selenizone low on the whorl face at mid height of the whorl.

Commozonospira Qiao, 1983 has the subsutural ridge in addition to a characteristic whorl profile, axial surface ornamentation and angular selenizone with sharp lunulae; therefore, is regarded as junior synonym of *Ruedemannia* herein.

Worthenia (*Worthenia*) *tabulata* (Conrad, 1835)
Figures 34, 35

*	1835	*Turbo tabulatus* Conrad, p. 267, pl. 12 fig. 1.
	1915	*Worthenia tabulata* Conrad; Girty, p. 152, pl. 22 figs 1–4a.
	1922	*Worthenia tabulata*; Plummer & Moore, pl. 22 figs 17–19 [non pl. 19 fig. 25].
	1941	*Worthenia tabulata* (Conrad); Knight, p. 385. pl. 34 fig. 1a–c.
	1967	*Worthenia tabulata* (Conrad); Yochelson & Saunders, p. 243 (for further synonymy).
	1972*a*	*Worthenia tabulata*; Batten, figs 15, 21, 24, 25.
	1982	*Worthenia tabulata* (Conrad); Schindel *et al.*, pl. 1 fig. 8.
	2001	*Worthenia tabulata* (Conrad); Kues & Batten, p. 32, fig. 7.1.

Material. A total of 249 specimens. 1 from the Virgilian of Kansas (Lawrence Formation, KSV–06): SNSB-BSPG 2020 LXVII. 10 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 11, and a further 9 specimens (SNSB-BSPG 2009 XXII). 107 from the Virgilian of Texas (Finis Shale Member Member, TXV–200): SNSB-BSPG 2020 XCI 6, 21–23, 40, and a further 102 specimens (86 from the surface sample, 16 from the bulk sample; SNSB-BSPG 2020 XCI). 77 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 1, 7, and a further 75 specimens (72 from the surface sample, 3 from the bulk sample; SNSB-BSPG 2020 LXXX). 4 from the Virgilian of Texas (Finis Shale Member, TXV–34): SNSB-BSPG 2020 LXXV 2, and a further 3 specimens (SNSB-BSPG 2020 LXXV). 20 from the Virgilian of Texas (Finis Shale Member, TXV–36): SNSB-BSPG 2020 LXXVI 4, and a further 19 specimens (SNSB-BSPG 2020 LXXVI). 1 from the Virgilian of Texas (Finis Shale Member, TXV–40): SNSB-BSPG 2020 LXXVII. 1 from the Virgilian of Texas (Finis Shale Member, TXV–44): SNSB-BSPG 2020 LXXVIII. 1 from the Virgilian of Texas (Finis Shale Member, TXV–54): SNSB-BSPG 2020 LXXIX. 1 from the Virgilian of Texas (Finis Shale Member, TXV–60): SNSB-BSPG 2020 LXXXI. 17 from the Virgilian of Texas (Finis Shale Member, TXV–120): SNSB-BSPG 2020 LXXXII. 1 from the Virgilian of Texas (Finis Shale Member, TXV–69): SNSB-BSPG 2020 LXXXIII. 1 from the Virgilian of Texas (Necessity Shale Member, TXV–66): SNSB-BSPG 2020 LXXXVI. 6 from the Virgilian of Texas (Wayland Shale Member, TXV–10): SNSB-BSPG 2020 LXXXVII. 1 from the Virgilian of Texas (Wayland Shale Member, BB-TXV–06): SNSB-BSPG 2020 LXXXVIII.

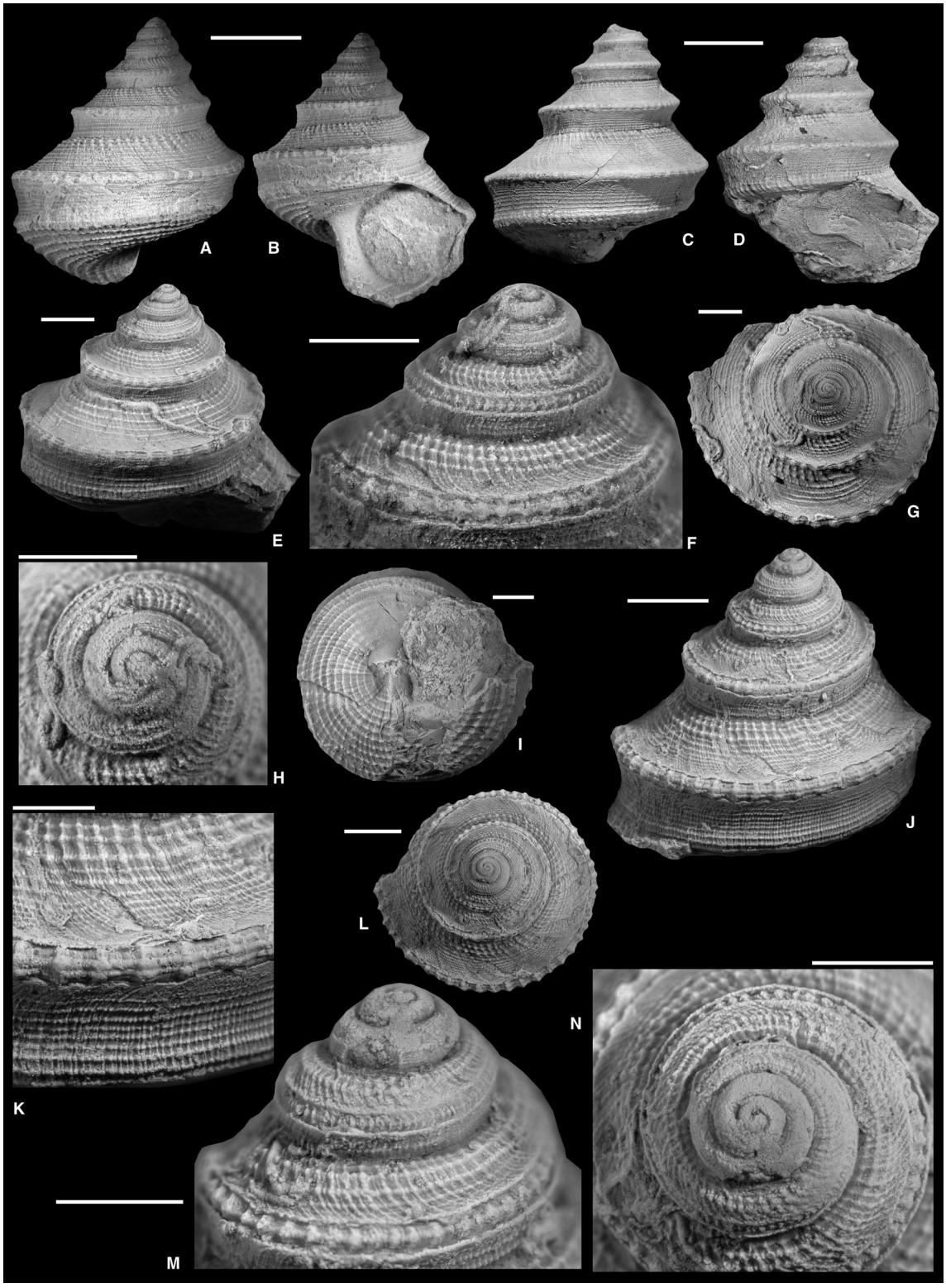

FIG. 34. *Worthenia* (*Worthenia*) *tabulata* (Conrad, 1835). A–B, SNSB-BSPG 2020 LXXX 1, from the Finis Shale Member (Virgilian, Texas). C–D, SNSB-BSPG 2020 LXXVI 4, from the Finis Shale Member (Virgilian, Texas). E–I, SNSB-BSPG 2009 XXII 11, from the Colony Creek Shale (Virgilian, Texas); F, oblique lateral view, detail of early whorls; H, apical view, detail of early whorls. J–N, SNSB-BSPG 2020 XCI 40, from the Finis Shale Member (Virgilian, Texas); K, oblique lateral view, detail of ornament and lunulae; N, apical view, detail of early whorls. Scale bars represent: 5 mm (A, B); 10 mm (C, D); 2 mm (E, G, I, J, L); 1 mm (F, H, K, M, N).

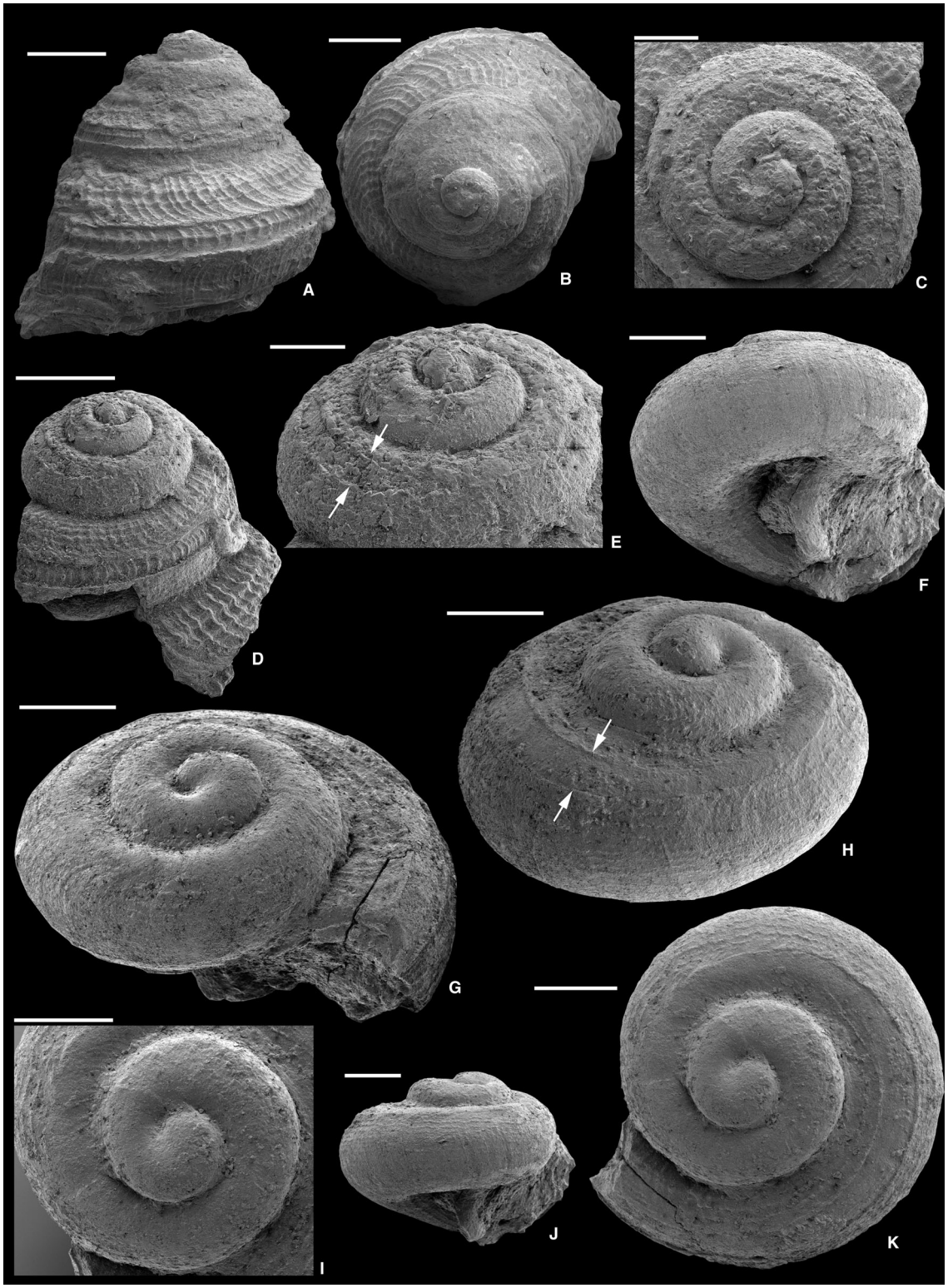

FIG. 35. *Worthenia* (*Worthenia*) *tabulata* (Conrad, 1835), juvenile specimens. A–C, SNSB-BSPG 2020 XCI 22, from the Finis Shale Member (Virgilian, Texas); C, apical view, detail of early whorls. D–E, SNSB-BSPG 2020 XCI 23, from the Finis Shale Member (Virgilian, Texas), arrows indicate selenizone margins. F–K, SNSB-BSPG 2020 LXXX 7, juvenile specimen showing gradual selenizone formation from U-shaped sinus, from the Finis Shale Member (Virgilian, Texas), arrows indicate selenizone margins; F, oblique basal view showing the umbilicus; I, apical view, detail of first whorl with a distinct protoconch-teleoconch boundary. Scale bars represent: 0.5 mm (A, B, D); 0.2 mm (C, E–K). All SEM images.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 XCI 40	7.7	7.8	76	0.32	3.9	4.1	0.5	0.11	0.12
2020 XCI 21	12.6	11.1	77	–	5.7	6.1	0.5	0.08	0.09
2020 LXXX 1	15.6	13.0	79	–	7.8	6.8	0.7	0.11	0.10
2020 XCI 6	21.6	20.6	82	–	10.6	9.2	1.0	0.11	0.09
2020 LXXVI 4	30.2	27.6	73	–	16.2	14.3	1.1	0.08	0.07
2020 LXXV 2	37.8	29.2	72	–	18.6	15.4	1.4	0.09	0.07

Description. Shell medium sized to relatively large (up to 40 mm), trochiform, higher than wide, largest specimen with 10 whorls; apical angle 70°; spire gradate, moderately high; suture shallow, situated at abapical angulation (basal edge); first whorl only slightly elevated, almost planispiral; early whorl with an apical angle >120°, phaneromphalous; protoconch consisting of less than one whorl, smooth, diameter *c.* 0.29 mm; first whorl diameter 0.33–0.36 mm; early teleoconch whorls largely smooth with ornament of fine spiral threads appearing on second whorl and then also with prosocline axial threads appear; later whorl face with two strong angulations, one at mid-whorl of spire whorls bearing the selenizone, the other at transition to base; ramp above selenizone inclining at about 45° angle, becoming convex near suture and concave near selenizone; later whorl face below selenizone concave, subparallel to shell axis, facing slightly abapically; whorl face above selenizone ornamented with spiral threads and less prominent but more closely spaced prosocline axial threads; spiral and axial ornamentation form faint nodes at intersections; prominence of spiral and axial ornamentation increases towards adapical suture, forming conspicuous nodes which are more widely-spaced than faint nodes; whorl face below selenizone ornamented with spiral threads and prosocyrt axial threads, curving backwards; spiral threads on whorl face up to 18 above selenizone, up to 9 below selenizone; selenizone starts to appear from U-shaped sinus at end of second whorl close to the adapical suture and moving downwards during ontogeny until reaching mid-whorl of spire whorls; early selenizone flush to slightly concave, devoid of strong ornament; subsequently lunulae and a central spiral cord appear; ornament and bordering spiral cords of selenizone increase in strength; finally, selenizone raised, convex, bordered above and below by sharp shell edges, situated on mid-angulation, forming median carina which represents periphery; selenizone covers 10% of whorl face width; selenizone of early whorls ornamented with prominent lunulae and one median thread; lunulae turn into equally-distant prominent nodes in later whorls and selenizone ornamented with 3–4 cords; base convex, with angular basal edge, ornamented with opisthocyrt axial threads or strengthened growth lines and with 11–14 equally prominent, nodose spiral cords; basal ornament more prominent than that on whorl face; aperture ovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex; base anomphalous.

Remarks. Worthenia (*W.*) *tabulata* is one of the most abundant gastropods from the Pennsylvanian of the US mid-continent. It is characterized by its relatively large size, the gradate spire, the convex, highly ornamented selenizone situated on the median angulation of the whorl face and the whorl face being densely ornamented by a mesh work of fine axial and spiral threads. Here, we can show details of the early ontogenetic shell including a vetigastropod-type protoconch and low-spired, rounded early whorls. The specimens at hand closely resemble topotypic material illustrated by Knight (1941, pl. 34 fig. 1b–c); the whereabouts of Conrad's (1835) type specimen are unknown.

Lintz (1958, p. 103, pl. 16 figs 18–20) erected a new species *W.* (*W.*) *castlemanensis* based on a single specimen from the Pennsylvanian of Maryland and differentiated it from *W.* (*W.*) *tabulata* by having a larger conch (41 mm in height) and sharply defined revolving lirae (spiral cords), lacking reticulate ornamentation on the base and lacking a spiral ornament on the selenizone. The size of *W.* (*W.*) *castlemanensis* is within the size range of the *W.* (*W.*) *tabulata* specimens studied herein and the ornament on the whorl face ornament is the same. The lack of spiral ornament on the selenizone and more closely spaced lunulae could be regarded as intraspecific variation and if that is so *W.* (*W.*) *castlemanensis* could be a junior synonym of *W.* (*W.*) *tabulata*. However, more information is needed for this synonymization.

As previously indicated by Knight (1945) and Yochelson & Saunders (1967, pp 243–244) the specimen identified as *W.* (*W.*) *tabulata* by Plummer & Moore (1922, pl. 19 fig. 25) belongs to *Glabrocingulum* (*Ananias*) *welleri* (Newell, 1935). *Glabrocingulum* (*A.*) *welleri* and *W.* (*W.*) *tabulata* form a good example of convergent evolution (Eldredge 1968). They resemble each other in adult shell morphology and surface ornamentation, but differ in early ontogeny and selenizone ornamentation.

Worthenia (*Worthenia*) *parvula* Hoare *et al.*, 1997
Figure 36

	1964*a*	*Worthenia* cf. *W. tabulata* (Conrad); Sturgeon, p. 209, pl. 32 fig. 6.
	1996	*Worthenia tabulata* (Worthen); Hoare & Miller, p. 154, fig. 13-3.9.
*	1997	*Worthenia parvula* Hoare *et al.*, p. 1031, figs 4.11–4.15.

Material. A total of 3 specimens. 2 from the Desmoinesian Allegheny Formation of Ohio: SNSB-BSPG 2020 I 20–21. 1 from the Desmoinesian of Oklahoma (Holdenville Formation, OKD–01): SNSB-BSPG 2020 LXIII 2.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 I 20	8.0	8.6	86	–	4.9	4.2	0.7	0.16	0.14
2020 I 21	10.8	10.6	79	–	5.3	5.3	0.6	0.11	0.11
2020 LXIII 2	[3.6]	4.7	91	0.37	1.8	1.9	0.2	0.12	0.13

Description. Shell of moderate size, trochiform; spire gradate; suture incised, situated below abapical edge of selenizone in early whorls, gradually shifting towards basal angulation during ontogeny; whorl embrace at basal angulation in mature whorls; first whorl very low-spired, about 0.4 mm in diameter; first two whorls convex, without visible ornament; third whorl

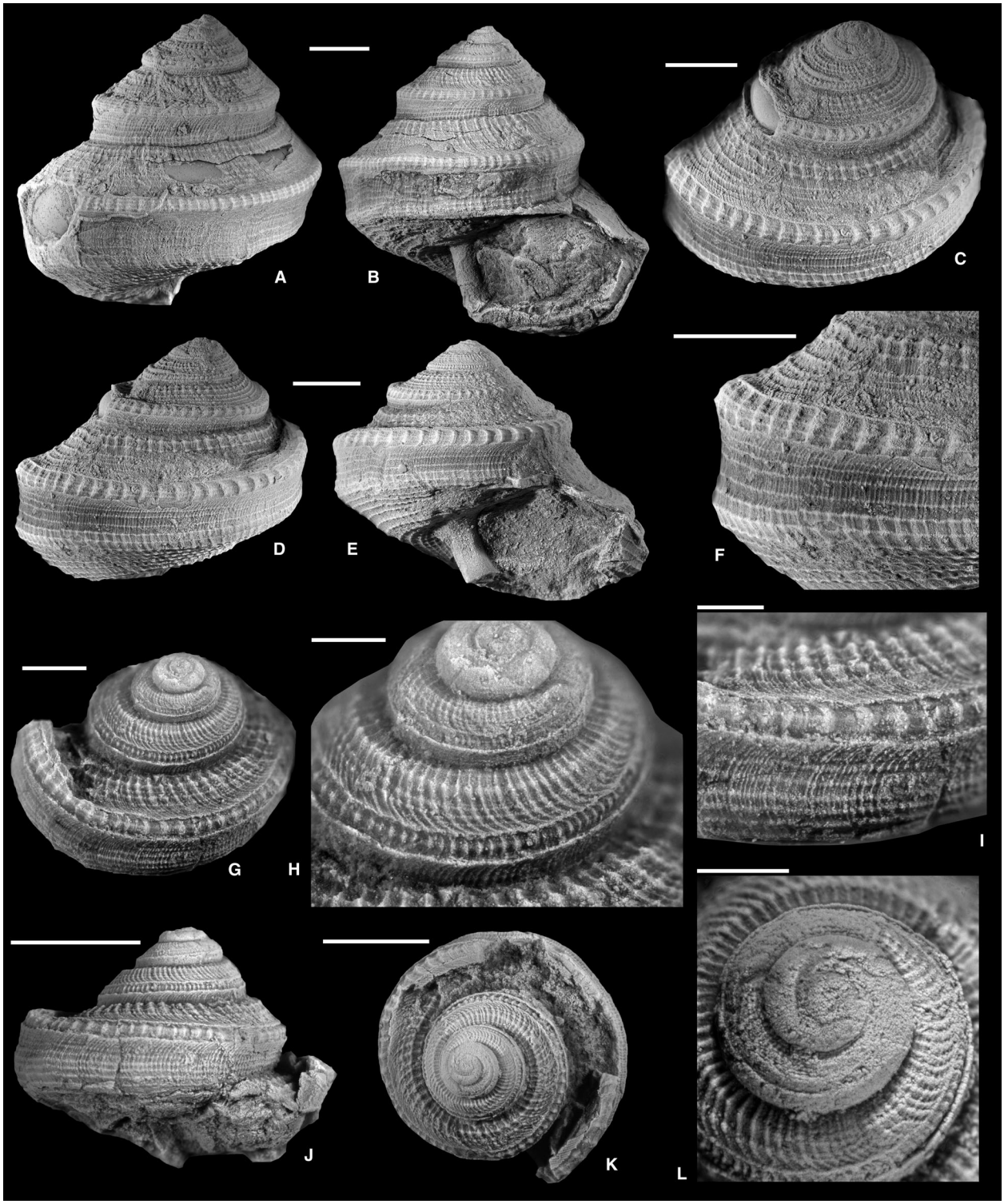

FIG. 36. *Worthenia* (*Worthenia*) *parvula* Hoare, Sturgeon & Anderson, 1997. A–B, SNSB-BSPG 2020 I 21, from the Allegheny Formation (Desmoinesian, Ohio). C–F, SNSB-BSPG 2020 I 20, from the Allegheny Formation (Desmoinesian, Ohio); F, lateral view, detail of ornament. G–L, SNSB-BSPG 2020 LXIII 2, from the Holdenville Formation (Desmoinesian, Oklahoma); H, oblique apical view, detail of ornament and lunulae on early whorls; I, (slightly oblique) lateral view, detail of surface ornament; L, apical view, detail of early whorls. Scale bars represent: 2 mm (A–F, J, K); 1 mm (G); 0.5 mm (H, I, L).

ornamented with spiral and axial threads, with angulation at mid whorl face, where selenizone appears; later whorl face with median and basal angulations; sutural ramp convex just below suture then concave, inclining at about 30°–45°, ornamented with spiral cords and prosocline axial threads/ribs, forming nodes at intersections; selenizone becomes visible at transition from second to third whorl, convex, bordered above and below by sharp shell edges, situated on median angulation, representing periphery; selenizone ornamented with lunulae and single median spiral thread in early ontogeny, later selenizone ornamented with widely spaced rib-like lunulae and three spiral threads; whorl face below selenizone concave, lying subparallel to shell axis, as equally wide as sutural ramp, ornamented with spiral cords/threads and prosocyrt axial threads and nodes at intersections; transition to base with rounded basal edge; base convex, ornamented with opisthocyrt radial growth lines/threads and node-bearing spiral cords; aperture slightly wider than high; base narrowly phaneromphalous.

Remarks. Worthenia (*W.*) *parvula* has only been reported from the Allegheny Formation of Ohio. The small specimens assigned herein to *W.* (*W.*) *parvula* from the Holdenville Formation of Oklahoma record the only occurrence outside Ohio.

Worthenia (*W.*) *legrandi* Kues & Batten, 2001 resembles *W.* (*W.*) *parvula* but differs in being higher spired and more slender as previously indicated by Kues & Batten (2001).

Worthenia (*Worthenia*) *speciosa* (Meek & Worthen, 1861)
Figure 37

*	1861	*Pleurotomaria speciosa* Meek & Worthen, p. 461.
	1866*b*	*Pleurotomaria speciosa* M.& W.; Meek & Worthen, p. 352, pl. 28 figs 5a–c.
	1967	*Worthenia speciosa* (Meek & Worthen); Yochelson & Saunders, p. 242.
	1989	*Worthenia speciosa* (Meek & Worthen); Batten, pl. 9 figs 10–12.
non	1995	*Worthenia speciosa* (Meek & Worthen); Batten, p. 19 fig. 25.
	2001	*Worthenia speciosa* (Meek & Worthen); Kues & Batten, p. 31 fig. 6.21–6.25.

Material. A total of 3 specimens. 2 from the Desmoinesian of Texas (Lazy Bend Formation, TXD–03): SNSB-BSPG 2020 LXIX 3–4. 1 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 12.

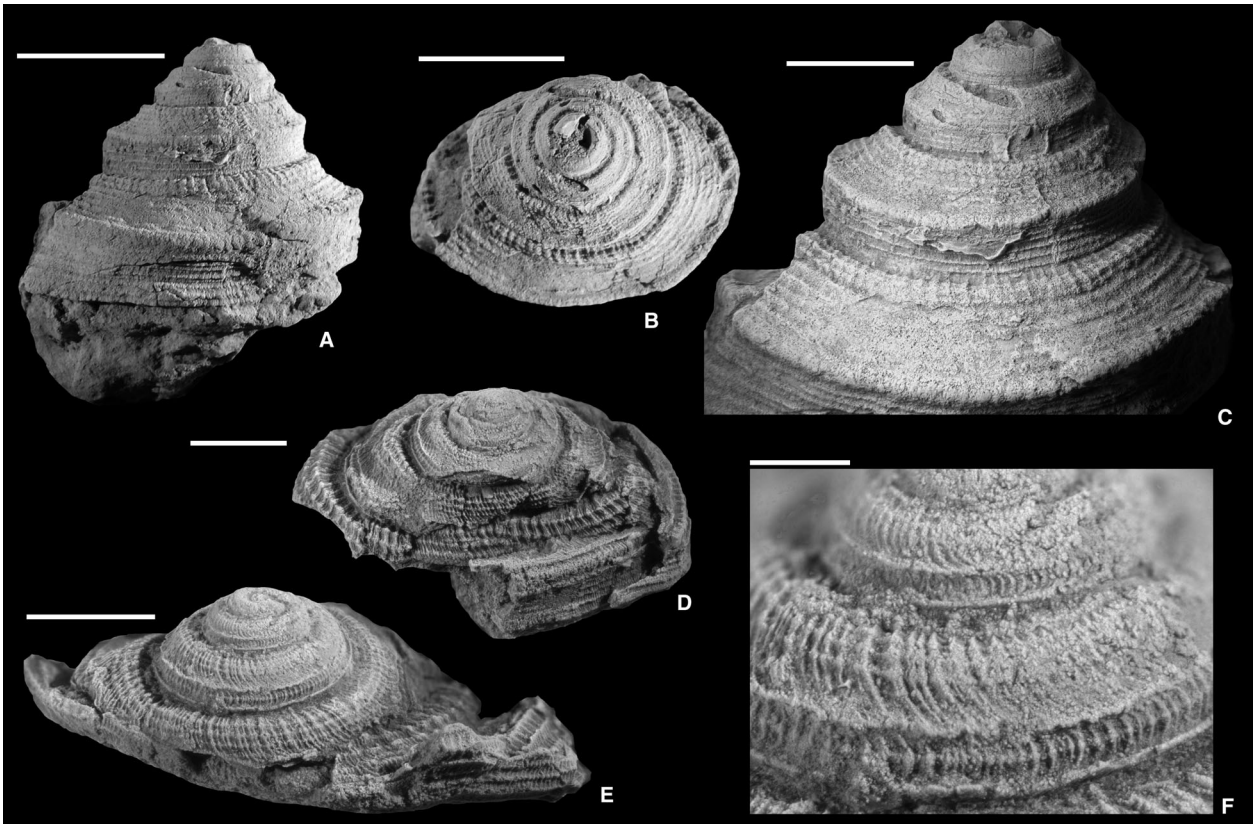

FIG. 37. *Worthenia* (*Worthenia*) *speciosa* (Meek & Worthen, 1861). A–C, SNSB-BSPG 2009 XXII 12, from the Colony Creek Shale (Virgilian, Texas). D, SNSB-BSPG 2020 LXIX 4, from the Lazy Bend Formation (Desmoinesian, Texas). E–F, SNSB-BSPG 2020 LXIX 3, from the Lazy Bend Formation (Desmoinesian, Texas); F, oblique apical view, detail of ornament and lunulae on early whorls. Scale bars represent: 10 mm (A, B); 5 mm (C); 2 mm (D, E); 0.5 mm (F).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 12	20.3	20.5	81	–	11.7	9.2	0.9	0.10	0.08
2020 LXIX 3	–	8.1	–	–	[2.53]	3.0	0.5	0.17	[0.20]

Description. Shell small to medium-sized (up to 20 mm), trochiform; spire gradate, moderately high; suture moderately deep, situated somewhat below selenizone in early whorls, shifting in abapical direction in later whorls; first whorl planispiral or very low-spired; early whorl face convex, ornamented with spiral and axial threads; later whorl face with subsutural, median and basal angulations; subsutural angulation forming narrow shoulder; whorl face between subsutural and median angulations concave, inclining at about 45° angle; whorl face below selenizone concave, lying parallel to shell axis; median and basal angulations situated equally distant to shell axis so that both represent periphery; whorl face between angulations equally wide; whorl face above selenizone ornamented with equally-prominent spiral cords and numerous closely spaced prosocline axial threads; some axial threads turn into equally-spaced axial ribs on subsutural angulation, forming nodes where they intersect with spiral cords; whorl face below selenizone ornamented with spiral cords and prosocyrt axial threads; spiral cords on whorl face increase to up to seven above and up to seven below selenizone; spiral and axial ornament forms reticulate pattern; selenizone convex, bordered above and below by sharp shell edges, situated on median angulation; selenizone of early whorls depressed, ornamented with sharp lunulae and one median spiral thread; selenizone ornamented with 3–4 cords in later whorls; base convex, with angular basal edge, ornamented with opisthocyrt axial threads or growth lines and spiral cords; aperture not visible; base narrowly phaneromphalous.

Remarks. We have at hand three crushed specimens from two different horizons; two of the specimens from Desmoinesian of Texas are small while the one from the Missourian of Texas is a relatively large specimen. Our specimens fit well into the range of variation reported by Batten (1989) who treated two forms (those in pl. 9 figs 10–11, and the specimen in fig. 12) as conspecific, which suggests some changes of whorl morphology during ontogeny (i.e. strengthening of the basal angulation and formation of a subsutural angulation in later whorls). Therefore, we consider the larger specimen (Fig. 37A–C) and the smaller ones (Fig. 37D–F) to be conspecific. The two small specimens from the Desmoinesian of Texas (TXD–03) do not develop multiple cords on the selenizone instead they have a single median spiral cord on throughout ontogeny.

Worthenia (*W.*) *speciosa* differs from *W.* (*W.*) *tabulata* in having a subsutural angulation, equally wide adapical and abapical whorl faces, with its lateral whorl face in being parallel to the shell axis and in having more closely spaced lunulae on the selenizone. *Phymatopleura preclara* Hoare *et al.*, 1997 is transferred herein to *W. preclara* (Hoare *et al.*, 1997) comb. nov. because it has the selenizone situated at a median whorl angulation. It can be differentiated from *W.* (*W.*) *speciosa* in the abapical suture being just below the selenizone. Hence, the vertical lateral whorl face in *W. preclara* can be seen only in the last whorl. *Worthenia* (*W.*) *humiligrada* Ketwetsuriya *et al.* 2020*a* from the Permian of Thailand resembles *W.* (*W.*) *speciosa* in whorl profile but *W.* (*W.*) *humiligrada* is a much smaller species, with lower spire (pleural angle of 90°–100°), wide umbilicus and the position of the suture is well below the selenizone in early whorls. The specimen assigned to *W. speciosa* by Batten (1995, p. 19 fig. 25) seems to be slightly higher-spired and with wider interspace between the lunulae; it probably represents *W.* (*W.*) *legrandi* Kues & Batten, 2001.

Subgenus YOCHELSONOSPIRA Thein & Nitecki, 1974

Type species. Yochelsonospira pagoda Thein & Nitecki, 1974 later synonymized with *Worthenia* (*Yochelsonospira*) *tenuilineata* (Girty, 1929) by Gordon & Yochelson (1983).

Remarks. The absence of a lower angulation and therefore an evenly convex transition from whorl face to base is the main diagnostic feature of this taxon according to Thein & Nitecki (1974). Gordon & Yochelson (1987) who assigned several Mississippian species to it, reduced *Yochelsonospira* to subgenus rank and questioned the taxonomic value of this character.

Here we assign the new species *Worthenia* (*Yochelsonospira*) *kuesi* to *Yochelsonospira* although it has a weak, rounded basal angulation. We consider *Yochelsonospira* to be a non-gradate form of *Worthenia*, as previously proposed by Gordon & Yochelson (1975, p. 985). Hence, we differentiate the two subgenera according to their translation rate, principally in the same way differentiating *Glabrocingulum* from *Ananias*. In *Yochelsonospira*, the subsequent whorl embraces the previous whorls just below the selenizone, so it does lack a median angulation and lateral whorl face in spire whorls.

Worthenia (*Yochelsonospira*) *kuesi* sp. nov.
Figure 38

LSID. urn:lsid:zoobank.org:act:37B96178-5D2D-4A0A-A46E-38CD2DFF50EF

Derivation of name. After Barry S. Kues, who made great contributions to the knowledge of the Carboniferous invertebrates of the USA.

Holotype. SNSB-BSPG 2020 LX 1

Type location & age. Desmoinesian, Wetumka Formation; centre north line of sec. 17, T. 7 N., R. 10 E., Lake Holdenville 7½′ Quadrangle, Hughes County, Oklahoma; pond dam (AMNH locality 5011; 35°05′11.37″N, 96°16′25.73″W).

Material. 1 specimen from the Desmoinesian of Oklahoma (Wetumka Formation, OKD–14): SNSB-BSPG 2020 LX 1.

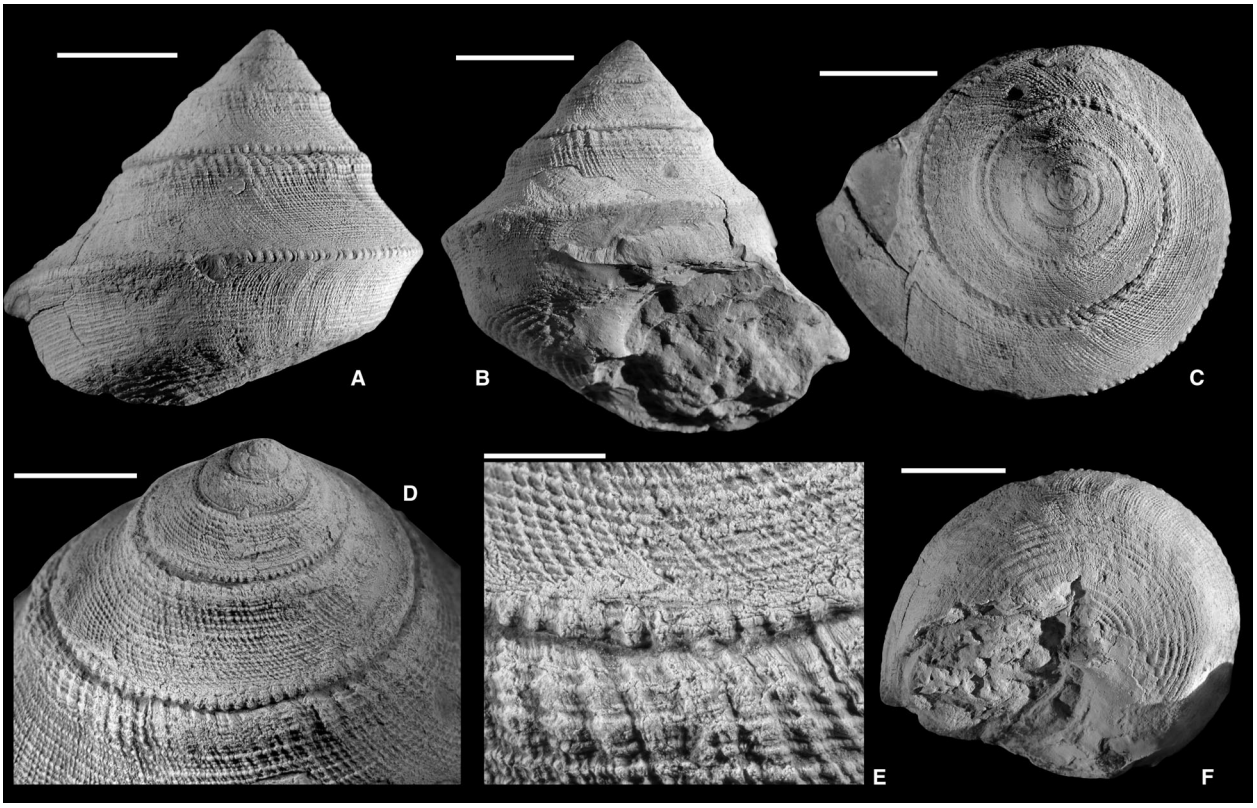

FIG. 38. *Worthenia* (*Yochelsonospira*) *kuesi* sp. nov., from the Wetumka Formation (Desmoinesian, Oklahoma). A–F, SNSB-BSPG 2020 LX 1, holotype; E, oblique apical view, detail of surface ornament and lunulae. Scale bars represent: 10 mm (A–C, F); 5 mm (D); 2 mm (E).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LX 1	31.4	31.6	82	–	19.1	13.0	0.9	0.07	0.05

Description. Shell relatively large (33 mm high), massive, conical, almost as high as wide, with *c.* 7 whorls; apical angle *c.* 80°; whorl face of spire whorls concave; suture distinct, situated just below selenizone; early whorl face slightly convex; adapical region of later whorl face adpressed, with face parallel to the shell axis, forming a subsutural bulge; rest of whorl face inclining at about 45°; whorl face generally concave; region between selenizone and basal angulation straight to slightly concave, sloping slightly adapically; whorl face above selenizone and the region below selenizone ornamented with equally prominent axial and spiral threads forming fine meshwork with faint nodes at intersections; axial threads becoming prominent subsuturally; spiral threads increase to up to 43 above and 21 below selenizone; axial threads prosocline above selenizone, prosocyrt below selenizone; selenizone narrow, convex, bordered above and below by sharp shell edges, situated on periphery, forming median carina of body whorl; selenizone ornamented with prominent nodes and three spiral threads; base flatly convex, with rounded angular basal edge, ornamented with opisthocyrt axial threads and with 12 equally prominent spiral cords; basal cords more prominent than those on whorl face; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex; base anomphalous.

Remarks. The studied specimen resembles *Pleurotomaria textiligera* Meek, 1871 in general shell morphology. However, the figure later provided by Meek (1875, p. 314, pl. 13 fig. 7a–b) suggests that *Ple. textiligera* lacks a concave whorl face and an adpressed zone including subsutural strengthened axial riblets. Our specimen has a bluntly angulated base while the base of *Ple. textiligera* is evenly rounded and more convex. The base of our species has a distinct spiral ornament that is entirely missing in Meek's figure. According to Gordon & Yochelson (1987, p. 75) *Ple. textiligera* represents *Mourlonia*.

Worthenia (*Yochelsonospira*) *kuesi* resembles the type species of *Yochelsonospira*, *W.* (*Y.*) *tenuilineata* (Girty, 1929) (= *Y. pagoda* Thein & Nitecki, 1974, see Gordon & Yochelson 1987) in having a subsutural bulge. However, in *W.* (*Y.*) *kuesi* the later whorls embrace the preceding whorls just below the selenizone so that the whorl face below selenizone in *W.* (*Y.*) *kuesi* is narrow or entirely covered.

Genus BORESTUS Thomas, 1940*a*

Type species. *Borestus wrighti* Thomas, 1940*a* from the Carboniferous of Scotland; original designation.

Diagnosis. Gradate turbiniform; outer (lateral) whorl face almost vertical, bordered by median and basal angulation; ramp broad almost straight to concave; selenizone situated in centre of outer whorl face (below median angulation), broad, depressed, concave with distinct lunulae, rarely with spiral thread, bordered by spiral cords; teleoconch ornamented by collabral axial and spiral threads of similar strength or smooth; early whorls very low-spired with convex whorls; initial whorl almost planispiral; early teleoconch with spiral threads starting within second whorl; base flatly convex with distinct spiral cords and finer collabral threads.

Remarks. Knight *et al.* (1960, p. 215, fig. 130.1) included *Borestus* in Phymatopleuridae and provided the following diagnosis: 'Gradate turbiniform, superficially resembling *Worthenia* but with depressed selenizone near mid-whorl and with shoulder on basal angulation sharp; ornament sharp and transverse threads.'

Borestus resembles *Phymatopleura* but the type species of *Phymatopleura* has an adapical angulation below the adapical suture (however, not all members assigned to *Phymatopleura* have this character) and the selenizone of *Borestus* lacks the conspicuous spiral ornament which is typical of *Phymatopleura* (in most cases a single spiral cord). *Borestus* develops the median angulation much earlier during ontogeny and the spiral cords above the median angulation are orthocline or slightly prosocline.

Borestus costatus Yoo, 1994 from the Lower Carboniferous of Australia, allegedly the oldest representative of the genus, is not typical of the genus; it lacks the vertical outer whorl face typical of *Borestus*. *Borestus costatus* has an inclining whorl face above the selenizone with a pronounced crest and the borders of the selenizone form prominent spiral ridges. This is not the case in the species studied herein (*Bo. pagoda*) or in the type species, *Bo. wrighti*. *Borestus costatus* resembles *Bembexia* Oehlert, 1888 (Knight 1941, p. 54, pl. 34 fig. 2a–d), *Kersadiella* Blodgett *et al.*, 1999 and *Spiroscala* in whorl shape, ornamentation and presence of prominent spiral ridges. However, *Bembexia* and *Kersadiella* do not have vertical plate-like extensions bordering the selenizone. *Borestus costatus* is assigned herein to *Spiroscala* due to the presence of vertical plate-like extensions (between the prominent spiral ridges) that border the selenizone (see Remarks on *Spiroscala shwedagoniformis*, above).

The Triassic (Norian) *Borestus*? sp. reported by Nützel & Erwin (2004) cannot be confirmed as species of the genus *Borestus*; its periphery is too convex and does not represent a vertical lateral whorl face, axial ornament is not visible in this species. *Pleurotomaria hamlingii* Whidborne, 1896 was assigned to *Borestus* by Amler & Heidelberger (2003). The selenizone of *Ple. hamlingii* is situated on whorl angulation and ornamented with nodes. Therefore, *Ple. hamlingii* certainly does not represent *Borestus* and is herein tentatively assigned to *Worthenia*: *Worthenia*? *hamlingii* (Whidborne, 1896) comb. nov.

Borestus pagoda (Newell, 1935)
Figure 39

*	1935	*Orestes pagoda* Newell, p. 346, pl. 36 figs 4–4a.
?	1940*a*	*Borestus procerus* Thomas, pl. 3 fig. 2a–b.
aff.	1949	*Borestus* aff. *B. pagoda* (Newell); Chronic, p. 142, pl. 28 fig. 3a–c.
	1967	*Borestus pagoda* (Newell); Yochelson & Saunders, p. 52.

Material. 2 specimens from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 6–7.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 6	11.6	9.3	62	0.4	4.2	4.9	0.7	0.15	0.17
2020 LVIII 7	9.9	7.3	58	0.4	4.4	3.4	0.5	0.15	0.12

Description. Shell small, trochiform, higher than wide, the largest specimen with about seven whorls; spire gradate, moderately high; suture shallow, situated at basal edge; first whorl planispiral or very low-spired with a diameter of 0.4 mm; selenizone starts at 1.5 whorls; early whorl face before the onset of the selenizone convex and ornamented with faint spiral threads then becoming angular and developing selenizone at the same time, ornamented with spiral and axial threads; later whorl face above median angulation concave, forming an angle of about 55° with axis; later whorl face below median angulation slightly concave, almost parallel to shell axis; whorl face above median angulation ornamented with equally prominent spiral cords and orthocline axial ribs, forming reticulate pattern and nodes at intersections; number of spiral cords increase up to 8; whorl face below median angulation ornamented with axial ribs and spiral cords; axial ribs prosocline between median angulation and selenizone, prosocyrt opisthocline below selenizone; selenizone flat, depressed, bordered above and below by spiral cords, situated between median and basal angulations; selenizone broad (12% of whorl face width); selenizone ornamented with distinct lunulae; base flatly convex, with angular basal edge, ornamented with opisthocyrt axial threads and 15 spiral cords; aperture subovate, slightly wider than high; outer lip angular, basal lip slightly convex, columellar lip slightly convex, curved backwards; base narrowly phaneromphalous.

Remarks. Newell (1935) had a single specimen from the Lansing Shale of Oklahoma. Our material agrees very well with it. According to Chronic (1949) *Borestus procerus* (Thomas, 1940*a*) differs from *Bo. pagoda* (Newell, 1935) in having a less prominent ornament, otherwise the shell morphology is similar. *Borestus chesterensis* (Meek & Worthen, 1861) from the Mississippian of the Illinois, USA, has a larger upper whorl face and its whorl angulation forms the periphery according to the figure given by Meek & Worthen (1866*b*, pl. 24 fig. 1). *Borestus texanus* Batten, 1995 has a smooth shell and *Bo. magdalenensis* Batten, 1995 has a largely smooth shell with an ornamented subsutural rib (both mentioned species are from the Pennsylvanian of the USA).

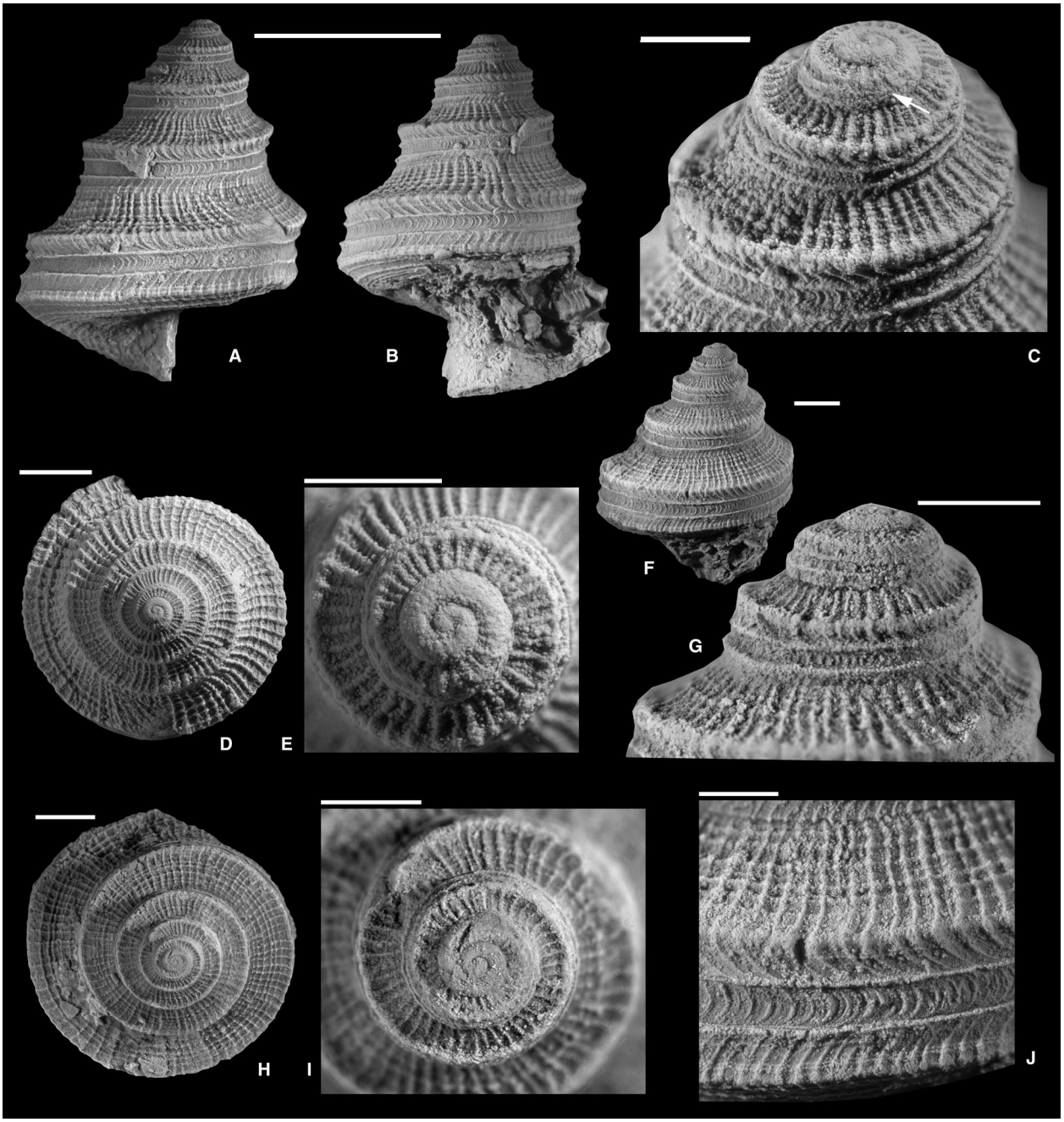

FIG. 39. *Borestus pagoda* (Newell, 1935) from the Gene Autry Shale (Morrowan, Oklahoma). A–E, SNSB-BSPG 2020 LVIII 7; C, oblique apical view, detail of early whorls, arrow indicating the onset of selenizone; E, apical view, detail of early whorls. F–J, SNSB-BSPG 2020 LVIII 6; G, lateral view, detail of early whorls; I, apical view, detail of early whorls; J, oblique lateral view, detail of ornament and selenizone. Scale bars represent: 5 mm (A, B); 1 mm (C, E, G, I, J); 2 mm (D, F, H).

Genus GLYPTOTOMARIA Knight, 1945

Type species. Glyptotomaria apiarium Knight, 1945 from the Carboniferous of Texas, USA; original designation.

Remarks. Glyptotomaria and *Dictyotomaria* were first defined as two distinct genera by Knight (1945). Batten (1958) treated *Dictyotomaria* as subgenus of *Glyptotomaria* and this was accepted by Knight *et al.* (1960). Gordon & Yochelson (1975) raised the rank of *Dictyotomaria* to genus level again due to orthocline growth lines on whorl face of *Di. scitula* (Meek & Worthen, 1861) as opposed to prosocline growth lines of *Glyptotomaria apiarium* Knight, 1945. We agree with the view of Gordon & Yochelson (1975, 1983) and treat *Dictyotomaria* and *Glyptotomaria* as distinct genera.

Glyptotomaria (Knight, 1945) is similar to the Triassic genus *Stuorella* Kittl, 1891 (see Karapunar & Nützel 2021) in shell shape, whorl profile, growth line pattern and ornamentation. However, *Stuorella* differs in having strong spiral cords on the early teleoconch whorls (Bandel 2009, pl. 2 fig. 18) and in developing the selenizone very late during ontogeny (Karapunar & Nützel 2021). Its type species, *Stuorella subconcava* (Münster, 1841), develops nodes on the selenizone but not all members of this genus do that. The early ontogeny of *Glyptotomaria* is not well known. Judging from the figures given by Knight (1945), the selenizone of *Glyptotomaria* seems to develop earlier than in *Stuorella* and the early shell of *Glyptotomaria* seems to be similar to that of *Dictyotomaria*. *Glyptotomaria* and *Stuorella* represent an example of convergent adult shell morphologies. *Glyptotomaria apiarium* is the only species belonging to *Glyptotomaria* (see Remarks on *Dictyotomaria*, below)

Glyptotomaria apiarium Knight, 1945
Figure 40

* 1945 *Glyptotomaria apiarium* Knight, p. 577, pl. 79 fig. 4a–c.
1967 *Glyptotomaria* (*Glyptotomaria*) *apiarium* (Knight); Yochelson & Saunders, p. 90.

Material. 2 specimens from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 13–14.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 13	[11.19]	[12.65]	62	–	3.5	3.5	0.7	0.20	0.19
2009 XXII 14	[13.06]	13.5	57	–	5.6	4.4	0.8	0.18	0.14

Description. Shell of moderate size, conical, higher than wide; flanks straight; spire angle 55°–60°, suture incised, situated just below basal bulge; early whorls not visible; whorl face flat, forming an angle of about 35° with axis, angulated at periphery with peripheral carina; whorl face flat, ornamented with spiral cords and equally-spaced prosocline/prosocyrt axial threads; few, widely spaced spiral cords near selenizone, more closely spaced at adapical half of whorl face and at peripheral carina; axial threads and spiral cords forming reticulate pattern; number of spiral cords increase up to seven above selenizone; axial threads prosocyrt below selenizone; area between abapical edge of selenizone and basal carina forming a shallow groove; selenizone concave, depressed, bordered above and below by spiral cords, situated at lower half of whorl face; selenizone ornamented with thread-like, densely spaced lunulae; base flat, slightly convex, with rounded

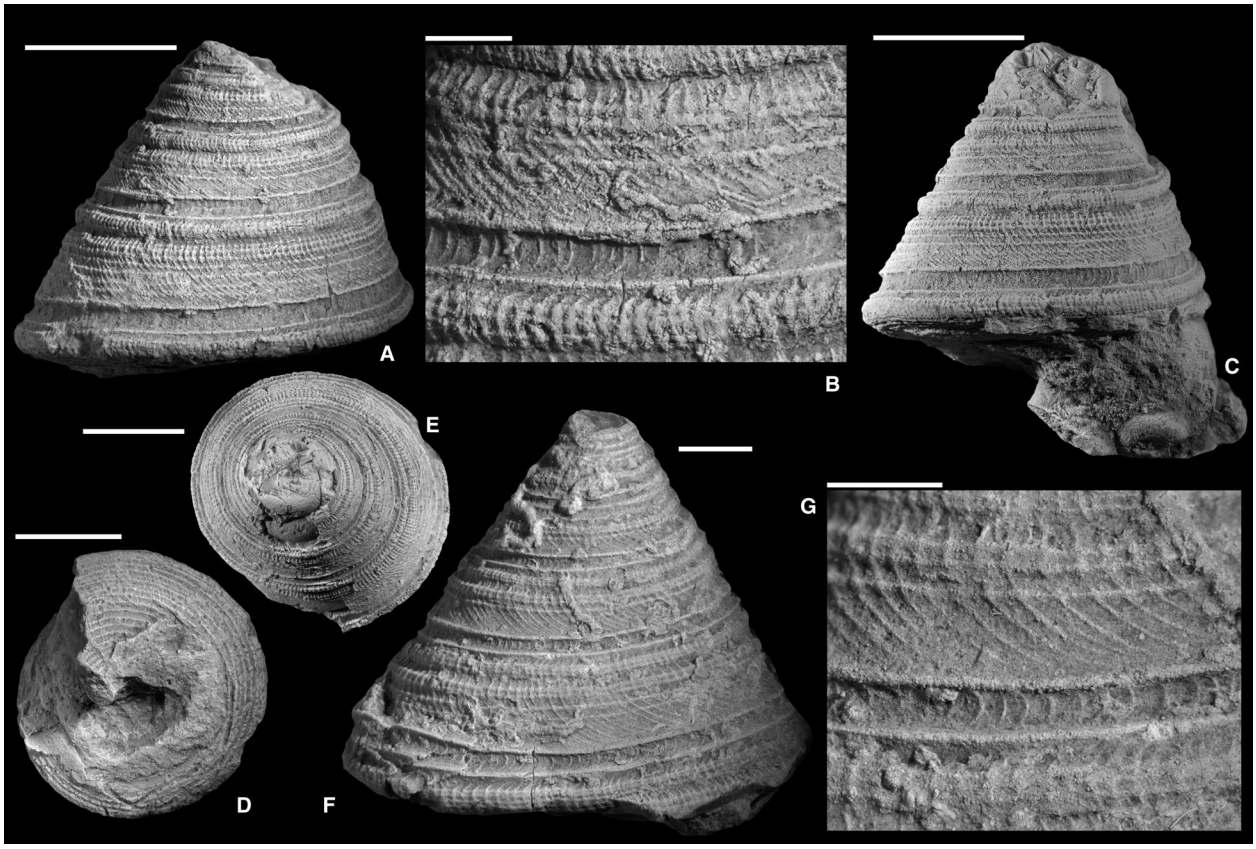

FIG. 40. *Glyptotomaria apiarium* Knight, 1945 from the Colony Creek Shale (Virgilian, Texas). A–E, SNSB-BSPG 2009 XXII 13. F–G, SNSB-BSPG 2009 XXII 14; G, lateral view, detail of ornament and selenizone. Scale bars represent: 5 mm (A, C–E); 1 mm (B, G); 2 mm (F).

basal edge, ornamented with sinuous axial threads and about 20 spiral cords; basal axial threads opisthocyrt near edge, prosocyrt near umbilical region; aperture subrectangular, wider than high; outer lip flat, basal lip sligthly convex, columellar lip slightly convex; base anomphalous.

Remarks. The studied specimens have a lower spire angle (55°–60°) compared to the holotype of *Glyptotomaria apiarium* (35°, Knight 1945); otherwise identical in morphology and ornamentation.

Genus DICTYOTOMARIA Knight, 1945

Type species. Pleurotomaria scitula Meek & Worthen, 1861 from the Carboniferous of Illinois, USA; original designation.

Remarks. The figured syntypes of *Dictyotomaria scitula* (Sturgeon 1964*b*, pl. 121 figs 6–9) are probably not fully-grown specimens and might not be conspecific with the specimen that was called hypotype by Knight (1945, pl. 79 figs 3a–b). In this case Knight would have misidentified the specimens as the type species of *Dictyotomaria*. The specimens designated as 'hypotype' by Knight (1945) are not from the type locality of *Di. scitula*. The syntypes as reported by Sturgeon (1964*b*), including the lectotype designated by this author, differ from Knight's (1945) specimen in having a median angulation rather than a convex whorl. We regard presence/absence of median angulation as variable character among the members of *Dictyotomaria* and continue to keep the species with convex ramp within *Dictyotomaria*. *Glyptotomaria* can be differentiated from *Dictyotomaria* in having a flat shell profile while the latter has a gradate shell profile with or without whorl angulations.

Batten (1958) reported two Permian species with an angulated whorl profile in *Glyptotomaria*: *Gly*. (*Gly*.) *marginata* Batten, 1958 and *Gly*. (*Gly*.) *pistra* Batten, 1958. Due to the pronounced median angulation these species represent rather *Dictyotomaria*. The same is true for the Middle Triassic species *Gly*. (*Gly*.) *triassica* Yin & Yochelson, 1983, that is actually quite similar to *Di. turrisbabel*. Therefore, we place all these species herein in *Dictyotomaria*: *Di. marginata* (Batten, 1958) comb. nov., *Di. pistra* (Batten, 1958) comb. nov. and *Di. triassica* (Yin & Yochelson, 1983) comb. nov. Thus, *Gly. apiarium* is the only member of *Glyptotomaria* at this point.

There are three Devonian species that are assigned to genus *Dictyotomaria*: *Pleurotomaria capillaria* Conrad, 1842 (as figured by Rollins *et al*. 1971, who assigned it to *Dictyotomaria*), *Di. quasicapillaria* Rollins, 1975 and *Di. eurocapillaria* Amler & Heidelberger, 2003. These three species have a narrower and more strongly concave selenizone than *Dictyotomaria* and they are therefore assigned herein to *Devonorhineoderma*: *Dev. capillaria* (Conrad, 1842) comb. nov., *Dev. quasicapillaria* (Rollins, 1975) comb. nov. and *Dev. eurocapillaria* (Amler & Heidelberger, 2003) comb. nov.

The Triassic species *Pleurotomaria subcancellata* d'Orbigny, 1850 was assigned to *Dictyotomaria* by Bandel (1991, 2009). This species is not considered to be *Dictyotomaria* any longer and represents the type species of *Cancellotomaria* (Karapunar & Nützel 2021).

Dictyotomaria turrisbabel sp. nov.
Figure 41

2014*b* unident. Pleurotomarioidea; Nützel, p. 68, fig. 1G.

LSID. urn:lsid:zoobank.org:act:2EE7CA02-FC2F-4696-A0C8-702097E5F0C3

Derivation of name. Referring to the Tower of Babylon.

Holotype. SNSB-BSPG 2009 XXII 15

Paratypes. SNSB-BSPG 2009 XXII 8, 16

Type location & age. Virgilian, Colony Creek Shale Member (Caddo Creek Formation), Lake Brownwood 7½′ Quadrangle, Brown County, Texas; hillside exposure (AMNH locality 5500; 31°50′25.33″N, 99°01′51.79″W).

Material. 12 specimens from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 8, 15–16, and a further 9 specimens (SNSB-BSPG 2009 XXII).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 15	9.7	10.8	68	–	4.7	4.1	0.7	0.16	0.14
2009 XXII 16	6.7	8.6	88	–	3.9	3.3	0.6	0.20	0.17
2009 XXII 8	7.4	10.0	93	–	3.6	3.7	0.6	0.16	0.16

Description. Shell of moderate size, conical, trochiform, slightly cyrtoconoid, wider than high, largest specimen with about seven whorls; whorl face angulated; suture shallow, indistinct, situated just below basal bulge; whorls ornamented with few crest-like spiral cords angulating whorl face and numerous axial threads; intersections of spiral cords not nodular; early whorl face angulated, ornamented with axial threads; later whorl face with subsutural angulation, median angulation and basal bulge forming peripheral keel; area between suture and subsutural angulation form horizontal to concave shoulder lying perpendicular or somewhat sloping to shell axis; whorl face between subsutural and median angulations concave, inclined at 45°; lateral whorl face steeply sloping, concave, bordered by basal bulge and pronounced median carina; whorl face above median carina occasionally with 2–3 spiral cords additional to subsutural angulation; whorl face ornamented with numerous, sharp collabral axial treads; axial threads nearly orthocline between adapical suture and median angulation, sharply curving backward between median angulation and selenizone and between basal bulge and selenizone; selenizone flatly concave, depressed, wide, bordered by spiral cords, situated below median angulation, with

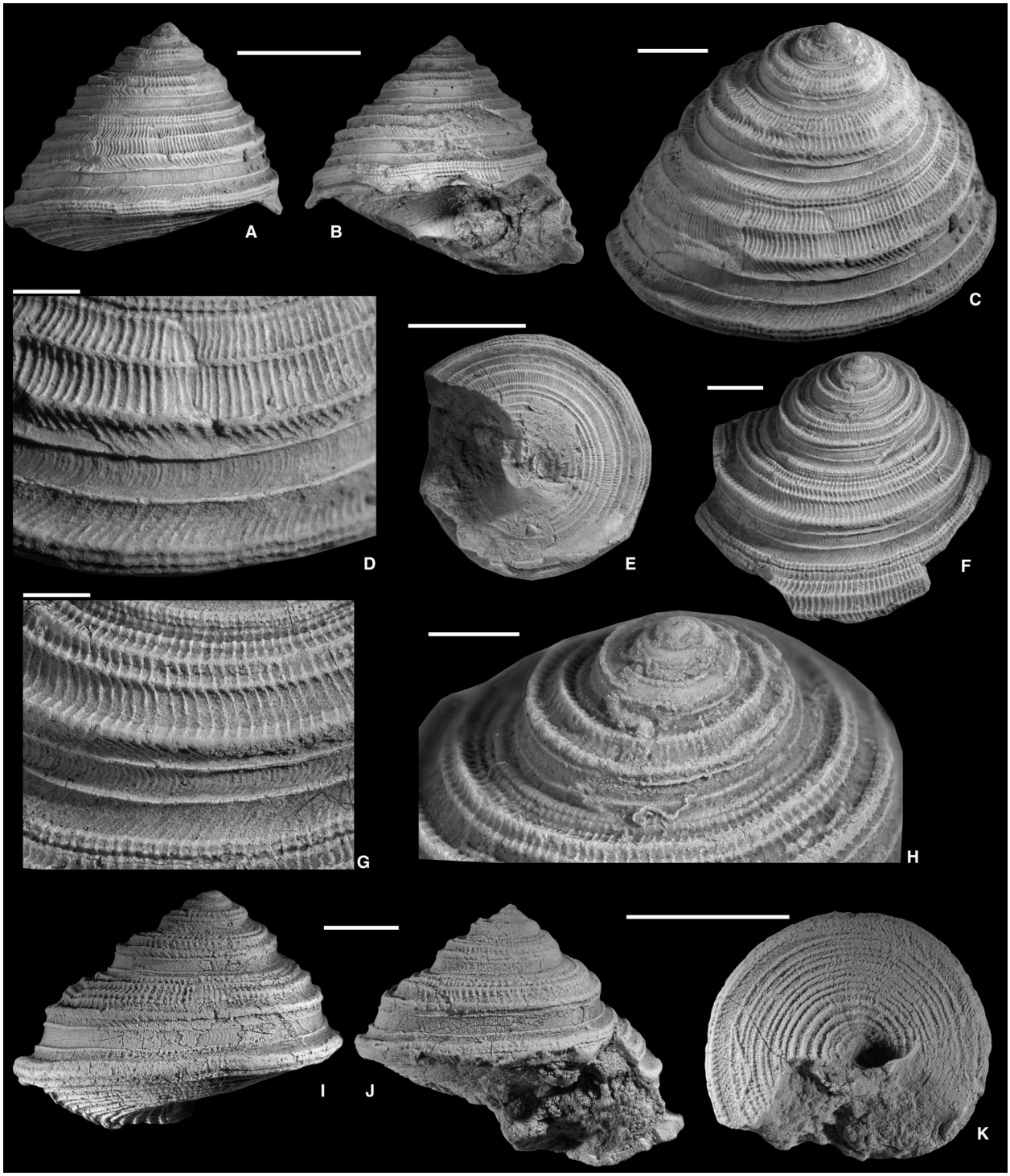

FIG. 41. *Dictyotomaria turrisbabel* sp. nov. from the Colony Creek Shale (Virgilian, Texas). A–E, SNSB-BSPG 2009 XXII 15, holotype; D, oblique apical view, detail of ornament and selenizone. F–H, SNSB-BSPG 2009 XXII 8, paratype; G, oblique apical view, detail of ornament and selenizone; H, oblique apical view, detail of early whorls. I–K, SNSB-BSPG 2009 XXII 16, paratype. Scale bars represent: 5 mm (A, B, E, K); 2 mm (C, F, I, J); 1 mm (D, G, H).

distinct thread-like lunulae; basal bulge forming angular transition to base, covered with equally prominent prosocyrt axial ribs and 4–6 spiral cords, 2–3 of which exposed on spire whorls, forming reticulate pattern; base convex, ornamented with sinuous axial threads and up to 15 spiral cords; basal axial threads opisthocyrt near basal edge, prosocyrt near umbilical region;

aperture subovate, almost as wide as high; outer lip angulated, basal lip slightly convex, columellar lip straight; base phaneromphalous.

Remarks. Dictyotomaria turrisbabel resembles *Di. scitula* (Meek & Worthen, 1861) (Sturgeon 1964*b*, pl. 121 figs 6–9) in the principal ornamentation and having an angulated whorl face but differs in having a prominent peripheral keel and more prominent angulations. As already indicated by Yochelson & Saunders (1967), *Ptychomphalus lineata* Sayre, 1930 represents *Dictyotomaria*. *Dictyotomaria lineata* resembles *Di. turrisbabel* in surface ornamentation but its whorl profile is less gradate and its basal bulge (peripheral keel) is less pronounced.

Family PORTLOCKIELLIDAE Batten, 1956

Original diagnosis. 'Characterized by dominant, usually rather coarse spiral ornament and a selenizone low on the whorls; shell shape ranging from globose to turreted; ornament on parietal surface resorbed or covered by a very thin inductura' (Batten 1956, p. 42).

Emended diagnosis. 'Turbiniform to trochiform, with notch or short labral slit giving rise to depressed selenizone low on whorl; spiral cords dominant, collabral threads also present. Dev.–M. Perm.' (Knight *et al.* 1960, p. I212).

Remarks. The type species of *Shansiella* (*Shansiella*), *Sh. altispiralis* Yin, 1932 from the upper Carboniferous of China, is not well known (Knight 1941). Its type material has never been studied since Yin (1932). Here, we follow Knight *et al.* (1960) and regard *Latischisma* Thomas, 1940*a* as younger synonym of *Shansiella* (*Shansiella*). However, if a revision of the type species of *Sh.* (*Shansiella*) reveals that it is not synonymous with *Latischisma*, then the species assigned to *Sh.* (*Shansiella*) herein should be placed in *Latischisma*.

The original composition of Portlockiellidae (Batten 1956; Knight *et al.* 1960) was based on the position of the selenizone and the dominant spiral ornament. *Shansiella* (*Sh.*) *carbonaria* has the same type of axial threads and strong spiral crests as *Portlockiella kentuckyiensis* (type species of *Portlockiella*). Hence the placement of *Shansiella* in Portlockiellidae is corroborated. However, the composition of the family Portlockiellidae seems to be artificial. The Devonian genus *Agniesella* has a selenizone positioned at or above mid-whorl and is widely phaneromphalous (Knight 1941) unlike the other members of the genera included and therefore this genus should be removed from Portlockiellidae. *Tapinotomaria* has more shared characters with the members of Phymatopleuridae (i.e. reticulate ornamentation, whorl profile, selenizone position and ornamentation). Therefore, this genus is assigned herein to Phymatopleuridae (see Remarks on Phymatopleuridae, above). The early ontogeny, dominant spiral ornamentation on whorl face, selenizone position and ornamentation suggest a close relationship between *Shansiella* and the Carboniferous genus *Abylea* Sturgeon, 1964*a*. The Permian species *Sh.* (*Sh.*) *tabulata* Batten, 1958 and *Sh.* (*Sh.*) *conica* Batten, 1958 develop a similar whorl morphology as *Abylea* species (also see Remarks on *Paragoniozona*, above). Therefore, *Abylea* can be assigned to Portlockiellidae. However, the general whorl profile, position of selenizone of *Sh.* (*Sh.*) *conica*, *Sh.* (*Sh.*) *tabulata* and members of *Abylea* also suggest a close affinity of *Shansiella* and *Abylea* to Phymatopleuridae. The classification of Pleurotomariida and the generic composition of Portlockiellidae proposed by Batten (1956) and Knight *et al.* (1960) was mainly based on the position of the selenizone since the position of the selenizone is highly informative if combined with other selenizone characters. However, additional characters regarding the early ontogeny seem to be as informative for higher classification. Since the early ontogeny of *Portlockiella* is unknown, it is not certain whether Portlockiellidae represents a synonym of Phymatopleuridae or not. The only character differentiating Portlockiellidae from Phymatopleuridae seems to be the dominance of spiral ornament in Portlockiellidae.

Genus SHANSIELLA Yin, 1932
Subgenus SHANSIELLA Yin, 1932

Type species. Shansiella altispiralis Yin, 1932 from the upper Carboniferous of Shanxi, China; original designation.

Shansiella (*Shansiella*) *carbonaria* (Norwood & Pratten, 1855)
Figure 42

* 1855 *Pleurotomaria carbonaria* Norwood & Pratten, p. 75, pl. 9 fig. 8.
1964*a* *Shansiella carbonaria* (Norwood & Pratten); Sturgeon, p. 209, pl. 32 figs 18–21.
1967 *Shansiella carbonaria* (Norwood & Pratten); Yochelson & Saunders, p. 201.
1972*a* *Shansiella carbonaria*; Batten, figs 1–5, 8–9, 11–14, 16–20, 22–23, 28.
2001 *Shansiella carbonaria* (Norwood & Pratten); Kues & Batten, figs 7.9, 7.10.

Material. A total of 5 specimens. 1 from the Virgilian of Texas (Colony Creek Shale Member, TXV–50): SNSB-BSPG 2020 LXXIII 1. 1 from the Desmoinesian Allegheny Formation of Ohio: SNSB-BSPG 2020 I 26. 1 from the Virgilian of Texas (Finis Shale Member, TXV–34): SNSB-BSPG 2020 LXXV 1. 2 from the Virgilian of Texas (Finis Shale Member, TXV–36): SNSB-BSPG 2020 LXXVI 2–3.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXIII 1	20.7	25.4	109	–	13.2	9.8	1.3	0.13	0.10
2020 I 26	24.8	27.8	102	–	17.3	14.2	1.6	0.11	0.09
2020 LXXV 1	33.3	35.6	94	–	22.7	18.6	2.0	0.11	0.09
2020 LXXVI 2	33.4	38.6	112	–	22.0	16.4	2.0	0.12	0.09

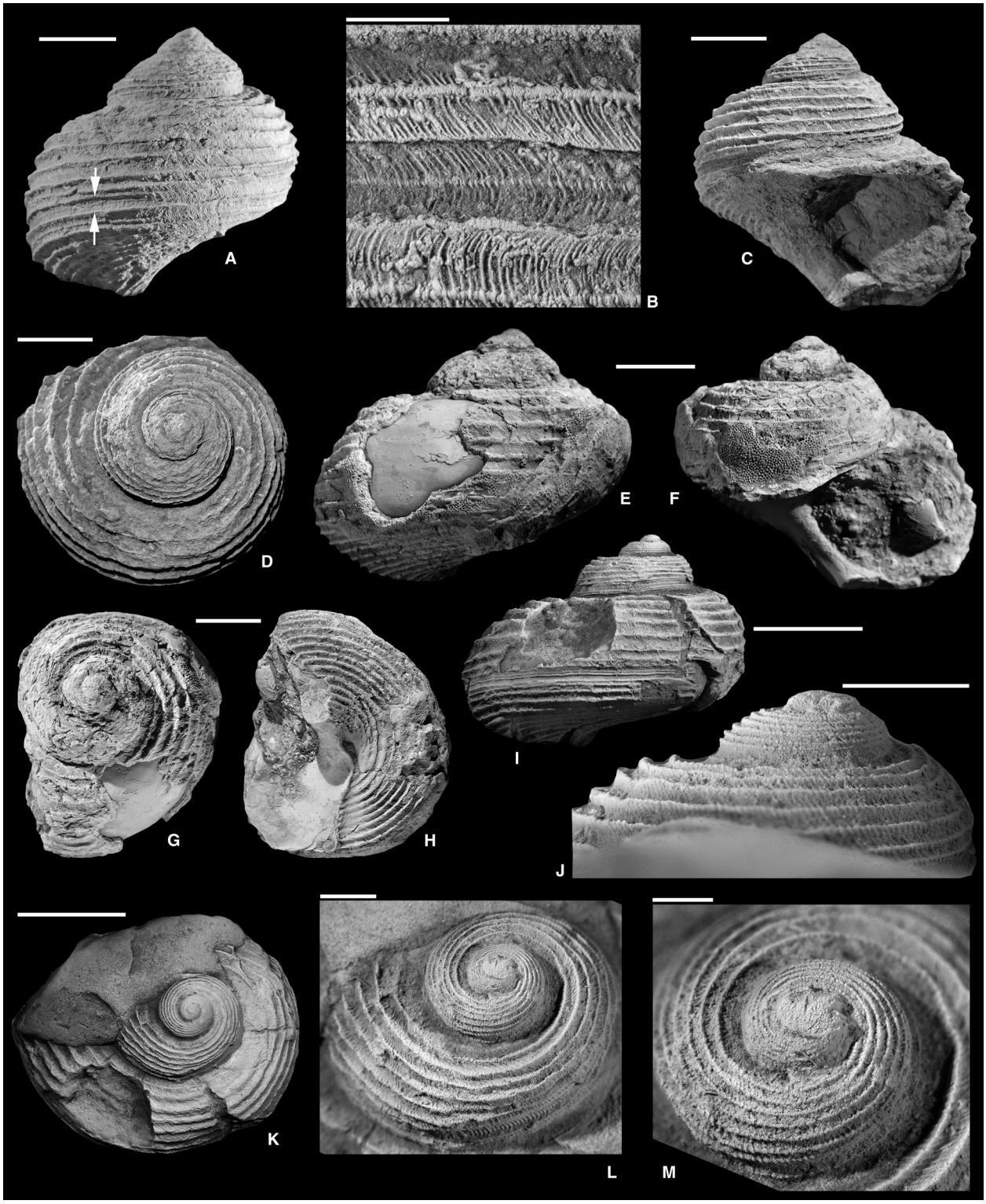

FIG. 42. *Shansiella* (*Shansiella*) *carbonaria* (Norwood & Pratten, 1855). A–D, SNSB-BSPG 2020 LXXV 1, from the Finis Shale Member (Virgilian, Texas); A, arrows indicate selenizone margins; B, lateral view, detail of selenizone. E–H, SNSB-BSPG 2020 LXXVI 2, from the Finis Shale Member (Virgilian, Texas). I–M, SNSB-BSPG 2020 LXXIII 1, from the Colony Creek Shale (Virgilian, Texas); J, lateral view, detail of early whorls; L–M, oblique apical view, detail of early whorls. Scale bars represent: 10 mm (A, C–I, K); 2 mm (B, J, L); 1 mm (M).

Measurements (mm). (Continued)

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXVI 3	22.5	28.9	128	–	16.1	15.8	1.9	0.12	0.12

Description. Shell relatively large, turbiniform, as wide as high, the largest specimen with *c.* 7 whorls; apical angle *c.* 100°–120°; suture moderately deep, situated just below selenizone; whorl face convex, whorl face (area between adapical and abapical sutures) ornamented with maximum of 10 sharp, strong spiral cords above and two spiral cords below selenizone; spiral cords from sharp ridges with strongly concave interspaces; growth lines strengthened, forming densely spaced threads, prosocline prosocyrt above selenizone, prosocyrt just below selenizone; selenizone flat, slightly depressed, bordered above and below by irregular shell edges, situated on lower half of whorl face; selenizone ornamented with one median spiral cord, occasionally one additional spiral cord and densely-spaced thread-like lunulae; base convex, ornamented with about 10–14 spiral cords and opisthocyrt growth threads; aperture ovate, slightly oblique, almost as wide as high; outer lip convex, basal lip convex, columellar lip convex, inner lip cover the umbilical region; base anomphalous.

Remarks. Two of the studied specimens from TXV–36 are encrusted by sponges (?*Chaetetes* sp.) around the selenizone. In one specimen (2020 LXXVI 3) the sponge has grown just on the selenizone in a small spot (2 mm in diameter) next to the broken aperture. In another specimen (2020 LXXVI 2) the sponge has grown along the last whorl without covering the whole shell. If the sponges encrusted the shells while the animal was still alive, then it might be an example of a commensal relationship. The sponges might have benefited passively from the exhalant current produced by the animal at the abapertural part of the slit. McKinzie (2003) mentioned the rarity of *Sh.* (*Sh.*) *carbonaria* and its presence in the sponge–echinoderm facies in the Pennsylvanian of Texas. Batten (1958, pp 169–170, pl. 42 fig. 9) reported *Glyptotomaria marginata* Batten, 1958 (= *Dictyotomaria*) within the cloaca of *Heliospongia* from the Permian of Texas and discussed a possible commensalism between the two species. A possible spongivory habit of *Dictyotomaria* or *Shansiella* cannot be ruled out given the fact that the recent members of the Order Pleurotomariida are spongivorous (Harasewych 2002).

Shansiella (*Shansiella*) *beckwithana* (McChesney, 1859)
Figure 43

* 1859 *Pleurotomaria beckwithana* McChesney, p. 61.
1868 *Pleurotomaria beckwithana*; McChesney, p. 47, pl. 2 fig. 17.
1964*a* *Shansiella beckwithana* (McChesney); Sturgeon, p. 210, pl. 33 figs 19–22.
1967 *Shansiella beckwithana* (McChesney); Yochelson & Saunders, p. 201.
2001 *Shansiella* beckwithana (McChesney); Kues & Batten, p. 38, fig. 7.7–7.8.

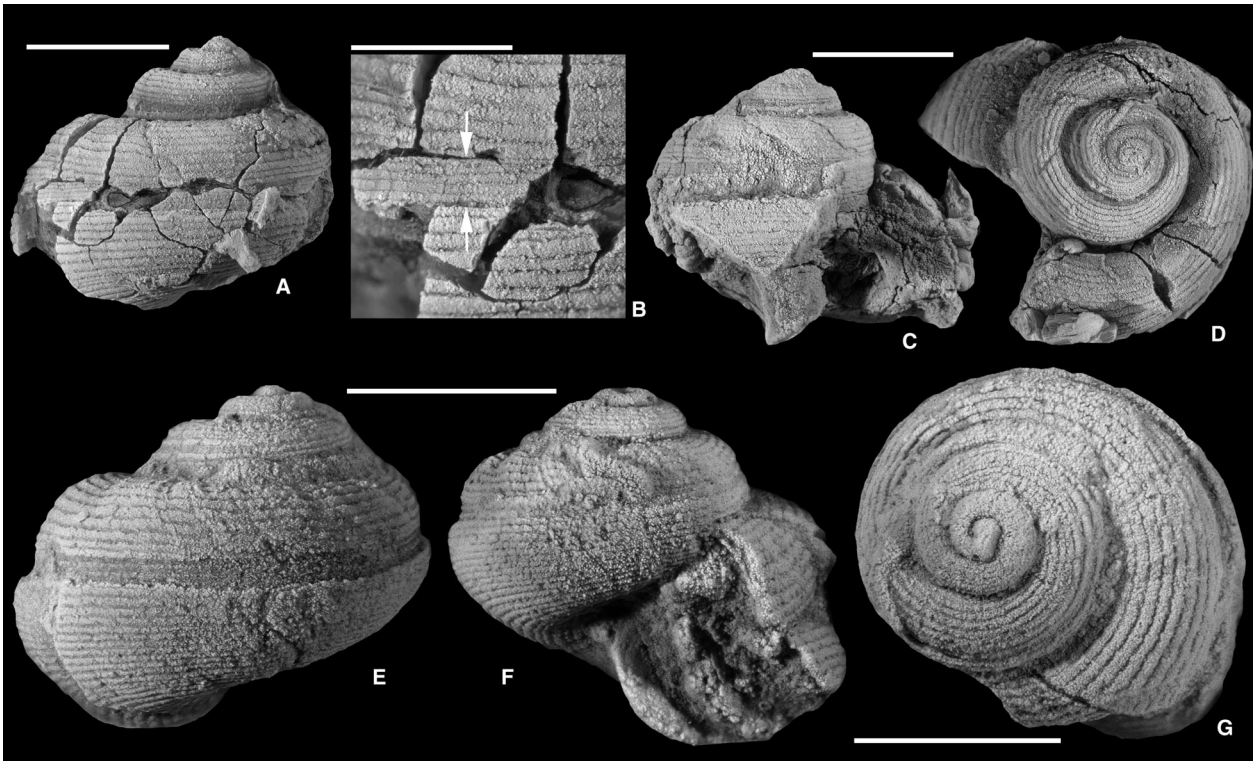

FIG. 43. *Shansiella* (*Shansiella*) *beckwithana* (McChesney, 1859). A–D, SNSB-BSPG 2020 XCI 24, from the Finis Shale Member (Virgilian, Texas); B, lateral view, detail of selenizone, arrows indicate selenizone margins. E–G, SNSB-BSPG 2009 XXII 17, from the Colony Creek Shale (Virgilian, Texas). Scale bars represent: 2 mm (A, C, D); 1 mm (B, E–G).

Material. A total of 2 specimens. 1 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 17. 1 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 24 (from bulk sample).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 XCI 24	3.9	4.3	103	–	2.8	1.9	0.3	0.16	0.11
2009 XXII 17	1.7	1.9	108	0.38	1.1	0.8	0.1	0.16	0.11

Description. Shell small, turbiniform, slightly wider than high, largest specimen with four whorls; apical angle *c.* 110°; suture moderately deep, impressed, situated somewhat below selenizone; first whorl convex, without visible ornament; spiral threads appear in second whorl; selenizone appears at the end of the second whorl, slightly above suture; whorl face convex throughout ontogeny; whorl face of largest specimen ornamented with prosocline growth lines and 14 spiral bands above selenizone; shallow grooves between spiral bands; occasionally with transverse undulations near adapical suture; selenizone flat, slightly sunken below whorl face, ornamented with four spiral bands separated by grooves, weak lunulae formed by growth lines; spiral bands on selenizone narrower than the bands on whorl face; abapical border of selenizone forming whorl periphery, situated slightly more abaxially than the adapical border; whorl face below selenizone (of largest specimen) with four spiral bands and prosocyrt growth lines/striae; base convex, ornamented as whorl face and with opisthocyrt growth lines; aperture ovate, slightly oblique, as wide as high; outer lip convex, basal lip convex, columellar lip convex and slightly thickened; base anomphalous.

Remarks. As discussed by Kues & Batten (2001), *Sh.* (*Sh.*) *planicostata* (Girty, 1937) might represent a younger synonym of *Sh.* (*Sh.*) *beckwithana* but Girty's species seems to have a narrower selenizone.

Subgenus OKLAHOMAELLA nov.

LSID. urn:lsid:zoobank.org:act:9D6A84FC-BA81-43A0-AF0E-8F1309E51513

Type species. Shansiella (*Oklahomaella*) *globilineata* from the Morrowan of Oklahoma, USA.

Derivation of name. From the type locality (Oklahoma, USA), where the species come from; gender feminine.

Diagnosis. Turbiniform, whorl face strongly convex; surface ornamented with several closely spaced spiral threads on early whorls, few and very prominent spiral cords on late whorls; selenizone wide, situated on lower half of whorl face on spire whorls, situated above mid whorl in last whorl; selenizone with median spiral cord and faint growth lines; base anomphalous.

Remarks. Shansiella (*Oklahomaella*) subgen. nov. and *Shansiella* (*Shansiella*) share the same shell shape, whorl profile, early whorl ornamentation and both are ornamented dominantly with spiral cords. However, *Sh.* (*Oklahomaella*) differs from all other *Sh.* (*Shansiella*) species by its very prominent and few (3–5) spiral cords on its late whorl face. Additionally, the selenizone is above mid whorl on the last whorl in *Sh.* (*Oklahomaella*), which is in contrast with other *Sh.* (*Shansiella*) species, where the selenizone is located below mid whorl.

Shansiella (*Oklahomaella*) *globilineata* sp. nov.
Figure 44

LSID. urn:lsid:zoobank.org:act:5B6A7662-9B4A-409F-8D46-DCA9B5FA364E

Derivation of name. From Latin *globi*, for the globular shape, and Latin *lineata*, for the prominent spiral cords characteristic of this species.

Holotype. SNSB-BSPG 2020 LVIII 8

Paratype. SNSB-BSPG 2020 LVIII 9

Type location & age. Morrowan, Gene Autry Formation exposed in gullies on east side of unnamed tributary of Sycamore Creek on the Daube Ranch, NW¼, NW¼, SW¼, sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7½′ Quadrangle, Oklahoma (AMNH locality 5270; 34°14′13.76″N, 96°52′42.02″W).

Material. 2 specimens from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 8–9.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 8	4.1	4.0	91	0.35	2.3	1.6	0.2	0.14	0.10
2020 LVIII 9	4.0	4.3	89	–	2.2	1.8	0.2	0.13	0.11

Description. Shell small, turbiniform, as wide as high, largest specimen comprising about five whorls; suture moderately deep, situated between two strong spiral cords below selenizone; initial whorl low-spired, almost flat, without visible ornament, 0.35 mm in diameter; early whorl face convex, ornamented with *c.* 10 spiral threads starting within second whorl; later ornament consisting of strong spiral cords, starting within third whorl; later whorl face convex, ornamented with three strong, crest-like spiral cords above and two spiral cords below selenizone; adapical spiral cord weaker than others, very weakly nodose; second and third spiral cords asymmetrical, shallow adapically, steep abapically; growth lines prosocline above selenizone, prosocline below selenizone; selenizone flat, sligthly depressed, starting at 1.5 whorls, bordered above and below by irregular shell edges, situated on lower half of whorl face; selenizone ornamented with one median cord and faint lunulae formed by growth lines; base convex, ornamented with *c.* 11 spiral cords; basal spiral cords weaker

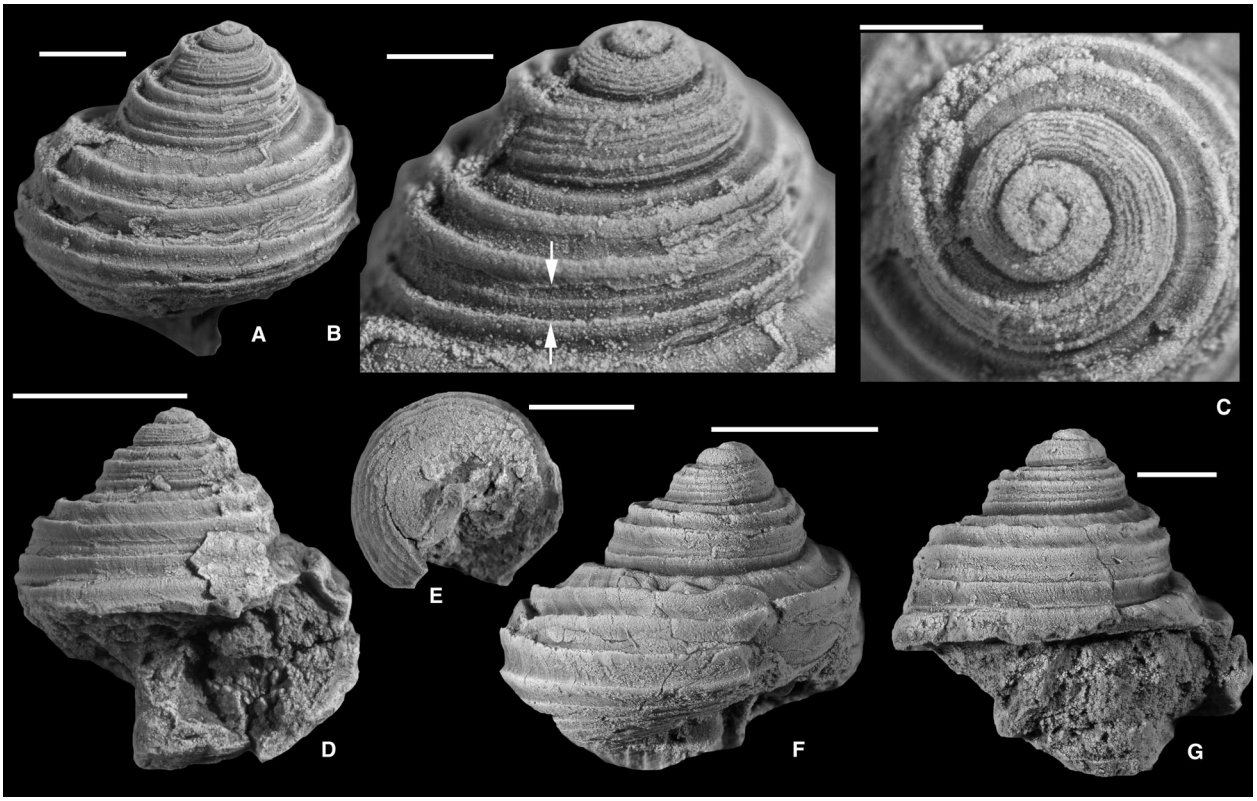

FIG. 44. *Shansiella* (*Oklahomaella*) *globilineata* subgen. et sp. nov. from the Gene Autry Shale (Morrowan, Oklahoma). A–E, SNSB-BSPG 2020 LVIII 8, holotype; B, oblique lateral view, detail of selenizone, arrows indicate selenizone margins; C, apical view, detail of early whorls. F–G, SNSB-BSPG 2020 LVIII 9, paratype. Scale bars represent: 1 mm (A, G); 0.5 mm (B, C); 2 mm (D–F).

than cords on whorl face; basal growth lines opisthocyrt; aperture ovate, slightly oblique, almost as wide as high; outer lip convex, basal lip convex, columellar lip straight; base anomphalous.

Remarks. The ornament of few but very strong spiral cords is unique among *Shansiella* species. *Shansiella* (*Oklahomaella*) *globilineata* differs from *Sh.* (*Sh.*) *carbonaria* in being smaller and having fewer but stronger spiral cords. *Shansiella* (*Sh.*) *globosa* (Thomas, 1940*a*) from the Carboniferous of Scotland is slightly larger with many sharp spiral cords. *Shansiella* (*Sh.*) *beckwithana* (McChesney, 1859) and *Sh.* (*Sh.*) *planicosta* (Girty, 1937) from the Carboniferous of the USA are similar in size but have more spiral bands that are flat and not crest-like. *Shansiella* (*Sh.*) *altispiralis* Yin, 1932, the type species of *Shansiella* (*Shansiella*) from the Carboniferous of Shanxi, is larger and has more spiral cords.

Subclass CAENOGASTROPODA Cox, 1960*b*
Superfamily ORTHONEMATOIDEA Nützel & Bandel, 2000
Family GONIASMATIDAE Nützel & Bandel, 2000

Genus PERUVISPIRA Chronic, 1949

Type species. Peruvispira delicata Chronic, 1949 from the Permian of Peru; original designation.

Remarks. Peruvispira was placed in the family Eotomariidae and the subfamily Neilsoniinae Knight, 1956 by Knight *et al.* (1960). *Peruvispira* sp., described below, is a typical member of *Peruvispira*. It has a clearly multi-whorled, heliciform caenogastropod-style larval shell of the planktotrophic type. This type of larval shell has been shown to be present in several late Palaeozoic caenogastropods including some having a selenizone on the teleoconch such as *Goniasma*, *Platyzona* and *Erwinispira* (Nützel & Bandel 2000; Pan & Erwin 2002; Nützel & Pan 2005). Hence, we place the present species and the genus *Peruvispira* in Caenogastropoda and Goniasmatidae. As mentioned, *Peruvispira* was previously placed in subfamily Neilsoniinae. The protoconch of the type species of *Neilsonia* is unknown but *Neilsonia nuda* Mazaev, 2015 from the Permian of Russia seems to have a protoconch of little more than one whorl that could be either a caenogastropod larval shell of the non-planktotrophic type or a vetigastropod protoconch. It is also possible that *Neilsonia nuda* represents *Peruvispira*, because the suture is situated well below the selenizone and is has a prominent base. *Wannerispira* Kaim & Nützel *in* Kaim *et al.*, 2010 (replacement name for *Pagodina* Wanner, 1941) obviously has the same type of caenogastropod larval shell as *Peruvispira* as can be seen in the Early Triassic *Wannerispira shangganensis* Kaim & Nützel *in* Kaim *et al.*, 2010 from China as figured by Sun *et al.* (2021, fig. 5x, y). Therefore, we place *Wannerispira* in Goniasmatidae and this represents the first evidence that this family survived the end-Permian mass extinction event.

The resemblance of selenizone development and selenizone width at the development in *Peruvispira* sp. with the Devonian murchisonioid genus *Diplozone* as figured by Frýda (2012, figs 4G, 12A) is remarkable. However, it is not sure whether the two taxa are closely related.

The Early Carboniferous *Peruvispira gundyensis* Yoo, 1988 from Australia (Yoo 1988, figs 29–32; Yoo 1994, pl. 8 figs 4–8) also has smooth early whorls but it is unclear whether they represent a caenogastropod larval shell. However, *Peruvispira gundyensis* Yoo, 1988 does not represent *Peruvispira*. Cook & Nützel (2005, p. 394) proposed to assign it to *Austroneilsonia* Sabattini, 1975 (type species *A. argentina* Sabattini, 1975 from the upper Carboniferous and lower Permian of Argentina). *Peruvispira gundyensis* shows the characteristic shell shape, whorl profile, position of selenizone and ornamentation of the Devonian genus *Lukesispira* Frýda & Manda, 1997; therefore, it is herein assigned to *Lukesispira*: *Lukesispira gundyensis* (Yoo, 1988) comb. nov.

Pleurocinctosa Fletcher, 1958 represents a younger synonym of *Peruvispira* (Taboada *et al.* 2015). *Cordispira* Qiao, 1983, with type species *Cordispira angulata* Qiao, 1983 from the Carboniferous of Xinjiang, very closely resembles *Peruvispira* and might represent a younger synonym of *Peruvispira*.

Peruvispira sp.
Figure 45

Material. A total of 2 specimens. 1 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 9. 1 from the Virgilian of Texas (Finis Shale Member, TXV–200): SNSB-BSPG 2020 XCI 39.

Description. Shell very small conical, relatively high-spired; largest specimen with four whorls (protoconch and 1.5 teleoconch whorls); suture impressed, situated well below selenizone; protoconch heliciform, consisting of *c.* 2.3–2.7 rounded, convex whorls; first whorl diameter 0.15 mm; late larval shell with minute pustules; larval shell ending abruptly at opisthocyrt ledge; teleoconch with slightly convex ramp followed by concave area towards selenizone; ramp ornamented with widely spaced sharp

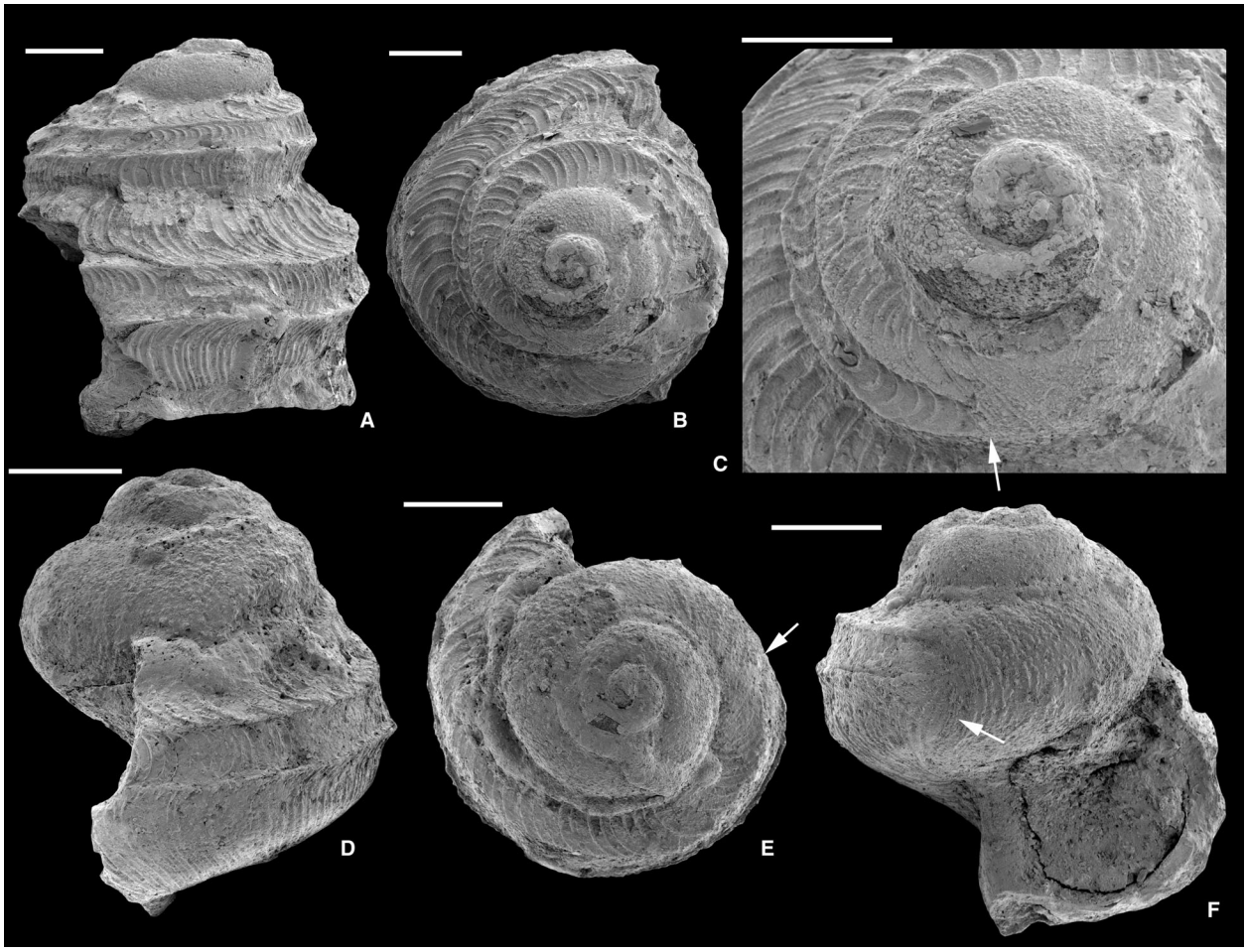

FIG. 45. *Peruvispira* sp. from the Finis Shale Member (Virgilian, Texas). A–C, SNSB-BSPG 2020 XCI 39; C, (slightly oblique) apical view, arrow indicates the margin of the protoconch II. D–F, SNSB-BSPG 2020 LXXX 9, arrows indicate the margin of the protoconch II. All scale bars represent 0.2 mm. All SEM images.

prosocyrt riblets; axial riblets over 25 per mm at 1.5 teleoconch whorls (whorl width slightly longer than 1 mm); whorl face below selenizone concave, ornamented with numerous prosocyrt, collabral axial riblets; selenizone starts abruptly after protoconch at mid-whorl face; selenizone flat, sunken, wide, covers quarter of whorl face, situated slightly below mid-whorl face of spire whorls, bordered above and below by projecting shell edges; abapical shell edge represents whorl periphery; lunulae sharp, at same number as axial riblets on whorl face; base convex, with opisthocyrt axial riblets; aperture subovate, outer lip convex, basal lip convex, columellar lip flat; base convex, anomphalous.

Remarks. Peruvispira sp. resembles *Pe. canningens*is from the lower Permian of Australia. *Peruvispira canningens*is seems to have fewer but slightly stronger axial ribs on the ramp. However, the number of ribs may change during ontogeny in *Peruvispira* species and *Pe. canningens*is is insufficiently documented also regarding protoconch morphology so a meaningful identification is impossible at this point.

Peruvispira delicata Chronic, 1949, the type species of *Peruvispira* from the Permian of Peru, is also ornamented with numerous sharp axial riblets (as is typical of that genus) but its whorl ramp seems to be more convex. The early ontogeny including the protoconch morphology of *Pe. delicata* is unknown.

Peruvispira oklahomaensis sp. nov.
Figure 46

LSID. urn:lsid:zoobank.org:act:D5044C17-E6AA-43F0-A7BD-D9E35D1A6026

Derivation of name. Referring to Oklahoma, where the specimens are found.

Holotype. SNSB-BSPG 2020 LVIII 18

Paratypes. SNSB-BSPG 2020 LVIII 19, 20, 21

Type location & age. Morrowan, Gene Autry Formation exposed in gullies on east side of unnamed tributary of Sycamore Creek on the Daube Ranch, NW¼, NW¼, SW¼, sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7½′ Quadrangle, Oklahoma (AMNH locality 5270; 34°14″13.76″N, 96°52′42.02″W).

Material. 4 specimens from the Morrowan of Oklahoma (Gene Autry Shale locality): SNSB-BSPG 2020 LVIII 18–21.

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 18	4.9	3.7	70	–	2.2	2.0	0.5	0.23	0.21
2020 LVIII 19	3.6	2.9	72	0.21	1.6	1.2	0.3	0.24	0.18
2020 LVIII 20	4.8	3.6	67	0.18	2.2	1.8	0.4	0.23	0.19
2020 LVIII 21	4.8	3.4	61	–	2.0	1.7	0.4	0.22	0.19

Description. Shell very small, conical, relatively high-spired; pleural angle 62°–65°; suture impressed, situated below basal edge; protoconch heliciform, consisting of *c.* 2.3–2.7 convex whorls; first whorl diameter 0.19 mm; larval shell ending abruptly at opisthocyrt ledge; teleoconch whorl face with rounded shoulder followed by concave area towards selenizone; whorl face above selenizone ornamented with prosocyrt growth lines which form sharp axial ribs on adapical half that disappear near selenizone; axial ribs are 6–9 per mm; whorl face below selenizone concave, ornamented with slightly prosocyrt riblets, sometimes with weak angulation (basal edge) at transition to convex base; riblets more pronounced on basal edge; selenizone starts abruptly after protoconch at mid-whorl face; selenizone flat, wide, situated at lower half of whorl face of spire whorls, bordered above and below by projecting shell edges; abapical shell edge represents whorl periphery; lunulae faint, formed by growth lines; base convex, smooth; basal growth lines slightly opisthocyrt; aperture subovate, outer lip convex, basal lip convex, columellar lip straight, reflexed; base anomphalous.

Remarks. The studied specimens resemble *Murchisonia insculpta* Hall, 1858 according to the original description given by Hall (1858, p. 26) and the drawings later given by Whitfield (1882, p. 85, pl. 9 fig. 18) and Hall (1883, p. 359, pl. 32 fig. 18). However, *M. insculpta* Hall, 1858 seems to be more slender, the axial ribs are not as oblique and the lunulae on the selenizone are more pronounced. We herein place *M. insculpta* in *Peruvispira* (*Peruvispira*? *insculpta* (Hall, 1858) comb. nov.) based on the typical axial ornamentation and sharp lunulae in the original drawings, but a better documentation of the holotype is needed for a certain generic assignment.

Peruvispira delicata Chronic, 1949, the type species of *Peruvisira* from the Permian of Peru, differs in having less prominent axial ribs that do not decrease in strength towards the selenizone. The specimen assigned to *Peruvispira* cf. *delicata* by Batten (1995) from the Pennsylvanian of Texas is higher-spired, with shorter whorl ramp and without axial ribs. *Peruvispira boreala* Beus & Lane, 1969 from the Pennsylvanian of Nevada has a nearly straight ramp and a finer ornament. *Peruvispira*? *deornata* (de Koninck, 1883) from the Carboniferous of Belgium and England (Batten 1966, p. 37, pl. 4 figs 13–14) is higher spired with well-rounded whorl profile, wider selenizone, without pronounced selenizone borders. *Peruvispira sueroi* Sabattini & Noirat, 1969 from the Carboniferous of Argentina differs in having a wider pleural angle (70°–76°), an evenly convex ramp and continuous axial ribs on the ramp. *Peruvispira teckaensis* Taboada *et al.*, 2019 from the Carboniferous of Argentina has a wider pleural angle (75° measured from Taboada *et al.* 2019, fig. 9M, but 58° according to Taboada *et al.* 2019, p. 652) and its axial ribs on the ramp do not fade towards the selenizone. *Peruvispira teckaensis* Taboada *et al.*, 2019 has the same surface ornamentation and pleural angle as *Pe. sueroi*; hence, it might represent a younger synonym of *Pe. sueroi*. *Peruvispira canningensis* Taboada *et al.*, 2015 has a narrower pleural angle (40°), more (9–10 per mm) and more closely spaced, continuous axial ribs on the ramp. *Peruvispira kuttungensis* Campbell, 1961 from the Carboniferous of New South Wales is much larger (18 mm in height), and has an evenly convex upper whorl face

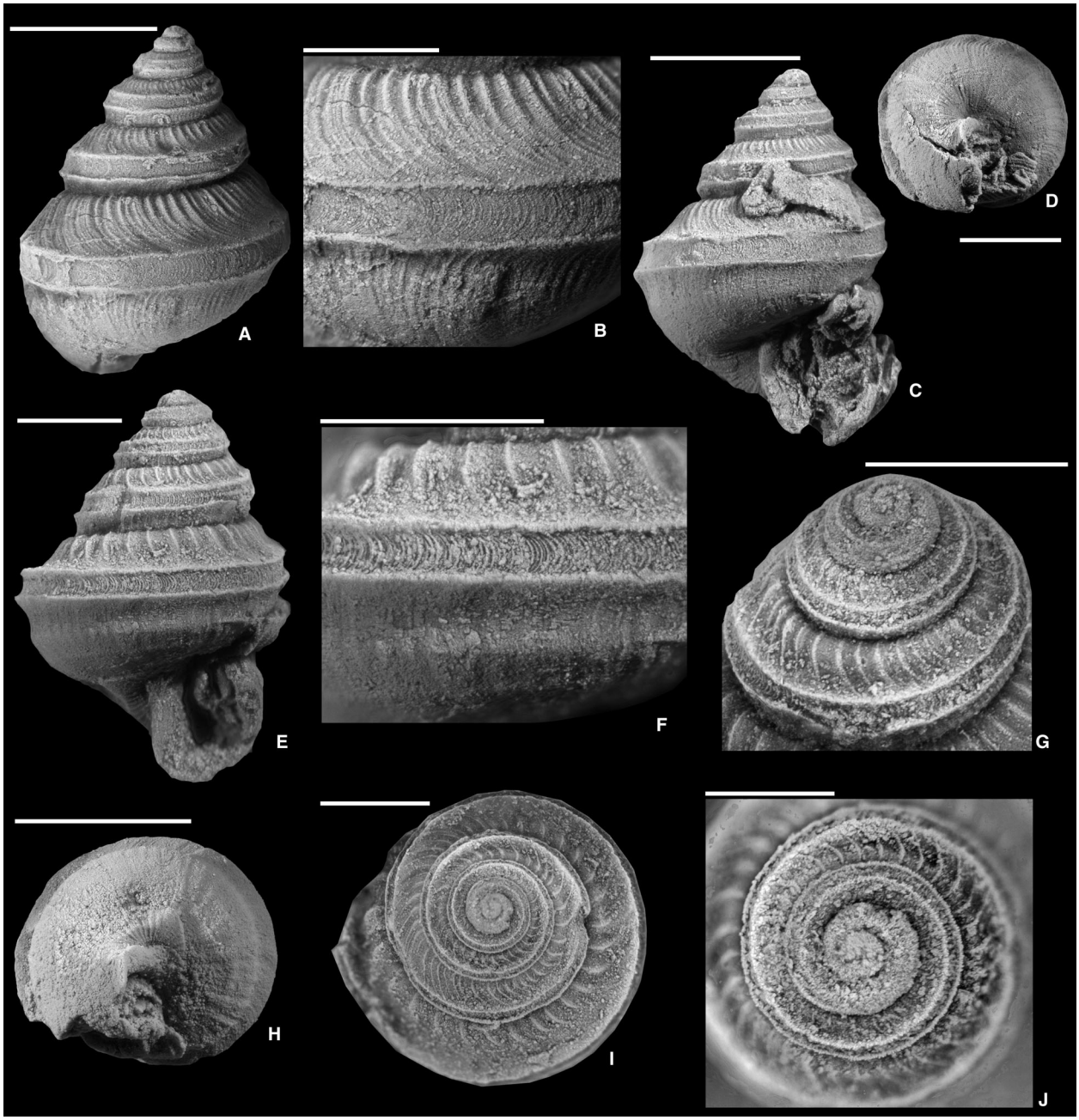

FIG. 46. *Peruvispira oklahomaensis* sp. nov. from the Gene Autry Shale (Morrowan, Oklahoma). A–D, SNSB-BSPG 2020 LVIII 18, holotype; B, lateral view, detail of surface ornament and selenizone. E–J, SNSB-BSPG 2020 LVIII 19, paratype; F, lateral view, detail of surface ornament and selenizone; G, oblique apical view, detail of early whorls; J, apical view, detail of early whorls. Scale bars represent: 2 mm (A, C, D, H); 1 mm (B, E–G, I); 0.5 mm (J).

ornamented with more widely spaced axial ribs (3–6 per mm). *Peruvispira kempseyensis* Campbell, 1962 from the Carboniferous of New South Wales is much larger (20 mm), has a narrower selenizone, many and less prominent axial ribs (6–7 per mm on second whorl and 15 per mm on last whorl). *Peruvispira fletcheri* (Waterhouse, 1987) from the upper Carboniferous and lower Permian of Australia resembles *Pe. oklahomaensis* in whorl profile but lacks prominent axial ribs. *Peruvispira promenata* (Waterhouse, 1987) is higher spired and has continuous axial ribs on the ramp. *Peruvispira* sp. in Ketwetsuriya *et al.* (2020*a*) from the Permian of Thailand resembles *Pe. oklahomaensis* in whorl profile but has a steeper ramp, a narrower pleural angle (55° from Ketwetsuriya *et al.* 2020*a*, fig. 12) and a weaker ornamentation.

The presence of subsutural nodes has been used to differentiate *Neilsonia* from *Peruvispira* by some authors (i.e. Knight *et al.*

1960; Beus & Lane 1969) together with the position of the selenizone. The subsutural nodes in the type species of *Neilsonia*, *N. roscobiensis* Thomas, 1940*a*, are axial ribs that fade towards selenizone. Axial ribs are present in most of the *Peruvispira* species including its type species. The main difference between *Neilsonia* and *Peruvispira* is that the selenizone is situated low and the suture is just below the selenizone in *Neilsonia*. *Neilsonia invisitata* Hoare *et al*., 1997 and *N. welleri* Thein & Nitecki, 1974 are herein placed in *Peruvispira* because the abapical suture is situated well below the selenizone in both species. The holotype of *Peruvispira invisitata* (Hoare *et al*., 1997) comb. nov. is more bulbous but its apical angle and bulbosity seems quite variable among its specimens (compare the holotype in fig. 4–5 and the specimen in fig. 4–6 in Hoare *et al*. 1997). The axial ribs on the ramp are stable in strength in *Pe. invisitata* while the axial ribs of *Pe. oklahomaensis* increase in prominence towards the adapical suture. *Peruvispira welleri* (Thein & Nitecki, 1974) comb. nov. is higher spired and has much shorter subsutural nodes. *Neilsonia coatesi* Peel, 2016 and *N. ganneyica* Peel, 2016 both from the Carboniferous of the UK, are herein placed in *Peruvispira* due to the position of the abapical suture well below the selenizone (*Pe. coatesi* (Peel, 2016) comb. nov. and *Pe. ganneyica* (Peel, 2016) comb. nov.) Both species closely resemble *Pe. oklahomaensis* in ornamentation and shell profile. However, the ramp below the susbsutural ribs is more strongly concave and longer in those two species.

Genus PLATYZONA Knight, 1945

Type species. Pleurotomaria trilineata Hall, 1858 from the Carboniferous of Indiana, USA; original designation.

Remarks. Platyzona comprises turbiniform shells with rounded convex whorls, an unusually wide selenizone and a spirally ornamented teleoconch. *Platyzona* was regarded as a member of superfamily Murchisonioidea Koken, 1896 and the family Pithodeidae Wenz, 1938 (= Plethospiridae Wenz, 1938) by Knight *et al*. (1960) but later placed in Gosseletinidae (Batten 1966; Batten 1972*b*; Kues & Batten 2001). Pan & Erwin (2002) assigned four species from the Permian of South China to the genus *Platyzona*. They could only document the protoconchs of *Platyzona pulchella* Pan & Erwin, 2002 and *Pla. luculenta* Pan & Erwin, 2002. Based on the caenogastropod type larval shell of these two species, the genus *Platyzona* was placed in the family Goniasmatidae (Nützel *et al*. 2002) and then to Family Pithodeidae (Nützel & Nakazawa 2012, p. 138). *Platyzona luculenta* resembles *Erwinispira* Nützel & Pan 2005 more than *Platyzona*, regarding the projecting spiral ridges at the selenizone borders and the lower whorl expansion rate. Therefore, it is herein placed in *Erwinispira*: *Erwinispira*? *luculenta* (Pan & Erwin, 2002) comb. nov. *Platyzona pulchella* is only known from its holotype, which is a juvenile specimen consisting of the protoconch and about two teleoconch whorls. It is unclear whether the Permian species *Pla. pulchella* is a representative of *Platyzona*; it could also be a representative of *Peruvispira*.

Here we document a caenogastropod type larval shell for a typical *Platyzona* species from the Carboniferous for the first time. The presence of a protoconch of distinctly more than one whorl terminating at a sinusigera in *Pla. hespera* from the Buckhorn Asphalt Quarry corroborates the view that *Platyzona* is a caenogastropod species with a selenizone.

High-spired slit bearing gastropods with caenogastropod type larval shell are classified within the superfamily Orthonematoidea and the family Goniasmatidae (Caenogastropoda) (Nützel & Bandel 2000; Nützel & Pan 2005; Bouchet *et al*. 2017; see Mazaev 2011 for an alternative view). Therefore, *Platyzona* is herein placed in the family Goniasmatidae.

Thomas (1940*b*) recognized this genus before Knight (1945) proposed the name *Platyzona* and she proposed *Semestropha* with type species *Helix*? *striatus* J. Sowerby, 1817 in her unpublished PhD thesis. Since her thesis has not been published according to ICZN Art. 8, *Semestropha* is not a valid name. *Helix*? *striatus* was later assigned to *Platyzona* by Batten (1966).

As mentioned by Batten (1972*b*), species of the genus *Platyzona* are quite similar to each other in morphology and ornamentation. However, there are some extreme forms, like the openly coiled *Pla. anguispira* Batten, 1989 from the Permian of the USA and *Pla. shikhanensis* Mazaev, 2019*a* with gradate spire. *Platyzona anguispira* resembles openly coiled siliquariid gastropods with a narrow deep slit (e.g. Bieler 2004). *Platyzona shikhanensis* resembles the phymatopleurid genus *Callitomaria* Batten, 1958 with a whorl angulation and a wide selenizone.

Platyzona hespera Kues & Batten, 2001
Figures 47, 48

* 2001 *Platyzona hespera* Kues & Batten, p. 38, figs 7.5–7.6.

Material. A total of 11 specimens. 1 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 19. 1 from the Virgilian of Texas (Finis Shale Member, TXV–56): SNSB-BSPG 2020 LXXX 4. 9 from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 82, 248–251, and a further 4 specimens (SNSB-BSPG 2011 X).

Measurements (mm).

	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LXXX 4	23.0	24.7	87	–	10.2	9.7	1.6	0.16	0.15
2009 XXII 19	10.1	11.8	93	–	4.9	5.5	1.0	0.19	0.21
2011 X 82	6.4	6.7	88	–	3.1	3.1	1.0	0.31	0.31

Description. Shell of moderate size, turbiniform, relatively high-spired; largest specimen with about 7–8 whorls; protoconch heliciform, consisting of 1.2–1.3 whorls, diameter 0.31 mm, first whorl diameter 0.28 mm; protoconch abruptly terminating at sinusigera with strengthened terminal ledge and abapical projection; suture impressed, situated below periphery; whorl face above selenizone convex, ornamented with up to eight spiral cords and prosocline growth lines; spiral cords band-like, irregularly spaced; subsutural cords weaker, others rather strong and broad; weak spiral cords intercalated between stronger ones in

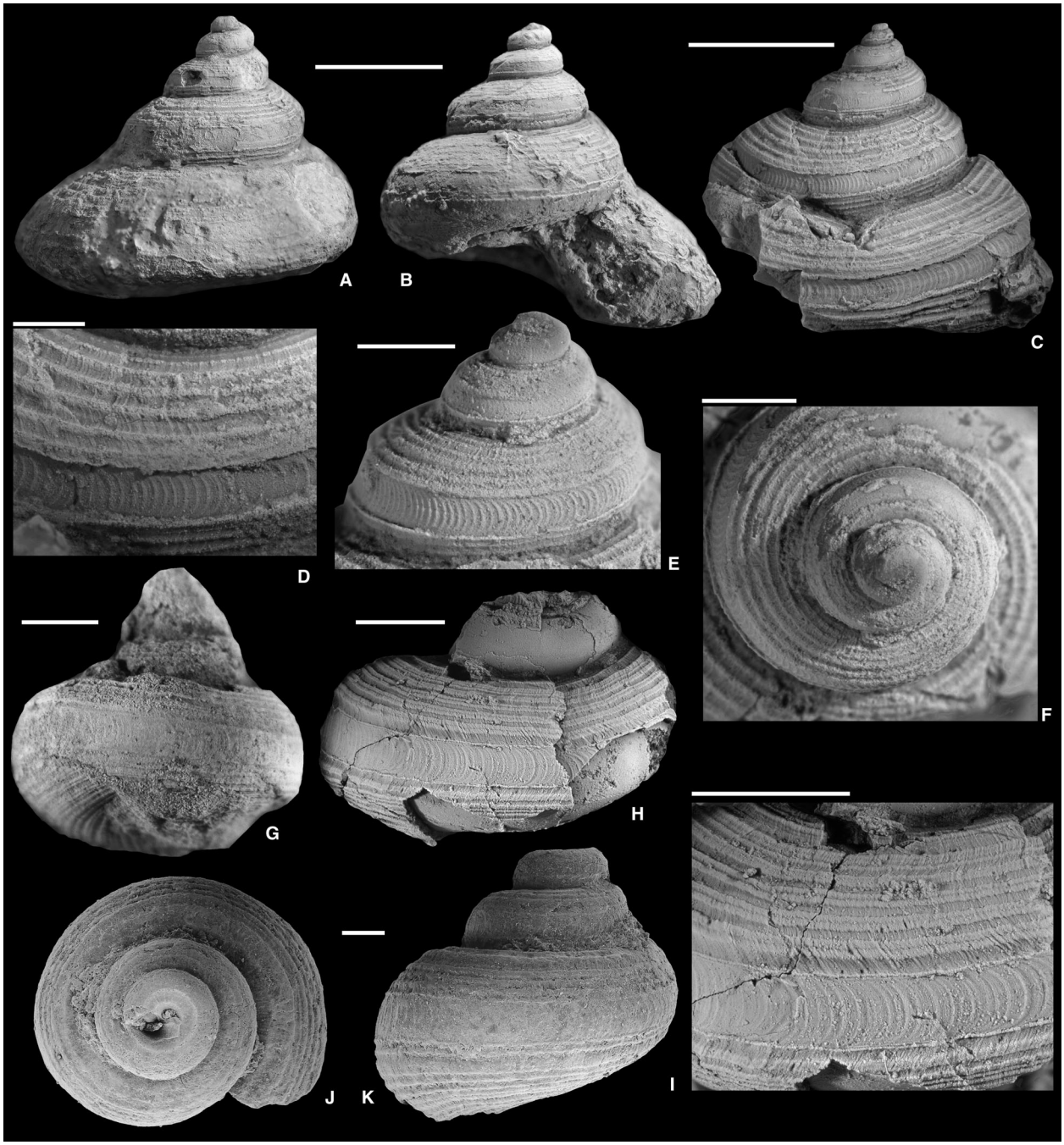

FIG. 47. *Platyzona hespera* Kues & Batten, 2001. A–B, SNSB-BSPG 2020 LXXX 4, from the Finis Shale Member (Virgilian, Texas). C–F, SNSB-BSPG 2009 XXII 19, from the Colony Creek Shale (Virgilian, Texas); D, lateral view, detail of surface ornament and selenizone; E, oblique apical view, detail of earlier whorls; F, apical view, detail of early whorls. G, SNSB-BSPG 2011 X 82, from the Buckhorn Asphalt (Desmoinesian, Oklahoma). H–I, SNSB-BSPG 2011 X 248, from the Buckhorn Asphalt (Desmoinesian, Oklahoma); I, lateral view, detail of surface ornament and selenizone. J–K, SNSB-BSPG 2011 X 251. Scale bars represent: 10 mm (A, B); 5 mm (C); 1 mm (D–F); 2 mm (G–I); 0.3 mm (J–K). J–K, SEM images.

last preserved whorls; growth lines form small opisthocyrt bows between spiral cords; whorl face below selenizone convex, ornamented with up to eight spiral cords and prosocyrt growth lines; selenizone flat, wide, depressed, situated at lower half of whorl face, bordered above and below by spiral cords; abapical edge of selenizone represents whorl periphery; lunulae formed by prominent, strengthened growth lines; base flatly convex, rounded, ornamented with spiral cords that are less prominent than the

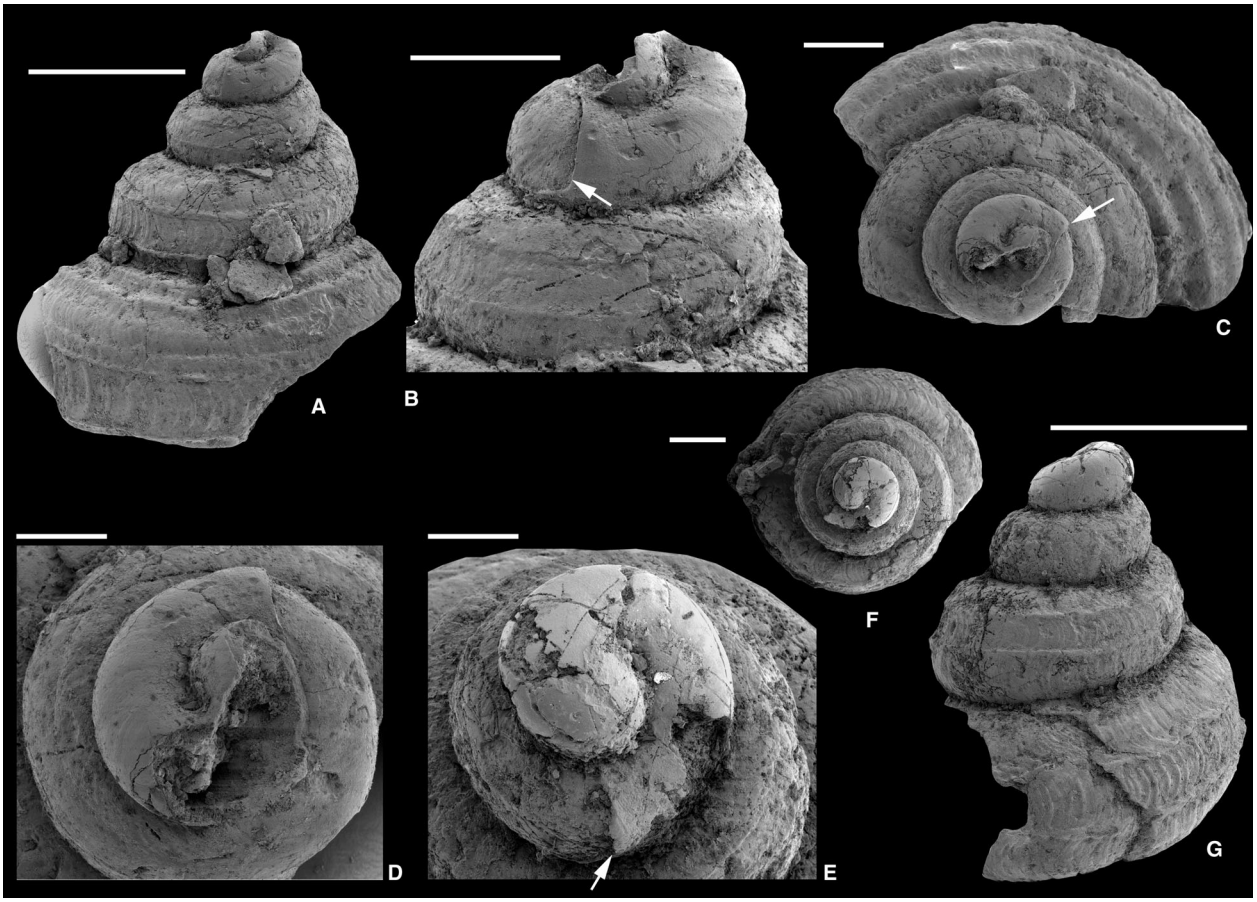

FIG. 48. *Platyzona hespera* Kues & Batten, 2001, juvenile specimens from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–D, SNSB-BSPG 2011 X 249, arrows indicate the margin of the protoconch II; D, apical view, detail of protoconch. E–G, SNSB-BSPG 2011 X 250; E, slightly oblique apical view, detail of protoconch, arrow indicates the margin of the protoconch II. Scale bars represent: 0.5 mm (A, G); 0.2 mm (B, C, F); 0.1 mm (D, E). All SEM images.

ones on whorl face; basal edge rounded; aperture subtrapezoidal, wider than high; outer lip and basal lip flatly convex, columellar lip straight; base phaneromphalous.

Remarks. The paucispiral protoconch of *Pla. hespera* comprises distinctly more than one whorl and has a relatively large diameter of the first whorl (0.28 mm) and terminates at a sinusigera. It thus reflects non-planktotrophic larval development and is typical of caenogastropods. The same protoconch of the planktotrophic type has been reported for the slit-bearing caenogastropods *Goniasma* and *Stegocoelia* from the Pennsylvanian of the USA (Nützel & Bandel 2000; Bandel *et al.* 2002).

The studied specimens from Texas are from two different horizons and only one of them has a poorly preserved aperture which is wider than high. They closely resemble the type specimens of *Pla. hespera* from the Pennsylvanian of New Mexico which is, however, slightly higher spired. The specimens from the Buckhorn Asphalt Quarry, Oklahoma closely resemble the specimens from Texas, but the specimens from the Buckhorn Asphalt Quarry occasionally develop a median groove on spiral cords (Fig. 47H–I). The Mississippian species *Pla. trilineata* (Hall, 1858) differs from *Pla. hespera* by having two spiral grooves and corresponding three spiral cords on its base. The Mississippian *Pla. americana* Thein & Nitecki, 1974 has 12 spiral cords above the selenizone, but is otherwise very similar to *Pla. hespera*.

Pleurotomaria broadheadi White, 1880 was placed in *Platyzona* by Knight (1945) and later assigned to *Shansiella* by Hoare (1961). The specimen assigned to *Sh. broadheadi* by Hoare can be confidently placed in *Platyzona* and might be considered as conspecific with *Pla. hespera* as proposed by Kues & Batten (2001). *Pleurotomaria broadheadi* is a large species (88 mm) with strongly convex whorls and its selenizone is not clearly known. Therefore, its generic affinity is unclear.

DISCUSSION

Predation

The well-preserved specimens studied herein show commonly healed shell fractures; good preservation is a pre-

requisite to recognize such shell repairs. Vermeij *et al.* (1981) used gastropod material from the Finis Shale Member and other Pennsylvanian Shale units from the USA for an analysis of shell repair frequency through time. Schindel *et al.* (1982) also analysed shell breakage frequencies (SBF) in abundant gastropod species from these shale units, among them five species belonging to Pleurotomariida: *Trepospira sphaerulata*, *Phymatopleura brazoensis*, *Glabrocingulum grayvillense*, *Glyptotomaria scitula*, *Worthenia tabulata* and *Ananias welleri*; all of these species except *Gly. scitula* are also treated herein. Schindel *et al.* (1982) reported that these pleurotomariid species had the highest SBF among gastropods (0.36, range 0.01–0.79) and that frequencies also depend on shell size. Differences in SBF have been found between pleurotomariid taxa from the Pennsylvanian Shale units from the USA (Schindel *et al.* 1982; Lindström 2003). Previous studies included only specimens >5 mm. We also studied abundant smaller specimens and present information on predation on these juvenile shells.

Some of the studied juvenile *Glabrocingulum* (*Glabrocingulum*) and *Glabrocingulum* (*Ananias*) specimens show repaired scars at a shell width of 1 mm (Figs 11E–H; 15A–B). This suggests that *Glabrocingulum* individuals were exposed to durophagous predation in very early stages of their life after benthic larval settlement (metamorphosis). The same is true for small *Trepospira* specimens (width *c.* 1 mm) that show repaired scars, indicating durophagous predation on juveniles after the benthic larval settlement. Previously, Schindel *et al.* (1982) found that *Trepospira* shows lower SBF compared to other genera such as *Glabrocingulum* and they concluded that *Trepospira* was less resistant to durophagous predation due to having a relatively lower spire height. Unlike most other pleurotomariid genera with reported SBF, *Trepospira* develops an infilling (callus) in its umbilicus. Most of the crushed *Trepospira* cf. *illinoiensis* shells have an uncrushed columella. The callus strengthens the columella and can be regarded as an antipredatory trait of this low-spired genus.

Small *Phymatopleura* specimens also were exposed to durophagous predation in very early stages of their life, after benthic larval settlement (Fig. 25). *Phymatopleura* differs from *Trepospira* and *Glabrocingulum* juveniles in having a larger initial whorl (*c.* 0.30 vs *c.* 0.15 mm) and in having prominent spiral cords on the earliest teleoconch. Spiral cords are regarded to strengthen the shell of planktotrophic gastropod larvae (Hickman 2001; Seuss *et al.* 2012; Nützel 2014*a*). The repaired fractures are observed in benthic post-larval shells in *Phymatopleura* and the same function of spiral cords can be assumed for these juvenile shells. Similar spiral cords are also present in some species of *Glabrocingulum* such as the specimens placed in *Glabrocingulum* (*Ananias*) cf. *talpaensis* in this study and *Glabrocingulum* (*Glabrocingulum*) *armstrongi* reported by Peel (2016, fig. 9Q).

Presence of repaired shell scars on the early whorls (preserved only in juvenile shells) show that these animals were predated throughout their life after metamorphosis. Durophagous predation on Carboniferous gastropods could be more important as a selective agent than previously assumed. This selective agent was acting both on juvenile (Figs 11E–H, 15A–B, 25) and adult members of species (Figs 6G–H, 10A, 23G–H, 27I, K, 34J–K, 38B, 41C–D). Therefore, antipredatory adaptations are expected to appear both on early and late ontogenetic shells. It is plausible to assume that different durophagous animals were hunting at different size ranges and hence the predation pressure differed in different size ranges.

Durophagous predation (chipping and breaking) on living planktotrophic gastropod larvae has been well documented (Hickman 2001). However, durophagous predation in the benthic post-larval stage of living gastropods at such small size (*c.* 1 mm) has not been documented yet. It is assumed that the nonplanktonic lecithotrophic larva is the ancestral larva type in gastropods from which planktonic larva was derived (Chaffee & Lindberg 1986). Occupation of the water column by planktonic larvae is thought to have occurred as a result of intense benthic predation in the early Palaeozoic (Signor & Vermeij 1994). Although our results represent the case well after the origin of planktonic or planktotrophic larvae in gastropods (Nützel *et al.* 2006; Parkhaev 2014), the discovery of repaired shell scars is direct evidence of predation within the size range of a gastropod larva (0.08–1 mm) in the Carboniferous marine benthos.

The diversity and relative abundance of Pleurotomariida in the Finis Shale Member

As outlined above, the order Pleurotomariida was one of the most diverse gastropod clades in the Carboniferous and the group had its highest generic diversity in the Carboniferous within its entire evolutionary history (e.g. Hickman 1984; Erwin 1990). Apart from this high standing diversity, quantitative data considering the relative abundance of Pleurotomariida in Carboniferous gastropod assemblages are rare (e.g. Batten 1995; Kues & Batten 2001). Considering the modifications in the classification made after the current study, Pleurotomariida constituted 31% of the gastropod species and 27% of the gastropod specimens in the Pennsylvanian Magdalena Formation from Texas (Batten 1995) and 18% of the gastropod species and 23% of the gastropod specimens from the Pennsylvanian Flechado Formation from New Mexico (Kues & Batten 2001).

In the surface samples gathered from the Colony Creek Shale at locality TXV–46, Pleurotomariida constitute 41% of the gastropod species (17 species) and 56% of the

gastropod specimens (545 specimens) (Fig. 49). In the surface samples gathered from the Finis Shale Member at locality TXV–200, Pleurotomariida constitute 41% of the gastropod species (17 species) and 59% of the gastropod specimens (192 specimens) (Fig. 50). This suggests that Pleurotomariida constituted the largest portion in the size fraction >5 mm at these localities. The high diversity and abundance in such late Palaeozoic shallow water assemblages is clearly anactualistic; it has not been observed in post-Triassic assemblages.

For the fauna from the Finis Shale Member, the surface sampling method neglects the small specimens (both, juveniles of larger growing species and small species), which can be only obtained by bulk sampling. Therefore, any conclusion drawn from only surface samples is biased. The relative abundance of Pleurotomariida is indeed exaggerated in the surface samples because almost all pleurotomariid species found in the Finis Shale Member (apart from *Shansiella* (*Sh.*) *beckwithana*) reach an adult size larger than 5 mm. In contrast, some species of other gastropod groups from the Finis Shale reach an adult size smaller than 5 mm (e.g. *Donaldina*, *Girtyspira*, and several Pseudozygopleuridae). In the size fraction >0.5 mm, Pleurotomariida constitute 39% of the total gastropod specimens (4141 specimens) and 26% of the total gastropod species (23 species) in a bulk sample from Finis Shale Member at locality TXV–200 (Fig. 51), in which 99.6% of the specimens are <5 mm. Thus, Pleurotomariida have a lower relative abundance in the fraction 0.5–5 mm than in the fraction >5 mm obtained by sieving at 5 mm mesh size or by surface collection in the field.

Species with a short life span (often small-bodied) or juveniles of the same species are expected to be more abundant in an assemblage than large-bodied, long-lived species or adult specimens of the same species (Kidwell 2001; Vermeij & Herbert 2004; also see Kidwell & Rothfus 2010). However, the size of species does not necessarily correlate with species longevity (e.g. Powell & Cummins 1985, table 1). The relative abundances of species in the various size fractions of a sample depend on their size frequency distribution and also their juvenile mortality. The decrease in relative abundance of Pleurotomariida in smaller size fractions of the Finis Shale Member is largely due to the small size of several non-pleurotomariid species, some of which are highly abundant (e.g. *Girtyspira minuta*). Apart from the decrease in the relative abundance of Pleurotomariida in comparison with other

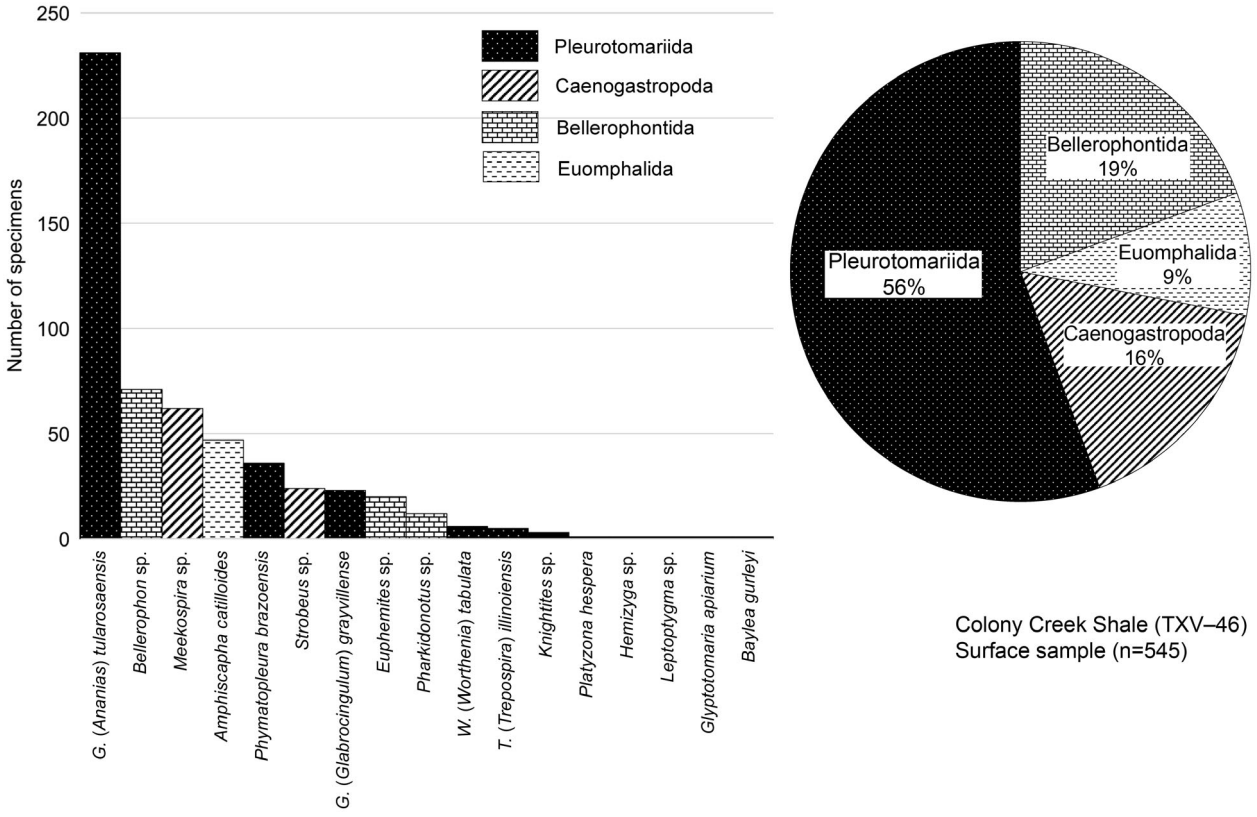

FIG. 49. Relative abundances of gastropods from the surface sample taken from the Colony Creek Shale (Virgilian, Texas) at locality TXV–46. Histogram shows species abundance distributions. Pie chart shows the relative abundances of the major gastropod groups.

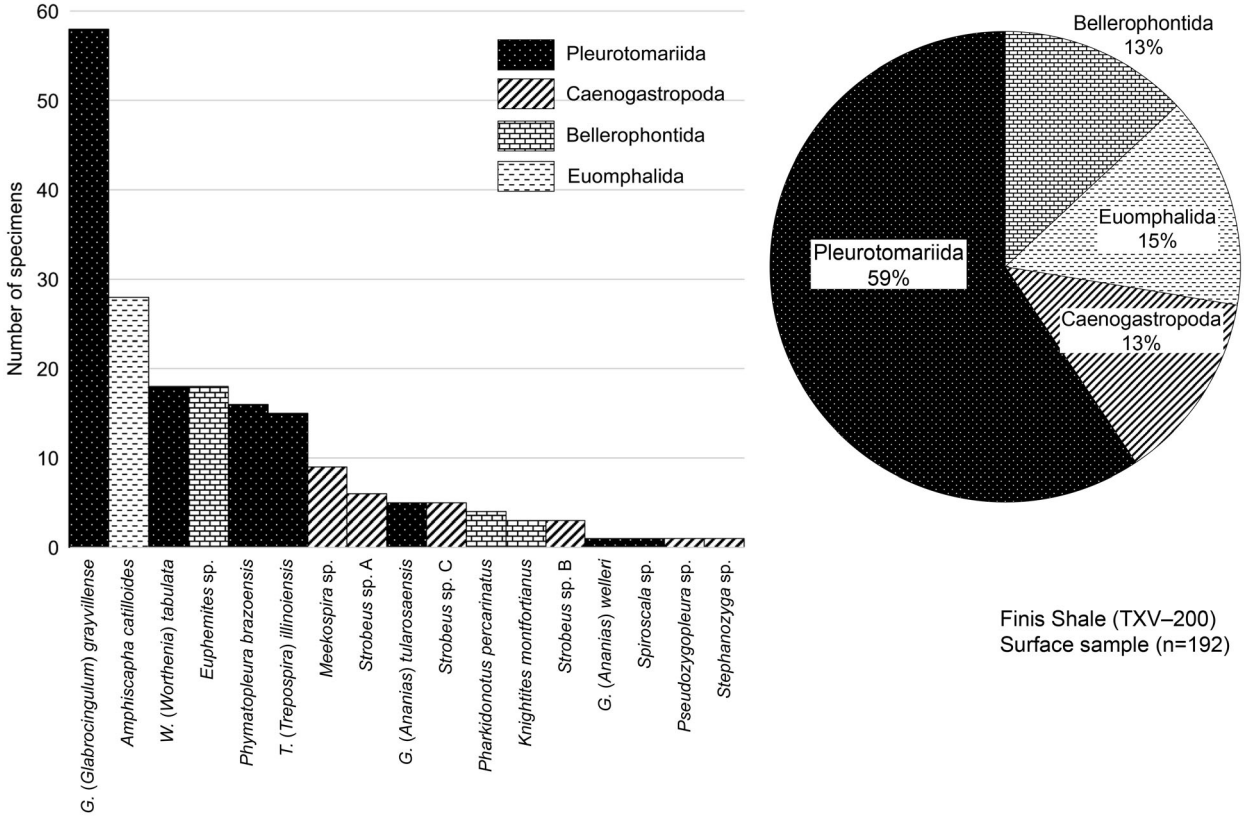

FIG. 50. Relative abundances of gastropods from the surface sample taken from the Finis Shale Member (Virgilian, Texas) at locality TXV–200. Histogram shows species abundance distributions. Pie chart shows the relative abundances of the major gastropod groups.

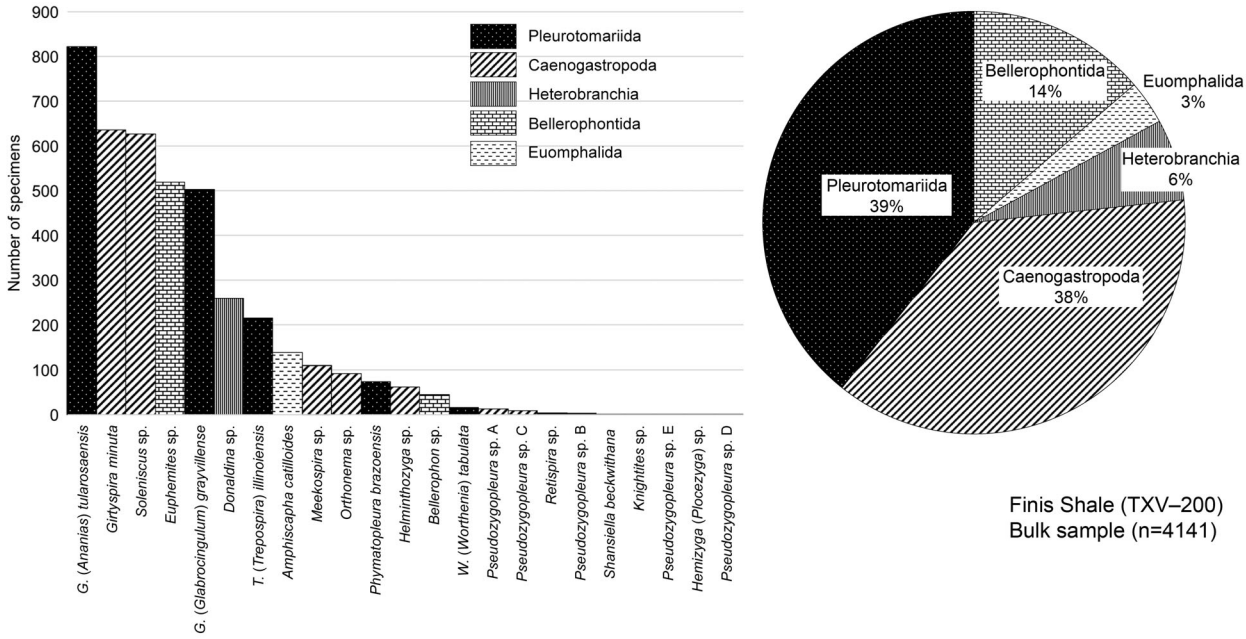

FIG. 51. Relative abundances of gastropods >0.5 mm from the bulk sample taken from the Finis Shale Member (Virgilian, Texas) at locality TXV–200. Histogram shows species abundance distributions. Pie chart shows the relative abundances of the major gastropod groups.

gastropod groups, there is a change in the relative abundances and rank abundance among five pleurotomariid species in different size fractions between 0.5 and 5 mm (Table 1). For instance, *Glabrocingulum* (*Ananias*) is rare (rank 5) in the surface sample but abundant (rank 1) in the size fraction <2 mm of the bulk sample. This suggests a high production of offspring but also a high juvenile mortality in this taxon. Generally, such changes in abundance between size classes can be explained by the different survival/mortality rates among the pleurotomariid taxa, which reach an adult size larger than 5 mm.

Forcino & Stafford (2020) compared the diversity between surface samples and bulk samples from the Finis Shale Member. They found a significantly higher richness in the surface samples and considerable variation in relative abundances of various taxa. Their study was based on the fraction >2 mm and hence most juvenile and microgastropod species were not included. In general, they found a pronounced brachiopod dominance in their samples, but we observed that this changes when the fraction 0.5–2 mm is also considered because abundant microgastropods are present in this fraction.

The human eye can hardly detect fossil specimens smaller than 2–3 mm in the field during surface collection. Smaller specimens can be picked from washed residues with the aid of a microscope. Therefore, the relative abundance or diversity of an assemblage are biased towards larger species in surface samples and they are biased towards smaller species and juveniles of larger species in bulk samples. The discrepancy reported by Forcino & Stafford (2020) thus basically reflects a mesh size effect (see also Kidwell 2002; Hausmann *et al.* 2018 and references therein). Forcino & Stafford (2020) used a mesh size of 2 mm when analysing their bulk samples. We analysed the bulk samples from the Finis Shale Member at mesh-sizes >0.5 mm, >1 mm, >2 mm, >4 mm at TXV–200 and TXV–56 and found considerable changes in the relative abundances of five common pleurotomariid species from the smaller size fractions to larger size fractions (e.g. from 0.5–2 mm to 2–4 mm) within the same bulk sample (Table 1).

If rank and relative abundances also change due to differential reproductive and survival rates, then the discrepancy in the abundance between bulk and surface samples cannot be explained solely by a methodological bias but is also constrained by life history traits and ecological interactions. Relative abundance variations in different fractions of bulk samples must also be influenced by the size frequency distributions of the species.

The question of which mesh size should be used to infer diversity and composition of the underlying living communities is disputable. Kidwell (2001) reported that the rank abundance of species in live–dead assemblages are significantly correlated when calculated with samples containing more than 100 specimens which are larger than 1 mm. Hausmann *et al.* (2018) reported that the species richness is much higher in the sieve size fraction >1 mm than >2 mm in Recent mollusc assemblages from the Gulf of Aqaba. This is also true for some Miocene mollusc assemblages (Kowalewski & Hoffmeister 2003, fig. 2). In the Finis Shale, most Pleurotomariida and slit-bearing caenogastropod species would be recovered using a mesh size of 2 mm (as suggested by Kidwell 2002). However, *Peruvispira* sp. would not be found since the largest *Peruvispira* sp. specimen is 1 mm in height. When it comes to Caenogastropoda and Heterobranchia, this picture would change. Many species of these groups are small and would be lost using a 2 mm mesh size. Thus, within Gastropoda, this mesh size would change the clade proportions within the sample dramatically. Therefore, as recommended by Forcino & Stafford (2020), both surface and bulk samples should be collected and analysed.

TABLE 1. The relative abundance of five pleurotomariid genera from the Finis Shale Member (Virgillian) at two localities in Texas.

	Trepospira	*G.* (*Glabrocingulum*)	*G.* (*Ananias*)	*Phymatopleura*	*Worthenia*
Finis Shale Member (TXV–200)					
Surface sample	16	56	6	15	18
Bulk sample (>4 mm)	6	7	3	3	3
Bulk sample (2–4 mm)	18	27	42	9	4
Bulk sample (1–2 mm)	116	120	199	35	5
Bulk sample (0.5–1 mm)	75	927		27	4
Finis Shale Member (TXV–56)					
Surface	36	167	8	20	67
Bulk sample (>4 mm)	3	3	7	4	2
Bulk sample (2–4 mm)	0	4	19	3	0
Bulk sample (1–2 mm)	72	34	20	2	1
Bulk sample (0.5–1 mm)	109	1316		23	9

Note: the differences in relative abundances between surface and bulk samples, and between different size fractions.

Abundance data need to be evaluated together with size and life history traits such as life span, reproductive rate and mortality. Although life history traits are difficult to infer from fossil specimens, body size can be reliably estimated from the shell size of molluscs. The body size of recent organisms is correlated with the basal metabolic rate of the organism (Gillooly *et al.* 2001) and shell size has been used to estimate metabolic rate of fossil gastropods (e.g. Finnegan *et al.* 2011). Considering both, size and abundance, we conclude that the Pleurotomariida were ecologically dominant among the gastropods of the Finis Shale in terms of resource utilization.

The gastropod assemblages from the Finis Shale Member and the Buckhorn Asphalt Quarry show that there is a 'hidden diversity' within smaller size fractions which can be studied only by picking fossils from washed residues under a microscope. By far the majority of the gastropod specimens from the Buckhorn Asphalt Quarry were obtained by processing bulk samples in this and other studies because most gastropod species in this locality are smaller than 5 mm (Bandel *et al.* 2002; Seuss *et al.* 2009). The Buckhorn Asphalt Quarry and the Finis Shale Member are categorized as Impregnation Lagerstätte and Liberation Lagerstätte respectively (Seuss *et al.* 2009; Roden *et al.* 2020) because it is relatively easy to extract small specimens from these deposits and they yield exceptionally well-preserved specimens. However, it is usually much more difficult to obtain small, well-preserved specimens from hard rocks such as limestones (lithification bias) unless the fossil material is not replaced by silica (e.g. Ketwetsuriya *et al.* 2020*b*). Alternatively, small specimens can be picked from washed residues of bulk samples taken from weathered out limestone (e.g. Nützel & Nakazawa 2012; Ketwetsuriya *et al.* 2020*a*). The 'hidden diversity' in smaller size fractions within the Finis Shale Member and Buckhorn Asphalt Quarry raises a question of whether the observed global diversity of the late Palaeozoic gastropods is biased by sampling methods ('mesh size effect') and reflects only the medium to large sized (>5 mm) gastropod diversity. If small gastropod species from the late Palaeozoic have been neglected either due to sampling method or preservational biases (e.g. lithification bias) then the known diversity of all gastropod groups including Pleurotomariida should be considered as the diversity of the medium to large sized gastropod species rather than the diversity of the late Palaeozoic Gastropoda as a whole.

CONCLUSION

Based on well-preserved specimens from Pennsylvanian aged shales on the North American Midcontinent, we discovered 35 Pleurotomariida species representing 17 genera/subgenera. In addition, we found three selenizone-bearing species belonging to the Caenogastropoda (Goniasmatidae). This diversity of Pleurotomariida in shallow marine soft bottom environments from a relatively short period of time (Morrowan–Virgillian, *c.* 15–20 myr, 320–300 Ma) and a single region is remarkably high and cannot be found in post-Triassic deposits. Previously published data and the present study of the Finis Shale show that Pleurotomariida are dominant both in terms of species diversity and rank abundance within gastropod assemblages of late Palaeozoic age. Pleurotomariida were still one of the dominant groups in several Triassic assemblages (Nützel *et al.* 2018, fig. 25) but seemingly the end-Triassic mass extinction event diminished the group at all hierarchical levels (Karapunar & Nützel 2021). For instance, they are only minor constituents in epi-continental dark shales of Europe that are comparable in facies to the Pennsylvanian aged shales of the North American Midcontinent (e.g. Kaim 2004, 2012; Schulbert & Nützel 2013; Nützel & Gründel 2015). Pleurotomariida contributed to shallow marine biota until the Late Cretaceous. For instance, Kiel & Bandel (2004) reported 6 pleurotomariidan species out of a total of 42 from the Cenomanian rocky shore deposits of the Kassenberg Quarry in Germany. After the end-Cretaceous mass extinction event, Pleurotomariida no longer played any role in shallow marine biota.

The good preservation of the studied gastropod material facilitated a taxonomic update for the involved species including type species of four pleurotomariidan genera. Special emphasis was put on the early ontogenetic shell. Most species have low-spired, almost planispiral initial whorls including a vetigastropod type protoconch matching the trochoid condition. However, distinctly immersed protoconchs as have been reported for some Triassic genera such as *Wortheniella* Schwardt, 1992 and *Schizogonium* Koken, 1889 were not found among the studied specimens (only *Baylea* sometimes has a slightly immersed initial whorl). In many of the studied species, the earliest teleoconch whorls are smooth whereas others have spiral cords or threads starting immediately after the protoconch. In the studied species, the onset of the selenizone is relatively late, commonly after the second or third whorl. By contrast, in Jurassic species of the family Pleurotomariidae the selenizone starts almost immediately after the protoconch together with a reticulated ornament (Kaim 2004; Nützel & Gründel 2015) and the same is true for living members of Pleurotomariidae (Harasewych 2002, fig. 3; Kaim 2004, fig. 136C). The taxonomic and phylogenetic implications of these differences in early shell ontogeny still need to be explored. Although not assessed quantitatively, we regularly found healed shell fractures in early juvenile specimens (at a shell width of 1 mm) of some of the taxa. This suggests a considerable predation pressure on early juveniles which may also have

caused a high mortality in some of the taxa. The diversity and rank abundances differ between samples collected at the same locality, depending on the sampling method (i.e. surface and bulk sampling). This discrepancy basically reflects a mesh size effect and caused primarily by species size ranges and secondarily by life history traits (reproductive rate and survival rate).

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/8BEDE5A1-F6C2-4CB6-9075-407C488B272A

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REFERENCES

AKTIPIS, S. W. and GIRIBET, G. 2012. Testing relationships among the vetigastropod taxa: a molecular approach. *Journal of Molluscan Studies*, **78**, 12–27.

AMLER, M. R. W. 1987. Fauna, paläogeographie und alter der Kohlenkalk-Vorkommen im Kulm des östlichen Rheinischen Schiefergebirges (Dinantium). *Geologische Abhandlungen Hessen*, **88**, 1–339.

AMLER, M. R. W. 2006. Gastropoden und Bellerophontiden. *Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften*, **41**, 106–120.

AMLER, M. R. W. and HEIDELBERGER, D. 2003. Late Famennian Gastropoda from South-West England. *Palaeontology*, **46**, 1151–1211.

ARCHIAC, E. J. A. D' and VERNEUIL, E. P. DE 1842. On the fossils of the older deposits in the Rhenish Provinces, preceded by a general survey of the fauna of the Palaeozoic rocks, and followed by a tabular list of the organic remains of the Devonian system in Europe. *Transactions of the Geological Society of London, Series 2*, **6**, 303–410.

BANDEL, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies*, **7**, 1–198.

BANDEL, K. 1991. Schlitzbandschnecken mit perlmutteriger Schale aus den triassischen St. Cassian Schichten der Dolomiten. *Annalen des Naturhistorischen Museums Wien, Reihe A*, **92**, 1–53.

BANDEL, K. 2009. The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St. Cassian Formation with evaluation of the taxonomic value of the selenizone. *Berliner paläobiologische Abhandlungen*, **10**, 5–47.

BANDEL, K. and GELDMACHER, W. 1996. The structure of the shell of *Patella crenata* connected with suggestions to the classification and evolution of the Archaeogastropoda. *Freiberger Forschungshefte, C*, **464**, 1–71.

BANDEL, K., NÜTZEL, A. and YANCEY, T. E. 2002. Larval shells and shell microstructures of exceptionally well-preserved Late Carboniferous gastropods from the Buckhorn Asphalt deposit (Oklahoma, USA). *Senckenbergiana Lethaea*, **82**, 639–690.

BATTEN, R. L. 1956. Some new pleurotomarian gastropods from the Permian of West Texas. *Journal of the Washington Academy of Sciences*, **46**, 42–46.

BATTEN, R. L. 1958. Permian Gastropoda of the southwestern United States. 2. Pleurotomariacea: Portlockiellidae, Phymatopleuridae, and Eotomariidae. *Bulletin of the American Museum of Natural History*, **114**, 153–246.

BATTEN, R. L. 1966. The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. *Palaeontographical Society Monographs*, **509**, 1–52.

BATTEN, R. L. 1967. Thoughts on the genus *Ptychomphalina* Fischer 1887 and the family Eotomariidae Wenz, 1938. *Journal of Paleontology*, **41** (1), 262–264.

BATTEN, R. L. 1972*a*. The ultrastructure of five common Pennsylvanian pleurotomarian gastropod species of eastern United States. *American Museum Novitates*, **2501**, 1–34.

BATTEN, R. L. 1972*b*. Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History*, **147**, 1–44.

BATTEN, R. L. 1989. Permian Gastropoda of the southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiriidae, Gosseletinidae. *American Museum Novitates*, **2958**, 1–64.

BATTEN, R. L. 1995. Pennsylvanian (Morrowan) gastropods from the Magdalena Formation of the Hueco Mountains, Texas. *American Museum Novitates*, **3122**, 1–46.

BEEDE, J. W. 1907. Invertebrate paleontology of the Upper Permian red beds of Oklahoma and the panhandle of Texas. *Kansas University Science Bulletin*, **4**, 113–171.

BEUS, S. S. and LANE, N. G. 1969. Middle Pennsylvanian fossils from Indian Springs, Nevada. *Journal of Paleontology*, **43**, 986–1000.

BIELER, R. 2004. Sanitation with sponge and plunger: western Atlantic slit-wormsnails (Mollusca: Caenogastropoda: Siliquariidae). *Zoological Journal of the Linnean Society*, **140**, 307–333.

BLAKISTON, T. and PRYER, H. 1880. Catalogue of the birds of Japan. *Transactions of the Asiatic Society of Japan*, **8**, 172–242.

BLODGETT, R. B. and JOHNSON, J. G. 1992. Early Middle Devonian (Eifelian) Gastropods of Central Nevada. *Palaeontographica, Abteilung A*, **222**, 85–139.

BLODGETT, R. B., FRÝDA, J. and RACHEBOEUF, P. R. 1999. Upper Middle Devonian (Givetian) gastropods from the Kersadiou Formation, Brittany, France. *Journal of Paleontology*, **73**, 1081–1100.

BOARDMAN, D. R. and HECKEL, P. H. 1989. Glacial-eustatic sea-level curve for early Late Pennsylvanian sequence in north-central Texas and biostratigraphic correlation with curve for midcontinent North America. *Geology*, **17**, 802–805.

BOARDMAN, D. R., WORK, D. M., MAPES, R. H. and BARRICK, J. E. 1994. Biostratigraphy of Middle and Late Pennsylvanian (Desmoinesian–Virgilian) ammonoids. *Kansas Geological Survey Bulletin*, **232**, 1–121.

BOSE, K., DAS, S. S. and MONDAL, S. 2021. An updated generic classification of Cenozoic pleurotomariid gastropods, with new records from the Oligocene and early Miocene of India. *Journal of Paleontology*, **95**, 763–776.

BOSTON, W. 1988. The surficial geology, paleontology, and paleoecology of the Finis Shale (Pennsylvanian Lower Virgilian) in Jack County, Texas. Unpublished PhD thesis, Ohio University, 293 pp.

BOUCHET, P., FRÝDA, J., HAUSDORF, B., PONDER, W. F., VALDÉS, Á. and WARÉN, A. 2005. Working classification of the Gastropoda. 239–397. *In* BOUCHET, P. and ROCROI, J.-P. (eds) *Classification and nomenclator of gastropod families*. Malacologia, **47**.

BOUCHET, P., ROCROI, J.-P., HAUSDORF, B., KAIM, A., KANO, Y., NÜTZEL, A., PARKHAEV, P., SCHRÖDL, M. and STRONG, E. E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, **61**, 1–526.

CAMPBELL, K. S. W. 1961. Carboniferous fossils from the Kuttung rocks of New South Wales. *Palaeontology*, **4**, 428–474.

CAMPBELL, K. S. W. 1962. Marine fossils from the Carboniferous glacial rocks of New South Wales. *Journal of Paleontology*, **36**, 38–52.

CHAFFEE, C. and LINDBERG, D. R. 1986. Larval biology of Early Cambrian molluscs: the implications of small body size. *Bulletin of Marine Science*, **39**, 536–549.

CHRONIC, H. 1949. Invertebrate paleontology (excepting fusulinids and corals). 46–173. *In* NEWELL, N. D., CHRONIC, B. J. and ROBERTS, T. G. (eds) *Upper Paleozoic of Peru*. Columbia University Press, 241 pp.

CHRONIC, H. 1952. Molluscan fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. *Geological Society of America Bulletin*, **63**, 95–166.

CONRAD, T. A. 1835. Description of five new species of fossil shells in the collection presented by Mr. Edward Miller to the Geological Society. *Transactions of the Geological Society of Pennsylvania*, **1**, 267–270.

CONRAD, T. A. 1842. Observations on the Silurian and Devonian systems of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, **8**, 228–280.

COOK, A. G. and NÜTZEL, A. 2005. New Devonian gastropods from the Broken River and their palaeoecology. *Memoirs of the Queensland Museum*, **51**, 391–397.

COOK, A. G., BLODGETT, R. B. and BECKER, T. 2003. Late Devonian gastropods from the Canning Basin, Western Australia. *Alcheringa*, **27**, 181–207.

COSSMANN, M. 1901. Paléoconchologie. *Revue Critique de Paléozoologie*, **5**, 132–160.

COX, E. T. 1857. A description of some of the most characteristic shells of the principal coal seams in the western basin of Kentucky. *Geological Survey of Kentucky Report*, **3**, 557–576.

COX, L. R. 1960*a*. Gastropoda, general characteristics of Gastropoda. I84–I169. *In* MOORE, R. C. (ed.) *Treatise on invertebrate paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press, 351 pp.

COX, L. R. 1960*b*. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London*, **33**, 239–261.

COX, L. R. and KNIGHT, J. B. 1960. Suborders of Archaeogastropoda. *Proceedings of the Malacological Society of London*, **33**, 262–264.

CUMINGS, E. R. 1906. Gasteropoda, Cephalopoda and Trilobita from the Salem limestone. *Indiana Department of Geology & Natural Resources Annual Reports,* **30**, 1335–1375.

CUNH A, T. J., DAVIS REIMER, J. and GIRIBET, G. 2021. Investigating sources of conflict in deep phylogenomics of vetigastropod snails. *Systematic Biology*, syab071.

DESHAYES, G.-P. 1824–1837. *Description des coquilles fossiles des environs de Paris. Tome 2*. Deshayes, Béchet, Baudouin, Treuttel & Wurtz, Paris. 1–80 (1824), 81–162 (1825), 163–290 (1832), 291–429 (1833), 430–494 (1834), 495–780 (1835), 781–814 (1837).

DICKINS, J. M. 1963. Permian pelecypods and gastropods from Western Australia. *Bureau of Mineral Resources, Geology & Geophysics Bulletin*, **63**, 1–203.

DIENER, C. 1926. 242. *Fossilium catalogus, I Animalia, 34, Glossophora triadica*. W. Junk, Berlin.

ELDREDGE, N. 1968. Convergence between two Pennsylvanian gastropod species: a multivariate mathematical approach. *Journal of Paleontology*, **42**, 186–196.

ERWIN, D. H. 1990. Carboniferous-Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. *Paleobiology*, **16**, 187–203.

ERWIN, D. H. 1993. *The great Paleozoic crisis: Life and death in the Permian*. Columbia University Press, 327 pp.

ERWIN, D. H. and SIGNOR, P. W. 1990. Extinction in an extinction-resistant clade: the evolutionary history of the Gastropoda. 152–160. *In* DUDLEY, E. C. (ed.) *The unity of evolutionary biology*. Proceedings of the Fourth International Congress of Systematics & Evolutionary Biology.

FINNEGAN, S., McCLAIN, C. M., KOSNIK, M. A. and PAYNE, J. L. 2011. Escargots through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution. *Paleobiology*, **37**, 252–269.

FISCHER, P. 1880–1887. *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mol-luscques vivants et fossiles*. F. Savy, Paris, 1569 pp.

FLETCHER, H. O. 1958. The Permian gastropods of New South Wales. *Records of the Australian Museum*, **24**, 115–164.

FOERSTE, A. F. 1914. Notes on the Lorraine faunas of New York and the Province of Quebec. *Bulletin of the Scientific Laboratories of Denison University*, **17**, 247–328.

FORCINO, F. L. and STAFFORD, E. S. 2020. The influence of collection method on paleoecological datasets: in-place versus surface-collected fossil samples in the Pennsylvanian Finis Shale, Texas, USA. *PLoS One*, **15**, e0228944.

FORCINO, F. L., STAFFORD, E. S., WARNER, J. J., WEBB, A. E., LEIGHTON, L. R., SCHNEIDER, C. L., MICHLIN, T. S., PALAZZOLO, L. M., MORROW, J. R. and SCHELLENBERG, S. A. 2010. Effects of data categorization in paleocommunity analysis: a case study from the Pennsylvanian Finis Shale of Texas. *Palaios*, **25**, 144–157.

FOSTER, W. J., DANISE, S. and TWITCHETT, R. J. 2017. A silicified Early Triassic marine assemblage from Svalbard. *Journal of Systematic Palaeontology*, **15**, 851–877.

FRÝDA, J. 1998. Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia). *Bulletin of the Czech Geological Survey*, **73**, 41–49.

FRÝDA, J. 2012. Phylogeny of Palaeozoic gastropods inferred from their ontogeny. 395–435. *In* TALENT, J. A. (ed.) *Earth and life: Global biodiversity, extinction intervals and biogeographic perturbations through time*. International Year of Planet Earth, Springer.

FRÝDA, J. and BLODGETT, R. B. 2004. New Emsian (late Early Devonian) gastropods from Limestone Mountain, Medfra B-4 Quadrangle, West-Central Alaska (Farewell terrane), and their palaeobiogeographic affinities and evolutionary significance. *Journal of Paleontology*, **78**, 111–132.

FRÝDA, J. and MANDA, S. 1997. A gastropod faunule from the *Monograptus uniformis* graptolite biozone (Early Lochkovian, Early Devonian) in Bohemia. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **80**, 59–121.

FRÝDA, J. and ROHR, D. M. 2004. Gastropods. 184–195. *In* WEBBY, B. D. and DROSER, M. L. (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press.

FRÝDA, J., NÜTZEL, A. and WAGNER, P. J. 2008. Paleozoic Gastropoda. 239–270. *In* PONDER, W. F. and LINDBERG, D. R. (eds) *Phylogeny and evolution of the Mollusca*. University of California Press, 469 pp.

GEIGER, D. L. 2012. *Monograph of the little slit shells*. Santa Barbara Museum of Natural History, 1291 pp.

GEIGER, D. L. and THACKER, C. E. 2005. Molecular phylogeny of Vetigastropoda reveals non-monophyletic Scissurellidae, Trochoidea, and Fissurelloidea. *Molluscan Research*, **25**, 47–55.

GEIGER, D. L., NÜTZEL, A. and SASAKI, T. 2008. Vetigastropoda. 297–330. *In* PONDER, W. F. and LINDBERG, D. R. (eds) *Phylogeny and evolution of the Mollusca*. University of California Press, 469 pp.

GEINITZ, H. B. 1866. Carbonformation und Dyas in Nebraska. *Verhandlungen der Kaiserlichen Leopoldino-Carolinischen deutschen Akademie der Naturforscher (Nova Acta Leopoldina)*, **33**, 1–91.

GEMMELLARO, G. G. 1889. La Fauna dei calcari con *Fusulina* della valle del fiume Sosio nella Provincia di Palermo. *Giornale di Science Naturali ed Economiche*, **20**, 97–182.

GILLOOLY, J. F., BROWN, J. H., WEST, G. B., SAVAGE, V. M. and CHARNOV, E. L. 2001. Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.

GIRTY, G. H. 1908. *The Guadalupian fauna*. Government Printing Office, Washington.

GIRTY, G. H. 1911. New genera and species of Carboniferous fossils from the Fayetteville Shale of Arkansas. *Annals of the New York Academy of Sciences*, **20**, 189–238.

GIRTY, G. H. 1912. On some new genera and species of Pennsylvanian fossils from the Wewoka Formation of Oklahoma. *Annals of the New York Academy of Sciences*, **21**, 119–156.

GIRTY, G. H. 1915. Fauna of the Wewoka formation of Oklahoma. *US Geological Survey Bulletin*, **544**, 1–353.

GIRTY, G. H. 1929. New Carboniferous invertebrates—I. *Journal of the Washington Academy of Sciences*, **19**, 135–142.

GIRTY, G. H. 1934. New Carboniferous invertebrates—IV. *Journal of the Washington Academy of Sciences*, **24**, 249–266.

GIRTY, G. H. 1937. Three Upper Carboniferous gastropods from New Mexico and Texas. *Journal of Paleontology*, **11**, 202–211.

GIRTY, G. H. 1939. Certain pleurotomariid gastropods from the Carboniferous of New Mexico and Texas. *Journal of the Washington Academy of Sciences*, **29**, 21–36.

GORDON, M. J. and YOCHELSON, E. L. 1975. Gastropoda, Cephalopoda, and Trilobita of the Amsden Formation (Mississippian and Pennsylvanian) of Wyoming. *Geological Survey Professional Paper*, **848-F**, 1–30.

GORDON, M. J. and YOCHELSON, E. L. 1983. A gastropod fauna from the *Cravenoceras hesperium* ammonoid zone (Upper Mississippian) in East-central Nevada. *Journal of Paleontology*, **57**, 971–991.

GORDON, M. J. and YOCHELSON, E. L. 1987. Late Mississippian Gastropods of the Chainman Shale, West-Central Utah. *US Geological Survey Professional Paper*, **1368**, 1–112.

GRECO, B. 1937. La fauna permiana del Sosio conservata nei musei di Pisa, di Firenze e di Padova; parte seconda, Gastropoda; Lamellibranchiata. *Palaeontographia Italica*, **37**, 57–114.

HALL, J. 1858. Description of new species of fossils from the Carboniferous Limestones of Indiana and Illinois. *Transactions of the Albany Institute*, **4**, 1–37.

HALL, J. 1883. Spergen Hill fossils. *Indiana Department of Geology & Natural History Annual Report*, **12**, 319–375.

HARASEWYCH, M. G. 2002. Pleurotomarioidean gastropods. *Advances in Marine Biology*, **42**, 237–294.

HARASEWYCH, M. G. and KIEL, S. 2007. Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagascar. *The Nautilus*, **121**, 76–89.

HARASEWYCH, M., ADAMKEWICZ, S. L., BLAKE, J. A., SAUDEK, D., SPRIGGS, T. and BULT, C. J. 1997. Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome c oxidase I sequences. *Molecular Marine Biology & Biotechnology*, **6**, 1–20.

HASZPRUNAR, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies*, **54**, 367–441.

HASZPRUNAR, G. 1993. The Archaeogastropoda. A clade, a grade or what else? *American Malacological Bulletin*, **10**, 165–177.

HAUSMANN, I. M., DOMANSKI, H. and ZUSCHIN, M. 2018. Influence of setting, sieve size, and sediment depth on multivariate and univariate assemblage attributes of coral reef-associated mollusc death assemblages from the Gulf of Aqaba. *Facies*, **64** (3), 20.

HEIDELBERGER, D. 2001. Mitteldevonische (givetische) Gastropoden (Mollusca) aus der Lahnmulde (südliches Rheinisches Schiefergebirge). *Geologische Abhandlungen Hessen*, **106**, 1–291.

HICKMAN, C. S. 1984. *Pleurotomaria*: pedigreed perseverance? 225–231. *In* ELDREDGE, N. and STANLEY, S. M. (eds) *Living fossils*. Springer.

HICKMAN, C. S. 1998. Superfamily: Pleurotomarioidea. 664–666. *In* BEESLEY, P. I., ROSS, G. J. B. and WELLS, A. (eds) *Mollusca: the southern synthesis. Vol. 5*. Fauna of Australia. Melbourne.

HICKMAN, C. S. 2001. Evolution and development of gastropod larval shell morphology: experimental evidence for mechanical defense and repair. *Evolution & Development*, **3**, 18–23.

HOARE, R. D. 1961. Desmoinesian Brachiopoda and Mollusca from Southwest Missouri. *University of Missouri Studies*, **26**, 1–263.

HOARE, R. D. and MAPES, R. H. 1985. New Mississippian and Pennsylvanian Polyplacophora (Mollusca) from North America. *Journal of Paleontology*, **59**, 875–881.

HOARE, R. D. and MILLER, B. B. 1996. Phylum Mollusca, Class Gastropoda. 151–165. *In* FELDMANN, R. M., ANSTEY, R. L. and HACKATHORN, M. (eds) *Fossils of Ohio*. Geological Survey of Ohio Bulletin, **70**.

HOARE, R. D., STURGEON, M. T. and ANDERSON, J. R. J. 1997. Pennsylvanian marine gastropods from the Appalachian Basin. *Journal of Paleontology*, **71**, 1019–1039.

HORNÝ, R. 1997. Ordovician Tergomya and Gastropoda (Mollusca) of the Anti-Atlas (Morocco). *Acta Musei Nationalis Pragae, Series B, Historia Naturalis*, **53**, 37–78.

HYDE, J. E. 1953. The Mississippian formations of central and southern Ohio. *Ohio Geological Survey Bulletin*, **51**, 1–355.

ISAJI, S. and OKURA, M. 2020. Microgastropods from the late Carboniferous limestone in Fukuji, Gifu Prefecture, central Japan. *Paleontological Research*, **24**, 192–202.

JABLONSKI, D., SEPKOSKI, J. J., BOTTJER, D. J. and SHEEHAN, P. M. 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. *Science*, **222**, 1123–1125.

JEFFERY, D. L., HOARE, R. D., MAPES, R. H. and BROWN, C. J. 1994. Gastropods (Mollusca) from the Imo Formation (Mississippian, Chesterian) of North-Central Arkansas. *Journal of Paleontology*, **68**, 58–79.

JUKES-BROWNE, A. J. 1912. *The student's handbook of stratigraphical geology*. E. Stanford, London, 668 pp.

KAIM, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaeontologia Polonica*, **62**, 1–182.

KAIM, A. 2012. Faunal dynamics of gastropods in the Bathonian (Middle Jurassic) ore-bearing clays at Gnaszyn, Kraków-Silesia Homocline, Poland. *Acta Geologica Polonica*, **62**, 367–380.

KAIM, A., NÜTZEL, A., BUCHER, H., BRÜHWILER, T. and GOUDEMAND, N. 2010. Early Triassic (Late Griesbachian) gastropods from South China (Shanggan, Guangxi). *Swiss Journal of Geosciences*, **103**, 121–128.

KARAPUNAR, B. and NÜTZEL, A. 2021. Slit-band gastropods (Pleurotomariida) from the Upper Triassic St. Cassian Formation and their diversity dynamics in the Triassic. *Zootaxa*, **5042**, 1–165.

KETWETSURIYA, C., KARAPUNAR, B., CHAROENTITIRAT, T. and NÜTZEL, A. 2020*a*. Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa*, **4766**, 1–47.

KETWETSURIYA, C., COOK, A. G. and NÜTZEL, A. 2020*b*. Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. *PalZ*, **94**, 53–77.

KIDWELL, S. M. 2001. Preservation of species abundance in marine death assemblages. *Science*, **294**, 1091–1094.

KIDWELL, S. M. 2002. Mesh-size effects on the ecological fidelity of death assemblages: a meta-analysis of molluscan live–dead studies. *Geobios*, **35**, 107–119.

KIDWELL, S. M. and ROTHFUS, T. A. 2010. The living, the dead, and the expected dead: variation in life span yields little bias of proportional abundances in bivalve death assemblages. *Paleobiology*, **36**, 615–640.

KIEL, S. and BANDEL, K. 2004. The Cenomanian Gastropoda of the Kassenberg quarry in Mühlheim (Germany, Late Cretaceous). *Paläontologische Zeitschrift*, **78**, 103–126.

KITTL, E. 1891. Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. I. Theil. *Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums*, **6**, 166–262.

KITTL, E. 1900. Trias-Gastropoden des Bakonyer Waldes. *Resultate der wissenschaftlichen Erforschung des Balatonsees*, **2**, 1–57.

KNIGHT, J. B. 1937. Genotype designations and new names for invalid homonyms among Paleozoic gastropod genera. *Journal of Paleontology*, **11**, 709–714.

KNIGHT, J. B. 1940. Gastropods of the Whitehorse sandstone. *Geological Society of America Bulletin*, **51**, 302–315.

KNIGHT, J. B. 1941. Palaeozoic gastropod genotypes. *Geological Society of America Special Papers*, **32**, 1–510.

KNIGHT, J. B. 1945. Some new genera of Paleozoic Gastropoda. *Journal of Paleontology*, **19**, 573–587.

KNIGHT, J. B. 1956. New families of Gastropoda. *Journal of the Washington Academy of Sciences*, **46**, 41–42.

KNIGHT, J. B., COX, L. R., KEEN, A. M., BATTEN, R. L., YOCHELSON, E. L. and ROBERTSON, R. 1960. Systematic descriptions. I169–I310. *In* MOORE, R. C. (ed.) *Treatise on invertebrate paleontology. Part I. Mollusca 1*. Geological Society of America & University of Kansas Press, 351 pp.

KOKEN, E. 1889. Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband*, **6**, 440–463.

KOKEN, E. 1896. Die Gastropoden der Trias um Hallstatt. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, **46**, 37–126.

KOKEN, E. 1897. Die Gastropoden der Trias um Hallstatt. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt*, **17**, 1–111.

KOKEN, E. and PERNER, J. 1925. Die Gastropoden des Baltischen Untersilurs. *Mémoires de L'Ácadémie des Sciences de Russie*, **37** (1), 1–186.

KOLATA, D. R., FREST, T. J. and MAPES, R. H. 1991. The youngest carpoid: occurrence, affinities, and life mode of a Pennsylvanian (Morrowan) mitrate from Oklahoma. *Journal of Paleontology*, **65**, 844–855.

KONINCK, L. G. DE 1842–1844. *Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique*. H. Dessain, Liege, 636 pp.

KONINCK, L. G. DE 1883. Faune du calcaire carbonifère de la Belgique. Quatrième partie, Gastéropodes (suite et fin). *Annales du Musée Royal d'Histoire naturelle de Belgique*, **8**, 1–240.

KOWALEWSKI, M. and HOFFMEISTER, A. P. 2003. Sieves and fossils: effects of mesh size on paleontological patterns. *Palaios*, **18**, 460–469.

KUES, B. S. 2004. Stratigraphy and brachiopod and molluscan paleontology of the Red Tanks Formation (Madera Group) near the Pennsylvanian-Permian boundary, Lucero uplift, west-central New Mexico. *New Mexico Museum of Natural History & Science Bulletin*, **25**, 143–210.

KUES, B. S. and BATTEN, R. L. 2001. Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico. *Journal of Paleontology*, **75**(suppl. 1), 1–95.

LÉVEILLÉ, C. 1835. Aperçu géologique de quelques localités très riches en coquilles sur les frontières de France et de Belgique. *Mémoires de la Société géologique de France*, **2**, 29–40.

LICHAREW, B. K. 1967. Scaphopods and gastropods—Archaeogastropoda (excluding the suborder Bellerophontina and suborder Neritopsina) from the Upper Paleozoic of southern Fergana. *Trudy Vsesouznogo Naucho-Issledovatelskogo Geologicheskogo, Instituta Biostratigraficheskiy sbornik, Novaya Seriya*, **116**, 1–115. [in Russian]

LINDSTRÖM, A. 2003. Shell breakage in two pleurotomarioid gastropods from the Upper Carboniferous of Texas, and its relation to shell morphology. *GFF*, **125**, 39–46.

LINDSTRÖM, A. and PEEL, J. S. 2005. Repaired injuries and shell form in some Palaeozoic pleurotomarioid gastropods. *Bulletin of Geosciences*, **85**, 541–550.

LINDSTRÖM, A. and PEEL, J. S. 2010. Shell repair and shell form in Jurassic pleurotomarioid gastropods from England. *Bulletin of Geosciences*, **85**, 541–550.

LINTZ, J. J. 1958. The fauna of the Ames and Brush Creek shales of the Conemaugh Formation of western Maryland. *Journal of Paleontology*, **32**, 97–112.

LONGSTAFF, J. 1912. Some new Lower Carboniferous Gasteropoda. *Quarterly Journal of the Geological Society*, **68**, 295–309.

MAPES, R. H. and MAPES, G. 1982. Removal of gypsum from microfossiliferous shales. *Micropaleontology*, **28**, 218–219.

MARK, C. G. 1912. The fossils of the Conemaugh Formation in Ohio. *Ohio Geological Survey Bulletin*, **17**, 261–318.

MAZAEV, A. V. 2006. Permian gastropods from Kulogory Formation of northern Moscow Syneclise. *Paleontological Journal*, **40**, 42–53.

MAZAEV, A. V. 2011. Pennsylvanian gastropods of the suborders Murchisoniina Cox et Knight, 1960 and Sinuspirina Mazaev subordo nov. from the central regions of the Russian Platform: morphology, taxonomy, and phylogeny. *Paleontological Journal*, **45**, 1533–1599.

MAZAEV, A. V. 2015. Upper Kazanian (Middle Permian) Gastropods of the Volga-Urals Region. *Paleontological Journal*, **49**, 869–986.

MAZAEV, A. V. 2016. Evolution of the Genus *Baylea* (Gastropoda) in the Kazan Paleobasin (Middle Permian, Volga-Ural Region). *Paleontological Journal*, **50**, 585–600.

MAZAEV, A. V. 2017. The role of fetalization in the morphogenesis of Kazanian gastropods (Middle Permian, Volga-Urals Region). *Paleontological Journal*, **51**, 357–367.

MAZAEV, A. V. 2019*a*. Lower Permian gastropods of Shakhtau (Asselian–Sakmarian boundary beds, southern Cisuralia). *Paleontological Journal*, **53**, 1237–1345.

MAZAEV, A. V. 2019*b*. Morphology and systematics of the late Paleozoic Gastropods *Deseretospira* Gordon and Yochelson and *Termihabena* gen. nov. *Paleontological Journal*, **53**, 455–464.

McCHESNEY, J. 1859. Descriptions of new species of fossils from the Palaeozoic rocks of the Western States. *Transactions of the Chicago Academy of Sciences*, [**Extract 1**], 1–76.

McCHESNEY, J. 1868. Descriptions of fossils from the Paleozoic rocks of the Western States. *Transactions of the Chicago Academy of Sciences*, **1**, 1–57.

McKINZIE, M. 2003. Lake Bridgeport Shale, sponge-echinoderm facies. 49–74. *In* McKINZIE, M. and McLEOD, J. (eds) *Pennsylvanian fossils of North Texas*. Occasional Papers of the Dallas Paleontological Society, Tampa.

MEEK, F. B. 1871. Descriptions of new species of fossils from Ohio and other western states and territories. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **23**, 159–184.

MEEK, F. B. 1875. A report on some of the invertebrate fossils of the Waverly Group and Coal Measures of Ohio. *Report of the Geological Survey of Ohio*, **2**, 269–347.

MEEK, F. B. and WORTHEN, A. H. 1861. Descriptions of new Carboniferous fossils from Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **12**, 447–472.

MEEK, F. B. and WORTHEN, A. H. 1866*a*. Contributions to the palaeontology of Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **18**, 251–275.

MEEK, F. B. and WORTHEN, A. H. 1866*b*. Descriptions of Invertebrates from the Carboniferous system. *Geological Survey of Illinois*, **2**, 145–411.

MEEK, F. B. and WORTHEN, A. H. 1873. Palaeontology. — Descriptions of invertebrates from Carboniferous System. *Illinois Geological Survey*, **5**, 223–619.

MILLER, S. A. 1877. *The American Palaeozoic fossils: A catalogue of the genera and species, with names of authors, dates, places of publication, groups of rocks in which found, and the etymology and signification of the words, and an introduction devoted to the stratigraphical geology of the Palaeozoic rocks*. The author, Cincinnati, Ohio, 334 pp.

MILLER, S. A. 1889. *North American geology and palaeontology for the use of amateurs, students, and scientists*. Western Methodist Book Concern, 664 pp.

MORGAN, G. D. 1924. Geology of the Stonewall Quadrangle, Oklahoma. *Oklahoma Bureau of Geology Bulletin*, **2**, 1–248.

MÜNSTER, G. Z. 1841. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. 25–152. *In* WISSMANN, H. L., MÜNSTER, G. Z. and BRAUN, K. F. (eds) *Beiträge zur Geologie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian*, Buchner, Bayreuth, 152 pp.

NELSON, L. A. 1947. Two new genera of Paleozoic Gastropoda. *Journal of Paleontology*, **21**, 460–465.

NETCHAEV, A. V. 1894. Fauna from the Permian beds of the eastern band of European Russia. *Trudy Obshchestva Estestvoispytatelei pri Imperatorskom Kazanskom Universitete*, **27**, 1–503. [in Russian]

NEWELL, N. D. 1935. Some Mid-Pennsylvanian invertebrates from Kansas and Oklahoma: II. Stromaporoidea, Anthozoa, and Gastropoda. *Journal of Paleontology*, **9**, 341–355.

NORWOOD, J. G. and PRATTEN, H. 1855. Notice of fossils from the Carboniferous Series of the Western States, belonging to the Genera *Spirifer*, *Bellerophon*, *Pleurotomaria*, *Macrocheilus*, *Natica* and *Loxonema*: with descriptions of eight new characteristics species. *Journal of the Academy of Natural Sciences of Philadelphia, Series 2*, **3**, 71–79.

NÜTZEL, A. 2014*a*. Larval ecology and morphology in fossil gastropods. *Palaeontology*, **57**, 479–503.

NÜTZEL, A. 2014*b*. Die Evolution der Gastropoden an der Perm/Trias-Grenze. *Freunde der Bayerischen Staatssammlung für Paläontologie und Historische Geologie München e.V. Jahresbericht 2013 und Mitteilungen*, **42**, 64–78.

NÜTZEL, A. and BANDEL, K. 2000. Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **9**, 557–569.

NÜTZEL, A. and ERWIN, D. H. 2004. Late Triassic (Late Norian) gastropods from the Wallowa Terrane (Idaho, USA). *Paläontologische Zeitschrift*, **78**, 361–416.

NÜTZEL, A. and GRÜNDEL, J. 2015. Early Jurassic (Pliensbachian) gastropods from Franconia, Southern Germany. *Palaeontographica, Abteilung A*, **305**, 1–89.

NÜTZEL, A. and NAKAZAWA, K. 2012. Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology*, **10**, 103–169.

NÜTZEL, A. and PAN, H.-Z. 2005. Late Paleozoic evolution of the Caenogastropoda: larval shell morphology and implications for the Permian/Triassic mass extinction event. *Journal of Paleontology*, **79**, 1175–1188.

NÜTZEL, A., PAN, H.-Z. and ERWIN, D. H. 2002. New taxa and some taxonomic changes of a latest Permian gastropod fauna from South China. *Documenta Naturae*, **145**, 1–10.

NÜTZEL, A., LEHNERT, O. and FRÝDA, J. Í. 2006. Origin of planktotrophy—evidence from early molluscs. *Evolution & Development*, **8**, 325–330.

NÜTZEL, A., KAIM, A. and GRĂDINARU, E. 2018. Middle Triassic (Anisian, Bithynian) gastropods from North Dobrogea (Romania) and their significance for gastropod recovery from the end-Permian mass extinction event. *Papers in Palaeontology*, **4**, 477–512.

OEHLERT, D.-P. 1888. Descriptions de quelques espèces dévoniennes du département de la Mayenne. *Bulletin de la Société d'Études Scientifiques d'Angers, Nouvelle Série*, **17**, 65–120. [1887]

ORBIGNY, A. C. d' 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques & rayonnés, faisant suite au Cours élémentaire de paléontologie et de géologie stratigraphiques, Tome I*. V. Masson, Paris, 394 pp.

PAN, H.-Z. 1997. Namurian (Lower Carboniferous) Gastropod Assemblages from Ninxia, China. *Journal of Paleontology*, **71**, 599–609.

PAN, H.-Z. and ERWIN, D. H. 2002. Gastropods from the Permian of Guangxi and Yunnan provinces, South China. *Journal of Paleontology*, **76** (S56), 1–49.

PARKHAEV, P. Y. 2014. Protoconch morphology and peculiarities of the early ontogeny of the Cambrian helcionelloid mollusks. *Paleontological Journal*, **48**, 369–379.

PEEL, J. S. 2016. Gastropods from the Carboniferous (Namurian) of Congleton Edge, Cheshire, UK. *Papers in Palaeontology*, **2**, 399–438.

PERNER, J. 1907. *Systême silurien du centre de la Bohême, par Joachim Barrande. 1ére partie: Recherches paléontologiques. Vol. 4. Gastéropodes*. Privately published, Prague, 380 pp.

PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire: or a description of the strata and organic remains; accompanied by a geological map, sections, and diagrams, and figures of the fossils. Part 2. The Mountain Limestone district*. John Murray, London, 253 pp.

PINILLA, M. 2012. The new species *Ananias riccardii* (Gastropoda, Eotomariidae) from the Cisuralian of Patagonia, Argentina. *Revue de Paléobiologie*, **11**, 357–364.

PLUMMER, F. B. and MOORE, R. C. 1922. Pennsylvanian stratigraphy of north central Texas. *The Journal of Geology*, **30**, 18–42.

PLUMMER, F. B. and SCOTT, G. 1937. The geology of Texas, Volume III, Part 1, Upper Paleozoic ammonites in Texas. *University of Texas (Austin) Bulletin*, **3701**, 13–411.

PONDER, W. F. and LINDBERG, D. R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society*, **119**, 83–265.

POWELL, E. N. and CUMMINS, H. 1985. Are molluscan maximum life spans determined by long-term cycles in benthic communities? *Oecologia*, **67**, 177–182.

QIAO, Z. 1983. Late Paleozoic gastropods from the Xinjiang Uygur Autonomous Region. 462–557. *In* REGIONAL GEOLOGICAL SURVEYING PARTY, BUREAU OF GEOLOGY AND MINERAL RESOURCES OF XINYIANG, INSTITUTE OF GEOLOGICAL SCIENCE, BUREAU OF GEOLOGY AND GEOLOGICAL SURVEY XINYIANG, BUREAU OF PETROLEUM, XINJIANG (eds) *Paleontological Atlas of Northwest China, Part II*. Geological Publishing House, Xinjiang. [in Chinese]

RODEN, V. J., HAUSMANN, I. M., NÜTZEL, A., SEUSS, B., REICH, M., URLICHS, M., HAGDORN,

H. and KIESSLING, W. 2020. Fossil liberation: a model to explain high biodiversity in the Triassic Cassian Formation. *Palaeontology*, **63**, 85–102.

ROLLINS, H. B. 1975. Gastropods from the Lower Mississippian Wassonville Limestone in Southeastern Iowa. *American Museum Novitates*, **2579**, 1–35.

ROLLINS, H. B., ELDREDGE, N. and SPILLER, J. 1971. Gastropoda and Monoplacophora of the Solsville member (Middle Devonian, Marcellus Formation) in the Chenango Valley, New York State. *Bulletin of the American Museum of Natural History*, **144**, 129–170.

SABATTINI, N. 1975. *Austroneilsonia* gen. nov. (Gastropoda) del Paleozoico superior de Argentina. *Ameghiniana*, **12**, 337–342.

SABATTINI, N. and NOIRAT, S. 1969. Algunos Gastropoda de las superfamilias Euomphalacea, Pleurotomariacea y Platyceratacea del Paleozoico superior de Argentina. *Ameghiniana*, **6**, 98–118.

SADLICK, W. and NIELSEN, M. F. 1963. Ontogenetic variation of some Middle Carboniferous Pleurotomarian Gastropods. *Journal of Paleontology*, **37**, 1083–1103.

SALVINI-PLAWEN, L. V. 1980. A reconsideration of systematics in the Mollusca. *Malacologia*, **19**, 249–278.

SASAKI, T. 1998. Comparative anatomy and phylogeny of the Recent Archaeogastropoda. *University Museum, The University of Tokyo Bulletin*, **38**, 1–223.

SAYRE, A. N. 1930. The fauna of the Drum Limestone of Kansas and western Missouri. *The University of Kansas Science Bulletin*, **19** (8), 75–203.

SCHINDEL, D. E. 1982. Punctuations in the Pennsylvanian evolutionary history of *Glabrocingulum* (Mollusca: Archaeogastropoda). *Geological Society of America Bulletin*, **93**, 400–408.

SCHINDEL, D. E., VERMEIJ, G. J. and ZISPER, E. 1982. Frequencies of repaired shell fractures among the Pennsylvanian gastropods of North-Central Texas. *Journal of Paleontology*, **56**, 729–740.

SCHULBERT, C. and NÜTZEL, A. 2013. Gastropods from the Early/Middle Jurassic transition of Franconia (Southern Germany). *Bulletin of Geosciences*, **88**, 723–778.

SCHWARDT, A. 1992. Revision der *Wortheniella*-Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten). *Annalen des Naturhistorischen Museums Wien, Serie A*, **94**, 23–57.

SEDGWICK, A. and MURCHISON, R. I. 1840. XLIII.—On the physical structure of Devonshire, and on the subdivisions and geological relations of its older stratified deposits, &c. *Transactions of the Geological Society of London*, **2**, 633–703.

SEUSS, B., NÜTZEL, A., MAPES, R. H. and YANCEY, T. E. 2009. Facies and fauna of the Pennsylvanian Buckhorn Asphalt Quarry deposit: a review and new data on an important Palaeozoic fossil Lagerstätte with aragonite preservation. *Facies*, **55**, 609.

SEUSS, B., NÜTZEL, A., SCHOLZ, H. and FRÝDA, J. 2012. The Paleozoic evolution of the gastropod larval shell: larval armor and tight coiling as a result of predation-driven heterochronic character displacement. *Evolution & Development*, **14**, 212–228.

SHIKAMA, T. and NISHIDA, T. 1968. 535. On some species of Carboniferous pleurotomariaceans from Akiyoshi: molluscan paleontology of the Akiyoshi Limestone Group-III. *Transactions & Proceedings of the Paleontological Society of Japan, new series*, **69**, 211–217.

SHUMARD, B. F. 1860. Descriptions of five new species of gasteropoda from the coal measures: and a brachiopod from the potsdam sandstone of Texas. *Transactions of the Academy of Science of St. Louis*, **1**, 624–627.

SIGNOR, P. W. and VERMEIJ, G. J. 1994. The plankton and the benthos: origins and early history of an evolving relationship. *Paleobiology*, **20**, 297–319.

SLOAN, R. E. 1955. The Carboniferous gastropod genus *Glabrocingulum* Thomas. *Fieldiana*, **10**, 275–281.

SMITH, A. G. and HOARE, R. D. 1987. Paleozoic polyplacophora: a checklist and bibliography. *Occasional Papers of the California Academy of Sciences*, **146**, 1–71.

SOWERBY, J. 1812–1821. *The mineral conchology of Great Britain*. B. Meredith, London. 4 vols: pp i–vii + 9–236, pl. 1–102 (1812–1814); pp 1–239, pl. 103–203 (1815–1818); pp. 1–186, pl. 204–306 (1818–1821); pp 1–104, pl. 307–327 (1821–1822).

STURGEON, M. T. 1964*a*. Allegheny fossil invertebrates from Eastern Ohio - Gastropoda. *Journal of Paleontology*, **38**, 189–226.

STURGEON, M. T. 1964*b*. New descriptions of hitherto inadequality known Pennsylvanian gastropods. *Journal of Paleontology*, **38** (4), 739–748.

SUN, X., QIU, X., TIHELKA, E., YANG, H., SUN, D., TONG, J. and TIAN, L. 2021. A diverse gastropod fauna from the shallow marine carbonate platform of the Yangou section (south China) in the immediate aftermath of the Permian–Triassic mass extinction. *Geological Journal*, **56**, 6199–6209.

SWAINSON, W. 1840. *A treatise on malacology; or the natural classification of shells and shell-fish*. Longman, London, 419 pp.

TABOADA, A. C., MORY, A. J., SHI, G.-R., HAIG, D. W. and PINILLA, M. K. 2015. An early permian brachiopod–gastropod fauna from the Calytrix Formation, Barbwire Terrace, Canning Basin, Western Australia. *Alcheringa*, **39**, 207–223.

TABOADA, A. C., PAGANI, M. A., PINILLA, M. K., TORTELLO, F. and TABOADA, C. A. 2019. Carboniferous deposits of northern Sierra de Tecka, central-western Patagonia, Argentina: paleontology, biostratigraphy and correlations. *Andean Geology*, **46**, 629–669.

TERMIER, H., TERMIER, G. and VACHARD, D. 1977. Monographie paléontologique des affleurements Permiens du Djebel Tébaga (sud Tunisien). *Palaeontographica, Abteilung A*, **156**, 1–109.

THEIN, M. L. and NITECKI, M. H. 1974. Chesterian (Upper Mississippian) Gastropoda of the Illinois basin. *Fieldiana Geology*, **34**, 1–238.

THIELE, J. H. 1929–1931. *Handbuch der systematischen Weichtierkunde*. Gustav Fischer, Jena.

THOMAS, E. G. 1940*a*. Revision of the Scottish Carboniferous Pleurotomariidae. *Geological Society of Glasgow Transactions*, **20**, 30–72.

THOMAS, E. G. 1940*b*. Anglo-Belgian Carboniferous Pleurotomariidae. Unpublished PhD thesis, University of Glasgow, 115 pp. http://theses.gla.ac.uk/id/eprint/80223

TRACEY, S., TODD, J. A. and ERWIN, D. H. 1993. Mollusca: Gastropoda. 131–167. *In* BENTON, M. J. (ed.) *The fossil record 2*. Chapman & Hall, 845 pp.

ULRICH, E. O. and SCOFIELD, W. H. 1897. The lower Silurian Gastropoda of Minnesota. *The Geology of Minnesota: Paleontology*, **3**, 813–1081.

VERMEIJ, G. J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**, 245–258.

VERMEIJ, G. J. and HERBERT, G. S. 2004. Measuring relative abundance in fossil and living assemblages. *Paleobiology*, **30**, 1–4.

VERMEIJ, G. J., SCHINDEL, D. E. and ZIPSER, E. 1981. Predation through geological time: evidence from gastropod shell repair. *Science*, **214**, 1024–1026.

VOLTZOW, J., MORRIS, P. J. and LINSLEY, R. M. 2004. Anatomy of and patterns of water currents through the mantle cavities of pleurotomariid gastropods. *Journal of Morphology*, **262**, 659–666.

WAGNER, P. J. 2002. Phylogenetic relationships of the earliest anisotrophically coiled gastropods. *Smithsonian Contributions to Paleobiology*, **88**, 1–152.

WANG, H. and XI, Y. (1980). Late Permian and Early Triassic gastropods of western Guizhou. 195–232. *In* NANKING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY (ed.) *Stratigraphy and palaeontology of Upper Permian coal bearing Formation in Western Guizhou and Eastern Yunnan, China*. Academia Sinica (Science Press). [in Chinese]

WANNER, C. 1941. Neue Beiträge zur Gastropoden-Fauna des Perm von Timor. *Geological Expedition to the Lesser Sunda Islands*, **4**, 1–71.

WATERHOUSE, J. B. 1987. Late Palaeozoic Mollusca and correlations from the south-east Bowen Basin, east Australia. *Palaeontographica, Abteilung A*, **198**, 129–233.

WELLER, J. M. 1929. The gastropod genus *Yvania*; contribution to the paleontology of Illinois. *Illinois State Geological Survey, Report of investigations*, **18**, 1–44.

WENZ, W. 1938–1944. Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. *In* SCHINDEWOLF, O. H. (ed.) *Handbuch der Paläozoologie. 6. Gastropoda*. Borntraeger, 1639 pp.

WHIDBORNE, G. 1896. A monograph of the Devonian Fauna of the South of England. Vol. III.—Part I. The fauna of the Marwood and Pilton Beds of North Devon and Somerset. *Monographs of the Palaeontographical Society*, **50**, 1–112.

WHITE, C. A. 1880. Contributions to invertebrate paleontology, No. 6; certain Carboniferous fossils from western states and territories. *US Geological and Geographical Survey of the territories, Annual Report*, **12**, 119–141.

WHITFIELD, R. P. 1882. On the fauna of the Lower Carboniferous of Spergen Hill, Indiana. *American Museum of Natural History Bulletin*, **1**, 39–97.

WILLIAMS, S. and OZAWA, T. 2006. Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics & Evolution*, **39**, 33–51.

WORTHEN, A. H. 1884. Descriptions of two new species of Crustacea, fifty-one species of Mollusca, and three species of crinoids, from the Carboniferous Formation of Illinois and adjacent States. *Illinois State Natural History Museum Bulletin*, **2**, 1–27.

WORTHEN, A. H. 1890. Description of fossil invertebrates. *Illinois Geological Survey*, **8**, 69–154.

YAKOWLEW, N. N. 1899. Fauna of the Upper Paleozoic deposits of Russia. I. Cephalopods and gastropods. *Trudy Geologicheskago Komiteta*, **15**, 1–140. [in Russian]

YIN, T. H. 1932. Gastropoda of the Penchi and Taiyuan series of North China. *Palaeontologica Sinica, Series B*, **11**, 1–53.

YIN, H.-F. and YOCHELSON, E. L. 1983. Middle Triassic Gastropoda from Qingyan, Guizhou Province, China: 1 - Pleurotomariacea and Murchisoniacea. *Journal of Paleontology*, **57**, 162–187.

YOCHELSON, E. L. 1956. Permian Gastropoda of the southwestern United States. 1. Euomphalacea, Trochonematacea, Anomphalacea, Craspedostomatacea, and Platyceratacea. *Bulletin of the American Museum of Natural History*, **110**, 179–275.

YOCHELSON, E. L. and SAUNDERS, B. W. 1967. A bibliographic index of North American Late Paleozoic Hyolitha, Amphineura, Scaphopda, and Gastropoda. *Geological Survey Bulletin*, **1210**, 1–271.

YONGE, C. M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society B*, **232**, 443–518.

YOO, E. K. 1988. Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. *Records of the Australian Museum*, **40**, 233–264.

YOO, E. K. 1994. Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. *Records of the Australian Museum*, **46**, 63–110.

YOON, S. H. and KIM, W. 2005. Phylogenetic relationships among six vetigastropod subgroups (Mollusca, Gastropoda) based on 18S rDNA sequences. *Molecules & Cells*, **19**, 283–288.

ZAPATA, F., WILSON, N. G., HOWISON, M., ANDRADE, S. C., JÖRGER, K. M., SCHRÖDL, M., GOETZ, F. E., GIRIBET, G. and DUNN, C. W. 2014. Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. *Proceedings of the Royal Society B*, **281**, 20141739.

APPENDIX 1

ADDITIONAL NEW COMBINATIONS AND OTHER CHANGES

Based on the original illustrations and descriptions, we propose generic re-assignments for several species below. The arguments for these new combinations are presented in the remarks of the Systematic Palaeontology section.

The following species are used in new combinations (comb. nov. [former combination]):

Phymatopleura? *missouriensis* (Bandel, 2009) comb. nov. [*Campbellospira missouriensis*]

Paragoniozona obesum (Yoo, 1994) comb. nov. [*Glabrocingulum obesum*]

Paragoniozona pustulum (Yoo, 1994) comb. nov. [*Glabrocingulum pustulum*]

Spiroscala? *costata* (Yoo, 1988) comb. nov. [*Borestus costatus*]

Spiroscala? *solida* (Hyde, 1953) comb. nov. [*Mourlonia solida*]

Euconospira conoides (Meek & Worthen, 1866*a*) comb. nov. [*Spiroscala conoides*]

Lamellospira catherinae (Gemmellaro, 1889) comb. nov. [*Luciella catherinae*]

Eirlysella hissingeriana (de Koninck, 1843) comb. nov. [*Trochus hissingerianus*]

Eirlysella squamula (Phillips, 1836) comb. nov. [*Pleurotomaria squamula*]

Eirlysella ocultabanda (Kues & Batten, 2001) comb. nov. [*Luciellina ocultabanda*]

Paragoniozona venustiformis (Licharew, 1967) comb. nov. [*Deseretospira venustiformis*]

Rhineoderma asiatica (Licharew, 1967) comb. nov. [*Paragoniozona asiatica*]

Rhineoderma nikitowkensis Yakowlew, 1899 (original generic attribution) [*Termihabena nikitowkensis*, see Mazaev 2019*b*]

Ruedemannia crenilunula (Yoo, 1994) comb. nov. [*Worthenia crenilunula*]

Yiningicus waterhousei (Ketwetsuriya *et al.*, 2020*b*) comb. nov. [*Worthenia*? *waterhousei*]

Worthenia preclara (Hoare *et al.*, 1997) comb. nov. [*Phymatopleura preclara*]

Worthenia? *hamlingii* (Whidborne, 1896) comb. nov. [*Borestus hamlingii*]

Dictyotomaria marginata (Batten, 1958) comb. nov. [*Glyptotomaria marginata*]

Dictyotomaria pistra (Batten, 1958) comb. nov. [*Glyptotomaria pistra*]

Dictyotomaria triassica (Yin & Yochelson, 1983) comb. nov. [*Glyptotomaria triassica*]

Devonorhineoderma capillaria (Conrad, 1842) comb. nov. [*Dictyotomaria capillaria*]

Devonorhineoderma quasicapillaria (Rollins, 1975) comb. nov. [*Dictyotomaria quasicapillaria*]

Devonorhineoderma eurocapillaria (Amler & Heidelberger, 2003) comb. nov. [*Dictyotomaria eurocapillaria*]

Lukesispira gundyensis (Yoo, 1988) comb. nov. [*Austroneilsonia gundyensis*]

Peruvispira? *insculpta* (Hall, 1858) comb. nov. [*Murchisonia insculpta*]

Peruvispira invisitata (Hoare *et al.*, 1997) comb. nov. [*Neilsonia invisitata*]

Peruvispira welleri (Thein & Nitecki, 1974) comb. nov. [*Neilsonia welleri*]

Peruvispira coatesi (Peel, 2016) comb. nov. [*Neilsonia coatesi*]

Peruvispira ganneyica (Peel, 2016) comb. nov. [*Neilsonia ganneyica*]

Erwinispira? *luculenta* (Pan & Erwin, 2002) comb. nov. [*Platyzona pulchella*]

Glabrocingulum sp. in Yoo (1994, pl. 7 figs 1–4) is assigned to *Rhineoderma*.

The specimen assigned to '*Glabrocingulum tongxinensis* (Guo)' by Pan (1997, fig. 2-18–19) represents *Worthenia* (*Worthenia*).

Borestus sp. in Jeffery *et al.* (1994, figs 7–20, 21) is assigned to *Spiroscala*.

Gosseletina nodosa Hoare *et al.*, 1997 represents a junior synonym of *Glabrocingulum* (*Glabrocingulum*) *beedei* (Mark, 1912).

Glyptotomaria (*Dictyotomaria*) *faceta* Hoare *et al.*, 1997 represents a junior synonym of *Phymatopleura nodosa* (Girty, 1912).

Euconospira sp. indet. 1 and *Euconospira* sp. indet. 2 in Thein & Nitecki (1974) are assigned to *Eirlysella* gen. nov.

Worthenia sp. in Yoo (1994, pl. 9, figs 9–11) is assigned to *Ruedemannia*.

Guizhouspira Wang *in* Wang & Xi, 1980 represents a junior synonym of *Baylea* de Koninck, 1883.

Commozonospira Qiao, 1983 represents a junior synonym of *Ruedemannia* Foerste, 1914.

APPENDIX 2

LOCALITIES

Original labels with the fossil samples and locations described by Boardman *et al.* (1994) are written in *italic*. Stratigraphic and locality information from Boardman *et al.* (1994) which is current and correct at this time, is kept without modification. Where necessary, this information was updated (in 2017) to be in agreement with the American Museum of Natural History (AMNH) locality log for fossil localities with specimens in the Mapes Collection in New York City, USA. As necessary, additional information and corrections were provided by Mr Curtis J. Faulkner and RHM in 2020.

Morrowan of Oklahoma

Gene Autry Shale

Gene Autry Shale locality on the Daube Ranch (*Coral Reef area*). Red shales of the Gene Autry Formation exposed

in gullies on east side of unnamed tributary of Sycamore Creek on the Daube Ranch in south central Oklahoma, NW¼, NW¼, SW¼, sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7½′ Quadrangle (Hoare & Mapes 1985; Smith & Hoare 1987; and especially Kolata *et al.* 1991). AMNH locality 5270 (34°14′13.76″N; 96°52′42.02″W).

Desmoinesian of Oklahoma

Boggy Formation (Deese Group)

Buckhorn Asphalt Quarry, 6.5 miles (10 km) south of Sulphur, Oklahoma (34°26′44″N; 96°57′41″W).

[Middle] Wetumka Formation (Little Osage Shale Member)

OKD–13. SW¼, SW¼, NE¼, sec. 8, T. 7 N., R. 10 E., Lake Holdenville 7½′ Quadrangle, Hughes County. Oklahoma; hillside exposure. AMNH locality 5010 (35°05′45.87″N; 96°16′16.98″W).

[Middle] Wetumka Formation (Little Osage Shale Member)

OKD–14. centre north line of sec. 17, T. 7 N., R. 10 E., Lake Holdenville 7½′ Quadrangle, Hughes County, Oklahoma; pond dam. AMNH locality 5011 (35°05′11.37″N; 96°16′25.73″W).

[Basal] Wetumka Formation (Little Osage Shale Member)

OKD–15. Locality 163 (Morgan 1924): NW¼, NW¼, NE¼, sec. 18, T. 3 N., R. 7 E., Stonewall 7½′ Quadrangle, Pontotoc County, Oklahoma; hillside exposure. AMNH locality 5012 (34°44′14.09″N; 96°36′31.38″W).

[Middle] Wewoka Formation (Anna Shale Member)

OKD–10. SE¼, SW¼, sec. 10, T. 13 N., R. 12 E., Okmulgee Lake 7½′ Quadrangle, Okmulgee County, Oklahoma; hillside exposure adjacent to OK–56. AMNH locality 3516 (35°36′44.67″N; 96°01′30.03″W).

[Upper] Wewoka Formation (Lake Neosho Shale Member)

OKD–11. Locality 2006 (Girty 1915): northern half of NW¼, sec. 5, T. 6 N., R. 9 E., Holdenville 7½′ Quadrangle, Hughes County, Oklahoma; hillside exposure. AMNH locality 3517 (35°01′40.52″N; 96°23′10.98″W).

[Upper] Holdenville Formation (Nuyaka Creek Shale Member)

OKD–01. Ranch of Mr Christianberry. Centre of sec. 35, T. 8 N., R. 8 E., Holdenville 7½′ Quadrangle, Hughes County, Oklahoma; gully used for trash dump. AMNH locality 5000 (35°07′29.14″N; 96°25′58.62″W).

Missourian of Oklahoma

[Lower] Barnsdall Formation (Eudora Shale Member)

OKM–02. Centre east line of sec. 9, T. 28 N., R. 13 E., Copan 7½′ Quadrangle, Washington County, Oklahoma. Roadfill on west side of US Highway 75. The fill is from the lower part of the roadcut (locality OKM-03) across the highway. Note: this locality is no longer collectable. AMNH locality 5142 (36°55′36.64″N; 95°55′04.16″W).

Coffeyville Formation (Mound City Shale Member)

Sampson Ranch *OKM–25 Missourian lower Tackett*. Centre S 1/2, SW¼, SE¼ sec. 1, T. 25 N., R. 14 E., Oglesby 7½′ Quadrangle, Nowata County, Oklahoma. Pond dam. AMNH locality 5167 (36°40′25.74″N; 95°45′55.78″W).

Virgilian of Kansas

Haskell Limestone Member and basal Robbins Shale Member (Lawrence Formation)

KSV–05. SW¼, NE¼, NE¼, sec. 14, T. 35 S., R. 12 E., Peru 7½′ Quadrangle, Chautauqua County, Kansas; road ditch. No AMNH locality number (37°00′26.81″N; 96°03′31.02″W).

KSV–06. Centre of sec. 22, T. 34 S., R. 12 E., Peru 7½′ Quadrangle, Chautauqua County, Kansas; roadcut. No AMNH locality number (37°04′32.14″N; 96°04′56.34″W).

Desmoinesian of Texas

Dickerson Shale

TXD–01 Ft. Walters Gate 2 (Bureau of Economic Geology locality 110–T–3). Dennis 7½′ Quadrangle, Hood County, Texas; shale in cutbank on south face of an isolated hill north of Evergreen drive on old Ft. Walters. AMNH locality 5410 (32°32′02.32″N; 98°00′54.03″W).

Lazy Bend Formation

TXD–03. Red shale in dry creek bank about 3.5 miles north-east of Lipan, Texas on county road 1189. Lipan 7½′ Quadrangle, Hood County, Texas. AMNH locality 5412 (32°49′12.79″N; 98°03′54.06″W).

Missourian of Texas

Lower Wolf Mountain Shale Member (Lake Bridgeport Shale) (Graford Formation)

TXM–01. Bridgeport West 7½′ Quadrangle, Wise County, Texas; hillside excavation. AMNH locality 5422 (33°09′35.69″N; 97°52′22.96″W).

Lower Placid Shale Member (Brad Formation)

TXM–14. Costello Island 7½′ Quadrangle, Palo Pinto County, Texas; roadcut on Park Road 36. AMNH locality 5435 (32°50′42.55″N; 98°07′28.28″W).

Virgilian of Texas

Colony Creek Shale Member (Caddo Creek Formation)

TXV–46. Lake Brownwood 7½′ Quadrangle, Brown County, Texas; hillside exposure. AMNH locality 5500 (31°50′25.33″N; 99°01′51.79″W).

TXV–49. Lake Brownwood 7½′ Quadrangle, Brown County, Texas; excavation for boat dock. AMNH locality 5503 (31°49′58.34″N; 99°02′41.75″W).

TXV–50. Caddo North-east 7½′ Quadrangle, Stephens County, Texas; roadcut on both sides of US Highway 180. AMNH locality 5504 (32°44′47.08″N; 98°32′05.31″W).

Finis Shale Member (Graham Formation)

TXV–29 (Bureau of Economic Geology locality 251-T-2). Lacasa 7½′ Quadrangle, Stephens County, Texas; pond dam exposure. Presented as Graham undifferentiated by Plummer & Scott (1937). AMNH locality 5483 (33°16′07.88″N; 98°06′25.77″W).

TXV–34 (Bureau of Economic Geology locality 214-T-27, presented as Graham Formation, undifferentiated). Cundiff 7½′ Quadrangle, Jack County, Texas; hillside exposure. AMNH locality 5488 (33°16′04.24″N; 98°06′23.81″W).

TXV–36 Ranger Oil Lease. Cundiff 7½′ Quadrangle, Jack County, Texas; hillside exposure adjacent to TXV–24. AMNH locality 5490 (33°16′40.55″N; 98°05′55.86″W).

TXV–40. Jacksboro North-east 7½′ Quadrangle, Jack County, Texas; hillside exposure. AMNH locality 5494 (33°12′36.22″N; 98°06′32.32″W).

TXV–44. Jacksboro North-east 7½′ Quadrangle, Jack County, Texas; roadcut on US Highway 380. AMNH locality 5498 (33°11′51.93″N; 98°06′13.84″W).

TXV–54. Jacksboro North-east 7½′ Quadrangle, Jack County, Texas; hillside exposure. AMNH locality 5508 (33°11′46.09″N; 98°06′18.54″W).

TXV–56. Jacksboro North-east 7½′ Quadrangle, Jack County, Texas; well pad exposure. AMNH locality 5510 (33°11′09.86″N; 98°06′14.20″W).

TXV–60 (= *BBTXV–113*). From creek to top of ridge to west, 2.8 km south of the Fort Richardson State Park office (Boston 1988, p. 211, fig. 8). AMNH locality 5514.

TXV–120 (Boston 1988). Jacksboro 7½′ Quadrangle, Jack County, Texas; hillside exposure in gulley AMNH locality 5561.

TXV–69 (= *BBTXV–121*) (Boston 1988). Jacksboro 7½′ Quadrangle, Jack County, Texas; hillside exposure. AMNH locality 5523.

TXV–200. Lost Creek Lake emergency spillway at dam, *c*. 4 km north-east of Jacksboro, Jack County, Texas on Texas Highway 59. AMNH locality 5562 (33°14′11.17″N; 98°07′11.33″W).

Un-named shale member (Graham Formation)

Jacksboro Airport. Un-named shale above Jacksboro Limestone at Jacksboro Municipal Airport, Jacksboro, Texas. Locality now destroyed by recent quarrying operations. No AMNH locality (33°13′24.22″N; 98°08′38.09″W).

Necessity Shale Member = Bluff Creek Shale Member (Graham Formation)

TXV–66 (Boston 1988, locality *BBTXV–145*). Johnson Lake 7½′ Quadrangle, Jack County, Texas; roadcut on unimproved road. AMNH locality 5520.

TXV–24 Schindel's locality. Lake Brownwood 7½′ Quadrangle, Brown County, Texas; roadcut on Park Road 15. AMNH locality 5478 (31°51′43.52″N; 99°03′13.86″W).

Wayland Shale Member (Graham Formation)

TXV–10. Lynn Creek 7½′ Quadrangle, Jack County, Texas (Bureau of Economic Geology locality 119–T–23; presented as Graham Formation, undifferentiated by Plummer & Scott 1937). Roadcut and hillside exposures on

south side US Highway 281. AMNH locality 5463 (33°15′20.98″N; 98°15′30.87″W).

TXV–06. Speck Mountain 7½′ Quadrangle, Coleman County, Texas; hillside exposure. AMNH locality 5458 (31°31′37.57″N; 99°16′07.98″W).

TXV–61 (Boston 1988, locality *BB TXV–107*), Graham 7½′ Quadrangle, Young County, Texas; shallow gullies adjacent to TXV–67. AMNH locality 5516.

Desmoinesian of Ohio

Sturgeon Collection (Allegheny Formation) Washingtonville unit exposed in the James Brothers strip mine, sec. 32 and sec. 33, Rose Tp., Carroll County, Ohio, Mineral City 7½′ quadrangle, Ohio Geologic Survey locality 15098 (Hoare *et al.* 1997). No AMNH locality.

CHAPTER 3

Ketwetsuriya, C., **Karapunar, B.**, Charoentitirat, T., & Nützel, A. (2020). Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa*, 4766(1): 1–47, https://doi.org/10.11646/zootaxa.4766.1.1.

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Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane

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Abstract

A new Permian gastropod assemblage from the Roadian (Middle Permian) Khao Khad Formation, Saraburi Group (Lopburi Province, Central Thailand) which is part of the Indochina Terrane, has yielded one of the most diverse Permian gastropod faunas known from Thailand. A total of 44 gastropod species belonging to 30 genera are described herein, including thirteen new species and one new genus. The new genus is *Altotomaria*. The new species are *Bellerophon erawanensis*, *Biarmeaspira mazaevi*, *Apachella thailandensis*, *Gosseletina microstriata*, *Worthenia humiligrada*, *Altotomaria reticulata*, *Yunnania inflata*, *Trachydomia suwanneeae*, *Trachyspira eleganta*, *Heterosubulites longusapertura*, *Platyzona gradata*, *Trypanocochlea lopburiensis* and *Streptacis*? *khaokhadensis*. Most of the species in the studied assemblage represent vetigastropods (35.6%) and caenogastropods (26.7%) and most of the species belong to Late Palaeozoic cosmopolitan genera. The studied faunas come from shallow water carbonates that are rich in fusulinids, followed by gastropods, ostracods, bivalves and brachiopods. The gastropod assemblage from the Khao Khad Formation shares no species with the gastropod assemblages from other Permian formations in Thailand, the Tak Fa Limestone and the Ratburi Limestone. However, it is similar to the Late Permian gastropod faunas from South China of the Palaeo-Tethys, therefore it suggests that the Indochina Terrane was not located far from South China.

Key words: Gastropoda, Mollusca, Saraburi Group, new species, diversity, Lopburi

Introduction

Permian marine invertebrate faunas from the Indochina Terrane of Thailand have been intensively studied over the past decade (e.g., fusulinids, brachiopods, bryozoan, corals and ostracods). The knowledge on the fauna together with the previous stratigraphic and sedimentological studies suggest the existence of a carbonate platform along the western edge of the Indochina Terrane during the Permian. Although gastropods are a major benthic invertebrate component in the limestones from the Indochina Terrane of Thailand, their taxonomy and diversity have been rarely studied until recently.

Permian gastropod faunas from Thailand have been studied in detail only during the last 6 years by Ketwetsuriya *et al*. (2014, 2016), who provided the first detailed study of the Middle Permian gastropods form the Tak Fa Limestone (Saraburi Group) of the Indochina Terrane and by Ketwetsuriya *et al*. (2020), who studied gastropods from the Ratburi Limestone of the Sibumasu Terrane. These studies reported numerous new species mostly representing typical Late Palaeozoic gastropod genera. Prior to these studies, only a few reports mentioned the presence of Permian gastropods from Thailand (Grant 1976; Waterhouse 1982; Sone 2010) without providing a detailed study.

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The present study describes a new Permian gastropod fauna from the Khao Khad Formation (Saraburi Group) at Erawan Hill, Lopburi Province, Central Thailand of the Indochina Terrane. The outcrops of the Khao Khad Limestone at Erawan Hill have yielded several species of the Permian marine invertebrate fossils including fusulinids, brachiopods, bryozoans, bivalves, ostracods and especially gastropods which form the most diverse group in this fauna. The studied gastropod assemblage represents one of the richest and most diverse Permian gastropod assemblages known from Thailand and provides important information on the distribution of Permian gastropods in the Palaeo-Tethys. Some species and genera suggest that the assemblage is related to the Late Permian gastropod faunas from South China, the Permian faunas from Cambodia and Japan and the Pennsylvanian and Permian faunas of the USA.

Geological setting

The Permian sedimentary rocks extending in central Thailand along the north–south orientation on the eastern side of the Chao Phraya Central Plain have been assigned to the Saraburi Group (informally known as Saraburi Limestone) (Nakornsri 1976, 1981; Bunopas 1981) which consists of widely exposed carbonate rocks along the western margin of the Indochina Terrane (Hinthong *et al*. 1985).

The Permian limestone in the study area forms part of the Khao Khad Formation of the Saraburi Group (Fig. 1). This formation was initially erected by Hinthong (1981) for the carbonate rocks that are exposed in an almost WNW–ESE direction in the Saraburi area through southern Lopburi area. It mainly comprises thin- to very thick-bedded limestone and locally interbedded with argillaceous limestone and clastic sedimentary rocks, i.e., shale, siltstone, sandstone and conglomerate. The bioclastic limestone lithology together with an abundant marine invertebrate fauna suggests shallow-marine deposition on a carbonate platform. Several invertebrate groups have been reported from this formation, e.g., fusulinids, brachiopods, gastropods, ostracods, bivalves, corals and ammonoids. However, only fusulinids have been investigated in detail which indicate an age ranging from Early to Middle Permian (Pitakpaivan 1965; Toriyama *et al*. 1974; Toriyama & Kanmera 1977, 1979; Dawson 1993). The studied limestone samples yield numerous fusulinids of *Verbeekina* sp. (Fig. 2A, B) indicating Kubergandian (= Roadian, Middle Permian) age based on Charoentitirat's informal identification for this study.

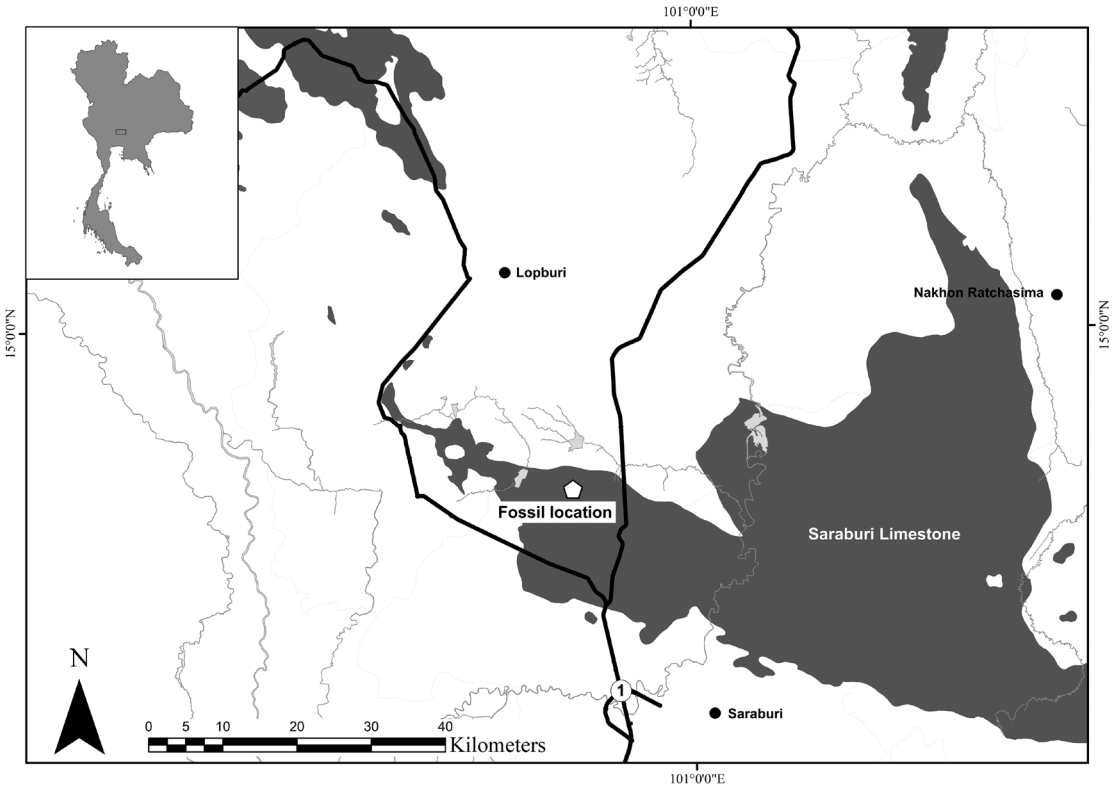

FIGURE 1. Geological map of the study location at Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand.

The faunas described herein were collected from the weathered limestone surface exposed at Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1). The samples were taken from several limestone outcrops that are exposed as lapiés (Fig. 3A, C) of 10 acres near the road No. 3334 at the western foot hill of Erawan Hill (GPS N21°56'24.5" and E96°30'11.2"). The outcrops composed predominantly of shallow marine limestone consisting generally of black to light grey limestone or recrystallized argillaceous limestone (Fig. 2C–D).

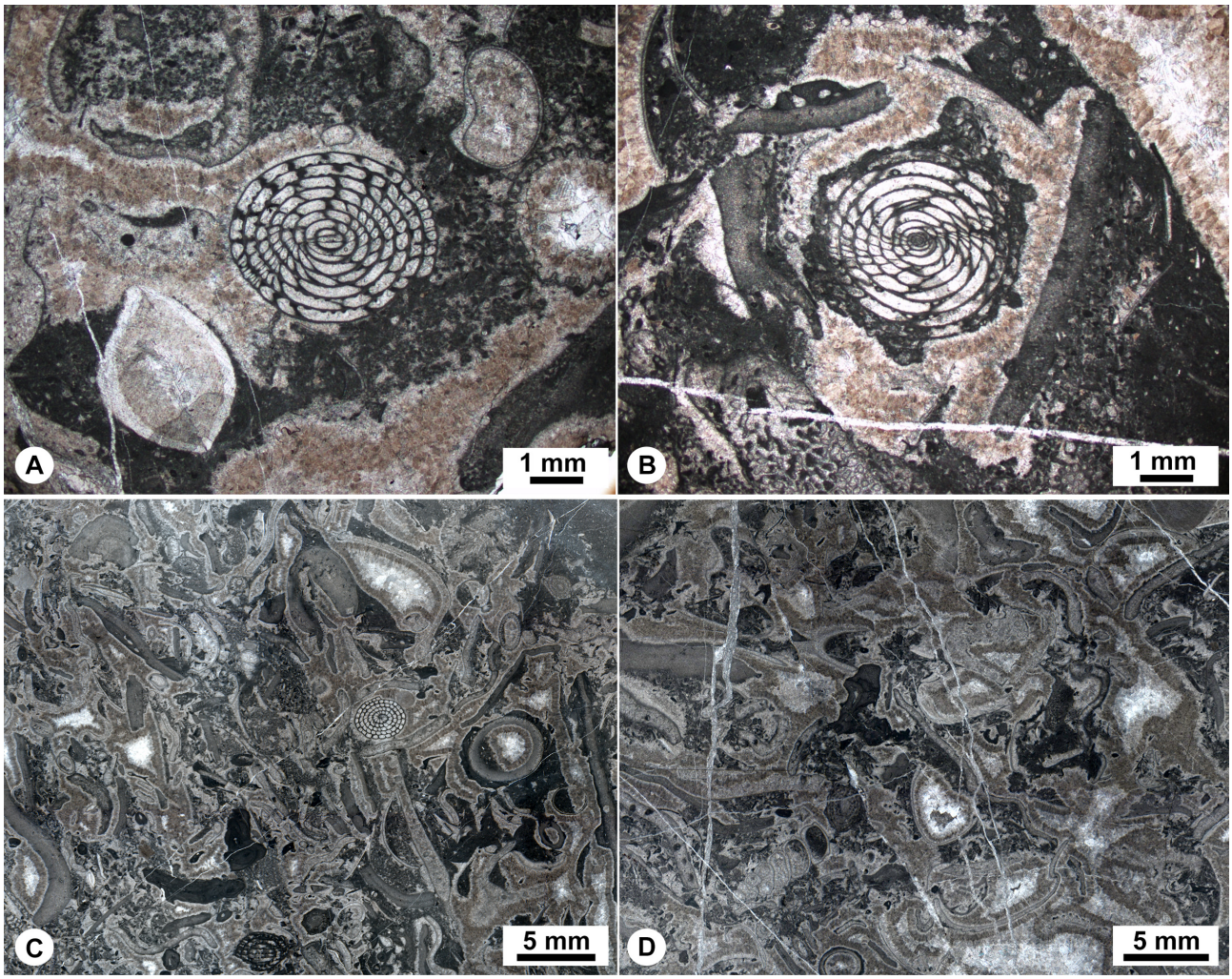

FIGURE 2. Photomicrographs of thin-sections of the studied fossiliferous limestone of the Khao Khad Formation at Erawan Hill, Lopburi Province, Central Thailand. A–B, the index taxa *Verbeekina* sp. C–D, Bioclastic packstone with gastropods, fusulinids, brachiopods, bivalves and dasycladacean algae.

Material and methods

The present fossil material was obtained by surface collection from weathered-out material at the surface of massive hard limestone blocks (Fig. 3B, D). Fossils could not be obtained from the unweathered parts of the hard, massive fossiliferous limestones. Sampling was performed in March 2017 and May 2018. In addition to collecting of fossils in the field, 5 kg of weathered-out scree sediments from six different exposures near the limestone block. Laboratory work was carried out at the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany. The sediments were wet sieved at mesh sizes of 0.2 mm, 0.5 mm and 5 mm and the residues were dried at 40 degrees Celsius for one day. All fossils were picked from the residues under a microscope. Fossils were sorted according to species and selected specimens were documented aided by microphotography (mostly whitened with ammonium chloride) or with SEM. Finally, gastropods were identified as far as possible. In addition, thin sections of rock samples were prepared for sedimentological analysis.

Repository. All type specimens of gastropods are housed in the Department of Earth Sciences, Faculty of Science, Kasetsart University (Bangkok, Thailand) under the general repository number ESKU-19-LP 1–221.

Classification. The classification used in this article follows Knight *et al*. (1960) and Bouchet *et al*. (2017). Bellerophontids are classified as a subclass of Gastropoda (Amphigastropoda). A recent discussion of the systematic placement of bellerophontids is given by Harper (2018). Euomphaloidea are classified as "Basal taxa that are certainly Gastropoda" (subclass unknown according to Harper 2018) because although it is sure that they represent Palaeozoic Gastropoda, their phylo-systematic position is disputed: see e.g. Bandel & Frýda (1998): Subclass Euomphalomorpha, and Nützel (2002): Subclass Vetigastropoda.

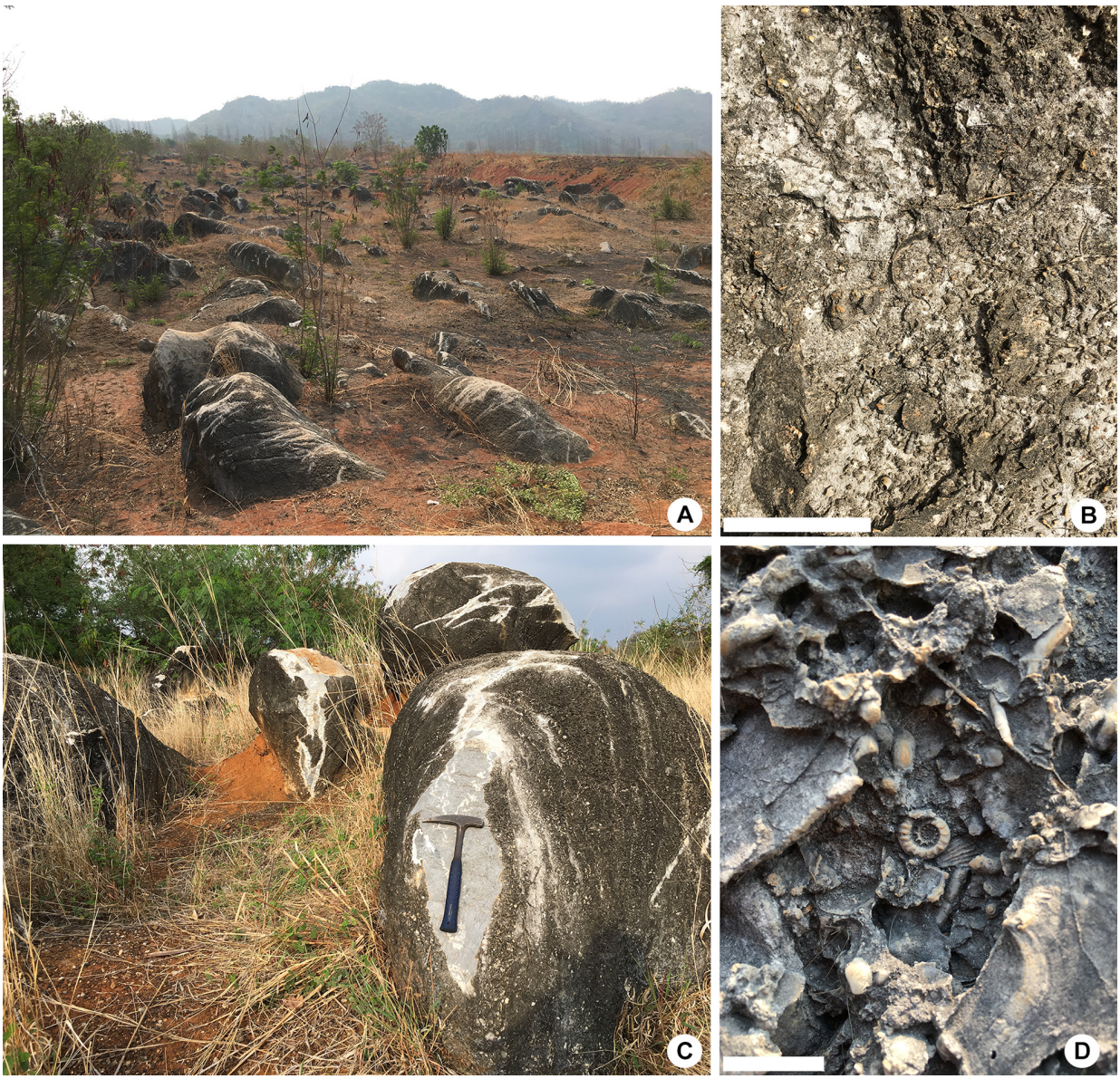

FIGURE 3. A, C, Limestone outcrops exposed as the lapiés at the west foot hill of Erawan hill; hammer in the right side for scale (C). B, D, Weathered surface limestones represented by bioclastic packstone as an example for preservation that the studied materials were collected; scale bars represent: 10 cm (B); 2 cm (D).

Results

The studied samples have yielded 221 gastropods representing 44 species belonging to 30 genera. Gastropoda is the most abundant and diverse group. The stratigraphy of this fauna is based on fusulinid foraminifera identified by T. Charoentitirat. Numerous fusulinids representing *Verbeekina* sp. (Fig. 2A, B) indicate an Kubergandian age (= Roadian, Middle Permian).

As in many other Permian faunas from Japan and Southeast Asia, the preservation of gastropods is commonly poor and shells are strongly and coarsely silicified. However, a number of specimens provided sufficient morphological characters for identification or characterization of new taxa.

The present gastropod assemblage from the Middle Permian of the Khao Khad Formation of Saraburi Group at Erawan Hill, Lopburi Province represents the most diverse Permian gastropod fauna known from Thailand. This fossiliferous limestone is rich in fusulinids and yields abundant gastropods together with ostracods, brachiopods, bivalves and some crinoids. Gastropods are the most diverse clade in this assemblage. The studied material comes from the shallow-marine carbonate platform of the Khao Kwang platform of the Indochina Terrane which is widely distributed in central and northeastern Thailand.

A total of 44 gastropod species have been described here, thirteen of which are new: namely *Bellerophon erawanensis*, *Biarmeaspira mazaevi*, *Apachella thailandensis*, *Gosseletina microstriata*, *Worthenia humiligrada*, *Altotomaria reticulata*, *Yunnania inflata*, *Trachydomia suwanneeae*, *Trachyspira eleganta*, *Heterosubulites longus-apertura*, *Platyzona gradata*, *Trypanocochlea lopburiensis* and *Streptacis*? *khaokhadensis*. The assemblage consists of several typical, cosmopolitan Late Palaeozoic genera such as *Bellerophon*, *Warthia*, *Worthenia*, *Anomphalus*, *Naticopsis*, *Trachydomia*, *Palaeostylus* and *Protostylus*.

The clade proportions of the gastropod faunas that have been reported from Thailand so far differ considerably from each other (Fig. 4). The clade proportion of the present gastropod fauna (Fig. 4A) shows that it is dominated by Vetigastropoda which comprise of 16 species (35.6%). Pleurotomariida is the most diverse group of Vetigastropoda and most of the new species belong to this group. High-spired caenogastropods are present with 11 species (24.4%) including several species of the superfamily Orthonematoidea. Neritimorpha are represented by at least 8 species (17.8%) containing various species of the genera *Naticopsis* and *Trachydomia* and followed by Bellerophontida at 11.1%. Only a single species (2.2%) of Euomphaloidea and Heterobranchia is present in this assemblage.

The Permian gastropod assemblages from the Tak Fa Limestone of the Saraburi Group reported by Ketwetsuriya *et al*. (2014, 2016) consists of 40 species and the relative quantitative data have been analyzed by Ketwetsuriya *et al*. (unpublished) from the Tak Fa Formation of the Nakhonsawan area, which is also located at the western margin of the Indochina Terrane (Sone & Metcalfe 2008). In contrast to the assemblage studied herein, however, Vetigastropoda of the Tak Fa assemblage are as diverse as Caenogastropoda (Fig. 4B) and each group contributes 32.5% of the total species diversity - with *Anomphalus* sp. being the most abundant.

Although the gastropod faunas from the Khao Khad Formation and the Tak Fa Formation come from the Indochina Terrane of the eastern Palaeo-Tethys, there is no species in common and thus their species composition differs distinctly from each other as discussed above. However, at the genus level, several typical Late Palaeozoic cosmopolitan genera are shared between the two localities: *Warthia*, *Bellerophon*, *Euomphalus*, *Anomphalus*, *Yunnania*, *Microdoma*, *Naticopsis*, *Trachydomia*, *Strobeus*, *Pseudozygopleura*, *Protostylus* and *Streptacis*. This result shows that there exists great variation in the diversity and composition of Permian gastropod assemblages in the Saraburi Limestone of the Indochina Terrane which probably reflects different environmental conditions within the carbonate platform of the Indochina Terrane.

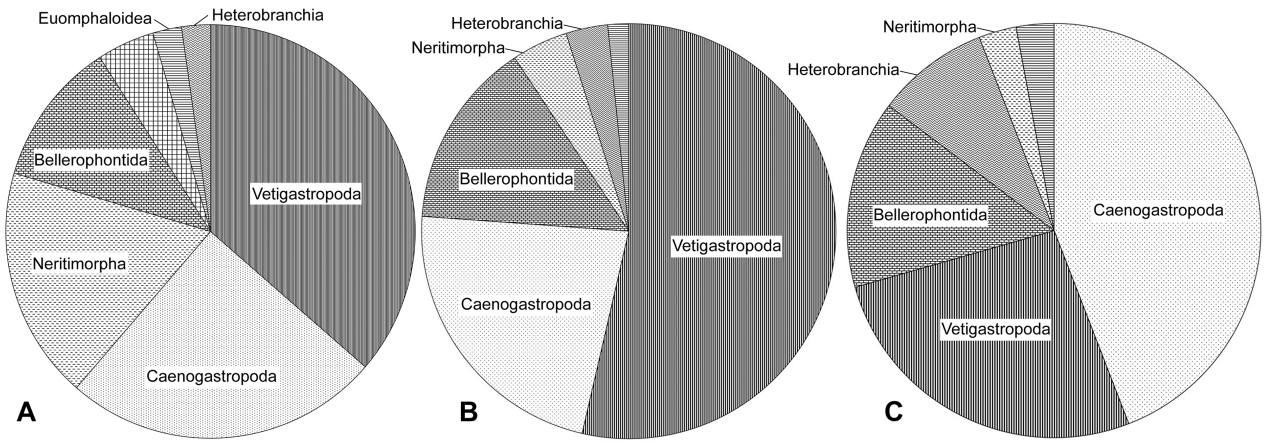

FIGURE 4. Relative species abundances of major clades of Middle Permian gastropod faunas in Thailand. The gastropod faunas from the Khao Khad Formation (this study), Lopburi province (A) from the Tak Fa Formation, Nakhonsawan province (B) as well as from the Ratburi Limestone, Ratchaburi province (C).

The gastropod fauna from the Permian Ratburi Limestone, Ratchaburi Province, Central Thailand, represents the first silicified Permian gastropod fauna known from the Sibumasu Terrane (Ketwetsuriya *et al*. 2020). It consists of 34 species. Caenogastropoda are the most diverse clade in this assemblage (44.1% of the total species; Fig. 4C), followed by Vetigastropoda which encompass 26.5% of the total number of species. Euomphaloidea are absent in the Ratburi Limestone. The studied assemblage from the Khao Khad Formation of the Indochina Terrane has no shared species and its species content differs strongly from the gastropod assemblage of the Ratburi Limestone. However, there are several typical Late Palaeozoic genera also shared between these two assemblages: *Warthia*, *Bellerophon*, *Peruvispira*, *Worthenia*, *Naticopsis*, *Pseudozygopleura*, *Protostylus* and *Streptacis*.

Caenogastropoda and Vetigastropoda contribute most to the species diversity of the Permian gastropods in Thailand. Neritimorpha and Bellerophontida are mainly represented by generally cosmopolitan genera while Heterobranchia and Euomphaloidea played a very minor role. However, the Permian gastropod fauna from the Khao Khad Formation of Erawan Hill studied herein shares no species with the gastropod faunas from the Tak Fa Limestone and the Ratburi Limestone. This suggests a high beta-diversity in this region and also that the Permian gastropod fauna of Thailand is still insufficiently studied.

On the genus level, many more taxa are shared between those three known faunas: *Warthia*, *Bellerophon*, *Peruvispira*, *Worthenia*, *Naticopsis*, *Pseudozygopleura*, *Protostylus* and *Streptacis*. However, they also have a cosmopolitan distribution. Several widespread Permian genera are recorded for the first time from the Permian in Thailand herein: *Porcellia*, *Araeonema*, *Biarmeaspira*, *Trachyspira*, *Platyzona* and *Knightella*.

The comparison of the studied fauna and other Permian eastern Palaeo-Tethys faunas suggests that the gastropods from the Khao Khad Formation of Erawan Hill are closely related to the Late Permian gastropod faunas from South China (Wang & Xi 1980; Wang 1982; Pan 1985; Pan & Yu 1993; Pan & Erwin 2002). The studied gastropod assemblage seems to have a connection with the faunas from South China, particularly the Guangxi and Yunnan provinces in South China. The presence of the species *Euomphalus* cf. *pronodocarinatus*, *Porcellia magninodosa*, *Naticopsis* cf. *heshanensis* and *Anomphalus* cf. *vanescens* further supports the idea that the Indochina Terrane and the South China Platform were palaeogeographically close to each other during the Permian period.

The studied gastropod fauna from the Khao Khad Formation of Erawan Hill (Middle Permian) is older than those of the South China (Late Permian). This could suggest that the gastropod faunas of South China migrated from the Indochina Terrane of Thailand to South China. Some species, e.g. *Worthenia* cf. *pagoda*, are commonly found from the Permian gastropod fauna of Cambodia (Mansuy 1914; Delpey 1941). The Permian gastropod fauna of the USA (Yochelson 1956, 1960; Batten 1989) and the Permian gastropod fauna of Japan (Nützel & Nakazawa 2012) also share some taxa with the present assemblage such as *Warthia* cf. *welleri*, *Anomphalus* cf. *vanescens*, *Anomphalus*? *blancus*, *Microdoma conicum* and *Trachydomia* cf. *nodosum*. However, the taxa reported from the richest known Permian gastropod fauna from Perak, Malaysia (Batten 1972, 1979, 1985) do rarely occur in the studied assemblage. The presence of several common taxa, especially on the genus level, in gastropod faunas from South China, Cambodia, Japan and the USA suggest a faunal connection and widespread palaeogeographic distribution of gastropods in the Palaeo-Tethys during the Permian.

In conclusion, the present Permian gastropod fauna from the Khao Khad Formation of Lopburi area has yielded about 44 species and represents one of the most diverse Permian gastropod faunas known from Southeast Asia. One genus (*Altotomaria*) and almost 30 % of the species described here are new. Vetigastropoda and Caenogastropoda are the most diverse groups in this fauna. This assemblage has no species in common with other Permian gastropod faunas in Thailand. However, a few taxa are shared with the Permian gastropod faunas from South China, Cambodia, Japan and the USA, especially with the Late Permian gastropod faunas from South China.

Systematics

Class Gastropoda Cuvier, 1795

Subclass Amphigastropoda Simroth, 1906

Order Bellerophontida Ulrich & Scofield, 1897

Superfamily Bellerophontoidea McCoy, 1852

Family Euphemitidae Knight, 1956

Subfamily Euphemitinae Knight, 1956

***Warthia* Waagen, 1880**

Type species. *Warthia brevisinuata* Waagen, 1880, Permian, Pakistan.

***Warthia* cf. *welleri* Yochelson, 1960**
(Fig. 5A–D)

cf. *Warthia welleri* Yochelson, 1960: 255–256, pl. 48, figs 20–26.

Material. One specimen: ESKU-19-LP 24.

Dimensions (mm): ESKU-19-LP 24: height = 6.5; width = 6.5; thickness = 6.6.

Description. Involute, globose and inflated shell; minutely phaneromphalous; dorsum moderately arched; inductura thick, smooth; whorls smooth with a distinct slit, approximately 20 percent of body-whorl circumference; lips thin; lateral lips gently curved joining anterior lips smoothly; anterior lips evenly straight and slightly curved back forming a slit; aperture gently expanded, kidney-shaped in transverse section with U-shaped indentation.

Remarks. This specimen has a smooth involute shell with a slit representing the genus *Warthia.* This specimen is the most similar to *Warthia welleri* Yochelson, 1960 from the Permian of the Southwestern USA in shape and having a short slit, but the aperture of *W. welleri* is more arcuate than in the present material. The present specimen has a wing-like turnout of lateral lips (see Mazaev 2015) covering large parts of the umbilicus, which differs from *W. welleri* with gently sickle-shaped lateral lips.

***Warthia* sp. 1**
(Fig. 5E–G)

Material. One specimen: ESKU-19-LP 20.

Dimensions (mm): ESKU-19-LP 20: height = 6.2; width = 4.9; thickness = 5.4.

Description. Compressed involute bellerophontiform shape, longer than wide; dorsum rounded; whorl seemingly geniculate in lateral view; whorls smooth without visible ornament, slit not observed; anomphalous; inductura smooth and thick; aperture kidney-shaped in transverse section but not broad; lateral lips gently sickle-shaped and thick, joining anterior lips at an angle of nearly 100 degrees; anterior lip curved and thin.

Remarks. This bellerophontiform shell is a typical representative of the genus *Warthia*, which is widespread and diverse in the Late Palaeozoic and has been reported from the Middle Permian of Thailand (e.g., Ketwetsuriya *et al*. 2016, 2020). However, the preservation of the material at hand is insufficient for species identification.

***Warthia*? sp. 2**
(Fig. 5H–J)

Material. One specimen: ESKU-19-LP 57.

Dimensions (mm): ESKU-19-LP 57: height = 11.1; width = 11.1; thickness = 8.9.

Remarks. This smooth bellerophontoid seems to be a representative of the genus *Warthia,* but the poor preservation prevents a certain generic assignment. The species can be differentiated from *Warthia* cf. *welleri* by being anomphalous and by the absence of an indentation on the aperture. It differs from *Warthia* sp. 1 by a more inflated shape and a wider aperture.

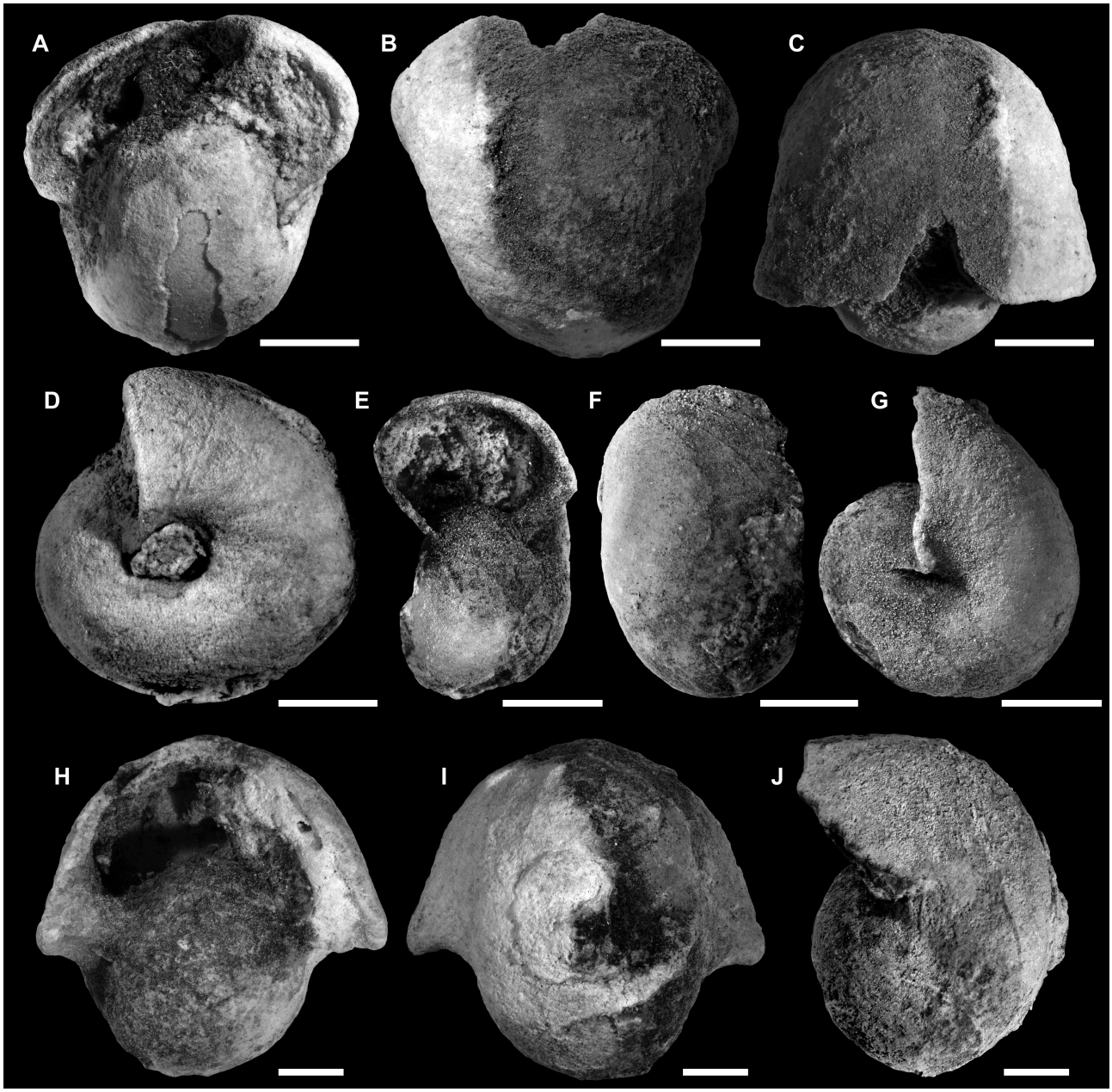

FIGURE 5. A–D, *Warthia* cf. *welleri* Yochelson, 1960, ESKU-19-LP 24. E–G, *Warthia* sp. 1, ESKU-19-LP 20. H–J, *Warthia*? sp. 2, ESKU-19-LP 57. All scale bars represent 2 mm.

Family Bellerophontidae McCoy, 1852

***Bellerophon* de Montfort, 1808**

Type species. *Bellerophon vasulites* de Montfort, 1808, Devonian, Germany.

***Bellerophon erawanensis* sp. nov.**
(Fig. 6A–G)

Etymology. After the Erawan Hill at which the studied gastropod material was found.

Holotype. ESKU-19-LP 55.

Paratypes. Three specimens, ESKU-19-LP 54, 56, 59.

Dimensions (mm): ESKU-19-LP 59: height = *c*. 11.7; width = 13.1; thickness = 10.6. ESKU-19-LP 55: height = 9.9; width = 8.1; thickness = 8.0. ESKU-19-LP 54: height = 9.5; width = *c*. 9.4; thickness = 7.1.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Bellerophontiform, subglobular and slightly compressed shell, higher than wide; anomphalous, umbilical region covered by distinct callus; dorsum evenly rounded; whorls with a distinct slit; slit narrow and rather shallow; whorls covered by numerous closely arranged strengthened growth lines forming almost ribs, growth lines slightly curved backwards towards selenizone at an angle of about 70 degrees; inductura thin, ornamented with several growth lines developed continuing from whorl face; selenizone at periphery, narrow (*c*. 0.3 mm wide), marked by short curved transverse lunulae, at almost the same distance as of growth lines; aperture reniform in transverse section, tiny V-shaped indentation at crest; lateral lip arched, somewhat angulated after wing-like turnout of lateral lips and smoothly joining anterior lips; outer lip sickle-shaped as suggested by course of growth lines.

Remarks. *Bellerophon* has previously been reported from the Middle Permian of Thailand (Ketwetsuriya *et al*. 2016, 2020) but it has been treated in open nomenclature because the preservation of that material is too poor for identification. *Bellerophon erawanensis* sp. nov. closely resembles *B*. *jonesianus* de Koninck, 1863 from the Permian of Pakistan (Chideru), which was also reported from the Permian of Pakistan (Salt Range) by Waagen (1880) and from the Permian of Japan (Akasaka Limestone) by Nützel & Nakazawa (2012). *Bellerophon jonesianus* has a similar ornamentation of pronounced growth lines, a narrow slit and a slightly elevated selenizone. However, *B*. *erawanensis* sp. nov. differs from *B*. *jonesianus* in having a less inflated shell, a narrower selenizone, a considerably higher number of fine threads formed by strengthened growth lines.

B. (*Bellerophon*) *sowerbyi*? d'Orbigny, 1840 as illustrated by Rollins (1975) from the Lower Mississippian of Southeastern Iowa is similar but this species has stronger growth lines and a slightly narrower selenizone. *B*. (*B*.) *kingorum* Yochelson, 1960 from the Permian of the Southwestern USA is also similar but has a more globular shape, thicker inductura and deeper slit. *B*. (*B*.) *huecoensis* Yochelson, 1960 can be differentiated by a deeper slit, a much more elevated selenizone, reflexed lateral lips and a very large size.

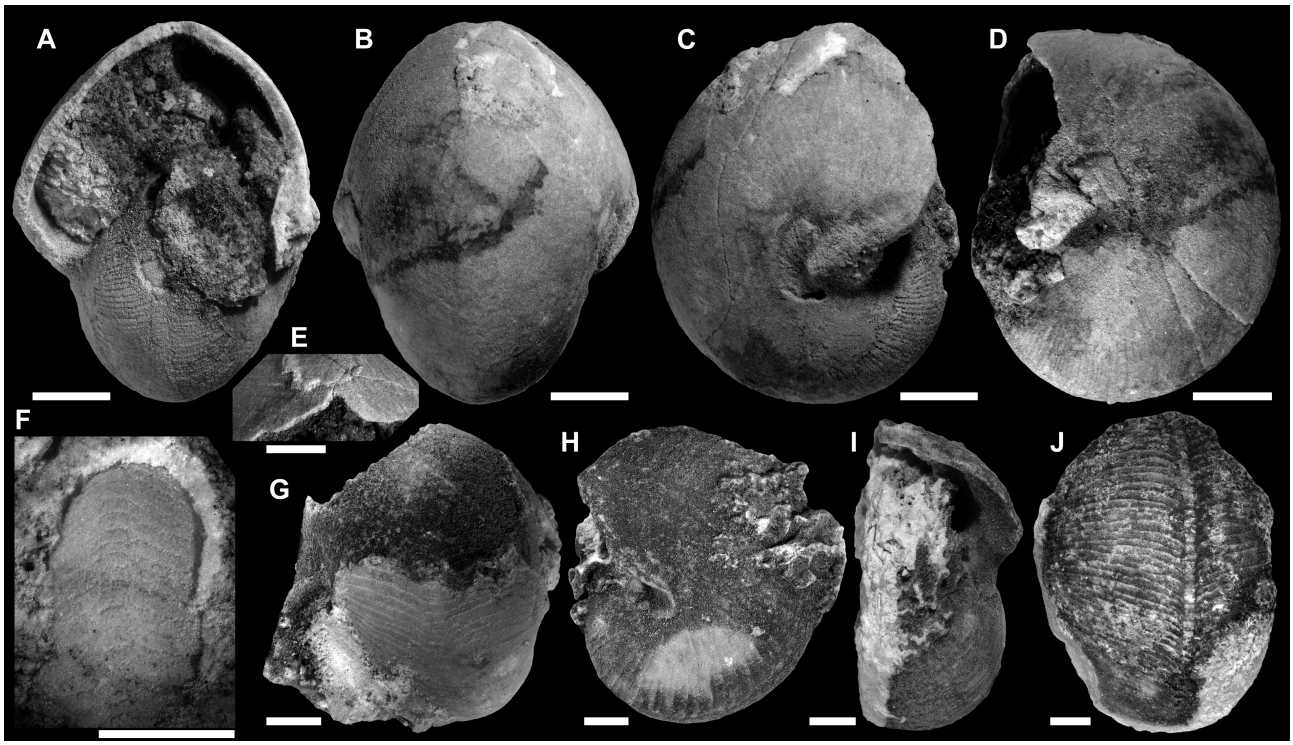

FIGURE 6. A–G, *Bellerophon erawanensis* sp. nov. A–E, ESKU-19-LP 55, holotype; E, shell showing V-shaped slit at crest. F, ESKU-19-LP 54, paratype; shell showing growth lines and position of selenizone. G, ESKU-19-LP 56, paratype. H–J, *Bellerophon* sp. H–I, ESKU-19-LP 58. J, ESKU-19-LP 59, shell fragment showing growth lines and position of selenizone. All scale bars represent 2 mm.

***Bellerophon* sp.**
(Fig. 6H–J)

Material. ESKU-19-LP 58.

Dimensions (mm): ESKU-19-LP 58: height = 13.3; width (half) = 6.6; thickness = 12.1.

Remarks. A single anomphalous bellerophontiform shell and a fragment show strengthened, thread-like growth lines and a distinct selenizone with slightly straight short lunulae, which are the general characteristics of the genus *Bellerophon*. The involute shell is slightly elongated and inflated and the whorl profile is moderately well rounded. The present specimens resemble *Bellerophon jonesianus* de Koninck, 1863. The specimens assigned as *B*. cf. *jonesianus* by Mansuy (1913*a*, p. 103, pl. 11, figs 1–2) from the Permian of Laos is the most similar form. The specimens assigned to *B*. *jonesianus* by Delpey (1941, p. 346, figs 21–22) from the Permian of Cambodia, by Waagen (1880, p. 135, pl. 8, figs 1–2) from the Permian of Pakistan and by Nützel & Nakazawa (2012, p. 109, fig. 8A–H) from the Permian of Japan also resemble the present specimens. The present specimens resemble *B*. *erawanensis* sp. nov. they have a more elongated shape, more distinct selenizone, stronger growth lines and wider interspaces between the thread-like growth lines.

Basal taxa that are certainly Gastropoda

Subclass uncertain

Order uncertain

Superfamily Euomphaloidea White, 1877

Family Euomphalidae White, 1877

***Euomphalus* Sowerby, 1814**

Type species. *Euomphalus pentangulatus* Sowerby, 1814, Carboniferous, Great Britain.

***Euomphalus* cf. *pronodocarinatus* Pan & Yu, 1993**
(Fig. 7)

cf. *Euomphalus pronodocarinatus* Pan & Yu, 1993: p. 36, pl. 2, fig. 4.

Material. Two specimens: ESKU-19-LP 61, 95.

Dimensions (mm): ESKU-19-LP 61: height = 1.7; width = 7.8. ESKU-19-LP 61: height = 2.0; width = 7.6.

Description. Small anisostrophic, discoidal shell; whorls rounded, convex, circular in transverse section, with the periphery at mid-whorl; whorls slowly increasing in diameter, only slightly embracing; suture deep; widely phaneromphalous with basal umbilicus deeper; whorl surface smooth with very faint and dense orthocline growth lines; rounded angulation on upper whorl surface at transition to upper umbilicus; base rounded; aperture subcircular, inner lip straight to somewhat concave.

Remarks. The present specimens closely resemble *Euomphalus pronodocarinatus* Pan & Yu, 1993 from the Lower Permian of Qixia Formation in Shangpingchuan, China in having a discoidal shape, a deep suture and numerous dense growth lines. However, the holotype of *E*. *pronodocarinatus* has nodes which are especially characteristic for this species that are absent in the studied material. *Straparollus* (*Straparollus*) *planorbiformis* de Koninck, 1881 as illustrated by Batten (1966*a*, p. 15, pl. 2, figs 12–14) from the Lower Carboniferous of the Hotwells Limestone, England is also similar in having rounded whorls with well-developed growth lines but it differs in being more high spired. Another similar species is *S*. (*Leptomphalus*) *micidus* Yochelson, 1956 (p. 220, pl. 12, figs 1–4) from the Middle Permian of Southwestern USA which is discoidal and has a weaker upper angulation. However, *S*. (*L*.)

micidus differs in having a sinus on the angulation of the upper whorl surface. There are other Permian euomphalid species which were reported from Southeast Asia such as *Discotropis* sp. from the Tak Fa Limestone of Thailand (Ketwetsuriya *et al*. 2016), *S.* (*Euomphalus*) sp. from Perak, Malaysia (Batten 1972), *E. khmerianus* Mansuy, 1912 from the Sisophon limestone of Cambodia (Mansuy 1912; Delpey 1941) and *E. subcircularis* Mansuy, 1912 (pl. 7, figs 7–8). In addition, the present species also resembles *S.* (*E.*) *alaskensis* Yochelson & Dutro, 1960 from the Permian Siksikpuk Formation, USA, but the present specimens lack an upper angulation on whorl and the former species is larger in size. The studied specimens might represent a new species of the genus *Euomphalus* but the present material too poorly preserved to characterize it sufficiently.

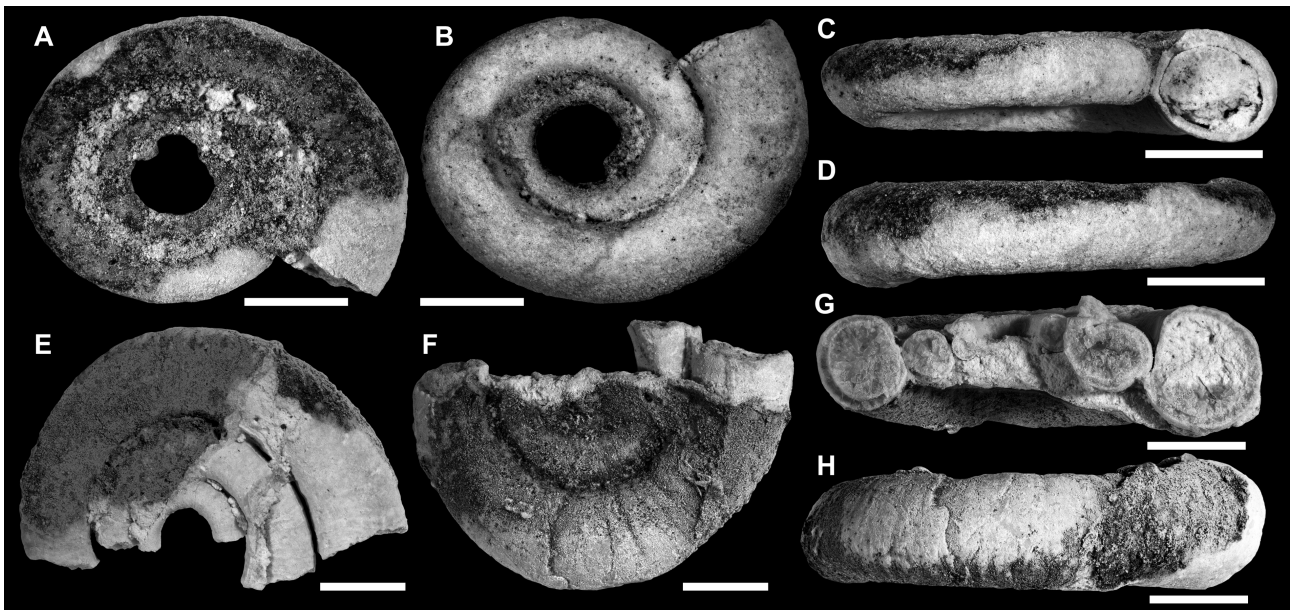

FIGURE 7. *Euomphalus* cf. *pronodocarinatus* Pan & Yu, 1993, A–D, ESKU-19-LP 61. E–H, ESKU-19-LP 95. All scale bars represent 2 mm.

Subclass Vetigastropoda Salvini-Plawen, 1980

Order uncertain

Superfamily uncertain

Family Holopeidae Cossmann, 1908

***Holopea* Hall, 1847**

Type species. *Holopea symmetrica* Hall, 1847, Middle Ordovician, USA.

***Holopea*? sp.**
(Fig. 8)

Material. Two specimens: ESKU-19-LP 2, 3.

Dimensions (mm): ESKU-19-LP 2: height = *c*. 3.8; width = 3.6. ESKU-19-LP 3: height = *c*. 6.3; width = 4.8.

Description. Turbiniform to naticiform, moderately high-spired shell consisting of three to four whorls (apex missing); whorls rapidly increasing strongly convex, rounded, embracing below periphery; whorl surface ornamented by prosocyrt, prosocline collabral ribs; ribs irregularly pace of unequal strength; suture impressed; base evenly convex; minutely phaneromphalous; aperture seemingly circular, columellar lip somewhat straight.

Remarks. These two incomplete specimens with deep suture, rounded whorls that bear collabral axial ribs

resemble the Ordovician genus *Holopea* which has never been reported from the Permian of Thailand. However, similar shell morphologies have been reported frequently from Palaeozoic and Mesozoic strata and were assigned to various other genera. For instance, *Coelostylina costata* Batten & Stoke, 1986, a putative representative of the basically Mesozoic genus *Coelostylina* from the Early Triassic of the U. S. is quite similar to our specimens. *H. bacca* Pan & Erwin, 2002 (p. 13, fig. 8.5–8.11) from the Permian of South China resembles the present specimens the most in general features. The coiling direction of the protoconch is important for species assignment and it is slightly oblique to the axis in *H. bacca*. The coiling direction of the protoconch in the studied specimens is poorly preserved, therefore the species treated in open nomenclature.

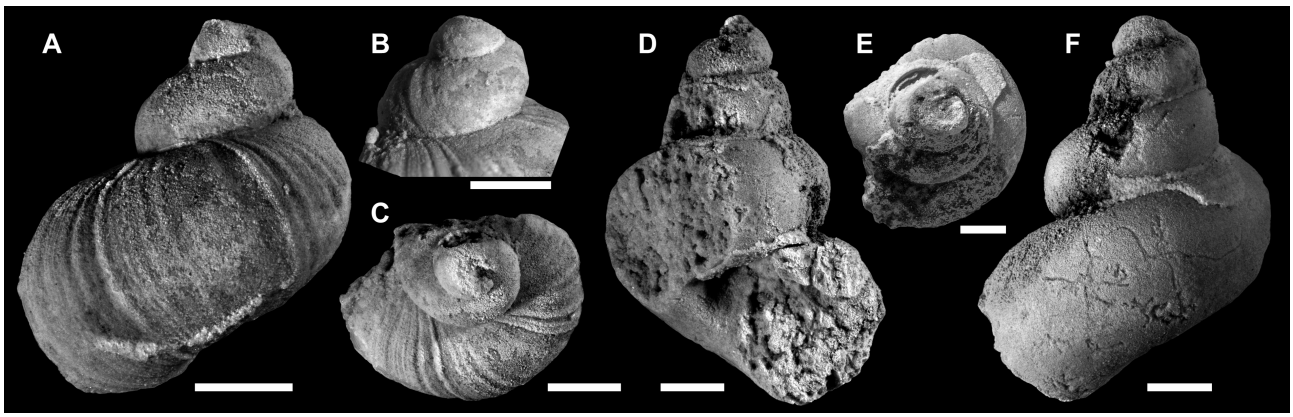

FIGURE 8. *Holopea*? sp., A–C, ESKU-19-LP 2. D–F, ESKU-19-LP 3. All scale bars represent 1 mm.

Order Pleurotomariida Cox & Knight, 1960

Superfamily Porcellioidea Koken in von Zittel, 1895

Family Porcelliidae Koken in von Zittel, 1895

Subfamily Porcelliinae Koken in von Zittel, 1895

***Porcellia* Léveillé, 1835**

Type species. *Porcellia puzo* de Koninck, 1883, Carboniferous, Belgium, original designation.

***Porcellia magninodosa* Pan, 1985**
(Fig. 9)

Porcellia magninodosa Pan, 1985: p. 35, pl. 2, fig. 10; Pan & Yu, 1993: 43, pl. 6, figs 1–4.

Material. Two specimens: ESKU-19-LP 91, 125, 126.

Dimensions (mm): ESKU-19-LP 91: height = 4.0; width = 11.7. ESKU-19-LP 125: height = 3.0; width = 7.4. ESKU-19-LP 126: height = 2.0; width = 9.4.

Description. Shell discoidal, pseudo-isostrophic, with 5 whorls; whorls well rounded; first whorl dextrally coiled, slightly elevated; later whorls planispirally coiled, expanding moderately; slit deep, extends one third of the whorl; selenizone narrow, concave, situated approximately at mid-whorl; selenizone bordered by two spiral lirae, representing periphery; upper and lower whorl face ornamented with *c*. 24 to 26 prominent, regularly spaced nodes or obliquely elongated (opisthocyrt) costae; suture deep and impressed; aperture subcircular.

Remarks. The present species is a typical representative of the genus *Porcellia* with its slightly elevated first whorls and nearly planispiral, dextrally coiled later whorls, with deep slit and very narrow selenizone. The present specimens closely resemble the type specimen of *Porcellia magninodosa* Pan, 1985 (p. 35, pl. 2, fig. 10) in shape,

size and ornaments as well as those assigned to *P. magninodosa* by Pan & Yu (1993, p. 43, pl. 6, figs 1–4) from the Late Permian of the Changxing Formation, China. Other similar species are *Porcellia paucituberculata* Pan & Erwin, 2002 (p. 10, fig. 5.10–13) from the Permian of Guangxi and Yunnan Provinces, South China and *P. nodosa* Hall, 1859. The latter was also reported from the Lower Permian Sisophon Formation, Cambodia (Delpey 1941, p. 365, fig. 39). *P. nodosa* differs from *P. magninodosa* in having a rectangular whorl profile and fewer costae. In *P. paucituberculata*, the nodes and the interspaces are wider and it has fewer costae compared to *P. magninodosa*.

This is the first known occurrence of the genus *Porcellia* in Thailand and the earliest occurrence of *P. magninodosa*. Our report extends the range of the species to the Middle Permian and expands its geographical range to further south in the Palaeo-Tethys.

The *Porcellia* species that have been recorded from the North America (e.g., Thein & Nitecki 1974; Kues 1984) and Europe (Haughton 1859; Batten 1966*a*) are from the Carboniferous of Panthalassa and the western Palaeo-Tethys, respectively. The *Porcellia* species reported from Asia are from the Permian of the eastern Palaeo-Tethys, e.g., *P. nodosa* Hall, 1859 from Cambodia (Delpey 1941), *P. puzoidea* Hayasaka, 1955 from Japan, *P. lingshuiensis* Pan, 1985 from China, *P. magninodosa* Pan, 1985 from China and Thailand and *P. paucituberculata* Pan & Erwin, 2002 from South China. Our report further fills the biogeographic gap between these Carboniferous and Permian occurrences.

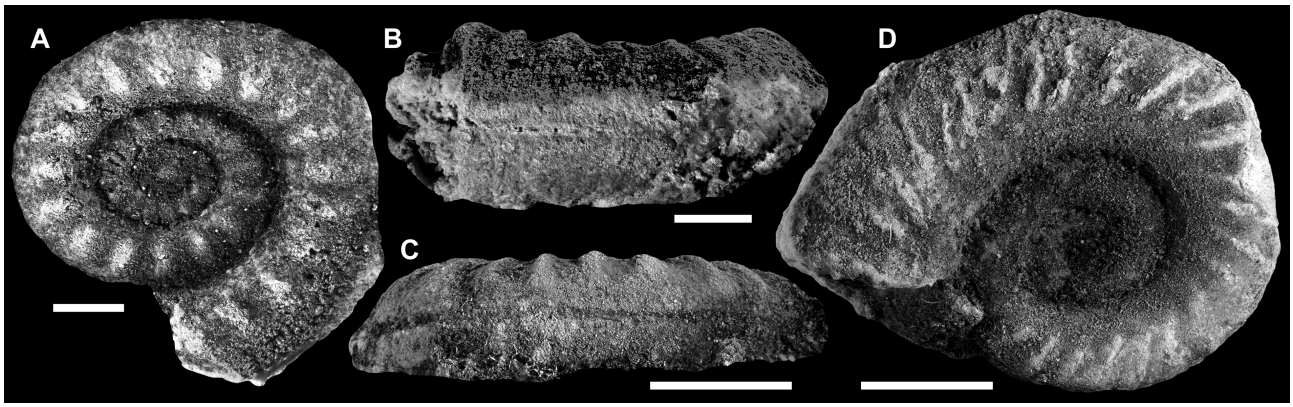

FIGURE 9. *Porcellia magninodosa* Pan, 1985, A–B, ESKU-19-LP 91. C, ESKU-19-LP 126. D, ESKU-19-LP 125. All scale bars represent 2 mm.

Superfamily Eotomarioidea Wenz, 1938

Family Eotomariidae Wenz, 1938

***Biarmeaspira* Mazaev, 2006**

Type species. *Biarmeaspira verideclinata* Mazaev, 2006, Permian, Russia.

Remarks. When Mazaev (2006) erected the genus *Biarmeaspira*, he tentatively placed it within the family Phymatopleuridae Batten, 1956 (see also Mazaev 2015). However, the characters regarding the selenizone suggest a placement within the family Eotomariidae. The members of Eotomariidae are characterized by a concave selenizone and the lower edge of their selenizone represents the shell periphery. The early shell development of genus *Biarmeaspira* as documented by Mazaev (2015) shares these characteristics with other Eotomariidae. As suggested by Mazaev (2006, 2015), *Biarmeaspira* probably derived from the eotomariid genus *Baylea*. This further supports its placement in the family Eotomariidae.

***Biarmeaspira mazaevi* sp. nov.**
(Fig. 10)

Etymology. After Alexey Mazaev for his work on the Late Palaeozoic gastropods and establishment of this genus.

Holotype. One specimen: ESKU-19-LP 1.

Dimensions (mm): ESKU-19-LP 1: height = 11.0; width = *c*. 9.5; apical angle = 100º.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell moderately high-spired, turbiniform, earliest whorls missing, 4 whorls preserved; early teleoconch whorls convex, ornamented by up to four spiral lirae; later spire whorls with sharp angulation at mid whorl face; upper whorl face above angulation develops a concave subsutural ramp; ramp ornamented with several spiral threads; selenizone narrow, angulated, situated at middle angulation, ornamented with obscure lunulae, bordered by two distinct spiral cords; lower whorl face flat to concave, subvertical inclined about 10 degrees from axis, ornamented with up to eight widely spaced fine spiral lirae; lower whorl face twice as wide as upper whorl face; suture shallow and indistinct; lower part of the lower whorl face ornamented by two strongest spiral cords, representing periphery, interspace between the two cords markedly concave, wide and ornamented with additional 2 fine spiral lirae, lowest cord represents the basal edge; profile near basal edge swollen; base convex, ornamented by numerous widely spaced fine spiral cords that are stronger and more widely spaced than those on ramp and lower whorl face; aperture unknown.

Remarks. This single specimen is placed in the genus *Biarmeaspira* due to the presence of an angular selenizone and a strong spiral ornament. The early teleoconch is absent and the growth lines and the aperture are poorly preserved so that this generic assignment is not entirely beyond doubt. Another genus having a prominent spiral ornament, a swollen basal edge and an angular selenizone is the Triassic genus *Sisenna*. *Sisenna* has a lower spire compared to *Biarmeaspira* and it possesses an angulation on the early whorl face which later turns into selenizone during ontogeny, a characteristic that is absent in *Biarmeaspira.*

Biarmeaspira mazaevi sp. nov. can be differentiated from other *Biarmeaspira* species by its ornamentation and by having a swollen basal edge. *B*.? *loatienensis* (Mansuy, 1914) from the Carboniferous of Loatien, Yunnan is very similar in shape, but is ornamented with more prominent spiral ribs on the upper and lateral whorl face. *B*.? *choueitangensis* (Mansuy, 1912, pl. 18, fig. 12) shows a similar whorl morphology and might be closely related.

Subfamily Neilsoniinae Knight, 1956

Apachella Winters, 1956

Type species. *Apachella translirata* Winters, 1956, Permian, USA.

Apachella thailandensis sp. nov.

(Fig. 11)

Etymology. After the country of Thailand.

Holotype. ESKU-19-LP 62.

Paratypes. Four specimens: ESKU-19-LP 25, 60, 89, 100.

Dimensions (mm): ESKU-19-LP 25: height = *c*. 9.4; width = 5.5; apical angle = 75º. ESKU-19-LP 62: height = 8.5; width = 5.2; apical angle = 60º. ESKU-19-LP 60: height = *c*. 4.6; width = *c*. 4.6. ESKU-19-LP 89: height = *c*. 7.1; width = *c*. 4.1; apical angle = 66º. ESKU-19-LP 100: height = *c*. 6.5; width = *c*. 4.8.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell high-spired, consisting of 8 whorls, first whorl planispiral; first two teleoconch whorls smooth, rounded, third whorl ornamented with spiral threads; selenizone starts within the 4th whorl; suture slightly impressed; subsutural ramp slightly convex, ornamented with 3–4 spiral ribs that are ornamented with nodes; selenizone concave, ornamented with very faint lunulae, bordered by two straight spiral ribs; lower rib forms periphery; lower whorl face twice as wide as the upper whorl face; lower whorl face slightly convex, ornamented with one spiral rib just above suture, equal in strength to spiral rib bordering the lower edge of selenizone; lower whorl face

further ornamented with two spiral threads between two spiral ribs; base convex, ornamented with several evenly spaced spiral ribs of same strength as ribs on lower whorl face; base convex, anomphalous; aperture unknown.

Remarks. *Apachella thailandensis* sp. nov. has a wider upper whorl face (above selenizone) than other species of *Apachella*. The ratio of the height of the upper and the lower whorl face of *A*. *thailandensis* sp. nov. is similar to that of *A*. *alimillana* (Girty, 1909). However, the latter lacks spiral ribs on upper whorl face. *A*. *powwowensis* Batten, 1995 has a wider selenizone, a median spiral lira on its selenizone and only one spiral rib on its upper whorl face. *A*. *franciscana* (Chronic, 1952) differs by having two faint spiral ribs on the upper whorl face adjacent to the suture, more prominent ribs bordering the selenizone, a stepped whorl profile and a higher whorl expansion rate.

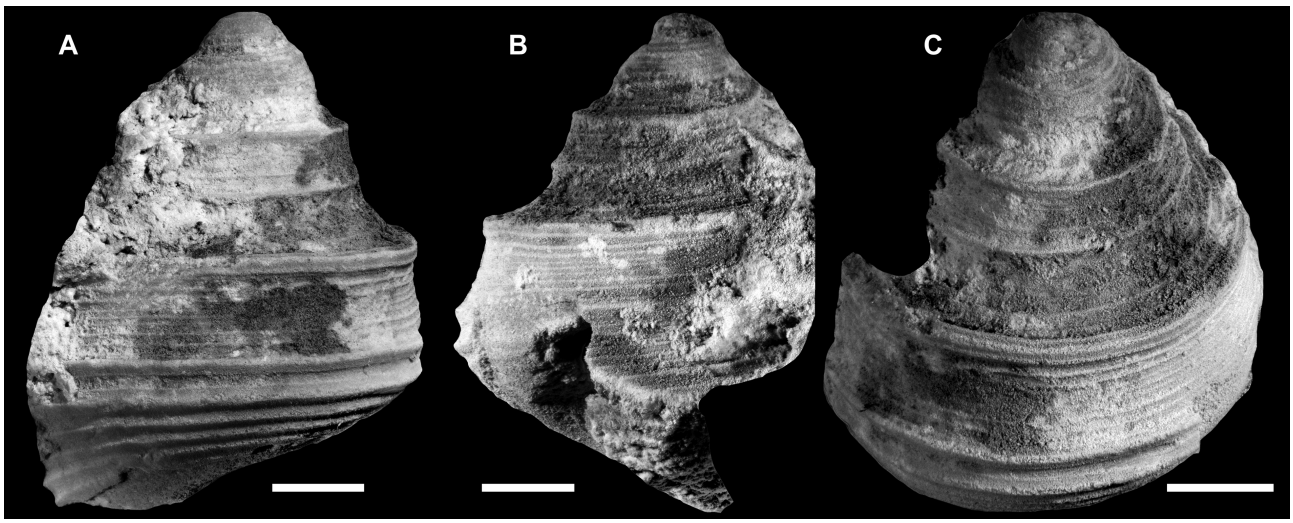

FIGURE 10. *Biarmeaspira mazaevi* sp. nov. ESKU-19-LP 1, holotype. All scale bars represent 2 mm.

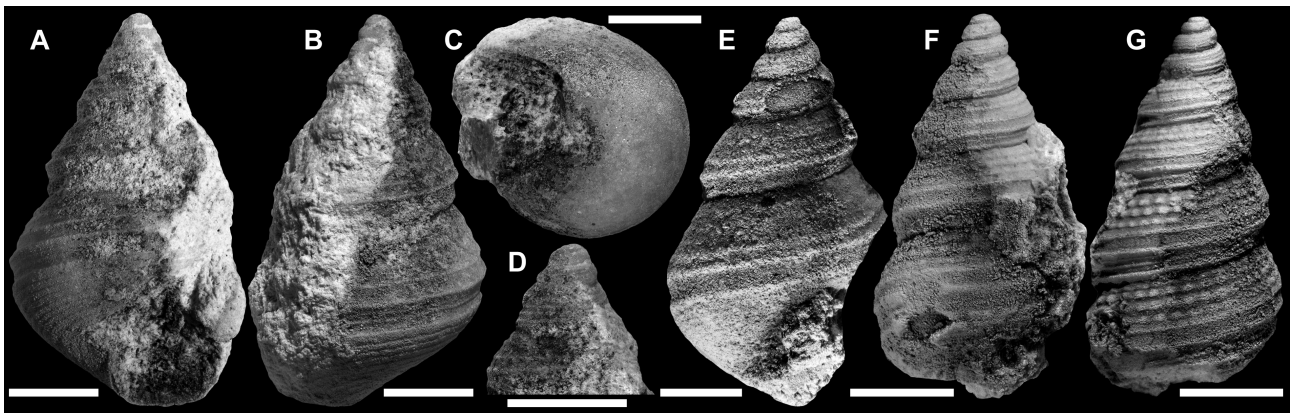

FIGURE 11. *Apachella thailandensis* sp. nov. A–D, ESKU-19-LP 62, holotype. E, ESKU-19-LP 25, paratype. F–G, ESKU-19-LP 89, paratype. All scale bars represent 2 mm.

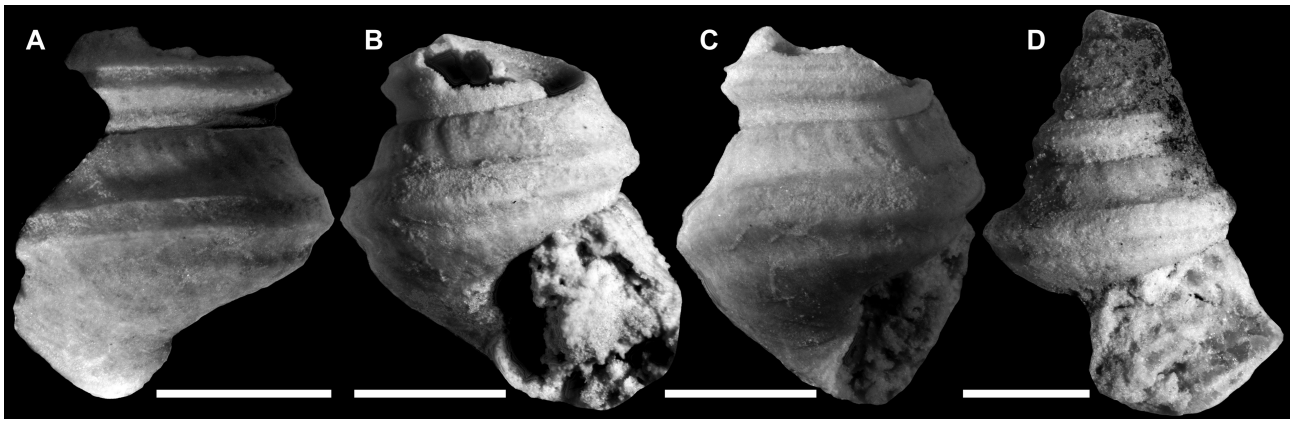

FIGURE 12. *Peruvispira* sp., A–C, ESKU-19-LP 10. D, ESKU-19-LP 68. All scale bars represent 1 mm.

***Peruvispira* Chronic, 1949**

Type species. *Peruvispira delicata* Chronic, 1949, Permian, Peru.

***Peruvispira* sp.**
(Fig. 12)

Material. Two specimens: ESKU-19-LP 10, 68.

Dimensions (mm): ESKU-19-LP 10: height = *c*. 2.7; width = *c*. 2.0. ESKU-19-LP 68: height = *c*. 3.3; width = 3.1.

Description. Shell small, conical, moderately high-spired; suture distinct, situated just below basal edge; whorl face above selenizone slightly convex near suture, concave above selenizone, ornamented with very faint, obliquely elongated, prosocline/prosocyrt subsutural nodes; upper whorl face three times as wide as the lower whorl face; selenizone wide, concave, slightly raised, situated at lower half of whorl face, bordered above and below by pronounced spiral cords; lower cord forms periphery; the whorl face below selenizone concave, smooth; basal edge rounded; base convex, smooth; aperture subovate, outer lip convex angular, basal lip convex, lower half of the columellar lip slightly reflexed; base anomphalous.

Remarks. The whorl profile is very similar to that of *Peruvispira turrita* Yu, 1980 from the Permian of Guizhou, but it is not clear whether the latter species has subsutural nodes or not. *P. allandalensis* Fletcher, 1958 and *P. trifilata* (Dana, 1847) from the Permian of Australia are other similar species but they differ in having collabral threads and a rather convex upper and lower whorl face.

Family Gosseletinidae Wenz, 1938

***Gosseletina* Fischer, 1885**

Type species. *Pleurotomaria callosa* de Koninck, 1843, Carboniferous, Belgium.

***Gosseletina microstriata* sp. nov.**
(Fig. 13)

Etymology. From Latin micro, meaning small, and Latin stria, meaning furrow, referring the tiny spiral ornaments.

Holotype. ESKU-19-LP 29.

Paratypes. Two specimens: ESKU-19-LP 5, 14.

Dimensions (mm): ESKU-19-LP 5: height = *c*. 3.8; width = *c*. 4.4. ESKU-19-LP 14: height = 2.2; width = 2.2. ESKU-19-LP 29: height = 7.3; width = 8.3.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Low-spired, globose shell, medium-sized, comprising *c*. 4.5 whorls; apex obtuse; spire distinctly elevated; body-whorl broad and inflated, covering approximately 80% of the entire height; whorls rapidly increasing; whorls distinctly convex; whorl surface with numerous very thin, faint spiral threads; whorls embracing at periphery; selenizone broad, situated high on whorl, above periphery, flush with whorl surface or very slightly convex, ornamented as on whorl face; suture impressed but shallow; base rounded; aperture unknown.

Remarks. *Gosseletina microstriata* sp. nov. differs from other *Gosseletina* species in several aspects. *G. aspeniana* (Girty, 1927) (Early Carboniferous, USA) is with faint spiral threads but differs by its whorl profile with distinctly convex whorl face above selenizone. *G. permiana* Batten, 1989 (Permian, USA) has a coarser spiral ornament and deeper sutures. *G. nodosa* Batten, 1966*a* (Early Carboniferous, England) has subsutural axial riblets

and lacks a spiral micro-striation. *G. portlockiana* (de Koninck, 1843) (Early Carboniferous, Europe) has a stronger spiral striation (Batten 1966*a*). *G. johnsoni* Thein & Nitecki, 1974 is more slender and has a cancellate ornament in subsutural position. *G. callosa* (de Koninck, 1843) (Carboniferous, Belgium), the type species of *Gosseletina*, lacks spiral ornament (Knight 1941). *G. persimplex* (Girty, 1915) (Pennsylvanian, USA) lacks spiral ornament and is more low-spired (Hoare 1961). *G. subglobosa* (Hall in Miller, 1877) (Early Carboniferous, USA) has a coarser spiral ornament. *G. spironema* (Meek & Worthen, 1866) (Pennsylvanian, USA) has a coarser spiral ornament and prosocyrt folds on whorl face above selenizone (Kues & Batten 2001).

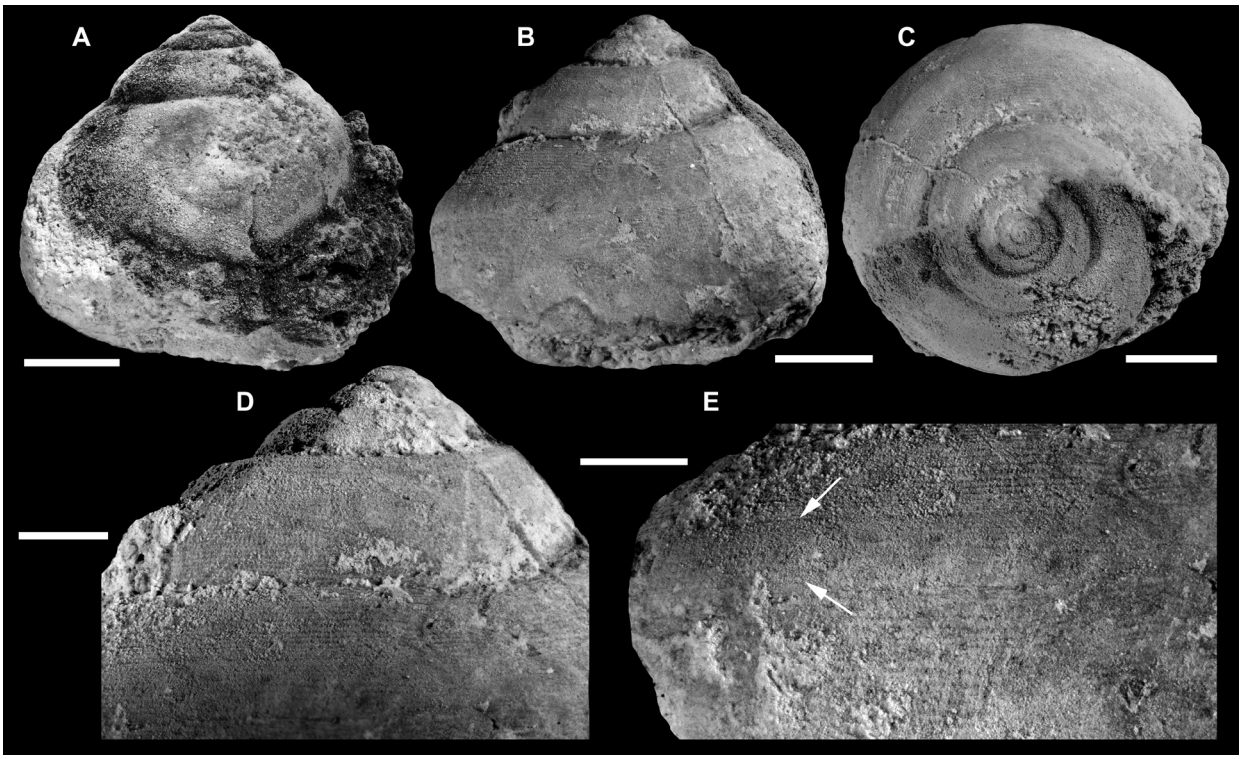

FIGURE 13. *Gosseletina microstriata* sp. nov., A–E, ESKU-19-LP 29, holotype. Scale bars represent: 2 mm (A–C); 1 mm (D–E). Arrows indicate the presence of selenizone.

Superfamily Pleurotomarioidea Swainson, 1840

Family Phymatopleuridae Batten, 1956

***Worthenia* de Koninck, 1883**

Type species. *Turbo tabulatus* Conrad, 1835, Carboniferous, Pennsylvania.

***Worthenia humiligrada* sp. nov.**
(Fig. 14A–I)

Etymology. From Latin humilis, meaning low, and Latin gradus, meaning step, referring to the low-stepped whorl profile.

Holotype. ESKU-19-LP 22.

Paratypes. ESKU-19-LP 23, 33, 34, 35, 74

Dimensions (mm): ESKU-19-LP 22: height = 6.8; width = 7.0; apical angle = 98º. ESKU-19-LP 23: height = 10.5; width = 12.7. ESKU-19-LP 33: height = *c*. 16.0; width = 13.8; apical angle = 92º. ESKU-19-LP 34: height = *c*. 9.0; width = 11.3; apical angle = 110º. ESKU-19-LP 35: height = *c*. 10.9; width = 13.6; apical angle = 110º. ESKU-19-LP 74: height = *c*. 1.7; width = *c*. 3.1.

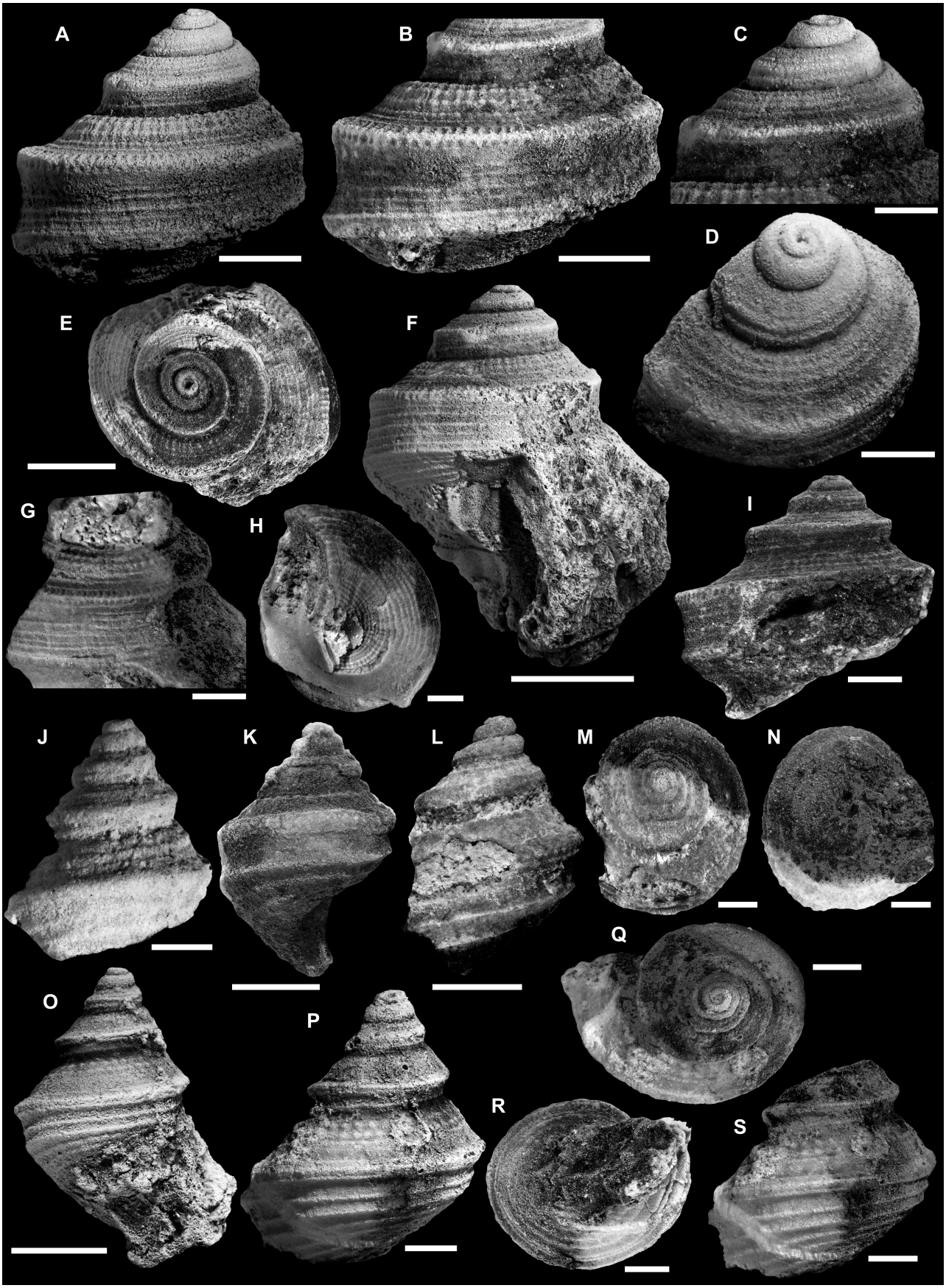

FIGURE 14. A–I, *Worthenia humiligrada* sp. nov. A–D, ESKU-19-LP 22. E–F, ESKU-19-LP 33. G–H, ESKU-19-LP 23. I, ESKU-19-LP 34. J–N, *Worthenia* cf. *pagoda* Mansuy, 1912, J, ESKU-19-LP 17. K–N, ESKU-19-LP 66. O–S, *Worthenia* sp., ESKU-19-LP 88. Scale bars represent: 2 mm (A, B, G, H, I, K, L, O); 1 mm (C, D, J, M, N, P–S); 5 mm (E, F).

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell low-spired for genus, gradate, trochiform; first whorl planispiral; early teleoconch whorls (about first two or three whorls) low-spired, smooth, convex, rounded; second and third whorls with fine spiral and axial ribs; suture distinct and impressed; later whorls sharply angulated at about mid-whorl face, the middle angulation separates subsutural ramp from subvertical lower whorl face; subsutural ramp slightly convex near adapical suture to concave on the remaining part; ramp inclining at an angle of 35–50°; subsutural ramp ornamented with up to eight spiral ribs and equally spaced prosocyrt fine collabral ribs or strengthened growth lines; spiral ribs and collabral ribs form nodes at intersections, forming fine reticulate pattern; ornamentation more prominent near adapical suture; lower whorl face subvertical, concave, ornamented with up to six strong spiral cords and numerous faint prosocyrt collabral threads or growth lines; mid angulation forms crest-like periphery of whorl where selenizone situated; selenizone sharply angular covered by v-shaped lunulae; lunulae form nodes when intersecting with angulation; selenizone bordered with fine spiral ribs, upper rib represents lowest spiral rib of subsutural ramp, while lower rib represents uppermost spiral rib of the subvertical lower whorl face; intersections of lunulae and angulation nodular; basal edge sharply angulated; base convex, ornamented by several evenly spaced spiral ribs and very weak opisthocyrt collabral threads; suture shallow, indistinct; narrowly phaneromphalous; aperture unknown.

Remarks. The convex early teleoconch whorls, the position and the ornamentation pattern of the selenizone suggest that this species belongs to the genus *Worthenia* de Koninck, 1883. The distinguishing characters of *Worthenia humiligrada* sp. nov. are the relatively low spire, wide umbilicus, weak subsutural convexity of the ramp, sharp angulation at the basal edge and nodular selenizone. The combination of these characters distinguishes *W. humiligrada* sp. nov. from the other species belonging to the genus *Worthenia*.

There are some similar Permian species in Southeast Asia which have been assigned to *Worthenia*, for instance *W. multicarinata* (Mansuy, 1912) from the Carboniferous of Yunnan, China (Mansuy 1912) and the Permian of Cambodia (Delpey 1941) and Malaysia (Batten 1972, p. 32, figs 36–38) is very similar in shape but it has more prominent subsutural nodes on the upper whorl face, a distinctly impressed suture and its basal edge is rounded angular and ornamented with nodes. The type specimens of *W. schirjaevensis* (Stuckenberg, 1905) from the Upper Carboniferous of Samara, Russia and the specimens assigned to *W. schirjaevensis* from the Permian of Cambodia (Delpey 1941, fig. 27) has a very similar whorl profile and ornamentation but they differ from *W. humiligrada* sp. nov. by having a higher spire. According to Batten (1972, fig. 38), *W. schirjaevensis* (Stuckenberg, 1905) lacks nodes on the selenizone. *W. arizonensis* Winters, 1963 from the Permian of Arizona is another species with planispiral early whorl but differs from *W. humiligrada* sp. nov. by having a narrower upper whorl face, a very prominent subsutural convexity, by lacking the sharp angulation at the basal edge and by having a very narrow or no umbilicus. *W. crenulata* Batten, 1989 from the Permian of southwestern United States, with steeper upper whorl face and more prominent nodes on its selenizone. The specimens assigned to *W. corrugata* Chronic, 1952 by Batten (1989) differ from *W. humiligrada* by having a stronger spiral ornament, a sharper collabral ornament and by the presence of axial folds on its upper whorl face. The specimens assigned to *W. corrugata* by Kulas & Batten (1997) from the Permian of Wyoming differ by having a narrow umbilicus and faint lunulae.

Worthenia cf. *pagoda* Mansuy, 1912

(Fig. 14J–N)

cf. *Worthenia pagoda* Mansuy, 1912: 39, pl. 7, fig. 6; Delpey, 1941: 353, fig. 26.

Material. Two specimens: ESKU-19-LP 17, 66.

Dimensions (mm): ESKU-19-LP 17: height = *c*. 6.6; width = 4.9. ESKU-19-LP 66: height = 5.5; width = *c*. 5.0; apical angle = 75º.

Description. Shell moderately high-spired, trochiform, consisting of 6 whorls; first three teleoconch whorls smooth, convex, rounded; mid angulation develops starting from the 4th whorl onward; the last quarter of the last whorl slightly deflected; suture slightly impressed; subsutural ramp with faint subsutural convexity, slightly concave on remaining part; ramp inclining at an angle of about 45–60°; subsutural ramp ornamented with three spiral ribs starting from 4th whorl and almost straight prosocline growth lines; spiral ribs ornamented with equally spaced

nodes; mid-angulation forms periphery where selenizone situated; selenizone prominent, wide, comprising about 1/7 of the whole whorl face of 5th whorl, ornamented with equally spaced strong nodes, bordered by fine spiral ribs; lower whorl face facing abapically, concave, ornamented with two nodular spiral ribs; lowest spiral rib stronger, situated at angulation, forming basal edge; base convex, ornamented by several evenly spaced nodular spiral ribs, narrowly phaneromphalous; aperture unknown.

Remarks. We tentatively assign the studied specimens to *Worthenia pagoda*, based on the whorl profile, the presence of three nodular spiral ribs on the upper whorl face and the nodular selenizone. Species with a similar whorl profile belonging to *Worthenia* are more common in the Triassic e.g., *W. annamensis* Mansuy, 1913*b* from Tonkin, Vietnam but are very rare in the Permian. *W.*? *psiche* (Gemmellaro, 1889) from the Permian of Italy has a similar shape but have only two spiral ribs on the upper whorl face.

Worthenia sp.

(Fig. 14O–S)

Material. One specimen: ESKU-19-LP 88.

Dimensions (mm): ESKU-19-LP 88: height = 6.4; width = 4.8; apical angle = 74º.

Description. Shell moderately high-spired, trochiform, consisting of at least 6 whorls; first two teleoconch whorls smooth, convex, rounded; third whorl ornamented with fine spiral threads; mid angulation develops starting from the 4th whorl; suture slightly impressed; subsutural ramp slightly convex, becoming concave just above selenizone; ramp inclining at an angle about 45–55°; subsutural ramp ornamented with four spiral ribs, uppermost two ribs ornamented with weak nodes, lowest one represents upper border of selenizone; mid angulation represents periphery where selenizone is situated; selenizone prominent, ornamented with equally spaced small nodes; lower whorl face concave just below the selenizone, slightly convex otherwise, ornamented with three spiral ribs, uppermost spiral rib represents lower border of selenizone; spiral ribs on lower whorl face stronger than ribs on ramp; suture situated between lowermost two ribs; base convex, ornamented with several evenly spaced, prominent spiral ribs of about same strength as ribs on lower whorl face; base anomphalous; aperture unknown.

Remarks. *Worthenia* sp. differs from *Worthenia* cf. *pagoda* in ornamentation pattern and has a narrower and less ornamented selenizone. The whorl profile of *Worthenia* sp. is similar to that of *W.*? *constantini* (Mansuy, 1912) from the Carboniferous of Yunnan, but the latter without nodular spiral ribs.

Altotomaria gen. nov.

Type species. *Altotomaria reticulata* sp. nov.

Etymology. From Latin alto, meaning high, referring both the high spire and the high position of the selenizone; -tomaria refers to the genus name *Pleurotomaria*, typical of the group Pleurotomarioidea to which the new genus belongs; gender feminine.

Diagnosis. Shell relatively high-spired; whorl face strongly ornamented with widely spaced spiral cords and narrowly spaced axial ribs or threads forming reticulate pattern; spiral cords more prominent than the axial ribs; periphery low on whorls in mature whorls, formed by strong spiral cord; selenizone above mid-whorl face, flush with the whorl face, bordered by two spiral cords, ornamented with widely spaced lunulae and median spiral thread; base anomphalous.

Remarks. Differences to other genera are discussed below.

Altotomaria reticulata sp. nov.

(Fig. 15)

Etymology. From Latin reticulata, meaning net-like, referring the reticulated ornament.

Holotype. Only specimen: ESKU-19-LP 83.

Dimensions (mm): Height = *c*. 5.8; width = 4.4.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell relatively high-spired, consisting of about 5 preserved whorls, whorls convex with periphery low on the whorl face; periphery in late teleoconch whorl with strong spiral cord angulating whorl face, first whorl(s) missing; first preserved whorl seemingly smooth (corroded), rounded; second whorl ornamented with spiral threads; whorl face above selenizone convex, narrow, ornamented with nearly orthocline regular axial threads and 2 spiral ribs, lower one bordering selenizone; selenizone situated above mid-whorl, flush with whorl face, ornamented regular with distinct lunulae and a median thread; selenizone bordered by two spiral cords; slit depth about 1/6 of last whorl; lower whorl face twice as wide as the upper whorl face; lower whorl face convex, ornamented with regularly spaced axial threads and 3 prominent, broad spiral cords, uppermost cord bordering selenizone; middle spiral cord strongest, representing periphery, interspace between spiral cords concave; suture slightly impressed, situated just below the lowermost spiral band; base convex, anomphalous, ornamented with axial threads and evenly spaced spiral cords of about same strength as those on upper whorl face; aperture unknown.

Remarks. The general whorl profile of *Altotomaria reticulata* sp. nov. is similar to that of species and genera of the subfamily Neilsoniinae but in *Altotomaria*, the lower edge of the selenizone does not represent the periphery and the selenizone is not raised above rest of the shell surface and as prominent as in neilsoniins. Median thread on selenizone has never been reported in Neilsoniinae. The reticulate ornament with stronger spiral cords, the relatively wide selenizone that is flush with the whorl face and bordered by two cords, the widely spaced regular lunulae that are in the same strength with the spiral ornaments, the presence of median thread on the selenizone suggest its affinity to the Triassic genera *Euryalox* Cossmann, 1897 and *Eymerella* Cossmann, 1897, therefore we tentatively place the new genus *Altotomaria* to Phymatopleuridae. The difference of the new genus from the latter two genera is the higher position of the selenizone. The position of the selenizone was regarded as informative for taxonomy and phylogeny (e.g., Knight *et al*. 1960). However, the position of the selenizone can differ among the species of the same genus (e.g., *Kokenella*, *Stuorella*) and may also change during ontogeny (e.g. *Pleurotomaria*, *Eirlysia*). *A. reticulata* sp. nov. resembles the neilsoniin species *Apachella exaggerata* Batten, 1989 (pl. 6, figs 3–10) from the Permian southwestern USA. Apart from the above discussed features that distinguish *Altotomaria* from the neilsoniin genera, *A. exaggerata* has less prominent spiral ornaments, sharper axial ornaments and differs in selenizone position.

Superfamily Seguenzioidea Verrill, 1884

Family Eucyclidae Koken, 1896

Ampezzalina Bandel, 1993

Type species. *Pleurotomaria calcar* Münster, 1841, Cassian Formation, Late Triassic, Carnian, Italy; original designation.

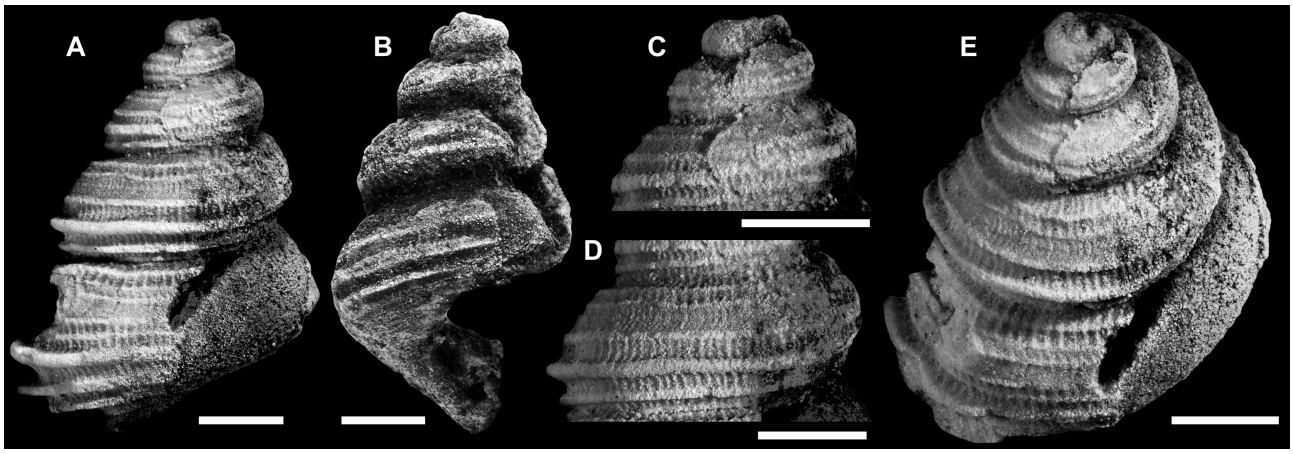

FIGURE 15. *Altotomaria reticulata* sp. nov. A–E, ESKU-19-LP 83, holotype. All scale bars represent 1 mm.

***Ampezzalina*? sp.**
(Fig. 16)

Material. One specimen: ESKU-19-LP 36.

Dimensions (mm): ESKU-19-LP 36: height = 8.9; width = 11.7.

Description. Shell trochiform, consisting of at least 2.5 whorl (apex missing); whorl face straight to slightly convex; whorl surface ornamented with at least seven spiral cords and equally spaced opisthocyrt fine collabral threads or strengthened growth lines; intersections between spiral cords and collabral threads forming a weak reticulate pattern with tiny nodes at intersections; six of the spiral cords equally strong; suprasutural spiral cord most prominent, representing shell periphery, with several coarse broken-off hollow spines; spines open in apertural direction, rounded convex in abapertural direction; base flatly convex, ornamented with spiral cords separated by concave interspace; the five strongest spiral cords situated at outer half of base; suture situated at outermost basal cord; basal cords evenly decreasing in prominence and more closely spaced toward umbilical area; minutely phaneromphalous; aperture not well-preserved but seemingly oblique.

Remarks. The single present shell probably represents a new species, but due to the state of preservation we refrain from erecting a new species. This shell is unique in that it has a well-developed spiny cord just above abapical suture. Spine-forming cords are known from Mesozoic vetigastropods e.g., in the family Eucyclidae (e.g., *Bandelastraea* Nützel & Kaim, 2014, *Ampezzalina* Bandel, 1993). *Ampezzalina* Bandel, 1993 and *Bandelastraea* Nützel & Kaim, 2014 might represent synonyms and their type species should be restudied. The single specimen has prominent suprasutural spines similar to type species of *Ampezzalina*; therefore, placed in *Ampezzalina* instead of *Bandelastraea*. *Ampezzalina* is so far only known from the Triassic. It is possible that the abapical spiny spiral cord of the present specimen is a selenizone and in that case it would represent a new genus. However, the preservation is insufficient to be sure.

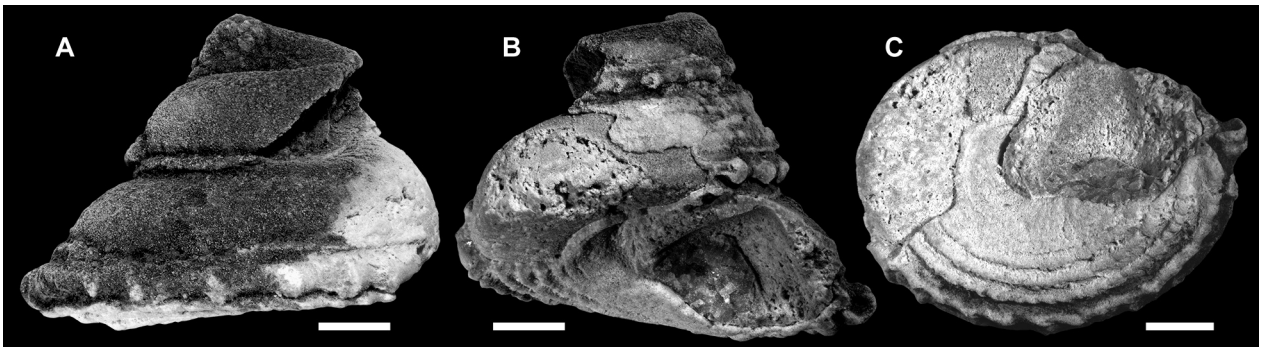

FIGURE 16. *Ampezzalina*? sp., A–C, ESKU-19-LP 36. All scale bars represent 2 mm.

Order Trochida Cox & Knight, 1960

Superfamily Trochoidea Rafinesque, 1815

Family Anomphalidae Wenz, 1938

***Anomphalus* Meek & Worthen, 1866**

Type species. *Anomphalus rotulus* Meek & Worthen, 1867, Carboniferous, USA.

***Anomphalus* cf. *vanescens* Yochelson, 1956**
(Fig. 17A–E)

cf. *Anomphalus vanescens* Yochelson, 1956: 253, pl. 22, figs 19–22; Pan & Yu, 1993: 46, pl. 9, fig. 3.

Material. Three specimens: ESKU-19-LP 30, 31, 50.

Dimensions (mm): ESKU-19-LP 30: height = 4.4; width = 7.7. ESKU-19-LP 31: height = *c*. 4.1; width = 6.7. ESKU-19-LP 50: height = 3.7; width = 5.5.

Description. Shell small, low-spired, rotelliform comprising about three whorls; whorls smooth, convex. embracing at periphery; whorls ornamented by numerous fine and dense prosocline collabral threads; upper whorl face somewhat flattened with convex periphery at mid-whorl; suture shallowly impressed, distinct; base flatly convex, narrowly phaneromphalous; umbilicus deep; aperture not certainly known.

Remarks. *Anomphalus vanescens* Yochelson, 1956 from the Permian of the Southwestern USA and from the Early Permian of China (Pan & Yu 1993, p. 46, pl. 9, fig. 3) is similar but has a flatter spire, whorls embrace above periphery and whorls are lower. *A. studiosus* Yochelson, 1956 (p. 254, pl. 22, figs 25–28) is also similar in shell shape as well as the rate of whorl expansion but has smaller size, a narrower umbilicus has a flatter spire and its whorls embrace above periphery. *A. fusuiensis* Pan & Erwin, 2002 from the Late Permian of South China is also similar but has lower, more rounded whorls, a wider umbilicus and a deeper suture. The Middle Permian species *A. lateumbilicatus* Nützel & Ketwetsuriya, 2016 from the Tak Fa Limestone of Thailand has a very wide umbilicus and consists of more whorls compared to the *A.* cf. *vanescens* at comparable size. *Anomphalus* sp. which is reported from the Tak Fa Limestone is also similar but has a wider umbilicus and a flatter spire. *Anomphalus* sp. from the Permian of Malaysia as reported by Batten (1979, p. 8, figs 10–11) is higher spired. The present specimens also resemble *A. japonicus* Nützel *in* Nützel & Nakazawa, 2012 from the Middle Permian of Japan but the latter has a wider umbilicus and a small umbilical ridge. The present species is probably undescribed but the preservation of the material is too poor for a safe species assignment, especially the aperture and the collabral threads is hardly visible in the studied specimens.

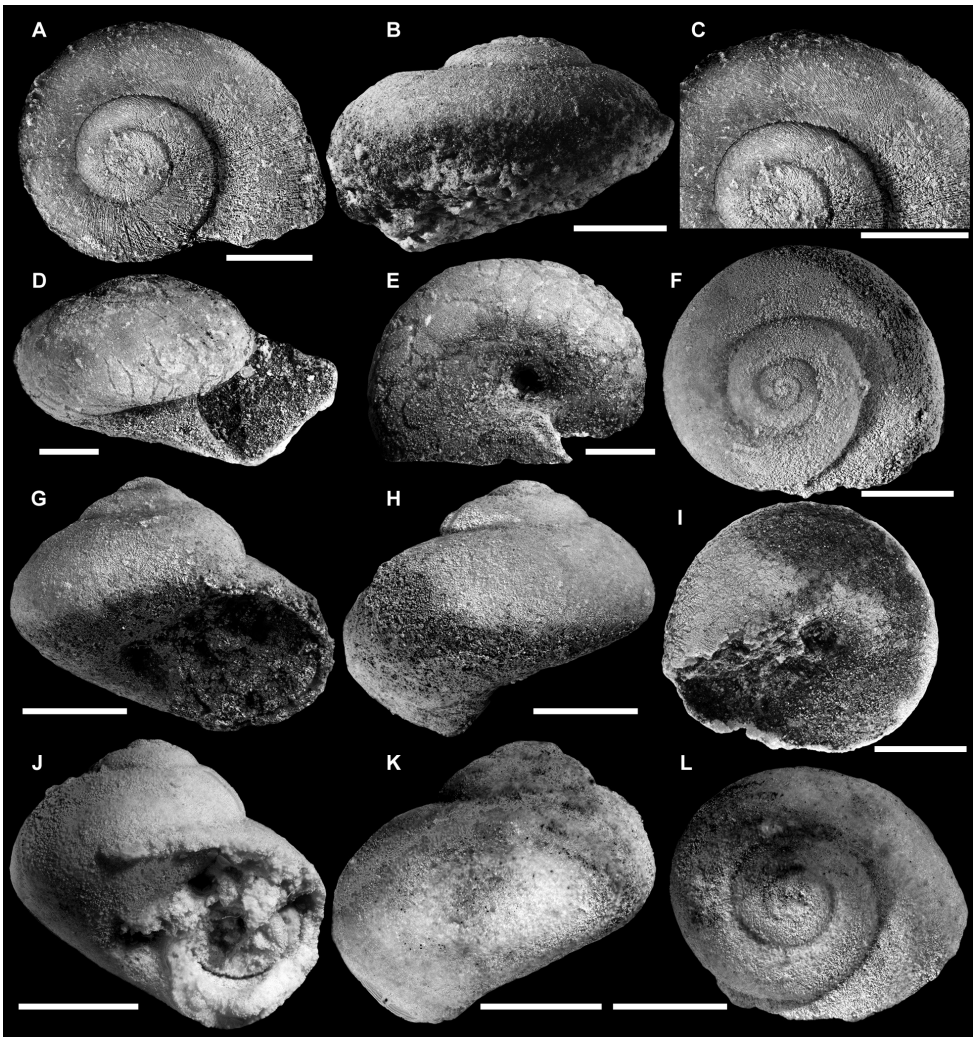

FIGURE 17. A–E, *Anomphalus* cf. *vanescens* Yochelson, 1956, A–C, ESKU-19-LP 30. D–E, ESKU-19-LP 50. F–L, *Anomphalus*? *blancus* Kues & Batten, 2001, F–I, ESKU-19-LP 67. J–L, ESKU-19-LP 96. Scale bars represent: 2 mm (A–C); 1 mm (D–L).

Anomphalus? *blancus* Kues & Batten, 2001
(Fig. 17F–L)

Anomphalus? *blancus* Kues & Batten, 2001: 44, figs 8.23–8.28.

Material. Two specimens: ESKU-19-LP 67, 96.

Dimensions (mm): ESKU-19-LP 67: height = 2.5; width = 3.0; apical angle = 124º. ESKU-19-LP 96: height = 2.3; width = 2.6; apical angle = 125º.

Description. Shell small, low-spired but spire clearly elevated, last whorl much higher than spire, turbiniform to naticiform, consisting of two to four whorls; whorls smooth, rounded, convex; whorls embrace at or slightly below periphery at mid-whorl; suture shallow but distinct; aperture somewhat circular, columellar lip straight to gently arched joining outer lip; base convex, minutely phaneromphalous.

Remarks. These specimens are very similar to the illustrations of *Anomphalus*? *blancus* Kues & Batten, 2001 (p. 44, fig. 8.23–8.28) from the Middle Pennsylvanian of New Mexico in shell shape and the whorl expansion rate. Kues & Batten (2001) assigned *A*.? *blancus* questionably to the genus *Anomphalus* due to its higher spired and more inflated shell which differs from typical species of *Anomphalus* in these respects that have low-spired or planispiral shells. The studied specimens also resemble the specimens assigned to *Anomphalus* sp. from the Permian of Malaysia by Batten (1979, p. 8, figs 10–11). However, the present specimens are more high-spired. Batten (1979) and Kues & Batten (2001) discussed that their specimens closely resemble the genus *Turbinilopsis* in shell shape and proportions of the shell, but *Turbinilopsis* is distinguished in having an obvious callus within the umbilicus. Other species of *Turbinilopsis* which have been reported from the Permian of Southeast Asia differ distinctly from the present material. *T*. *rotundus* Delpey, 1941 (p. 276, fig. 18) from Cambodia (see also Batten 1979) has a much more straight whorl face and a blunt apex. The specimens assigned to *Turbinilopsis*? sp. by Mansuy (1914, pl. 4, fig. 11) have a lower spire and hence a greater apical angle. The present specimens are placed tentatively in the genus *Anomphalus.* They are rather high-spired for this genus and hence become similar to the genus *Anematina* which generally is even more high-spired.

Family Araeonematidae Nützel *in* Nützel & Nakazawa, 2012

Remarks. *Yunnania*, *Araeonema* and *Rhabdotocochlis* were previously placed in Gyronematidae by Knight *et al*. (1960) but were placed in Araeonematidae by Nützel (2012) because these genera lack angulations.

Yunnania Mansuy, 1912

Type species. *Yunnania termieri* Mansuy, 1912, Late Carboniferous, China.

Yunnania inflata sp. nov.
(Fig. 18A–J)

Etymology. From Latin inflata, for having swollen, inflated whorl.

Holotype. ESKU-19-LP 9.

Paratypes. ESKU-19-LP 8, 16, 21, 38, 65, 98, two juvenile specimens: ESKU-19-LP 205, 212.

Dimensions (mm): ESKU-19-LP 8: height = 4.3; width = 3.9; apical angle = 87º. ESKU-19-LP 9: height = 5.0; width = 4.1; apical angle = 85º. ESKU-19-LP 16: height = 3.2; width = 2.8; apical angle = 80º. ESKU-19-LP 21: height = 8.9; width = 5.6; apical angle = 75º. ESKU-19-LP 38: height = 4.9; width = 3.9; apical angle = 87º. ESKU-19-LP 65: height = 5.4; width = 4.9; apical angle = 85º. ESKU-19-LP 98: height = 4.5; width = 4.6; apical angle = 87º. ESKU-19-LP 205: height = *c*. 1.9; width = *c*. 1.9; apical angle = 90º. ESKU-19-LP 212: height = *c*. 1.8; width = *c*. 1.9; apical angle = 96º.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district,

located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell small, turbiniform, cyrtoconoid with strong reticulate ornament; holotype comprising *c*. 5 whorls; first three to four whorls slightly convex, evenly rounded and low-spired, dome-shaped, without ornament or ornamented by very faint spiral threads; later whorls distinctly convex and inflated; periphery at about mid-whorl; suture impressed; whorls convex, embracing at about mid-whorl, slightly below periphery; whorls ornamented with about 10 evenly spaced spiral cords and numerous weaker collabral axial ribs; axial ribs prosocline slightly prosocyrt; spiral cords and axial ribs forming reticulate ornament with slightly nodular intersections; nodes strongest near upper suture; base convex with evenly rounded transition to whorl face, ornamented with up to 10 strong equally spaced spiral cords; base convex, anomphalous; aperture approximately circular; columellar lip straight.

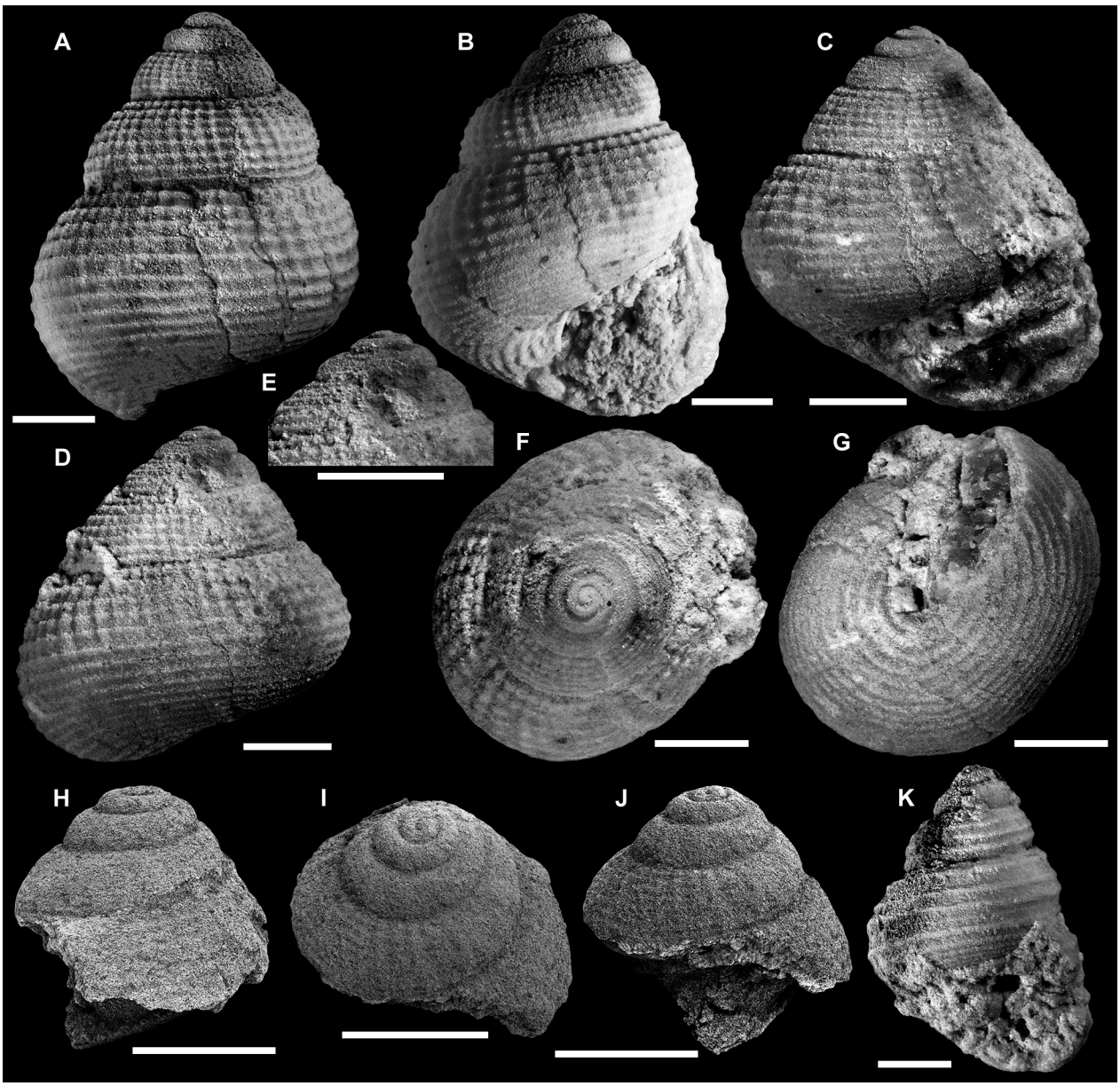

FIGURE 18. A–J, *Yunnania inflata* sp. nov. A–B, ESKU-19-LP 9, holotype; C–G, ESKU-19-LP 65, paratype. H–J, juvenile specimens, H–I, ESKU-19-LP 205. J, ESKU-19-LP 215. K, *Araeonema* cf. *tenuistriata* (Netchaev, 1894), ESKU-19-LP 99. All scale bars represent 1 mm.

Remarks. *Yunnania inflata* sp. nov. closely resembles *Yunnania meridionalis* Mansuy, 1914 (p. 41, pl. 4, fig. 10a–c) from the Permian Productus Limestone of Cambodia in shell shape, size and ornament on whorl face and base but *Y. meridionalis* has a deeper suture, its spiral cords are more pronounced and the axial ribs are less pronounced and less numerous *Y. meridionalis* has also been reported from another Permian deposits of Cambodia by

Delpey (1941) and from the Permian of Malaysia (Batten 1979). *Y. inflata* sp. nov. also resembles *Y. pulchra* Nützel & Ketwetsuriya, 2016 from the Middle Permian of the Tak Fa Limestone from Thailand (Ketwetsuriya *et al*. 2016, p. 499, fig. 16A–H) in shell shape and ornamentation but *Y. pulchra* has fewer but stronger spiral cords, the axial ribbing is denser, axial ribs are sharper, it has more convex and inflated whorls as well as the axial ribs of *Y. pulchra* are more distinct, dense and thinner. *Y. inflata* sp. nov. has much more inflated whorls than *Y. meridionalis* and *Y. pulchra*. *Y. inflata* sp. nov., improves our knowledge on the distribution of *Yunnania* in this region of the Indochina Terrane.

Araeonema Knight, 1933*a*

Type species. *Araeonema virgatum* Knight, 1933*a*, Pennsylvanian, USA.

Araeonema cf. *tenuistriata* (Netchaev, 1894)
(Fig. 18K)

cf. *Turbo tenuistriata* Netchaev, 1894; 349, pl. 11, fig 17.
cf. *Araeonema tenuistriata* (Netchaev, 1894); Mazaev 2015: 954, pl. 31, figs 1–8.

Material. One specimen: ESKU-19-LP 99.

Dimensions (mm): ESKU-19-LP 99: height = 4.2; width = 2.9; apical angle = 80º.

Description. Shell small, turbiniform; blunt apex; whorls weakly convex, evenly rounded; whorls ornamented by 4 strong spiral cords, and fifth emerging at abapical suture; spiral cords equally spaced with concave interspaces; base convex with rounded transition to whorl face, bordered by a strong spiral cord; base ornamented with 12 narrowly spaced spiral cords; sutures deep, distinct; aperture seemingly circular.

Remarks. The single specimen at hand closely resembles *Araeonema tenuistriata* (Netchaev, 1894) as reported by Mazaev (2015, p. 954, pl. 31, figs 1–8) from the Middle Permian of the Volga-Ural Region, Russia in shell shape, size and principal ornamentation. However, *A. tenuistriata* has a broader shell, more and weaker spiral cords and more convex whorls. *A. tenuistriata* is narrowly phaneromphalous but the umbilical area is not visible in the specimen at hand. *A. tenuistriata* is similar to *A. panthalassica* Nützel *in* Nützel & Nakazawa, 2012 from the Upper Middle Permian Akasaka Limestone, Japan but *A. panthalassica* is smaller, weaker spiral cords and a flatter apex. *A. virgatum* Knight, 1933*a* (p. 52, pl. 9, fig. 3) from the Pennsylvanian of the Labette Shale, Missouri, USA has more and much finer spiral cords and its whorl are less convex. Both, *A. novamexicanum* Kues, 2004 from the Laborcita Formation, New Mexico and *A. microspirulata* Yoo, 1994 from the Early Carboniferous of Australia are similar to the present specimen but those species are broader and have very fine and many more spiral cords. *A. problematicum* Wang *in* Wang & Xi, 1980 from the Permian of China is similar in shell shape but the ornamentation cannot be compared meaningfully because of its poor preservation. *A.* cf. *tenuistriata* resemble *Amaurotoma*? sp. as illustrated by Ketwetsuriya *et al*. (2016, p. 494, fig. 12A–C) from the Middle Permian Tak Fa Limestone, Thailand in having strong spiral cords, but differs in having a higher spire, steeper ramp and an angulated whorl profile. This is the first species which is referred to the genus *Araeonema* from Thailand and Southeast Asia.

Family Microdomatidae Wenz, 1938

Microdoma Meek & Worthen, 1867

Type species. *Microdoma conicum* Meek & Worthen, 1867, Pennsylvanian, USA.

Microdoma conicum Meek & Worthen, 1867
(Fig. 19A–C)

Microdoma conicum Meek & Worthen, 1867: 269, pl. 9, fig. 1; Knight 1933*a*: 48–49, pl. 9, fig. 1; Batten 1995: 25, fig. 34.

Material. One specimen: ESKU-19-LP 69.

Dimensions (mm): ESKU-19-LP 69: height = 4.5; width = 3.9.

Description. Shell conical, turbiniform consisting of *c*. 3 whorls (apex and early teleoconch whorls missing); whorl face nearly straight to slightly convex; periphery low on whorl just above suture; whorls ornamented by several collabral ribs which are separated in three rows of coarse nodes by two spiral grooves; suture shallow; base rounded and convex without ornament; seemingly minutely phaneromphalous; aperture sub-oval.

Remarks. The present material is very close to *Microdoma conicum* Meek & Worthen, 1867 as illustrated by Knight (1933*a*) from the Pennsylvanian of Missouri and by Batten (1995) from the Pennsylvanian of Texas, USA. The feature of ornamentation in the later whorls is identical with this species, although the present material lacks the early whorls. This species has been known only from the Pennsylvanian of USA. This is the first report of this species in the Palaeo-Tethys.

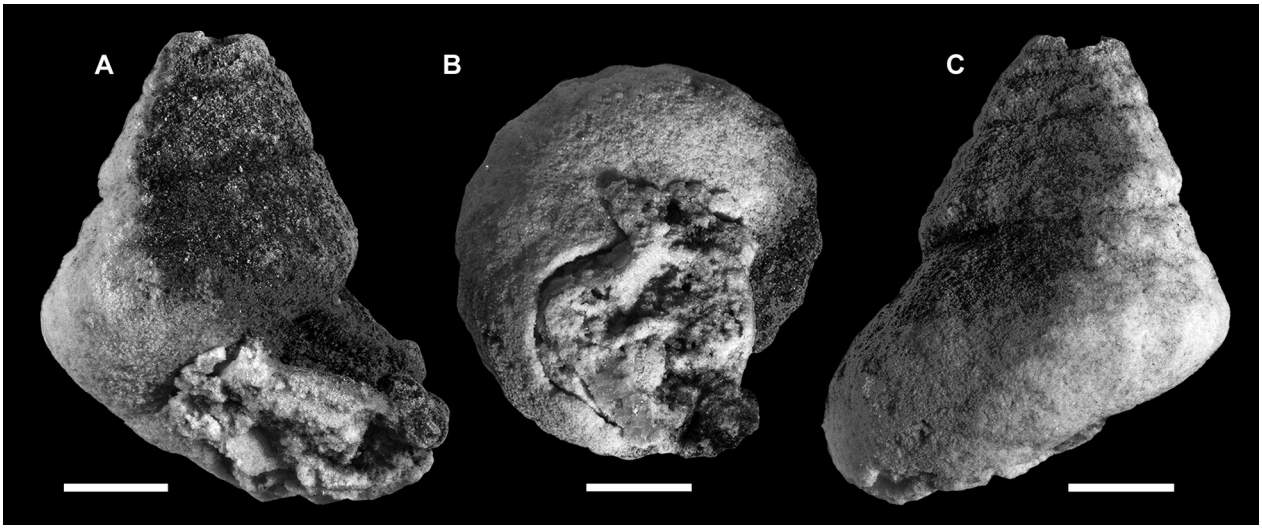

FIGURE 19 A–C, *Microdoma conicum* Meek & Worthen, 1867, ESKU-19-LP 69. All scale bars represent 1 mm.

Subclass Neritimorpha Koken, 1896

Superfamily Naticopsoidea Waagen, 1880

Family Naticopsidae Waagen, 1880

Subfamily Naticopsinae Waagen, 1880

***Naticopsis* McCoy, 1844**

Type species. *Naticopsis philippsii* McCoy, 1844, Early Carboniferous, Ireland.

***Naticopsis* sp. 1**
(Fig. 20A–C)

Material. One specimen: ESKU-19-LP 47.

Dimensions (mm): ESKU-19-LP 47: height = *c*. 8.3; width = 11.3; apical angle = 115º.

Remarks. The present specimen at hand shows 3 teleoconch whorls that are inflated and rapidly increasing. The shell is low-spired. Whorls are convex and the whorl profile is quite elongated. The surface of whorls is smooth. The suture is impressed and embraces the upper whorl surface. The aperture is broken, but it seems to be ovate with distinctly thickened callus on the parietal area. Judging from a single shell exhibiting the spire and half of the last body-whorl, the whorl profile of the studied specimen is similar to *Naticopsis khurensis* Waagen, 1880 (p. 100, pl.

9, fig. 10) from the Permian of Pakistan (Salt Range) but the latter differs in the absence of a callus. In contrast to the type specimen, the specimens illustrated and described as *N. khurensis* by Batten (1979, p. 13, fig. 15) from the Permian of Perak, Malaysia exhibits a callus. Nevertheless, the present specimen differs from the Malaysian specimen in having a more swollen upper whorl surface of the body-whorl. The specimens identified as *Neritina khurensis* by Delpey (1941, p. 271, fig. 13) from the Permian of Cambodia has a lower spire and its upper whorl surface is less inflated. Batten (1979) discussed that the degree of whorl curvature is highly variable in *N. khurensis*, so we cannot completely rule out the possibility that the studied specimen is conspecific to *Naticopsis khurensis*.

***Naticopsis* sp. 2**
(Fig. 20D–F)

Material. One specimen: ESKU-19-LP 46.

Dimensions (mm): ESKU-19-LP 46: height = 9.3; width = 10.3; apical angle = 112°; apertural height = 7.5; apertural width = 7.7.

Description. Moderately low-spired shell, naticiform, consisting of three rapidly expanding whorls; whorls smooth, strongly convex, rounded, embracing at periphery; spire low but distinctly elevated; body-whorl inflated, very large and much higher than spire with height about 90% of total height; periphery at about mid-whorl; base convex; suture shallow but impressed; anomphalous; aperture evenly rounded in cross section, lip thin, inner lip arched.

Remarks. *Naticopsis* sp. 2 differs from *Naticopsis* sp. 1 in having more flattened upper whorl surface, lacking callus, having a higher whorl expansion rate and a rounded aperture. It resembles *Naticopsis subovata* Worthen *in* Meek & Worthen (1873) as illustrated by Knight (1933*b*, p. 379, pl. 43, fig. 2a–j) in size, shell shape and pleural angle. *N. wortheni* Knight, 1933*b* (p. 377, pl. 43, fig. 3a–k) is also similar. Knight (1933*b*) mentioned that these two species, *N. subovata* and *N. wortheni,* are very close to each other but *N. subovata* can be differentiated from *N. wortheni* in having a swelling just above the mid-whorl height, and by the shape of the columellar lip, which is evenly crescent-shaped in *N. subovata* while it is slightly angled in *N. wortheni*. Although the parietal area of the present specimen is obscure it seems closer to *N. subovata*. The present specimen is also similar to the specimens illustrated and described as *N. praealta* Wanner, 1922 by Batten (1979; p. 14, fig. 16a–b) from the Permian of Perak, Malaysia but the latter specimens are more slender and relatively high-spired.

***Naticopsis*? sp. 3**
(Fig. 20G–I)

Material. One specimen: ESKU-19-LP 32.

Dimensions (mm): ESKU-19-LP 32: height = 5.3; width = 7.8; apical angle = 108°.

Description. Shell flatly turbiniform to naticiform with about three whorls (apex missing); spire elevated; rate of whorl expansion rapidly increasing; body-whorl broad, approximately 70% of the entire height; whorls rounded, strongly convex, with undulating, irregular axial ribs; base rounded; aperture unknown.

Remarks. The undulating, irregular axial ribs on the whorl surface and the broader body-whorl distinguish *Naticopsis* sp. 3 from the others present in this fauna. It might represent a new species, but the poor preservation prevents a further taxonomic assignment.

***Naticopsis*? sp. 4**
(Fig. 20J)

Material. One specimen: ESKU-19-LP 52.

Dimensions (mm): ESKU-19-LP 52: height = 6.0; width = 8.0; apical angle = 126°; apertural height = 4.2; apertural width = 5.2.

Remarks. The present specimen is low-spired with the spire only somewhat protruding, consisting of three

smooth rapidly increasing whorls. The body-whorl is very inflated, the height of the last whorl is about 90% of the total shell height. The aperture is broad with a thick inductura and seems to develop a columellar fold which has never been observed in *Naticopsis*. However, the preservation of the aperture is insufficient to be sure that a fold is really present.

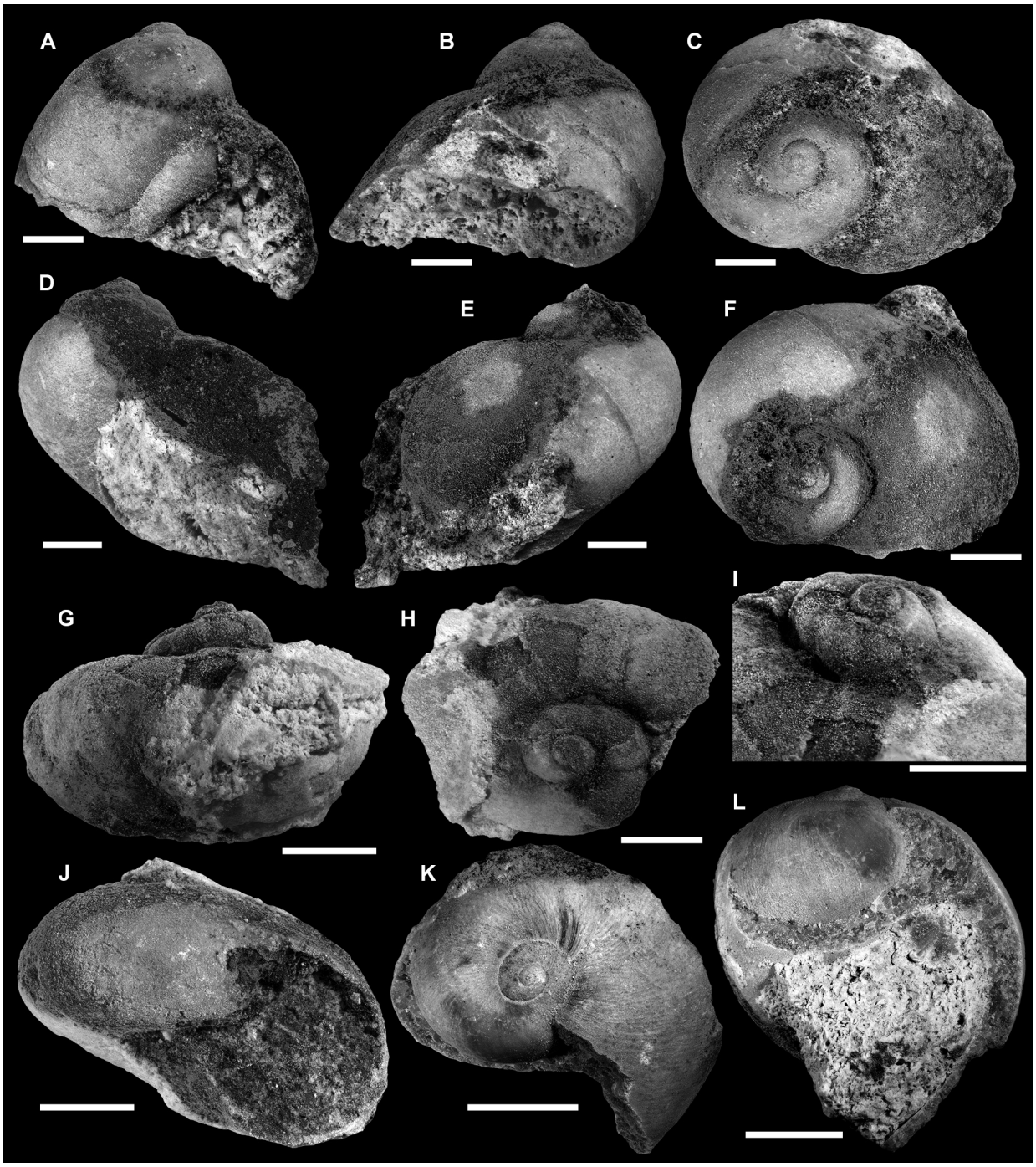

FIGURE 20. A–C, *Naticopsis* sp. 1, ESKU-19-LP 47. D–F, *Naticopsis* sp. 2, ESKU-19-LP 46. G–I, *Naticopsis*? sp. 3, ESKU-19-LP 32. J, *Naticopsis*? sp. 4, ESKU-19-LP 52. K–L, *Naticopsis* cf. *heshanensis* Pan & Erwin, 2002, ESKU-19-LP 44. Scale bars represent: 2 mm (A–J); 5 mm (K–L).

Naticopsis cf. *heshanensis* Pan & Erwin, 2002

(Fig. 20K–L)

cf. *Naticopsis* (*Naticopsis*) *heshanensis* Pan & Erwin, 2002: 21, fig. 11.12–11.17.

Material. One specimen: ESKU-19-LP 44.

Dimensions (mm): ESKU-19-LP 44: height = 19.0; width = 16.2; apical angle = 124°.

Description. Subglobose shell, very low-spired, medium-sized, comprising *c*. 3.5 whorls; apex obtuse; whorls rapidly increasing; body-whorl large and inflated, with flatly convex periphery; whorls embracing on preceding whorl, well above periphery; whorl surface with numerous fine, prosocyrt, distinct growth lines; suture adpressed; base convex; aperture unknown.

Remarks. This single globose shell with distinct, dense growth-lines resembles *Naticopsis* (*Naticopsis*) *heshanensis* Pan & Erwin, 2002 (p. 21, fig. 11.12–11.17) as reported from the Permian of Guangxi Provinces, South China, although the present specimen has a much lower spire than the holotype of *N*. (*N*.) *heshanensis*. The Permian species *N*. *permica* Netchaev, 1894 as illustrated by Mazaev (2015, p. 959, pl. 33, figs 1–5) from the Middle Permian of Volga Region, Russia is similar but has a higher spire, more convex whorls and less distinct growth lines.

Family Trachyspiridae Nützel, Frýda, Yancey & Anderson, 2007

***Trachydomia* Meek & Worthen, 1866**

Type species. *Naticopsis nodosa* Meek & Worthen, 1860, Carboniferous, USA.

***Trachydomia suwanneeae* sp. nov.**
(Fig. 21A–D)

Etymology. In honor of Suwannee Phomprasith for her work in biodiversity in Thailand.

Holotype. ESKU-19-LP 26.

Paratypes. ESKU-19-LP 27, 94.

Dimensions (mm): ESKU-19-LP 26: height = 12.1; width = 9.2; apical angle = 82°. ESKU-19-LP 27: height = 6.4; width = 5.7. ESKU-19-LP 94: height = 5.4; width = 4.2.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell naticiform to turbiniform; spire acute; whorls round, convex; body whorl distinctly higher than spire; whorls ornamented with distinct small nodes which are especially well-developed on the body whorl and weak or absent on the earliest preserved whorls; nodes roughly arranged in opisthocline arranged nodes; distance between nodes exceeds diameter of nodes; suture distinct; whorls convex with periphery at mid-whorl of body whorl but below mid-whorl of whorl face of spire whorls, with narrow subsutural ramp; base convex with gradually embracing of body whorl at transition below the periphery; aperture unknown; anomphalous.

Remarks. Based on the shell characters of the studied specimens such as having a naticiform shell and pustules on whorl face, the present material represents undoubtedly the genus *Trachydomia*. *Trachydomia suwanneeae* sp. nov. resembles most closely *T*. *dussaulti* Mansuy, 1913*a* (p. 101, pl. 11, fig. 5a–b) from the Permian Productus Limestone of Laos in shape and ornaments that was also reported by Batten (1979, p. 17, fig. 20) from the Permian of Perak, Malaysia and by Delpey (1941, p. 268, fig. 10) from the Permian of Cambodia. However, *T. dussaulti* is not as high-spired and hence its spire is not as acute. *T. dussaulti* has more nodes and the nodes are more densely spaced. The specimen illustrated as *T*. *dussaulti* Mansuy, 1913*a* by Delpey (1941) has a more distinctly inflated body whorl, a blunter spire and finer nodes, whereas the specimens assigned to *T*. *nodusum* (Meek & Worthen, 1866) by Delpey (1941, p. 268, fig. 9) is more similar to the present specimens in having an acute spire and a rather elongated shape. Knight (1933*b*) has reported several specimens of *T*. *nodusum* from the Pennsylvanian, USA (from which this species was originally described) differs distinctly from the studied specimens in having a lower spire, a broader and more pronounced ramp, stronger and coarser nodes and more inflated body whorl. *T*. *suwanneeae* sp. nov. also resembles *T*. *whitei* Knight, 1933*b*, both in having small and widely spaced nodes and a similar whorl profile but *T*. *whitei* differs from *T*. *suwanneeae* sp. nov. by its wider, more pronounced subsutural ramp, by being broader and by having stronger nodes. *T*. *suwanneeae* sp. nov. is also similar to *T*. *takhliensis* Nützel & Ketwetsuriya, 2016

(Ketwetsuriya *et al*. 2016, p. 502, fig. 19J–M) from the Middle Permian of the Tak Fa Limestone, Thailand. However, the shell of *T. takhliensis* is broader, its spire is less acute and it has more inflated body whorl. *T. takhliensis* has more densely spaced, somewhat coarser and more protruded nodes and a more pronounced ramp.

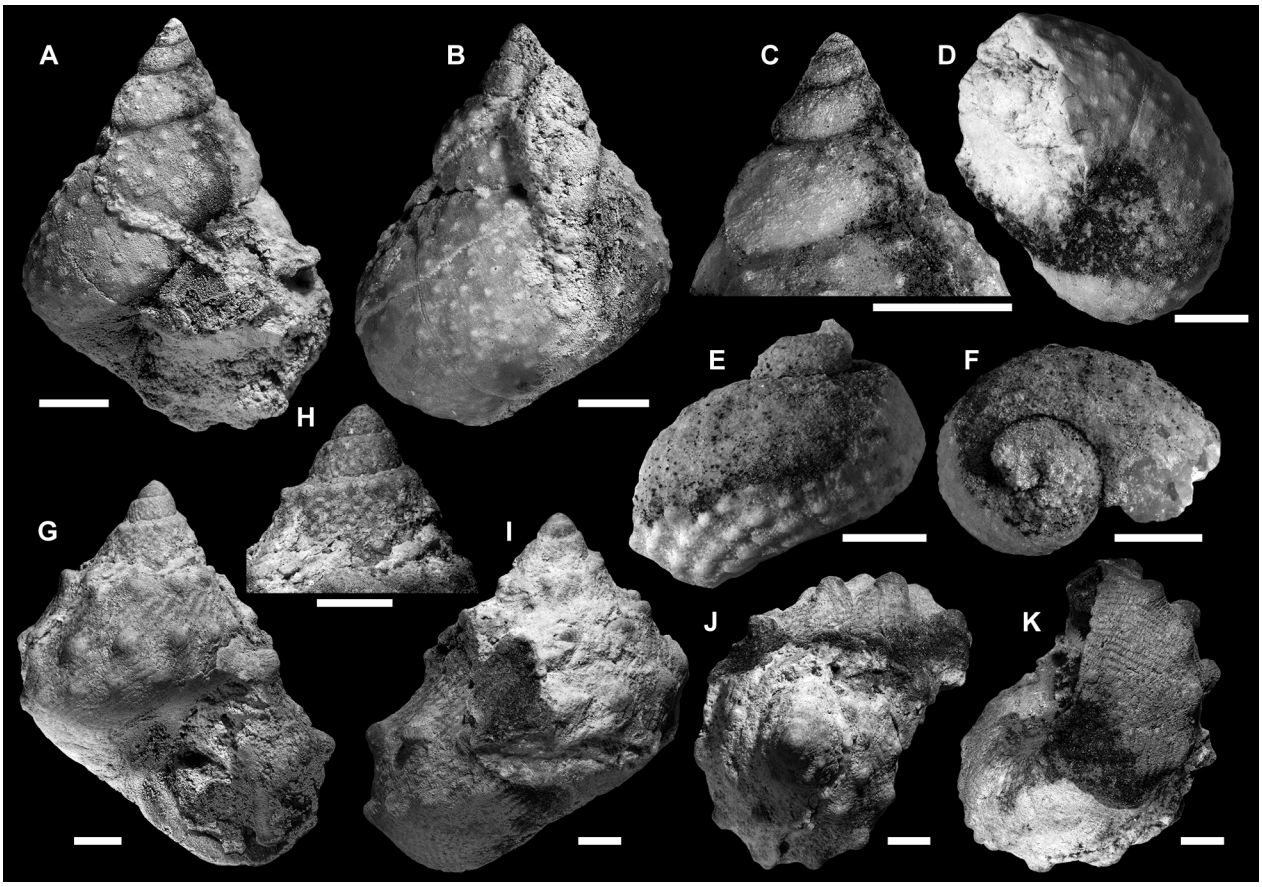

FIGURE 21. A–D, *Trachydomia suwanneeae* sp. nov., ESKU-19-LP 26, holotype. E–F, *Trachydomia* cf. *nodusum* (Meek & Worthen, 1866), ESKU-19-LP 92. G–K, *Trachyspira eleganta* sp. nov., ESKU-19-LP 28, holotype. Scale bars represent: 2 mm (A–D, G–K); 1 mm (E–F).

Trachydomia cf. *nodosum* (Meek & Worthen, 1866)

(Fig. 21E–F)

cf. *Trachydomia nodosum* (Meek & Worthen, 1866); Knight 1933: 383, pl. 45, fig. 2a–i.

Material. One specimen: ESKU-19-LP 92.

Dimensions (mm): ESKU-19-LP 92: height = *c*. 2.9; width = 3.2.

Remarks. The single specimen at hand represents has the general characteristics of the genus *Trachydomia*. It is naticiform, ornamented with distinct nodes on whorl face and has a rather deep suture. It seems to resemble *Trachydomia nodusum* (Meek & Worthen, 1866) as illustrated by Knight (1933*b*) from the Pennsylvanian of the U.S.A. This specimen can be differentiated from *T.* cf. *dussaulti* as described above in having coarser and denser nodes, an impressed suture, a subsutural ramp and a distinctly broader body whorl. The present specimen is too poorly preserved for a safe identification.

Trachyspira Gemmellaro, 1889

Type species. *Trachyspira delphinuloides* Gemmellaro, 1889, Permian, Italy; subsequent designation by Cossmann 1916.

***Trachyspira eleganta* sp. nov.**
(Fig. 21G–K)

Etymology. From Latin, meaning elegant, beautiful.

Holotype. Only one specimen ESKU-19-LP 28.

Dimensions (mm): ESKU-19-LP 28: height = 17.6; width = 13.3; apical angle = 75°.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Medium-size, moderately high-spired shell, conical , subturbiniform, consisting of approximately 5 whorls; apex acute, spire angle 75°; body whorl height about 80 percent of the total height; suture adpressed; earliest two whorls without visible ornament (preservation?), convex; following whorl with fine pustules and narrow shoulder; last two preserved whorls ornamented with two categories of nodes, large nodes arranged in spiral rows and fine, densely spaced nodes arranged in opisthocline rows tending to fuse to opisthocline ribs; body whorl with three rows of nodes,10–14 nodes per row; uppermost nodular row near adapical suture, forming edge of narrow ramp; middle row of nodes strongest, situated near abapical suture; third row with weakest nodes, situated on base; whorl angulated at nodular rows; whorl face concave between nodular rows; base rounded, anomphalous, ornamented with numerous spiral cords consisting of small pustules representing continuations of opisthocline rows on whorl face; aperture acute adapically, outer and anterior lip evenly rounded.

Remarks. This single specimen at hand is assigned to the genus *Trachyspira* Gemmellaro, 1889 which is characterized by having two different size-categories of nodes: numerous small pustules, aligned in opisthocline rows and few large nodes arranged in spiral rows (Knight *et al*. 1960). It is the first report of this genus from Thailand.

Trachyspira eleganta sp. nov. from the Khao Khad Limestone resembles the specimens illustrated and described as *T. obliquinodula* Wang, 1982 by Pan & Erwin (2002) from the Permian of Guangxi and Yunnan Provinces, South China. The type material of this species as illustrated by Wang (1982) is poorly preserved and not well-documented. However, these specimens as well as those illustrated by Pan & Erwin (2002) are much broader and stouter and hence have a larger apical angle (> 90°) and the nodules are much coarser.

The type species *T. delphinuloides* Gemmellaro, 1889 as illustrated by Batten (1979, p. 21, figs 29–31) from North Africa and Malaysia is also similar to *T. eleganta* sp. nov. in having three principal rows of nodes with the second row dominant but Batten's (1979) specimen have a larger apical angle and the second order pustules are larger in the African specimen. However, the original illustration of *T. delphinuloides* given by Gemmellaro (1889) shows a specimen with relatively small first order nodules that are spirally elongated. Knight (1941, pl. 56) figured a specimen form the type series that differs considerably from Gemmellaro's (1889) figure. Nevertheless, Knight (1941) identified this specimen as possible holotype. This specimen (probably the one used for the drawing in the Treatise, Knight et al. 1960, fig. 182/6) differs from our specimen in having a broader ramp, finer second order and stronger first order nodes, especially the adapical ones. *T. heshanensis* Pan & Erwin, 2002 (p. 25, fig. 12.11–12.14) from the Late Permian of China has a larger apical angle (close to 90°), the first order nodes are weaker at comparable growth stages and it lacks a third row of first order nodes on the base. *T. quangxiensis* Pan & Erwin, 2002 (p. 25, fig. 12.9–12.10) from the Late Permian of China has more convex whorls, a wider ramp and three instead of two rows of first order nodes on the whorl face.

Subclass Caenogastropoda Cox *in* Knight *et al*., 1960

Superfamily Soleniscoidea Knight, 1931*a*

Family Soleniscidae Knight, 1931*a*

Subfamily Soleniscinae Knight, 1931*a*

***Strobeus* de Koninck, 1881**

Type species. *Strobeus ventricosus* de Koninck, 1881, Mississippian, Belgium.

***Strobeus*? sp. 1**
(Fig. 22A–C)

Material. Two specimens: ESKU-19-LP 49, 90.

Dimensions (mm): ESKU-19-LP 49: height = *c*. 10.4; width = *c*. 10.9; apical angle = 90°. ESKU-19-LP 90: height = 6.5; width = 5.9; apical angle = 82°.

Description. Subglobose, broad, low-spired shell with elevated, acute spire; approximately four whorls; whorl embracing above periphery; whorls smooth; spire-whorls very slightly convex; periphery convex. Rounded; body-whorl very inflated, strongly convex, rounded; suture shallow; base evenly rounded, inductura seemingly thick; aperture acute adapically, broken abapically.

Remarks. The incomplete specimens resemble *Strobeus welleri* Knight, 1931*a* (p. 219, pl. 23, fig. 1) from the Desmoinesian (Pennsylvanian) Labette Shale of Missouri, USA. This species has also been reported from the Permian of Cambodia (Delpey, 1941; p. 61, fig. 54), the Middle Pennsylvanian of New Mexico (Kues & Batten, 2001; p. 85, fig. 16.30) and the Permian of Mexico (Sour-Tovar *et al*. 2005). The present specimens also resemble several other Late species representing *Strobeus* but it more low-spired than most of them. However, the broken aperture prevents an identification; presence or absence of columellar folds are important characters that cannot be seen in the present material.

***Strobeus*? sp. 2**
(Fig. 22D–E)

Material. Two specimens: ESKU-19-LP 217, 220.

Dimensions (mm): ESKU-19-LP 217: height = 1.4; width = 1.0; apical angle = 76°. ESKU-19-LP 220: height = 1.3; width = 1.0; apical angle = 78°.

Description. Shell fusiform, distinctly higher than wide with about three whorls (apex missing); periphery evenly rounded, convex; whorls embracing at or slightly above periphery; spire whorls slightly convex; whorls smooth; body-whorl inflated; suture shallow; base rounded, convex; anomphalous; aperture unknown.

Remarks. The two specimens resemble *Strobeus dongluoensis* (Pan & Yu, 1993) from the Upper Permian Changxing Formation, China (see also Pan & Erwin 2002; Nützel & Nakazawa 2012). The identification of the present specimens remains doubtful due to insufficient preservation.

Family Meekospiridae Knight, 1956

***Girtyspira* Knight, 1936**

Type species. *Bulimella canaliculata* Hall, 1856, Carboniferous, USA.

***Girtyspira*? sp.**
(Fig. 22F)

Material. One specimen: ESKU-19-LP 222.

Dimensions (mm): ESKU-19-LP 222: height = *c*. 1.0; width = 0.6.

Remarks. This very small single specimen is smooth and has slightly convex whorl with blunt apex and possess triangular-shaped aperture. It resembles *Girtyspira yodai* Erwin, 1988 from the Permian Cathedral Mountains Formation of West Texas. However, *Girtyspira yodai* species has much more slender shell and impressed suture.

Heterosubulites* Bandel, 2002*a

Type species. *Ceraunocochlis blatta* Knight, 1931*a*, Pennsylvanian, USA.

***Heterosubulites longusapertura* sp. nov.**
(Fig. 22G)

Etymology. Latin, because of the long-shape aperture.

Holotype. Only one specimen: ESKU-19-LP 215.

Dimensions (mm): ESKU-19-LP 215: height = 1.6; width = 0.9; apical angle = 82°.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell very small, fusiform; whorls smooth; whorls embracing high on the whorls; whorls evenly convex with periphery above mid-whorl; spire whorls only slightly convex; spire small, blunt, rounded; body-whorl inflated, much higher than spire with height about 90% of total height; sutures indistinct; base flat; aperture elongated, narrow, with wide and short anterior siphonal canal; outer lip almost straight.

Remarks. *Heterosubulites longusapertura* sp. nov. is very close to the type species *H. blatta* (Knight, 1931*a*, p. 203–204, pl. 21, fig. 2a–d) (see also Bandel 2002*a*) from the Pennsylvanian of Missouri, USA in shape, size and shell proportions, but *H. longusapertura* n. sp. differs from *H. blatta* having a narrower aperture, a much broader anterior siphonal canal and a much more arched outer lip. *H. fusiformis* Nützel, 2012 from the Middle Permian Akasaka Limestone, Japan is also similar but its shell is larger, the shell is more slender, whorls embrace lower on preceding whorl, its aperture is wider and its anterior siphonal canal is narrower.

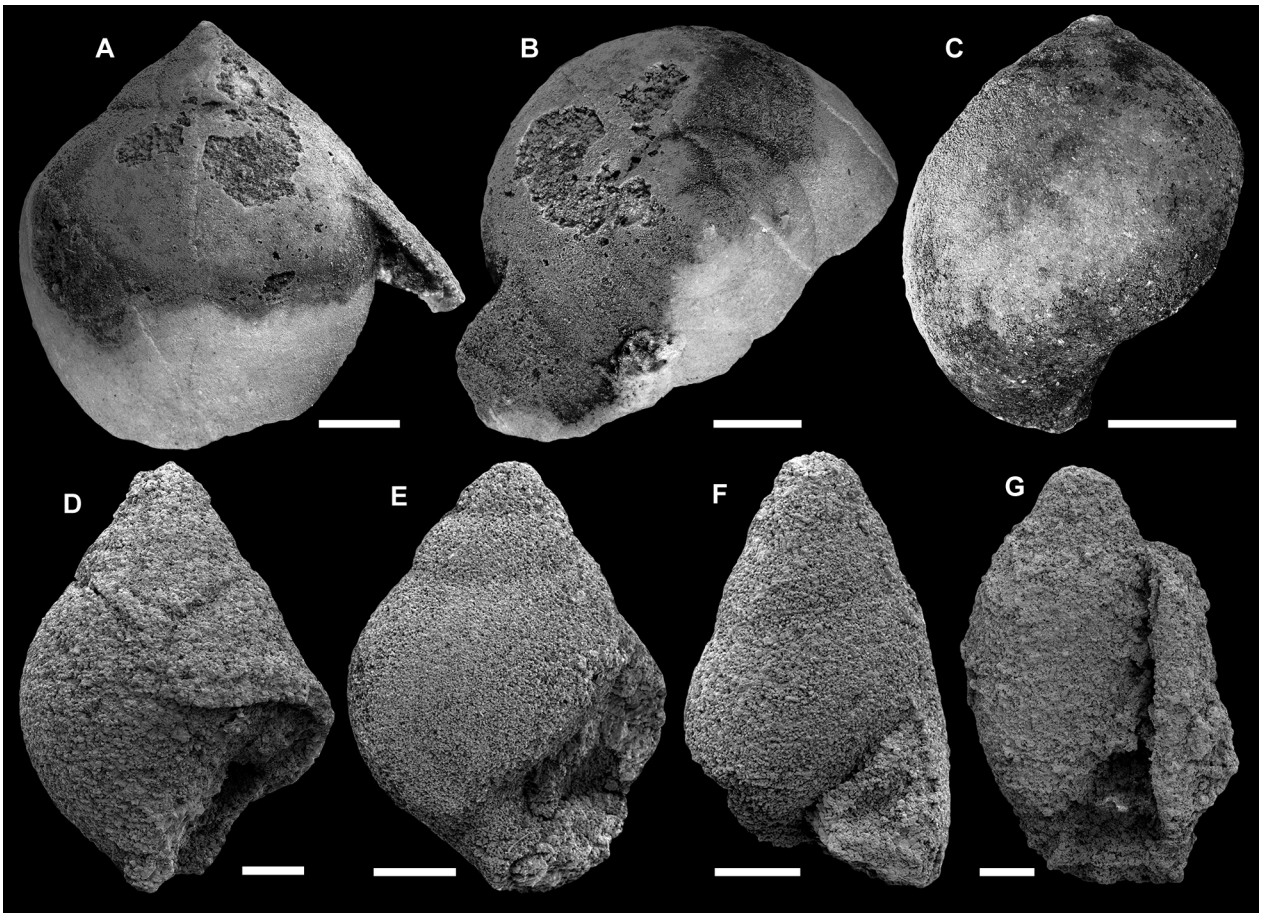

FIGURE 22. A–C, *Strobeus*? sp. 1, A–B, ESKU-19-LP 49. C, ESKU-19-LP 90. D–E, *Strobeus*? sp. 2, D, ESKU-19-LP 217. E, ESKU-19-LP 220. F, *Girtyspira*? sp., ESKU-19-LP 222. G, *Heterosubulites longusapertura* sp. nov. ESKU-19-LP 215, holotype. Scale bars represent: 2 mm (A–C); 200 μm (D–G).

Superfamily Palaeostyloidea Wenz, 1938

Family Pithodeidae Wenz, 1938

***Platyzona* Knight, 1945**

Type species. *Platyzona trilineata* (Hall, 1856), Carboniferous, USA.

Remarks. Nützel *in* Nützel & Nakazawa (2012) placed *Platyzona* in Caenogastropoda because Pan & Erwin (2002) reported the presence of caenogastropod larval shell of this genus from the latest Permian of South China.

***Platyzona gradata* sp. nov.**
(Fig. 23)

Etymology. From Latin gradata, because of the gradate spire.

Holotype. Only one specimen: ESKU-19-LP 11.

Dimensions (mm): ESKU-19-LP 11: height = 11.6; width = 8.3; apical angle = *c*. 72°.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Moderately high-spired, turbiniform shell consisting of 6 whorls (apex missing) with a step-like whorl profile; early teleoconch whorls (first three whorls) rounded, convex, with an ornament of faint spiral threads (maybe due to preservation); upper whorl surface of later whorls developing wide, steeply inclined ramp; ramp slightly convex to straight ornamented by *c*. 8 to 10 equally spaced spiral threads; selenizone wide and flat, approximately 0.8 mm wide, covering almost half of whorl height of body-whorl, situated below ramp; adapical border of ramp at about mid-whorl, forming also angulated border of ramp; outer whorl surface of selenizone almost straight, parallel to shell axis, bordered by two spiral threads followed by strong spiral cords; selenizone with curved transverse lunulae; adapical spiral rib forming periphery; abapical spiral somewhat above lower suture; whorls embracing somewhat below abapical spiral rib; suture distinctly impressed; base flatly convex with numerous evenly spaced spiral threads, shallowly phaneromphalous; aperture not well-preserved, seemingly with straight columellar lip.

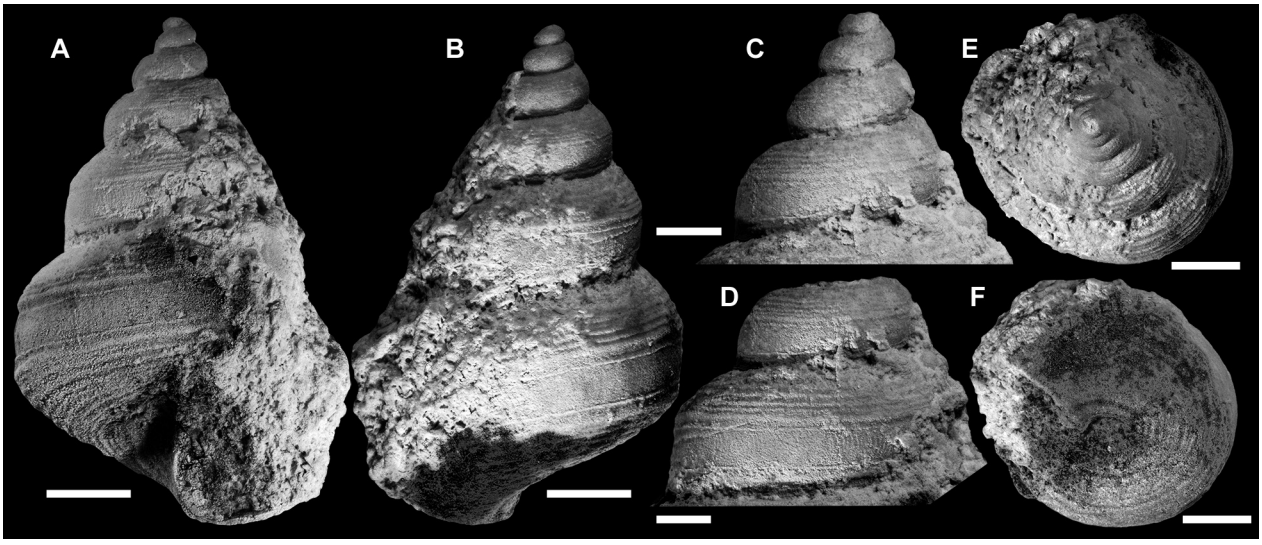

FIGURE 23. *Platyzona gradata* sp. nov., A–F, ESKU-19-LP 11, holotype. Scale bars represent: 2 mm (A–B, E–F); 1 mm (C–D).

Remarks. *Platyzona* is reported from Thailand for the first time. Several species of this genus have been reported from other Permian assemblages from Asia e.g., from Cambodia (Mansuy 1913*a*; Delpey 1941), Perak, Malaysia (Batten 1972), South China (Pan & Erwin 2002) and from the Akasaka Limestone, Japan (Nützel & Nakazawa 2012). It has also been reported from the USA (Batten 1989).

The single specimen at hand resembles the paratype of *Platyzona dongluoensis* (Pan & Yu, 1993) from the Upper Permian Changxing Formation of south China (Pan & Yu 1993, pl. 8, fig. 3a–c). However, the holotype of this species differs considerably from the paratype and from the present specimen in having a narrow selenizone at mid-whorl and in other characters (Pan & Yu 1993, pl. 8, fig. 2a–b). The paratype of *P. dongluoensis* represents the genus *Platyzona* but the holotype and hence the species itself does not, the species reported by Pan & Erwin (2002) as of *P. dongluoensis* from the Late Permian of China resembles the misidentified paratypes of this species and *P. gradata* sp. nov. and could be conspecific.

P. nodohumerosa Batten, 1972 from the Permian of Malaysia resembles *P. gradata* sp. nov. but has a nodular ornament and distinct spiral cords or lirae on the selenizone. *P. eulkaiensis* (Reed, 1927) as illustrated by Batten (1972) from the Permian of Malaysia and by Nützel & Nakazawa (2012) form the Permian of Japan is also similar but has a narrower selenizone that is lower on the whorls (just above the suture) and a weaker spiral ornament.

Three Late Permian species from South China have been assigned to *Platyzona* by Pan & Erwin (2002): *P. pulchella* Pan & Erwin, 2002 lacks spiral cords and has more pronounced growth-lines. *P. nitella* Pan & Erwin, 2002 is broader and has more pronounced lunulae. *P. luculenta* Pan & Erwin, 2002 is based on an early juvenile specimen (protoconch and 1.5 teleoconch whorls). In contrast to *P. gradate* sp. nov., it has strong spiral cords on the earliest teleoconch and the selenizone is higher on the whorls.

Four Permian species from SW USA have been assigned to *Platyzona* by Batten (1989): *P. rotunda* Batten, 1989 is broader and has entirely rounded whorls. *P. cancellata* Batten, 1989 has a much narrower selenizone and a cancellate ornament. *P. pagoda* Batten, 1989 is more slender and has a concave selenizone and has entirely rounded whorls. *P. anguispira* Batten, has uncoiled whorls.

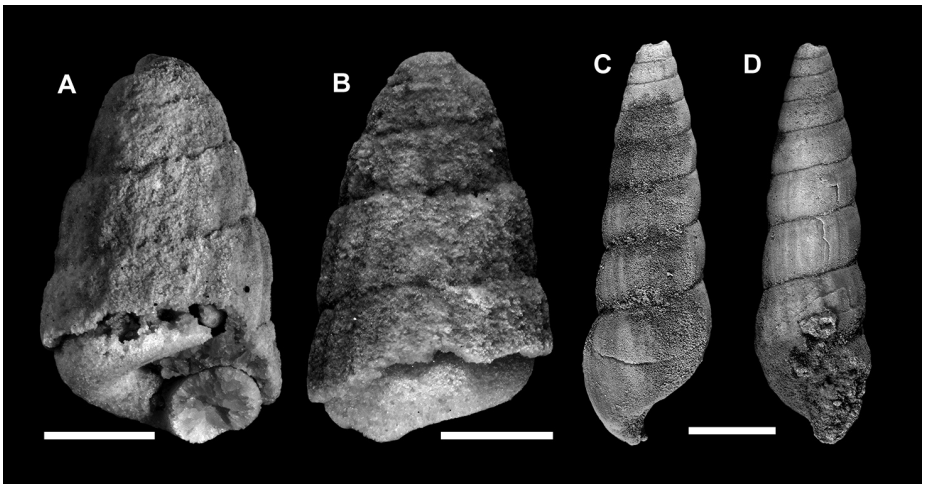

FIGURE 24. A–B, *Palaeostylus* sp., ESKU-19-LP 7. C–D, *Pseudozygopleura*? sp., ESKU-19-LP 63. Scale bars represent: 1 mm (A–B); 2 mm (C–D).

Family Palaeostylidae Wenz, 1938

Subfamily Palaeostylinae Wenz, 1938

***Palaeostylus* Mansuy, 1914**

Type species. *Palaeostylus pupoides* Mansuy, 1914, Permian, Cambodia.

***Palaeostylus* sp.**
(Fig. 24A–B)

Material. One specimen: ESKU-19-LP 7.

Dimensions (mm): ESKU-19-LP 7: height = 3.6; width = 2.2; apical angle = 84°.

Remarks. This small, high-spired, cyrtoconoid, shell has a straight whorl face that is ornamented by slightly

opisthocline axial ribs, forming node-like extensions situated immediately adjacent to the adapical suture. The whorls are low as is typical for the genus *Palaeoestylus*. Similar shells do also occur in the genera *Pseudozygopleura* Knight, 1930 and *Zygopleura* Koken, 1892. The present specimen is too fragmentary for an identification.

Superfamily Pseudozygopleuroidea Knight, 1930

Family Pseudozygopleuridae Knight, 1930

***Pseudozygopleura* Knight, 1930**

Type species. *Loxonema semicostatum* Meek, 1971, Carboniferous, USA.

***Pseudozygopleura*? sp.**
(Fig. 24C–D)

Material. One specimen: ESKU-19-LP 63.

Dimensions (mm): ESKU-19-LP 63: height = *c*. 9.2; width = 2.6.

Description. Shell high-spired, slender, turritelliform, slightly cyrtoconoid comprising at least 8 whorls with apex missing; whorls twice as wide as high; whorls gently convex, ornamented by straight faint collabral ribs numbering about 10 to 14 per whorl; ribs presumably reduced on last preserved whorl; sutures shallow but distinct; transition to base gradually convex; base rounded; anomphalous; aperture elongated suboval (higher than wide) with indistinct siphonal notch, columellar lip nearly straight.

Remarks. This single specimen resembles several species from the Pennsylvanian of the USA (Knight 1930; Hoare & Sturgeon 1985) but the preservation is insufficient for an identification. Pseudozygoppleuridae have a typical larval shell and hence knowledge of the protoconch is needed for a save family and genus assignment. Similar shells as the present one may also occur in Palaeostylidae and other groups. Several species that have been recorded from the Permian of the Palaeo-Tethys from Thailand (Ketwetsuriya *et al*. 2016) and Malaysia (Batten 1985) have been reported but those species have a more distinct axial ornament.

Superfamily Orthonematoidea Nützel & Bandel, 2000

Family Orthonematidae Nützel & Bandel, 2000

Donaldospira* Batten, 1966*b

Type species. *Murchisonia pertusa* de Koninck, 1883, Early Carboniferous, Europe

***Donaldospira*? sp.**
(Fig. 25A)

Material. One specimen: ESKU-19-LP 85.

Dimensions (mm): ESKU-19-LP 85: height = 10.4; width = 3.1.

Description. Turritelliform, high-spired, slender shell, comprising about five whorl (apex missing); whorls gradually increasing; whorls generally gently convex with median angulation; whorls with two fine spiral cords new near upper and lower suture; third cord strongest, situated at mid-whorl, forming crest-like periphery; upper whorl face forming evenly concave ramp; lower whorl face slightly concave, inwardly sloping from angulation to suture; suture distinct; base evenly rounded; anomphalous; aperture elongated suboval in shape with thin lip, columellar lip nearly straight.

Remarks. Due to the preservation a possibly present selenizone on the angulation at mid-whorl, this specimen

can only be assigned to *Donaldospira* tentatively. The Permian species *Murchisonia* (*Donaldospira*) *malaysia* Batten, 1985 from Perak, Malaysia is similar but has a straighter whorl face and finer spiral cords on the whorls above and below the selenizone. *M. gubleri* Delpey, 1941 (p. 367, fig. 41) from the Lower Permian Sisophon Formation, Cambodia is similar but it has a much more protruding peripheral carina and lacks spiral cords near the sutures. *M. fischeri* Stuckenberg, 1905 as illustrated by Delpey (1941) is much similar in whorl profile but it develops selenizone at the periphery which is bordered by two spiral ribs.

Knightella Longstaff, 1933

Type species. *Knightella irregularis* (Longstaff, 1933), Carboniferous, Scotland.

Knightella irregularis (Longstaff, 1933)

(Fig. 25B–E)

Knightia irregularis Longstaff, 1933: 118, pl. 12, figs 4–5; Knight, 1941: 164, pl. 49, fig. 6a–b.

Material. Two specimens: ESKU-19-LP 41, 84.

Dimensions (mm): ESKU-19-LP 41: height = *c*. 16.6; width = 6.1. ESKU-19-LP 84: height = 8.9; width = 4.0; apical angle = 42°.

Description. Shell high-spired, slender; largest specimen consisting of 10 whorls; protoconch smooth, seemingly about two orthostrophic whorls; whorls low, gently increasing; whorls smooth; whorl face evenly convex or somewhat pendent with periphery at mid-whorl or somewhat below; sutures moderately deep, distinct; base evenly convex, rounded; anomphalous; aperture unknown.

Remarks. The present specimens closely resemble the type species, *Knightella irregularis* (Longstaff, 1933) from the Carboniferous, Scotland as re-described and illustrated by Knight (1941, p.165, pl. 49, fig. 6a–b), although the present specimens are much larger. The general features of this species (i.e., high spire, sharply rounded and somewhat pendent whorl profile, a body whorl which is two-fifths of the total height, rounded base, anomphalous shell and slightly protruding protoconch) are obviously identical with the present specimens. Other similar species are *K. hydrobiformis* Nützel, 2012 and *Knightella* sp. from the Middle Permian Akasaka Limestone of Japan (Nützel & Nakazawa, 2012) and also several *Knightella* species which have been reported by Nützel (1998) from the Pennsylvanian of the USA. However, these species are smaller and have less convex whorls. *Loxonema karabolkensis* Licharev, 1975 (p. 78, pl. 13, figs 5–8) from the Pennsylvanian of Russia is similar but it differs in having a dense spiral ornament on the whorls. The present specimens are also similar to *Protostylus*; however, this genus has flatter whorls. This is the first known member of the genus *Knightella* in Thailand which extends the range of this species and genus to the Middle Permian and expands its distribution to the eastern Palaeo-Tethys.

Protostylus Mansuy, 1914

Type species. *Protostylus lantenoisi* Mansuy, 1914, Carboniferous, SE Asia.

Protostylus sp.

(Fig. 25F–H)

Material. Two specimens: ESKU-19-LP 39, 64.

Dimensions (mm): ESKU-19-LP 39: height = *c*. 16.8; width = 7.8. ESKU-19-LP 64: height = *c*. 6.9; width = 2.9.

Description. Shell high-spired, slender, consisting of approximately 7 whorls (apex missing); whorls smooth; whorls slightly convex to almost straight, periphery somewhat below mid-whorl; base evenly rounded, convex; anomphalous; sutures shallow but distinct; aperture unknown.

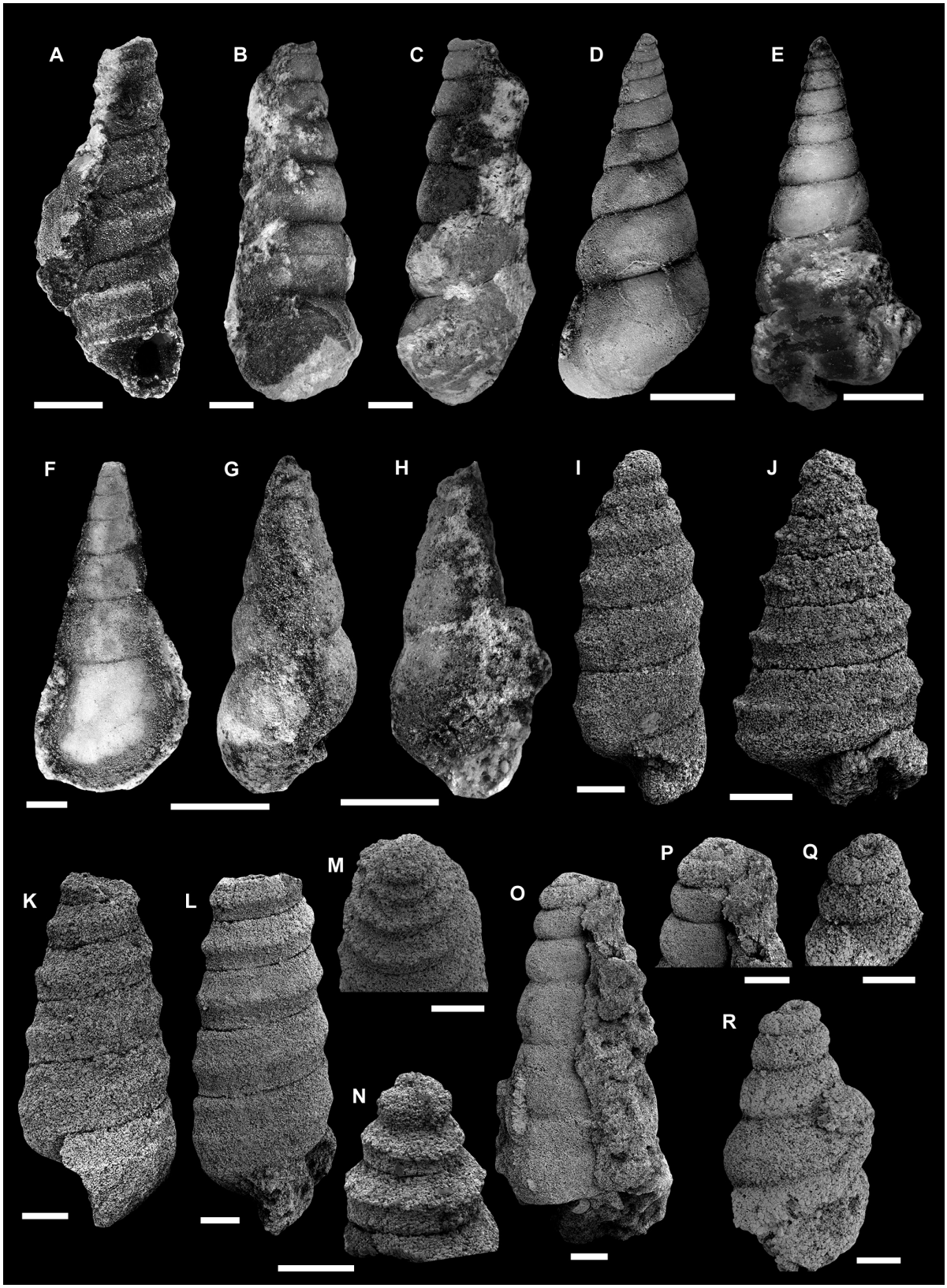

FIGURE 25. A, *Donaldospira* sp., ESKU-19-LP 85. B–E, *Knightella irregularis* (Longstaff, 1933), B–C, ESKU-19-LP 41. D–E, ESKU-19-LP 84. F–H, *Protostylus* sp., F, ESKU-19-LP 39. G–H, ESKU-19-LP 64. I–N, *Trypanocochlea lopburiensis* sp. nov. I, M, ESKU-19-LP 210, holotype; oblique view of early whorls to show protoconch. J, ESKU-19-LP 201, paratype. K, ESKU-19-LP 203, paratype. L, ESKU-19-LP 206, paratype; lateral view of early whorls to show protoconch. N, ESKU-19-LP 221, paratype. O–R, *Streptacis*? *khaokhadensis* sp. nov., O–P, ESKU-19-LP 214, holotype. Q–R, ESKU-19-LP 213, paratype. Scale bars represent: 2 mm (A–H); 200 μm (I–R).

Remarks. These unornamented high-spired shells resemble several Permian *Protostylus* species e.g. from the Middle Permian Tak Fa Limestone from Thailand (Ketwetsuriya *et al*. 2016) but the body-whorl of the present specimens seems to be more inflated. The Japanese *Protostylus* species from the Middle Permian Akasaka Limestone (Nützel & Nakazawa 2012) are much smaller. *Protostylus* sp. from the Permian of Ratburi Limestone, Thailand (Ketwetsuriya *et al*. 2020) is more slender in shape. The type species, *Protostylus lantenoisi* Mansuy, 1914 from the Carboniferous of South China (Yunnan) and the specimens illustrated by Batten (1985) from the Permian of Malaysia, differ from the present specimens in being more slender smaller and having lower whorls. The Permian Malaysian species *Omphaloptychia paleozoica* Batten, 1985 is similar in having high whorls, but it has a moderately high-spired turbiniform shape and a more step-like whorl profile. The studied specimens are also similar to *Knightella irregularis* (Longstaff, 1933) but its whorls are somewhat lower and less convex, and it has shallower sutures.

Family Goniasmatidae Nützel & Bandel, 2000

***Trypanocochlea* Tomlin, 1931**

Type species. *Trypanocochlea cerithioides* (Koken,1896), Late Triassic, Carnian.

***Trypanocochlea lopburiensis* sp. nov.**
(Fig. 25I–N)

Etymology. After the Lopburi Province in which the studied gastropod material was found.

Holotype. ESKU-19-LP 210

Paratypes. ESKU-19-LP 201, 203, 204, 206, 211, 218, 221.

Dimensions (mm): ESKU-19-LP 201: height = *c*. 1.1; width = 0.6. ESKU-19-LP 203: height = *c*. 1.1; width = 0.5. ESKU-19-LP 204: height = *c*. 1.0; width = 0.5. ESKU-19-LP 206: height = *c*. 1.9; width = 0.8. ESKU-19-LP 210: height = 1.5; width = 0.6. ESKU-19-LP 211: height = *c*. 1.1; width = 0.6. ESKU-19-LP 218: height = 1.3; width = 0.5. ESKU-19-LP 221: height = *c*. 0.7; width = *c*. 0.4.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian**.**

Description. Shell very small, high-spired, turritelliform, slightly cyrtoconoid comprising about six whorls; earliest two whorls (probably protoconch) convex, without visible ornament, somewhat mammilated; suture distinct; whorls low with evenly increasing whorl expansion after early first whorl, angulated at about mid-whorl with concave subsutural ramp; lower whorl below angulation concave; strong spiral cord located at mid-whorl at angulation forming periphery, with numerous small nodules (crenulated); additional weak spiral threads situated at subsutural position and second spiral thread located emerging from lower suture; whorl face on ramp and lower whorl smooth without visible ornament; base flatly convex without ornament; shallowly minutely phaneromphalous or anomphalous; aperture not well-preserved, seemingly circular with short slit.

Remarks. These tiny shells are assigned to the genus *Trypanocochlea* due to their high spire and the nodular spiral keel which is situated at the mid-whorl. However, due to preservation it is unclear whether a selenizone is present on the keel in the present specimens. *Trypanocochlea parva* Nützel, 2012 from the Akasaka Limestone, Japan is the only other Permian nominate species; it has much larger nodes on the keel, the keel is more pronounced, it is not cyrtoconoid but conical. Both species share a mammilate protoconch probably representing a larval shell of the caenogastropod type. The genus *Donaldospira* holds similar species but this genus lack nodes on the median keel. *Donaldospira taosensis* Kues & Batten (2001, fig. 9.30) from the Middle Pennsylvanian of New Mexico is similar but has higher whorls and several spiral threads above and below the carina (that lacks crenulation), which are not present in the present specimens. *D. carinata* Bandel, 2002*b* from the East Mount Shale, Pennsylvanian of Texas, USA has a much more protruding peripheral carina. The present specimens are much smaller than the other Permian *Donaldospira* species and the spiral cord at mid-whorl is weaker in the other species and the carina is not

crenulated. *Trypanocochlea lopburiensis* is established as a new species that yields approximately 10 specimens in the present collection.

Subclass Heterobranchia Burmeister, 1837

Superfamily Streptacidoidea Knight, 1931b

Family Streptacididae Knight, 1931b

***Streptacis* Meek, 1871**

Type species. *Streptacis whitfieldi* Meek, 1871, Carboniferous, USA.

***Streptacis*? *khaokhadensis* sp. nov.**
(Fig. 25O–R)

Etymology. After the Khao Khad Formation in which the studied gastropod material was found.

Holotype. ESKU-19-LP 213.

Paratype. ESKU-19-LP 214.

Dimensions (mm): ESKU-19-LP 213: height = *c*. 2.4; width = *c*. 0.8. ESKU-19-LP 214: height = *c*. 1.3; width = *c*. 0.7.

Type locality and stratigraphical range. Erawan Hill, Chong Sarika sub-district, Phatthana Nikhom district, located about 13 km east of Lopburi Province, Central Thailand (Fig. 1), Khao Khad Formation, Saraburi Group, Middle Permian, Roadian.

Description. Shell very small, high-spired, slender, largest specimen consisting of 7 whorls; protoconch smooth, seemingly coaxially heterostrophic; whorls low, smooth; earliest teleoconch whorls low, markedly convex with periphery at mid-whorl; later whorls higher, less convex; sutures deep; base and aperture unknown.

Remarks. Both specimens at hand are close to the Permian Japanese species *Knightella hydrobiformis* Nützel, 2012 from the Akasaka Limestone as reported by Nützel & Nakazawa (2012) in shell shape and size. However, in *K. hydrobiformis* convexity of the whorl face and height of the whorl does not change during ontogeny in contrast to the specimens at hand. The protoconch of the present material shows coaxial heterostrophy as does a specimen representing *K.* aff. *hydrobiformis* illustrated by Nützel & Nakazawa (2012, fig. 20N, O). However, the holotype of *K. hydrobiformis* does not display heterostrophy (maybe due to preservation) and was hence assigned to the caenogastropod genus *Knightella* (see Nützel 1998). *Streptacis* is characterized by transaxial heterostrophy i.e., the protoconch axis is more or less perpendicular to the shell axis of the teleoconch. However, *Streptacis*? *khaokhadensis* sp. nov. shows coaxial heterostrophy as does for instance the Jurassic genus *Usedomella* Gründel, 1998 and the Pennsylvanian *Mapesella* Bandel, 2002*a*. However, in *Usedomella* the width of the protoconch exceeds that of the early teleoconch and *Mapesella* has axial threads on the teleoconch whorls, both is not the case in *S*.? *khaokhadensis* sp. nov.. Therfore we tentaively place *S*.? *khaokhadensis* sp. nov. in *Streptacis*. *S*.? *khaokhadensis* sp. nov. differs from *K. irregularis* (Longstaff, 1933) in whorl profile that is somewhat pendent and in being larger.

Genus and species indeterminate 1
(Fig. 26A–C)

Material. One specimen: ESKU-19-LP 4.

Dimensions (mm): ESKU-19-LP 4: height = 3.9; width = 3.1; apical angle = 82°.

Remarks. This small, moderately high-spired, barrel-shaped shell has a prominent ornament of three spiral cords on convex whorl face, a forth emerging at the lower and flattened, planispiral early whorls (with earliest whorls missing). It represents clearly a distinct species in the present collection. However, the present specimen is too poorly preserved for a safe identification. It resembles the genus *Stegocoelia* Donald, 1889 but this genus has no

flattened early whorls and it is unclear whether the present specimen has a selenizone. Otherwise, it resembles several Late Palaeozoic species, for instance *Stegocoelia akasakaensis* Nützel, 2012 from the Middle Permian Akasaka Limestone of Japan but its spiral cords are much more prominent. It is also similar to some species from the Middle Pennsylvanian of New Mexico as described by Kues & Batten (2001).

Genus and Species indeterminate 2
(Fig. 26D)

Material. One specimen: ESKU-19-LP 207.

Dimensions (mm): ESKU-19-LP 207: height = *c*. 1.0; width = 0.9.

Remarks. This tiny incomplete specimen has several coarse orthocline ribs on whorl face and one spiral rib at abapical suture. is similar to *Hemizyga* (*Plocezyga*) sp. 1 as illustrated and described by Kues & Batten (2001) from the Middle Pennsylvania of New Mexico but the studied specimen differs in having a spiral rib at lower suture. The present specimen could represent a trochid or a caenogastropod but is too poorly preserved for an identification.

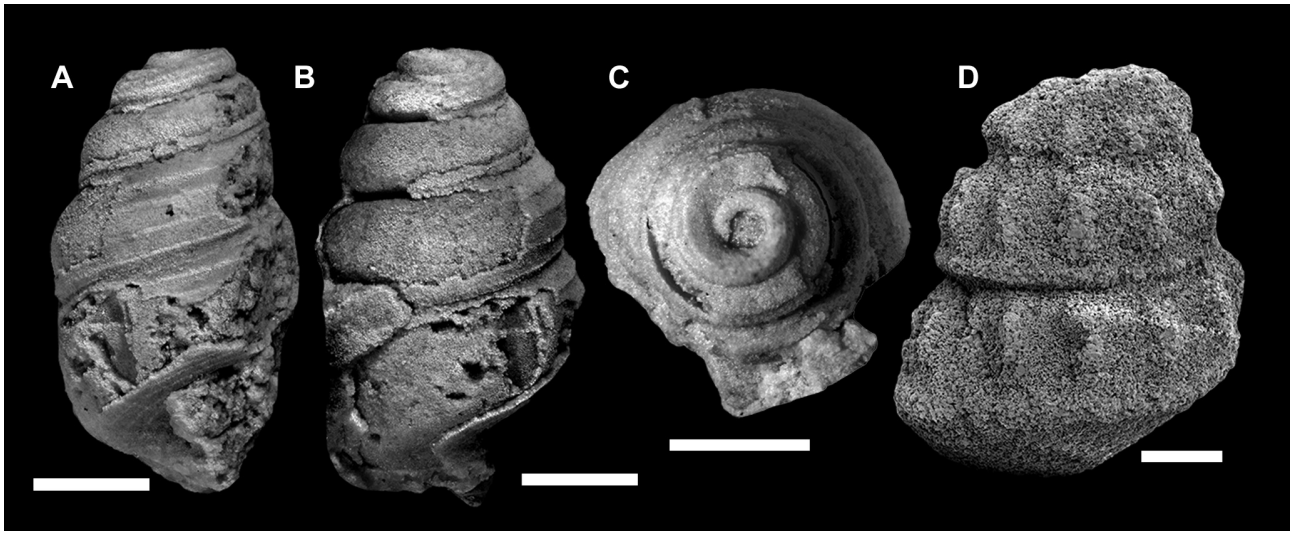

FIGURE 26. A–C, Genus and Species indeterminate 1, ESKU-19-LP 4. D, Genus and Species indeterminate 2, ESKU-19-LP 207. Scale bars represent: 2 mm (A–C); 200 μm (D).

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References

Bandel, K. (1993) Trochomorpha (Archaeogastropoda) aus den St. Cassian-Schichten (Dolomiten, Mittlere Trias). *Annalen des Naturhistorischen Museums Wien*, Reihe A, 95, 1–99.

Bandel, K. (2002*a*) About the Heterostropha (Gastropoda) from the Carboniferous and Permian. *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg*, 86, 45–80.

Bandel, K. (2002b) Reevaluation and classification of Carboniferous and Permian Gastropoda belonging to the Caenogastropoda and their relation. *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg*, 86, 81–188.

Bandel, K. & Frýda, J. (1998) The systematic position of the Euomphalidae. *Senckenbergiana lethaea*, 78, 103–131. https://doi.org/10.1007/BF03042762
Batten, R.L. & Stokes, W.L. (1986) Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *American Museum Novitates*, 2864, 1–33.
Batten, R.L. (1956) Some new pleurotomarian gastropods from the Permian of west Texas. *Journal of the Washington Academy of Sciences*, 46 (1), 42–44.
Batten, R.L. (1966*a*) The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. Part I. *Palaeontographical Society Monographs*, 119, 1–52.
Batten, R.L. (1966*b*) The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset. Part II. *Palaeontographical Society Monographs*, 119, 53–109.
Batten, R.L. (1972) Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History*, 147, 1–44.
Batten, R.L. (1979) Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids, and neritids. *American Museum Novitates*, 2685, 1–26.
Batten, R.L. (1985) Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids. *American Museum Novitates*, 2829, 1–40.
Batten, R.L. (1989) Permian Gastropoda of the Southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiriidae, Gosseletinidae. *American Museum Novitates*, 2958, 1–64.
Batten, R.L. (1995) Pennsylvanina (Morrowan) gastropods from the Magdalena Formation of the Hueco Mountains, Texas. *American Museum Novitates*, 3122, 1–46.
Bouchet, P., Rocroi, R.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, 61, 1–526. https://doi.org/10.4002/040.061.0201
Burmeister, H. (1837) *Handbuch der Naturgeschichte. Vol. 2. Zoologie*. Enslin, Berlin, pp. 369–858.
Bunopas, S. (1981) *Paleogeographic history of Western Thailand and Adjacent Parts of South-east Asia - A plate tectonics interpretation*. PhD thesis, Victoria University of Wellington, New Zealand, 810 pp. [Reprinted 1982 as Geological Survey Division, Department of Mineral Resources, Thailand, Geological Paper. No. 5. Special Issue]
Chronic, B.J. (1949) Invertebrate paleontology (excepting fuslinids and corals). *Upper Paleozoic of Peru*, 1949, 46–173.
Chronic, H. (1952) Molluscan fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. *Geological Society America Bulletin*, 63 (2), 95–166. https://doi.org/10.1130/0016-7606(1952)63[95:MFFTPK]2.0.CO;2
Conrad, T.A. (1835) Description of five new species of fossil shells in the collection presented by Mr. Edward Miller to the Geological Society. *Transactions of the Geological Society of Pennsylvania*, 1, 267–270.
Cossmann, M. (1897) Die Gastropoden der Trias um Hallstatt. Von E. Koken (1). *Revue critique Paléozoologie*, 1, 139–143.
Cossmann, M. (1908) [Review of] Système silurien du centre de la Bohème, 1ère partie. Recherches paléontologiques. Vol. IVn Gastropodes. Tom. II. Par J. Perner. *Revue Critique de Paléozoologie*, 12 (2), 91−95.
Cox, L.R. & Knight, J.B. (1960) Suborders of the Archaeogastropoda. *Proceedings of the Malacological Society of London*, 33, 262–264.
Cuvier, G. (1795) Second mémoire sur l'rorganisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordres, lu à la Société d'histoire naturelle de Paris, le 11 Prairial, an 3. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2, 433–449.
Dana, J.D. (1847) Descriptions of fossil shells of the collections of the exploring expedition under the command of Charles Wilkes, USN, obtained in Australia, from the lower layers of the coal formation in Illawarra, and from a deposit probably of nearly the same age at Harper's Hill, Valley of the Hunter. *American Journal of Science and Arts*, Series 2, 4, 151–160.
Dawson, O. (1993) Fusuline foraminifera1 biostratigraphy and carbonate facies of the Permian Ratburi Limestone, Saraburi, central Thailand. *Journal of Micropalaeontology*, 12, 9–33. https://doi.org/10.1144/jm.12.1.9
Delpey, G. (1941) Les Gastéropodes permiens du Cambodge. *Journal de Conchyologie*, 84, 255–278, 345–369.
Delpey, G. (1942) Les Gastéropodes permiens du Cambodge. *Journal de Conchyologie*, 85, 50–83.
Donald, J. (1889) Descriptions of new species of Carboniferous gastropods. *Quarterly Journal of the Geological Society of London*, 45, 619–625. https://doi.org/10.1144/GSL.JGS.1889.045.01-04.39
d'Orbigny, A. (1840) Chapter on *Bellerophon*. *In*: Ferussac, A. de & d'Orbigny, A. (Eds.), *Histoire naturelle générale et particulière des cephalopods acetabulifères vivants et fossils*. *Vol. 1*. Antiquariaat Junk, Amsterdam, pp. 180–218.
Erwin, D.H. (1988) Permian Gastropoda of the Southwestern United States: Cerithiacea, Acteonacea, and Pyramidellacea. *Journal of Paleontology*, 62, 566–575.
Fischer, P. (1885) *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des molluscques vivants et fossils*, 8, 1–1369.
Fletcher, H.O. (1958) The Permian gastropods of New South Wales. *Records of the Australian Museum*, 24 (10), 115–164. https://doi.org/10.3853/j.0067-1975.24.1958.648
Gemmellaro, G.G. (1889) La Fauna dei Calcari Con Fusulina della Valle del Fiume Sosio nella Provincia di Palermo, Fasc 2.

Nautiloidea e Gastropoda. *Giornale di Scienze Naturali e Economiche*, 20, 97–182. https://doi.org/10.5962/bhl.title.10774
Girty, G.H. (1909) Paleontology of the Manzano group. *In*: Lee, W.T. & Girty, G.H. (Eds.), *The Manzano group of the Rio Grande Valley, New Mexico*. *Bulletin of the U. S. Geological Survey*. Government Printing Office, Washington, D.C., pp. 40–141.
Girty, G.H. (1915) The fauna of the Wewoka Formation of Oklahoma. *United States Geological Survey Bulletin*, 544, 1–353.
Girty, G.H. (1927) Descriptions of new species of Carboniferous and Triassic fossils (from southeastern Idaho). *United States Geological Survey Professional Paper*, 152, 411–446.
Grant, R.E. (1976) Permian brachiopods from southern Thailand. *Paleontological Society Memoir*, 9, 1–269. https://doi.org/10.1017/S0022336000061795
Gründel, J. (1998) Heterostropha (Gastropoda) aus dem Dogger Norddeutschlands und Nordpolens. II. Weitere Allogastropoda. *Freiberger Forschungsheft*, C 474, Paläontologie, Stratigraphie, Fazies, 6, 1–37.
Hall, J. (1847) Containing descriptions of the organic remains of the lower division of the New York system (equivalent of the Lower Silurian rocks of Europe). *Paleontology of New York*, 1, 1–338.
Hall, J. (1856) Description of new species of fossils from the Carboniferous limestones of Indiana and Illinois. *Transactions of the Albany Institute*, 4, 1–36.
Hall, J. (1859) Contributions to the palaeontology of Iowa; being descriptions of new species of Crinoidea and other fossils. *Iowa Geological Survey*, 1 (2), 1–92.
Harper, J.A. (2018) Gastropods from the Gilmore City Formation (Lower Mississippian) of North-Central Iowa: Part 1, geology and systematics of Bellerophontoidea and Euomphaloidea. *Annals of the Carnegie Museum*, 85, 61–90. https://doi.org/10.2992/007.085.0104
Haughton, S. (1859) On some fossil Pyramidellidae from Carboniferous Limestone of Cork and Clonmel. *Proceedings of the Dublin University Zoology and Botany Association*, 1, 281–283.
Hayasaka, I. (1955) A new Permian species of Porcellia from Japan. *Journal of the Faculty of Science, Hokkaido University*, Series 4, Geology and Mineralogy, 9, 21–24.
Hinthong, C. (1981) *Geology and mineral resources of the Changwat Phranakorn Sri Ayutthaya (Map ND 47–8), scale 1:250,000*. Department of Mineral Resources, Geological Survey Report No. 4. Department of Mineral Resources, Geological Survey, Bangkok, 105 pp. [in Thai, English summary]
Hinthong, C., Chuaviroj, S., Kaewyana, W., Srisukh, S., Pholprasit, C. & Pholachan, S. (1985) *Geological map of Changwat Phranakorn Sri Ayutthaya, Thailand 1: 250 000 (ND 47–8)*. Geological Survey Division of the Department of Mineral Resources, Bangkok, Thailand. [in Thai]
Hoare, R.D. (1961) Desmoinesian Brachiopoda and Mollusca from southwest Missouri. *Missouri University Studies*, 36, 1–262.
Hoare, R.D. & Sturgeon, M.T. (1985) The Pennsylvanian gastropod *Pseudozygopleura* (Pseudozygopleura) from the Appalachian Basin: II. *Journal of Paleontology*, 59 (1), 60–78.
Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2014) A new Permian gastropod fauna from the Tak Fa Limestone, Nakhonsawan, Northern Thailand—a report of preliminary results. *Zitteliana A*, 54, 137–146.
Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2016) Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences*, 91, 481–513. https://doi.org/10.3140/bull.geosci.1617
Ketwetsuriya, C., Cook, A.G. & Nützel, A. (2020) Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. *Palaöntologische Zeitschrift*, 94, 53–77. https://doi.org/10.1007/s12542-019-00463-0
Knight, J.B. (1930) The gastropods of the St. Pseudozygopleurinae. *Journal of Paleontology*, 4 (1), 1–89.
Knight, J.B. (1931*a*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: the Subulitidae. *Journal of Paleontology*, 5 (3), 177–229.
Knight, J.B. (1931*b*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: *Aclisina* and *Streptacis*. *Journal of Paleontology*, 5, 1–15.
Knight, J.B. (1933*a*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: V. The Trocho-Turbinidae. *Journal of Paleontology*, 7 (1), 30–58.
Knight, J.B. (1933*b*) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: VI. The Neritidae. *Journal of Paleontology*, 7 (4), 359–392.
Knight, J.B. (1936) Notes on Paleozoic Gastropoda. *Journal of Paleontology*, 10 (6), 520–534.
Knight, J.B. (1941) Paleozoic gastropod genotypes. *Geological Society of America Special Paper*, 32, 1–510. https://doi.org/10.1130/SPE32-p1
Knight, J.B. (1945) Some new genera of the Bellerophontacea. *Journal of Paleontology*, 19, 333–340.
Knight, J.B. (1956) New families of Gastropoda. *Journal of the Washington Academy of Sciences*, 46, 41–42.
Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. (1960) Systematic descriptions. *In:* Moore, R.C. (Ed.), *Treatise on invertebrate paleontology*. *Part I. Mollusca 1*. Geological Society of America & University of Kansas Press, Kansas, pp. I169–I310.
Koken, E. (1892) Ueber die Gastropoden der rothen Schlernschichten nebst Bemerkungen über Verbreitung und Herkunft eini-

ger triassischer Gattungen. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 1892, 25–36.
Koken, E. (1896) Die Gastropoden der Trias um Hallstadt. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, 46, 37–126.
Koninck, L.G. de (1843) *[1842–44]. Description des animaux fossiles qui se trouvent dans le terrain carbonifere de Belgique.* Dessain, Liége, 651 pp.
Koninck, L.G. de (1863) *Meìmoire sur les Fossiles Paleìozoiques Recueillis dans l'Inde par M. le Docteur Fleming*. H. Dessaain, LieÌge, 44 pp.
Koninck, L.G. de (1881) Faune du calcaire carbonifère de la Belgique, 3e partie, Gastéropodes. *Annales du Musée Royal d'Histoire Naturelle de Belgique, serie Paleontologie*, 6, 1–170.
Koninck, L.G. de (1883) Faune du calcaire carbonifére de la Belgique. 4. Gastéropodes (suite en fin). *Annales du Musée Royale d'Histoire Naturelle Belgique*, 8, 1–240.
Kues, B.S. (1984) Pennsylvanian stratigraphy and paleontology of the Taos area, north-central New Mexico. *Rio Grande Rift: Northern New Mexico. New Mexico Geological Society Guidebook*, 35, 107–114.
Kues, B.S. (2004) Stratigraphy and brachiopod and molluscan paleontology of the Red Tanks Formation (Madera Group) near the Pennsylvanian–Permian boundary, Lucero uplift, west-central New Mexico. *Carboniferous —Permian transition at Carrizo Arroyo, Central New Mexico*, 25, 143–210.
Kues, B.S. & Batten, R.L. (2001) Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico. *Journal of Paleontology*, 75 (Supplement 1), 1–95.
https://doi.org/10.1666/0022-3360(2001)75[1:MPGFTF]2.0.CO;2
Kulas, H.A. & Batten, R.L. (1997) Silicified gastropods from the Permian Phosphoria rock complex of Wyoming. *Contributions to Geology, University of Wyoming*, 31 (2), 33–58.
Léveillé, C. (1835) A perçu géologique de quelques localités très riches en coquilles sur les frontiers de France et de Belgique. *Mémoires de la Société géologique de France*, 2 (1), 29–40.
Licharev, B.K. (1975) Carboniferous gastropods from the region of the River Karabolka. *Trudy Vsesoyuzniei Navcho-Issledovatelbskii Geologicheskii Institut*, 206, 5–183.
Longstaff, J.D. (1933) A revision of the British Carboniferous Loxonematidae, with descriptions of new forms. *Quarterly Journal of the Geological Society of London*, 89 (2), 87–124.
https://doi.org/10.1144/GSL.JGS.1933.089.01-04.05
Mansuy, H. (1912) Paléontologie. *In*: Mansuy, H. & Deprat, J. (Eds.), *Etude géologique du Yun-Nan oriental. Actes de la Société Géologique de l'Indo-Chine*, 1 (2), pp. 1–146.
Mansuy, H. (1913*a*) Faunes des calcaires à Productus de l'Indochine. *Mémoires du Service Géologique de l'Indochine*, 2 (4), 1–133.
Mansuy, H. (1913*b*) Paléontologie de L'Annam et du Tonkin. *Mémoires du Service Géologique de L`Indochine*, 2 (3), 1–48.
Mansuy, H. (1914) Nouvelle contribution à la paléontologie du Yunnan. *Mémoires du Service Géologique de l'Indochine*, 3 (2), 1–190.
Mazaev, A.V. (2006) Permian gastropods from the Kulogory Formation of the northern Moscow Syneclise. *Paleontological Journal*, 40, 391–403.
https://doi.org/10.1134/S0031030106040046
Mazaev, A.V. (2015) Upper Kazanian (Middle Permian) gastropods of the Volga-Urals Region. *Paleontological Journal*, 49, 869–986.
https://doi.org/10.1134/S0031030115080018
McCoy, F. (1844) *A Synopsis of the Characters of Carboniferous Limestone fossils of Ireland*. McGloshan & Gill, Dublin, 274 pp.
https://doi.org/10.5962/bhl.title.11559
McCoy, F. (1852) *A synopsis of the classification of the British Palaeozoic rocks [by the Rev. Adam Sedgwick] with a systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge [by Frederick McCoy] with figures of the new and imperfectly known species*. Parker & Son, London, 661 pp.
Meek, F.B. (1871) Descriptions of new species of invertebrate fossils from Ohio and other western states and territories. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 23, 159–184.
Meek, F.B. & Worthen, A.H. (1860) Description of new Carboniferous fossils from Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 12, 447–472.
Meek, F.B. & Worthen, A.H. (1866) Descriptions of invertebrates from the Carboniferous system. *Geological Survey of Illinois*, 2, Palaeontology, 143–411.
Meek, F.B. & Worthen, A.H. (1867) Contributions to the paleontology of Illinois and other western states. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 18, 251–275.
Meek, F.B. & Worthen, A.H. (1873) Descriptions of invertebrates from the Carboniferous System. *Illinois Geological Survey*, 5 (2), 321–619.
Montfort, P.D. de (1808) *Conchyliologie systématique et classification méthodique de coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Coquilles univalves, cloisonnées. Vol. 1*. F. Schoell, Paris, 409 pp.
Miller. S.A. (1877) *The American Palaeozoic fossils: a catologue of the genera and species. 2nd Edition.* Published by author,

Ohio, 334 pp.
Münster, G.zu. (1841) Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. *In*: Wissmann, H.L., Münster, G. zu & Braun, K.F. (Eds.), *Beiträge zur Geognosie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. Heft 4*. Buchner, Bayreuth, pp. 25–152.
Nakornsri, N. (1976) *Geological Map of Ban Mi Sheet ND 47–4. Scale 1:250,000*. Geological Survey Division. Department of Mineral Resources, Bangkok, 132 pp. [in Thai]
Nakornsri, N. (1981) *Geology and Mineral Resources of Amphoe Ban Mi (ND 47–4). Department of Mineral Resources, Geological Survey Report No. 3*. Department of Mineral Resources, Geological Survey, Bangkok, 1 map. [in Thai]
Netchaev, A.V. (1894) Fauna from the Permian beds of the eastern band of European Russia. *Tr. Ob-va Estestvoispyt. Kazan. Imp. University*, 27 (4), 1–503.
Nützel, A. (1998) Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen*, Serie E, Palaeobiologie, 26, 1–229.
Nützel, A. & Bandel, K. (2000) Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 2000 (9), 557–569. https://doi.org/10.1127/njgpm/2000/2000/557
Nützel, A. (2002) An evaluation of the recently proposed Palaeozoic gastropod subclass Euomphalomorpha. *Palaeontology*, 45, 259–266. https://doi.org/10.1111/1475-4983.00236
Nützel, A., Frýda, J., Yancey, T.E. & Anderson, J.R. (2007) Larval shells of Late Palaeozoic naticopsis gastropods (Neritopsoidea: Neritimorpha) with a discussion of the early neritimorph evolution. *Palaeontologische Zeitschrift*, 81 (3), 213–228. https://doi.org/10.1007/BF02990173
Nützel, A. & Nakazawa, K. (2012) Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology*, 10, 103–169. https://doi.org/10.1080/14772019.2010.549659
Nützel, A. & Kaim, A. (2014) Diversity, palaeoecology and systematics of a marine fossil assemblage from the Late Triassic Cassian Formation at Settsass Scharte, N Italy. *Paläontologische Zeitschrift*, 88, 405–431. https://doi.org/10.1007/s12542-013-0205-1
Pan, H.-Z. & Erwin, D.H. (2002) Gastropods from the Permian of Guangxi and Yunnan provinces, South China. *Journal of Paleontology*, 78 (Supplement 56), 1–49. https://doi.org/10.1666/0022-3360(2002)76[1:GFTPOG]2.0.CO;2
Pan, Y.-T. (1985) Fossil Gastropoda from the Permian of Sichuan, Guizhou, Yunnan, and Gaungxi. *Acta Palaeontologica Sinica*, 24 (1), 29–37
Pan, Y.-T. & Yu, W.Z. (1993) *Permian Gastropoda of China*. Ocean Press, Beijing, 68 pp.
Pitakpaivan, K. (1965) Fusulines of the Rat Buri Limestone of Thailand. *Memoirs of the Faculty of Science, Kyushu University*, Series D, Geology, 17, 3–69.
Rafinesque, C.S. (1815) *Analyse de la nature, ou tableau de l'univers et des corps organisées*. Jean Barravecchia, Palerme, 223 pp. https://doi.org/10.5962/bhl.title.106607
Reed Cowper, F.R. (1927) Upper Carboniferous fossils from Argentina. *Carnegie Institute of Washington*, 381, 129–158.
Rollins, H.B. (1975) Gastropods from the Lower Mississippian Wassonville Limestone in Southeastern Iowa. *American Museum Novitates*, 2579, 1–35.
Salvini-Plawen, L.von. (1980) A consideration of systematics in the Mollusca (Phylogeny and higher classification). *Malacologia*, 19, 249–278.
Simroth, H. (1906) Versuch einer neuen Deutung der Bellerophontidae. *Sitzungsberichte der Natuforschenden Gesellschaft zu Leipzig*, 32, 3–8. [dated 1905]
Sone, M. (2010) A new species of the rare neritopsid gastropod *Magnicapitatus* from the Guadalupian (Middle Permian) of East Thailand (the Indochina Terrane). *Alcheringa*, 34, 1–6. https://doi.org/10.1080/03115510903277709
Sone, M. & Metcalfe, I. (2008) Parallel Tethyan sutures in mainland Southeast Asia: New insights for Palaeo-Tethys closure and implications for the Indosinian orogeny. *Comptes Rendus Geosciences*, 340 (2), 166–179. https://doi.org/10.1016/j.crte.2007.09.008
Sour-tovar, F., Alvarez, F. & Chacon, M.L.M. (2005) Lower Mississippian (Osagean) spire-bearing brachiopods from Canon de la Peregrina, north of Ciudad Victoria, Tamaulipas, northeastern Mexico. *Journal of Paleontology*, 79 (3), 469–485. https://doi.org/10.1666/0022-3360(2005)079%3C0469:LMOSBF%3E2.0.CO;2
Sowerby, J. (1812–1822) *The mineral conchology of Great Britain; or coloured figures and descriptions of those remains of testaceous animals or shells, which have been preserved at various times and depths in the Earth*. Benjamin Meredith, London, 803 pp. https://doi.org/10.5962/bhl.title.14408
Stuckenberg, A. (1905) Die Fauna der obercarbonischen Suite des Wolgadurchbruches bei Samara. *Geologie Kommitte Trudy Memoir*, 23, 1–115.
Swainson, W. (1840) *A treatise on malacology or shells and shell-fish*. Longman, London, viii + 419 pp.

Thein, M. L. & Nitecki, M.H. (1974) Chesterian (Upper Mississippian) Gastropoda of the Illinois basin. *Fieldiana: Geology*, New Series, 34, 1–238.
Tomlin, J.R.B. (1931) Some preoccupied generic names. III. *Proceedings of the Malacological Society of London*, 19, 174–175.
https://doi.org/10.1093/oxfordjournals.mollus.a064001
Toriyama, R. & Kanmera, K. (1977) Fusuline fossils from Thailand, Part X. The Permian fusulines from the Limestone Conglomerate Formation in the Khao Phlong Phrab area, Sara Buri, Central Thailand. *In*: Kobayashi, T., Toriyama, R. & Hashimoto, W. (Eds.), *Geology and Palaeontology of Southeast Asia*. *Vol. 18.* University of Tokyo Press, Tokyo, pp. 1–27.
Toriyama, R. & Kanmera, K. (1979) Fusuline fossils from Thailand. Part XII. Permian fusulines from the Ratburi Limestone in the Khao Khao area, Sara Buri, Central Thailand. *In*: Kobayashi, T., Toriyama, R. & Hashimoto, W. (Eds.), *Geology and Palaeontology of Southeast Asia*. *Vol. 20.* University of Tokyo Press, Tokyo, pp. 43–61.
Toriyama, R., Kanmera, K., Kaewbaidhoam, S. & Hongnusonthi, A. (1974) Biostratigraphic zonation of the Rat Buri Limestone in the Khao Phlong Phrab area, Sara Buri, Central Thailand. *In*: Kobayashi, T. & Toriyama, R. (Eds.), *Geology and Palaeontology of Southeast Asia*. *Vol. 14.* University of Tokyo Press, Tokyo, pp. 25–48.
Ulrich, E.O. & Scofield, W.H. (1897) Chapter X: the lower Silurian Gastropoda of Minnesota. *In*: Ulrich, E.O., Scofield, W.H., Clarke J.M. & Winchell, N.H. (Eds.), *The geology of Minnesota. Part 2 of the final report: paleontology. Vol. 3*. Harrison & Smith, Minneapolis, pp. 813–1081.
Verrill, A.E. (1884) Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent part of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 6 (1), 139–194.
https://doi.org/10.5962/bhl.part.7412
Waagen, W. (1880) Salt-Range Fossils. I. Productus Limestone fossils. 2. Pisces-Cephalopoda: supplement Gasteropoda. *Memoirs of the Geological Survey of India (Palaeontologia Indica)*, 13, 1–183.
Wang, H.J. (1982) Late Permian gastropods from Heshan of Laibin, Guangxi Province. *Acta Palaeontologica Sinica*, 21, 491–496.
Wang, H.J. & Xi, Y.H. (1980) Late Permian to Early Triassic gastropods from Western Guizhou Province. *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan*, 1980, 195–240.
Wanner, C. (1922) Die Gastropoden und Lamellibranchiaten der Dyas von Timor. *Palaontologie von Timor*, 11, 1–82.
Waterhouse, J.B. (1982) An Early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine*, 119, 337–354.
https://doi.org/10.1017/S0016756800026261
Wenz, W. (1938–1944) Gastropoda. Teil 1: Allgemeiner Teil und Prosobranchia. *In*: Schindewolf, O.H. (Ed.), *Handbuch der Paläozoologie. 6. Gastropoda*. Borntraeger, Berlin, pp. 1–1639.
White, C.A. (1877) Report upon the invertebrate fossils collected in portions of Nevada, Utah, Colorado, New Mexico, and Arizona, by parties of the expeditions of 1871, 1872, 1873, and 1874. *In*: *Report upon United States geographical surveys west of the one hundredth meridian, Paleontology*. *Vol. 4.* Government Printing Office, Washington, pp. 1–219.
https://doi.org/10.5962/bhl.title.51607
Winters, S.S. (1956) New Permian gastropod genera from eastern Arizona. *Journal of the Washington Academy of Sciences*, 46 (2), 44–45.
Winters, S.S. (1963) Supai Formation (Permian) of eastern Arizona. *Geological Society of America Memoir*, 89, 1–99.
https://doi.org/10.1130/MEM89-p1
Yochelson, E.L. (1956) Permian Gastropoda of the southwestern United States. 1. Euomphalacea, Trochonematacea, Anomphalacea, Craspedostomatacea, and Platyceratacea. *Bulletin of the American Museum of Natural History*, 110, 179–275.
Yochelson, E.L. (1960) Permian Gastropoda of the southwestern United States. *Bulletin of the American Museum of Natural History*, 119, 205–294.
Yochelson, E.L. & Dutro, J.T. Jr. (1960) Late Paleozoic Gastropoda from Northern Alaska. *U.S. Geological Survey Professional Paper*, 334-D, 111–147.
https://doi.org/10.3133/pp334D
Yoo, E.K. (1994) Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia. *Records of the Australia Museum*, 46 (2), 63–120.
https://doi.org/10.3853/j.0067-1975.46.1994.18
Yu, W.Z. (1980) Taxonomic names, in Late Permian to Early Triassic gastropods from Western Guizhou Province. *Stratigraphy and Palaeontology of Upper Permian Coal-bearing Formation in Western Guizhou and Eastern Yunnan, China*, 1980, 195–232.
Zittel, K.A.von. (1895) *Grundzüge der Paläontologie (Paläozoologie). Abt. I. Invertebrata*. München & Leipzig, Oldenburg, 971 pp.

CHAPTER 4

Karapunar, B., Ketwetsuriya, C., & Nützel, A. (in review). A low-diversity *Peruvispira*-dominated gastropod assemblage from the Permian Ratburi Group of Central Thailand. *Alcheringa*, 1–9, https://doi.org/10.1080/03115518.2022.2050814.

A low-diversity *Peruvispira*-dominated gastropod assemblage from the Permian Ratburi Group of Central Thailand

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ABSTRACT

Permian gastropods from Thailand have been extensively studied over the last few years. The earliest known gastropod collection from the Permian deposits of Thailand was gathered in 1967, but has never been figured or described. Here, we document this historically important gastropod assemblage recovered from the Permian Ratburi Group of Khao Mang Lat in the Ban Kao District of Kanchanaburi Province, Central Thailand. The material comprises approximately 200 specimens, almost exclusively of a new species, *Peruvispira kanchanaburiensis* sp. nov., (family Goniasmatidae) together with a single individual of *Orthonychia* sp. (family Orthonychiidae =?Platyceratidae). This exceptionally low diversity community is unusual in comparison to Permian gastropod faunas from elsewhere, and could be due to a low temperature palaeoenvironmental setting or priority effects.

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KEYWORDS: Gastropoda; Platyceratidae; diversity; Kanchanaburi; Sibumasu Terrane.

THE PRESENCE of gastropods in the Permian deposits of Thailand was first mentioned by Grant (1976). Although the Permian gastropod faunas from several other localities in Thailand have since been studied (e.g., Ketwetsuriya *et al*. 2016, 2020a, 2020b), this original collection has yet to be fully described. Grant's (1976) material was derived from strata of the Ratburi Group exposed on Khao (= 'hill') Mang Lat in the Ban Kao District of Kanchanaburi Province, Central Thailand (Fig. 1). Associated faunal elements included brachiopods, fenestellid,

fistuliporoid, and 'rhomboporoid-sized' bryozoans, sponges, and pleurotomariidan and platyceratid gastropods (Grant 1976). Ketwetsuriya *et al*. (2020a) recently documented a diverse range of gastropod taxa from the Ratburi Group at Khao Phrik in Ratchaburi Province in Western Thailand; however, the relationships of this assemblage with Grant's (1976) historical collection from Khao Mang Lat remain uncertain. Consequently, in this paper we document these earliest recognised Permian gastropod fossils from Thailand and assess their palaeoecological implications.

Geological setting

Thailand represents the continental core of Southeast Asia, being formed by a latest Palaeozoic to early Mesozoic collision of the western Sibumasu (= 'Shan-Thai') Terrane and eastern Indochina Terrane along at least two major suture zones (e.g., Metcalfe 2011, 2013, Sone & Metcalfe 2008, Ueno & Charoentitirat 2011, Ueno *et al*. 2012). The Sibumasu and Indochina terranes are Gondwanan in origin and were inundated by the Palaeo-Tethys Ocean from the Devonian to Triassic (e.g., Metcalfe 2013). During the Permian, western and Peninsular Thailand constituted part of the Sibumasu Terrane (Fig. 1A), which was separated from Gondwana in the late Early Permian by opening of the Meso-Tethys (Metcalfe 2013). The Permian sequences today exposed on the Sibumasu Terrane and represent shelf carbonate platforms that bordered this oceanic palaeoenvironmental setting (Ueno & Charoentitirat 2011).

The Permian limestone deposits of the Sibumasu Terrane have been assigned to the Ratburi Group (also informally referred to as the 'Ratburi Limestone'), which consists of massive carbonates interbedded with argillaceous limestones and dolostones and fossiliferous chert nodules (Ueno & Charoentitirat 2011). The Ratburi Group has yielded various marine invertebrate remains, including foraminifers (e.g., Sakagami 1969, Brönnimann *et al*. 1978, Ingavat-Helmcke 1993), corals (e.g., Fontaine 1986, 1988), algae (Fontaine & Salyapongse 2001), brachiopods (e.g., Waterhouse & Piyasin 1970, Yanagida 1970, Grant 1976), bryozoans (e.g., Sakagami 1965, 1970, 1973) and gastropods (Ketwetsuriya *et al*. 2020a). Collectively, these assemblages indicate a latest Early Permian to Late Permian (Ueno & Charoentitirat 2011).

The studied gastropod assemblage is coming from the Ratburi Group at Khao Mang Lat in the Ban Kao District of Kanchanaburi Province, Central Thailand (Fig. 1B). The brachiopod fauna from Khao Mang Lat was correlated with those from Khao Phrik and from Ko Muk (an

island off the southern Andaman coast of Southern Thailand). The age of the outcrops at these localities were interpreted as Artinskian (late-Early Permian) and Wordian (Middle Permian) by different authors (Grant 1976, Ketweturiya *et al*. 2020a). Therefore, the age of the assemblage at Khao Mang Lat is regarded herein as ranging from the Artinskian to Wordian.

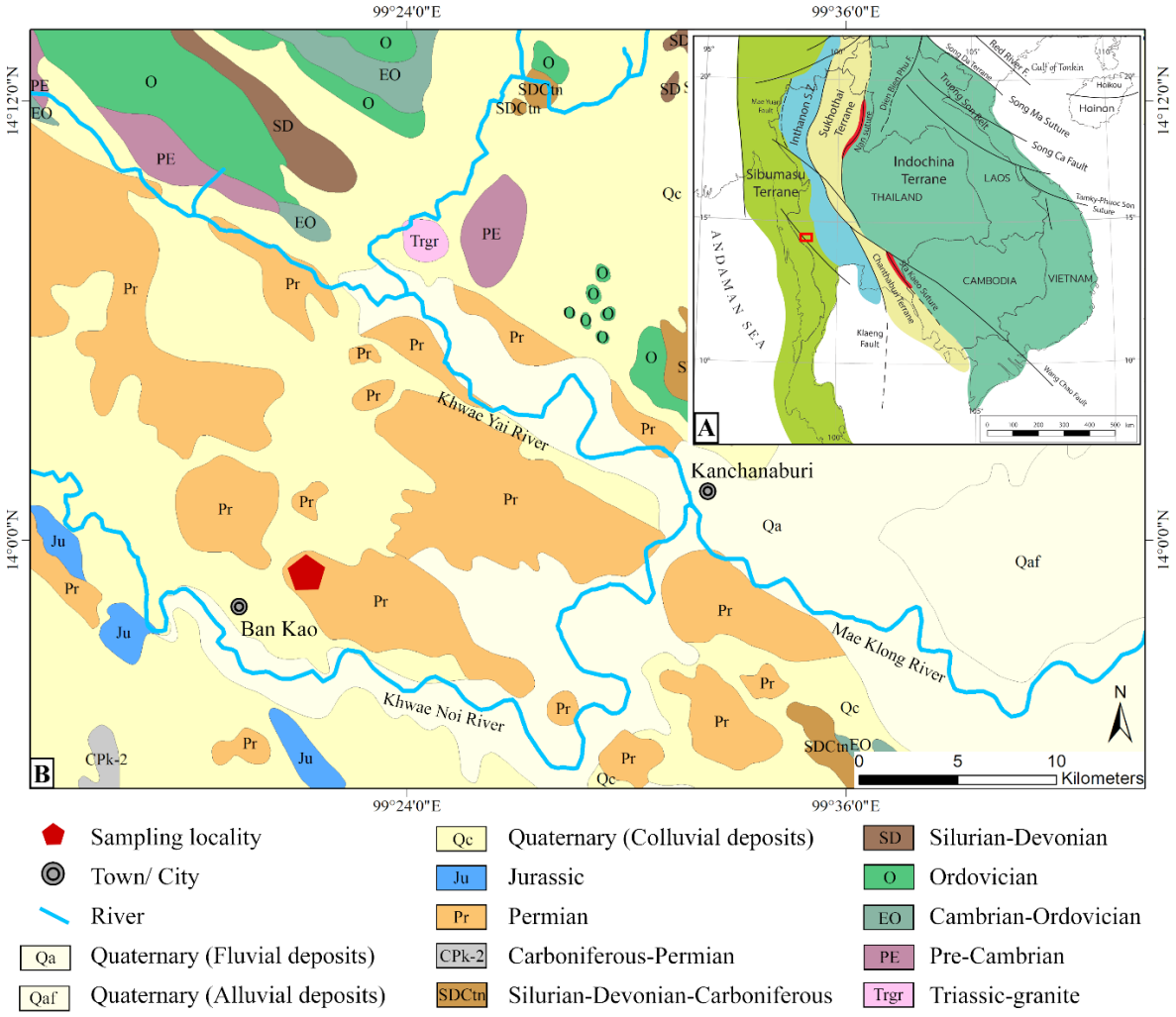

Figure 1. A, Geotectonic subdivision of mainland Thailand including the Sibumasu and the Indochina terranes (modified from Sone & Metcalfe 2008). **B**, Geological map of the sampling locality at Khao Mang Lat in the Ban Kao District of Kanchanaburi Province and adjacent areas (modified from Department of Mineral Resources of Thailand, 1999).

Materials and Methods

The Khao Mang Lat gastropod fossils were collected from USNM Locality 9266 in January 1967 by Richard E. Grant and a team from the Department of Mineral Resources, Thailand (Grant 1976). The bulk limestone samples were prepared at the National Museum of Natural History (USNM) Smithsonian Institution, Washington DC, USA, with more than 1350 brachiopod specimens picked from the residues (Grant 1976). The accompanying ca. 200

gastropod fossils are mostly fragmentary and lack initial whorls because of coarse silicification; however, some specimens show sufficient diagnostic characters for taxonomic assignment. The figured specimens were coated with ammonium chloride (NH_4Cl) prior to photography.

Specimen repository

All of the gastropod fossils recovered from Khao Mang Lat has been accessioned at USNM, and has the *Zoobank* Life Science Identifier (LSID): urn:lsid:zoobank.org:pub:486B13BE-B705-4C40-A172-9D36CBDB7428.

Systematic palaeontology

Subclass CAENOGASTROPODA Cox, 1960

Superfamily ORTHONEMATOIDEA Nützel & Bandel, 2000

Family GONIASMATIDAE Nützel & Bandel, 2000

Peruvispira Chronic, 1949

Type species

Peruvispira delicata Chronic, 1949; original designation.

Remarks

Peruvispira is a globally distributed early Carboniferous to Late Permian gastropod genus typified by small and high-spired to trochiform shells with a selenizone that is bordered by prominent spiral cords. The ramp is commonly ornamented with axial riblets or strengthened by growth lines. Karapunar & Nützel (2022) reported a caenogastropod-type larval shell from a Pennsylvanian *Peruvispira* and thus classified the genus within the caenogastropod family Goniasmatidae.

Peruvispira kanchanaburiensis sp. nov.

(Fig. 2)

Diagnosis

Shell small, murchisoniform, with pleural angle of 45°–60°; ramp convex in adapical half, concave in abapical half; whorl face ornamented with sharp prosocyrt ribs (eight/mm on last

whorl), extending from suture to selenizone; selenizone wide, covering about 1/6th of late whorl face, lunulae sharp, separated by interspaces equal to two–three times width of lunula.

LSID: urn:lsid:zoobank.org:act:177AD8A2-249D-4FAD-A58E-9F4350337C11

Etymology

After Kanchanaburi Province, the region where the specimens were collected.

Holotype

USNM PAL 768628.

Referred material

Paratypes: USNM PAL 768622; USNM PAL 768627; USNM PAL 768630. Additional specimens: USNM PAL 768615; USNM PAL 768616; USNM PAL 768617; USNM PAL 768618; USNM PAL 768619; USNM PAL 768620; USNM PAL 768621; USNM PAL 768623; USNM PAL 768624; USNM PAL 768625; USNM PAL 768629; USNM PAL 768631.

Type locality, unit and age

USNM Locality 9266, Khao Mang Lat in the Ban Kao District of Kanchanaburi Province, Central Thailand; Ratburi Group, Artinskian–Wordian (upper-Lower–Middle Permian).

Table 1. Measurements of *Peruvispira kanchanaburiensis*. Abbreviations: H, shell height; W, shell width; PA, pleural angle.

Specimen number	Figure	Number of whorls	H (mm)	W (mm)	PA
USNM PAL 768628, holotype	2A–C	5.5	4.8	3.7	59º
USNM PAL 768622, paratype	2E–H	4	5.1	3.6	51º
USNM PAL 768627, paratype	2I–J	5	5.6	3.8	47º
USNM PAL 768630, paratype	2K–L	5.5	4.8	3.2	51º

Description

Shell small (largest specimen ~6 mm in maximum height: Table 1), murchisoniform, and moderately high-spired with a variable pleural angle of ~45°–60°. The spire profile is gradate and the suture incised. The largest specimens preserve 5–6 whorls, with the initial whorls usually being broken or poorly preserved. The ramp is convex in the early whorls and the selenizone covers about a quarter of the early whorl face. In late whorls, the adapical half of

the ramp is convex, but becomes concave in abapical half and inclined at 40°–55°. The shell ornamentation comprises sharp prosocyrt ribs (eight/mm on the last whorl). The selenizone is concave and wide, covering about a sixth of the late whorl face and situated low on the spire whorls; it is bordered by prominent spiral cords (= projections of the former edges of the slit). The abapical (lower) edge of the selenizone is situated at about mid-whorl along the body whorl. The lunulae are crescentic, sharp and separated by spaces equating to two–three times the width of a lunula. The whorl face below the selenizone is concave and abapically facing with oblique prosocyrt growth lines and a maximum convexity near the abapical suture; the transition to base has a slight angulation where the suture is situated. The base has slightly opisthocyrt growth lines or ribs, and is anomphalous with a circular aperture that thickens at the basal to inner lip connection.

Remarks

The number of axial ribs/mm in last whorl has been used to distinguish between the Permian species of *Peruvispira* (e.g., Sabattini & Noirat 1969, Sabattini 1980, Taboada *et al*. 2015), but this can vary intra-specifically (Karapunar *et al*. 2022). *Peruvispira kanchanaburiensis* has eight axial ribs/mm, but whether this number varies cannot be assessed because of poor preservation. Apart from that, the shell form, whorl morphology and ornamentation differ from *Peruvispira* sp. in the Khao Khad Formation of Central Thailand, in which the abapical edge of the selenizone is more distinctly projecting and the selenizone is more gently inclined (Ketwetsuriya *et al.* 2020b). *Peruvispira delicata* Chronic, 1949, from the Lower Permian Copacabana Group of Peru also differs in lacking a concave region on the lower half of the ramp; instead, the ramp is slightly convex and more steeply inclined. *Peruvispira canningensis* Taboada, Mory, Shi, Haig & Pinilla, 2015 from the Lower Permian Calytrix Formation of Australia is lower spired, has a straighter ramp, and more closely spaced axial ribs numbering 9–10/mm. *Peruvispira brasilensis* Simões, Neves, Taboada, Pagani, Varejão & Assine, 2019 from the Lower Permian Taciba Formation of Brazil differs in having a concave ramp. *Peruvispira turrita* Yu, 1980 (in Wang & Xi) from the Changhsingian (Upper Permian) Xuanwei Formation of Guizhou, China likewise differs in having a slightly higher and somewhat coeloconoid spire and more elongate aperture with longer inner lip. *Peruvispira allandalensis* Fletcher, 1958 from the Sakmarian (Lower Permian) Allandale Formation of Australia is distinguished by its evenly convex ramp and narrower selenizone. *Peruvispira uralensis* Mazaev, 2019 from the Asselian–Sakmarian boundary beds (Lower

Permian) of Shakhtau in Russia similarly differs by possessing a convex ramp and rounded whorl profile.

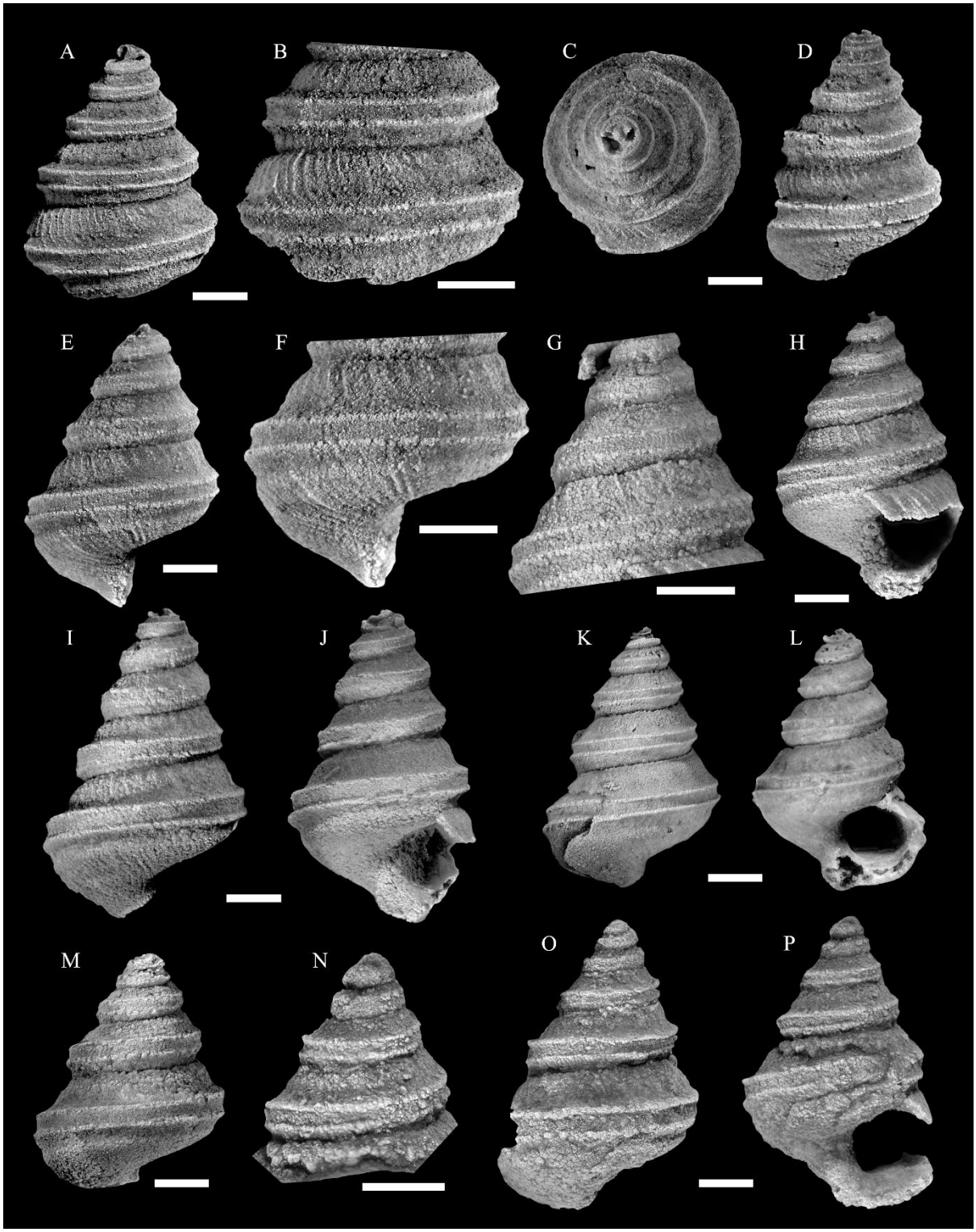

Figure 2. *Peruvispira kanchanaburiensis*. **A–C**, Holotype (USNM PAL 768628). **D**, Referred specimen (USNM PAL 768631). **E–H**, Paratype (USNM PAL 768622). **I–J**, Paratype (USNM PAL 768627). **K–L**, Paratype (USNM PAL 768630). **M**, (USNM PAL 768618). **N–P**, (USNM PAL 768615). Scale bar = 1 mm.

Peruvispira kirillowensis (Licharew, 1913) from the Lower Kazanian (Middle Permian) of Russia differs in its wider ramp, absence of sharp axial ribs, and more prominent selenizone borders (see Mazaev 2018). In addition, *P. kanchanaburiensis* is distinct from Carboniferous *Peruvispira* species, including both *Peruvispira teckaensis* Taboada, Pagani, Pinilla, Tortello & Taboada, 2019 from the Pampa de Tepuel Formation, and *Peruvispira sueroi* Sabattini & Noirat, 1969 from the Mojon de Hierro Formation of Argentina, which are lower spired (see also Karapunar *et al*. 2022). *Peruvispira reedi* Sabattini, 1980 from the San Eduardo Formation of Argentina differs in its narrower selenizone and evenly convex ramp. *Peruvispira promenata* (Waterhouse, 1987) from the Kasimovian (Upper Carboniferous) Fairyland Formation of Australia differs in its ramp profile, which is flat to slightly concave instead of convexo-concave. *Peruvispira oklahomaensis* Karapunar & Nützel, 2022 (in Karapunar *et al*. 2022) from the Morrowan (Pennsylvanian) Gene Autry Formation of the USA has a lower spire and the axial ribs that disappear near the selenizone. Finally, *Peruvispira coatesi* (Peel, 2016) from the Namurian Morridge Formation UK can be distinguished by its distinctly concave ramp and axially elongate subsutural nodes, rather than continuous axial ribs and nodes restricted to the peri-basal angulation as in *P. kanchanaburiensis*.

Subclass NERITIMORPHA Koken, 1896
Order CYRTONERITIDA Bandel & Frýda, 1999
Family ORTHONYCHIIDAE Bandel & Frýda, 1999 (=?Platyceratidae Hall, 1879)

Orthonychia Hall, 1843

Type species
Orthonychia subrectum (Hall, 1859); by monotypy.

Remarks
Orthonychia Hall, 1843 had long been considered a close relative of *Platyceras* Conrad, 1840, and has even been treated as a subgenus of *Platyceras* (e.g., Knight *et al*. 1960). Due to the presence of an open coiled, 'fishhook-like' protoconchin *Orthonychia*, Bandel & Frýda (1999) erected a new order Cyrtoneritimorpha (= Cyrtoneritida) and included *Orthonychia* in this new order, and placed *Platyceras* and Platyceratidae in their other new order Cycloneritimorpha (=Cycloneritida). The protoconch of the type species and other species of *Platyceras* has not been documented yet, thus its differentiation from the openly coiled protoconch of *Orthonychia*

remains uncertain. Frýda *et al*. (2009) reported a tightly coiled protoconch in a juvenile specimen whic they assigned to *Platyceras* sp.; however, protoconch of more clearly identified *Platyceras* specimens, especially the protoconch of the type species of *Platyceras* is needed to justify the distinction of *Orthonychia* from *Platyceras* at the family level. If the protoconch is openly coiled in clearly documented representatives of *Platyceras* as that of *Orthonychia*, then the family Orthonychiidae represents probably a junior synonym of Platyceratidae as also concluded by Frýda *et al*. (2009). Here, we follow Bouchet *et al*. (2017) in provisionally retaining Orthonychiidae, but do not consider *Orthonychia* and *Platyceras* to be distinct at family or order-level. These genera differ from all other Palaeozoic gastropods in possessing markedly irregular growth lines, which reflect their specialised feeding ecology on crinoids (e.g., Frýda *et al*. 2008).

Orthonychia sp.
(Fig. 3)

Referred material
USNM PAL 768629, an incomplete shell.

Locality, unit and age
USNM Locality 9266, Khao Mang Lat in the Ban Kao District of Kanchanaburi Province, Central Thailand; Ratburi Group, Artinskian–Wordian (upper-Lower–Middle Permian).

Description
The shell is small (height = 3.2 mm, width = 3.7 mm, length = 5.5 mm), openly coiled and cap-shaped, with a posteriorly pointing apex. The early shell is not preserved due to coarse silicification. The shell surface is smooth and consists of two regions; the right region is well-rounded comprising two-thirds of the whorl, and having prosocyrt growth lines; the left region is convex and comprises one-third of the whorl, and having prosocyrt growth lines. These two regions form an acute, V-shaped sinus at their confluence. The aperture is sub-ovate in shape.

Remarks
The present specimen (USNM PAL 768629) displays shell morphology and growth lines consistent with *Orthonychia*. Shells referred to this genus can vary inter-specifically both in their growth lines and aperture outline (e.g., Yochelson 1956); this conforms to the shape of

their crinoid host (Frýda *et al*. 2008). Comparisons between species are therefore challenging, especially when based on only a single specimen.

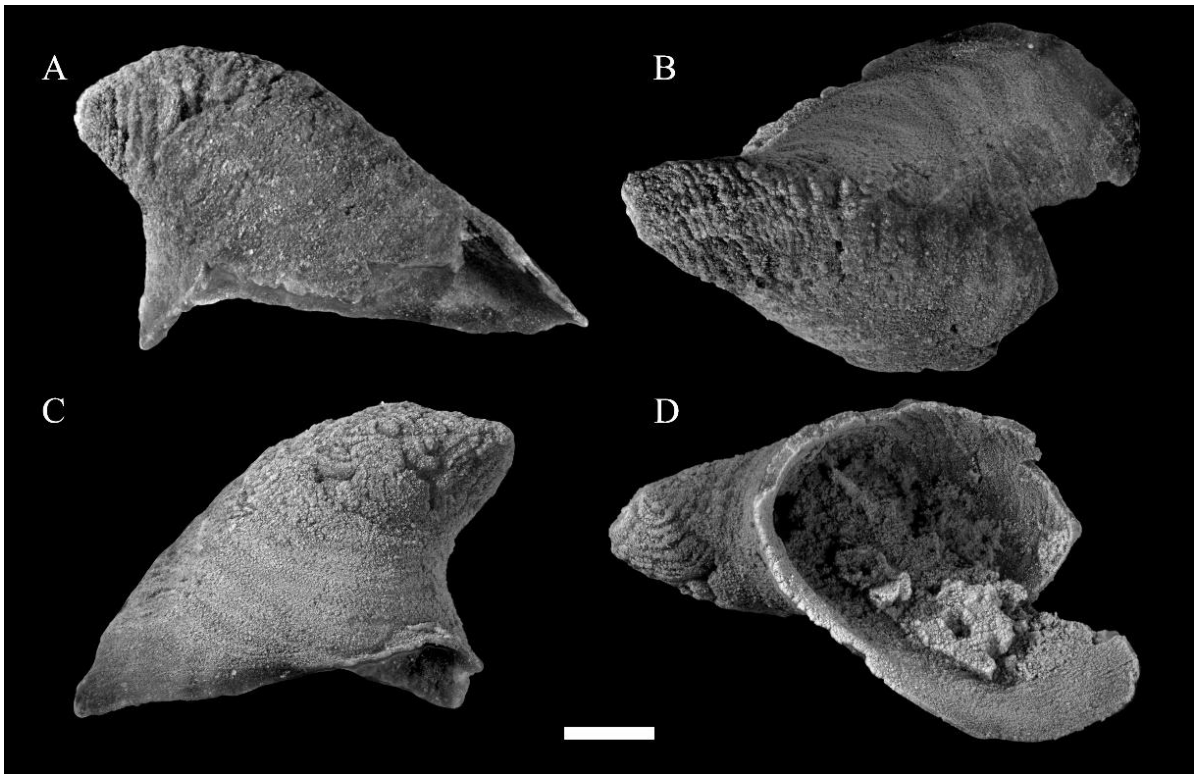

Figure 3. *Orthonychia* sp. (USNM PAL 768629). Scale bar = 1 mm.

Amongst the Permian species of *Orthonychia*, the studied specimen most closely resembles *Orthonychia bowsheri* Yochelson, 1956 from the Roadian (Middle Permian) Word Formation of Texas, USA, and *Orthonychia abundans* (Wanner, 1922) from the Artinskian (LowerPermian) Niki Niki Formation of Timor (Wanner 1922, 1941), the Wuchiapingian (Upper Permian) Chhidru Formation of Pakistan (see Reed, 1944, p. 347, pl. 58, figs 9a–b), and Sakmarian–Artinskian (Lower Permian Fossil Cliff Member of the Holmwood Formation of Australia (Dickins 1963). Although the degree of tightness of coiling is variable in *O. abundans* (Wanner, 1922, pl. 152, figs 8–10), the whorls seem to be more tightly coiled than the present specimen (see Dickins 1963, pl. 25, figs 7–18). Wanner (1941) later classified *O. abundans* as subspecies of *Orthonychia varians* (Wanner, 1922), but this was rejected by Dickins (1963). Wanner (1922) proposed several species of *Platyceras* (under the name *Capulus*). Some of these species may represent synonyms given the variability in shell shape and growth lines in this taxon. Because of this high variability, Yochelson (1956) did not provide comparisons for *Orthonychia bowsheri* Yochelson, 1956 with the previously erected

species, and instead justified species-level distinction by the absence of nominate *Orthonychia* species in the Permian of the USA. We therefore use the same basis (the paleogeographic distance) for excluding USNM PAL 768629 from *O. bowsheri*, and note that this specimen represents the only documented platyceratid *sensu lato* from the Permian of Thailand.

Discussion

Grant (1976) reported that the Khao Mang Lat fossil gastropod assemblage contained several pleurotomariidans in addition to a platyceratid. However, the present study revealed the presence of only *Peruvispira kanchanaburiensis* sp. nov. and *Orthonychia* sp. *Peruvispira* had long been considered as a pleurotomariidan genus (e.g., Knight *et al*. 1960), thus we assume that by mentioning several pleurotomariidan genera Grant (1976) was referring to the material identified herein as *Peruvispira kanchanaburiensis*. Karapunar *et al*. (2022) assigned *Peruvispira* to Goniasmatidae (Caenogastropoda) based on its planktotrophic protoconch. *Orthonychia* was removed from Platyceratidae and assigned to Orthonychiidae and to a distinct order (Bandel & Frýda 1999) but this classification needs re-consideration (see remarks on *Orthonychia*).

The Khao Mang Lat assemblage is virtually monospecific, with ca. 200 specimens attributed to *P. kanchanaburiensis* versus a single individual of *Orthonychia*. The low species diversity contrasts starkly with the diversity of other silicified Permian gastropod faunas from Thailand, such as those from the Tak Fa Limestone, Khao Khad Formation and other outcrops of the Ratburi Group, which have collectively yielded a rich diversity of 34–44 species in approximately equivalent abundances (Ketwetsuriya *et al*. 2016, 2020a, 2020b). The limestones from the Early Permian Khao Khad Formation of Central Thailand exhibits a facies dominated by several gastropod species including rather large specimens (Ketwetsuriya et al. 2020c). Similar to the low diversity of gastropods at Khao Mang Lat, the diversity of brachiopod assemblage (12 species, belonging to 12 genera based on ca. 1,350 specimens) is also relatively low compared to brachiopod assemblages from other coeval localities reported by Grant (1976). Grant (1976) attributed this diversity difference to low sampling effort, which he quantified with an index value of 0.5 derived from “Families found minus Cosmopolitan Dominants found, divided by Cosmopolitan Dominants found” (see Stehli & Grant 1971). In our opinion this index simply reflects the diversity of the fauna rather than sampling efficiency. The number of gastropods species ranges between 25–60 in the various known Middle Permian gastropod assemblages recovered across Southeast Asia at a sample size of 200 specimens in

rarefaction curves (see Ketwetsuriya *et al*. 2021). This shows that the gastropod fauna from Khao Mang Lat is much less diverse than other Middle Permian faunas and that the low diversity is an original attribute of the fauna rather than result of a sampling artefact.

Grant (1976) hypothesised that the low brachiopod diversity encountered at Khao Mang Lat might have been caused by sedimentary and energy regime. Based on the sandy-silty limestone lithology (or fine-grained sandstone with 10% sand and 15% silt content and calcareous cement according to Grant 1976) and inferred brachiopod ecologies, Grant (1976) interpreted the paleoenvironment as a shallow near-shore setting with clastic influx. The significant portion of the brachiopod specimens (95%) at Khao Mang Lat (Ban Kao District) were epifaunal either held by pedicular threads or supported by their spines, and some 5% were attached to the substrate by their pedicle but none cemented to the substrate (Grant 1976, table 2). The seafloor was accordingly interpreted as sparsely populated and topographically flat, firm and lacking bioherms or reefs (Grant 1976). The Khao Mang Lat assemblage also contained bryozoans and rare sponges, but no corals, implying a predominantly suspension-feeding benthic fauna, with the possible exception of *Peruvispira*, which does not have any shell features indicating a sedentary or suspension feeding life habit (e.g., flat base, open coiling, radial aperture or very low whorl expansion rate; e.g., Peel 1984 and references therein). Considering the small size and high abundance, an active predatory behaviour can be discarded. *Peruvispira* could be interpreted as a grazer either on algae or on sedentary animals (e.g., brayozoans and sponges).

The environmental preferences of Palaeozoic gastropods are not well-studied, thus the impact of particular habitat settings on diversity is uncertain. Grant (1976)discussed that the index he used might be temperature sensitive and the low index value of Khao Mang Lat brachiopod assemblage might indicate lower temperatures. Waterhouse (1982) reported presence of *Peruvispira* within a Lower Permian (Asselian) low-diversity cold-water assemblage from the Phuket Group on Ko Phi Phi, Thailand. Dickins (1961) also reported a monotaxic gastropod assemblage containing only *Peruvispira vipersdorfensis* Dickens, 1961 from the Lower Permian (Sakmarian–lower Artinskian) glacial deposits (Dwyka tillites) of South Africa. These two examples demonstrate that at least some species of *Peruvispira* were able to tolerate very low temperatures and cold-water environments. Low diversity can also be caused by increased salinity, oxygen deficiency, or geographic isolation (e.g., within lagoons), yet there is no indication of such conditions at Khao Mang Lat.

Domination of the Khao Mang Lat assemblage by *Peruvispira* rather than other cosmopolitan Permian gastropod taxa, such as *Bellerophon* Montfort, *Worthenia* de Koninck and *Naticopsis* McCoy, is notable given that these tend to be prolific in other faunas (e.g.,

Ketwetsuriya *et al*. 2021, table 6). However, both *Peruvispira* (Karapunar *et al*. 2022) and *Orthonychia* (see Yochelson 1956, Frýda *et al*. 2009) have planktotrophic protoconchs and therefore could have wider dispersal capacity than gastropods with non-planktotrophic larvae (Jablonski & Lutz 1983, Nützel 2014). The prevalence of *Peruvispira* at Khao Mang Lat could alternatively suggest a priority effect, with their planktotrophic larvae being able to establish early and exclude other ecologically equivalent gastropod taxa from the local habitat (see Fukami 2015).

Orthonychiids (and platyceratids) are known to feed on crinoids (e.g., Yochelson 1956, Baumiller & Gahn 2002, Webster & Donovan 2012, Nützel 2021) and on brachiopods (Baumiller *et a*l. 1999), but some may have been detritus feeders (Horný 2000, Frýda *et al*. 2008). Grant (1976) reported that crinoids were absent from the Khao Mang Lat assemblage, Thus, the occurrence of *Orthonychia* sp. in a crinoid-free assemblage raises a question whether it was a brachiopod predator or scavenger. Apart from that, the rarity of this taxon indicates that the environment was generally unfavourable for this particular species.

Conclusions

The taxonomic study of the earliest known Permian gastropod assemblage from Thailand revealed that the diversity of the gastropod fauna at the Khao Mang Lat is much lower than previously estimated. The gastropod assemblage is strongly dominated by *Peruvispira kanchanaburiensis*. Monotaxic gastropod assemblages with *Peruvispira* were previously reported in cool water deposits. Hence, low temperatures might be the primary cause of the low diversity and composition of the studied assemblage. Alternatively, priority effects might have played a role. The single *Orthonychia* specimen is the only record of this genus and of a platyceratid (*sensu lato*) in the Permian deposits of Thailand. The current taxonomic classification of *Orthonychia* in a distinct family than Platyceratidae based on the protoconch morphology is not justified since the protoconch of *Platyceras* has not yet been clearly documented.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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References

Bandel, K. & Frýda, J., 1999. Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. *Geologica et Palaeontologica* 33, 219–235.

Baumiller, T.K. & Gahn, F.J., 2002. Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. *The Paleontological Society Papers* 8, 195–210.

Baumiller, T.K., Leighton, L.R. & Thompson, D.L., 1999. Boreholes in Mississippian spiriferide brachiopods and their implications for Paleozoic gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 147, 283–289.

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

Brönnimann, P., Whittaker, J.E. & Zaninetti, L., 1978. *Shanita*, a new pillared miliolacean foraminifer from the Late Permian of Burma and Thailand. *Rivista Italiana di Paleontologia e Stratigrafia* 84: 63–92.

Chronic, B.J., 1949. Invertebrate paleontology (excepting fusulinids and corals). In *Upper Paleozoic of Perú*. Newell, N.D., Chronic, J. & Roberts, T.G., eds, Columbia University, New York, 46–173.

Conrad, T.A., 1840. *Third annual report on the Paleontological Department of the Survey*. New York Geological Survey, Annual Report 4, 199–207.

Cox, L.R., 1960. Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London* 33, 239–261.

Department of Mineral Resources of Thailand, 1999. *Geological Map of Thailand, Scale 1:2,500,000*. Bangkok.

Dickins, J., 1961. *Eurydesma* and *Peruvispira* from the Dwyka beds of South Africa. *Palaeontology* 4, 138–148.

Dickins, J.M., 1963. Permian pelecypods and gastropods from Western Australia. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 63, 1–203.

Fletcher, H.O., 1958. The Permian gastropods of New South Wales. *Records of the Australian Museum* 24, 115–164.

Fontaine, H., 1986. The Permian of Southeast Asia. *CCOP Technical Bulletin* 18, 1–111.

Fontaine, H., 1988. Permian corals of West Thailand. *CCOP Technical Bulletin* 20, 112–127.

Fontaine, H., Salyapongse, S., 2001. Permian corals of peninsular Thailand and other associated fossils. *CCOP Newsletter* 26, 14–19.

Frýda, J., Racheboeuf, P.R. & Frydova, B., 2008. Mode of life of early Devonian *Orthonychia protei* (Neritomorpha, Gastropoda) inferred from its post-larval shell ontogeny and muscle scars. *Bulletin of Geosciences* 83, 491–502.

Frýda, J., Racheboeuf, P.R., Frydova, B., Ferrova, L., Mergl, M. & Berkyova, S., 2009. Platyceratid gastropods–stem group of patellogastropods, neritimorphs or somethingelse?. *Bulletin of Geosciences* 84, 107–120.

Fukami, T., 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46, 1–23.

Grant, R.E., 1976. Permian brachiopods from southern Thailand. *The Paleontological Society Memoir* 50(S9), 1–269.

Hall, J., 1843. *Geology of New York*. Comprising the survey of the fourth geological district. Albany, Carroll and Cook.

Hall, J., 1859. Contributions to the palaeontology of New York: being some of the results of investigations made during the years 1855, '56, '57 & '58. *Annual Report of the Regents of the University on the condition of the State Cabinet of Natural History* 12.

Hall, J., 1879. Palaeontology, Vol. 5, Part 2, Text, containing descriptions of the Gasteropoda, Pteropoda, and Cephalopoda of the Upper Helderberg, Hamilton, Portage and Chemung Groups. Geological Survey of the State of New York. Van Benthuysen, Albany, 492 pp.

Horný, R.J., 2000. Mode of life of some Silurian and Devonian platyceratids. *Bulletin of Geosciences* 75, 135–143.

Ingavat-Helmcke, R., 1993. Contribution to the Permian fusulinacean faunas of Peninsular Thailand. *Journal of Southeast Asian Earth Sciences* 8, 67–75.

Jablonski, D. & Lutz, R.A., 1983. Larval ecology of marine benthic invertebrates: Paleobiological implications. *Biological Reviews* 58, 21–89.

Karapunar, B., Nützel, A., Seuss, B. & Mapes, R.H., 2022. Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA. Papers in Palaeontology.

Ketwetsuriya, C., Cook, A.G. & Nützel, A., 2020a. Permian gastropods from the Ratburi Limestone, Khao Phrik, Central Thailand. *Paläontologische Zeitschrift* 94, 53–77.

Ketwetsuriya, C., Hausmann, I.M. & Nützel, A., 2021. Diversity patterns of Middle Permian gastropod assemblages from the Tak Fa Formation, Central Thailand. *Palaeobiodiversity and Palaeoenvironments* 101, 907–925.

Ketwetsuriya, C., Karapunar, B., Charoentitirat, T. & Nützel, A., 2020b. Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa* 4766, 1–47.

Ketwetsuriya, C., Nose, M., Charoentitirat, T. & Nützel, A., 2020c. Microbial-, fusulinid limestones with large gastropods and calcareous algae: an unusual facies from the Early Permian Khao Khad Formation of Central Thailand. *Facies* 66, 1–21.

Ketwetsuriya, C., Nützel, A.& Kanjanapayont, P., 2016. Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences* 91, 481–513.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R., 1960. Systematic descriptions. In *Treatise on Invertebrate Paleontology, Part 1, Mollusca 1*. Moore, R.C., ed, Geological Society of America and University of Kansas Press, Kansas, I169–I310.

Koken, E., 1896. Die Gastropoden der Trias um Hallstatt. Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt, 46, 37–126.

Mazaev, A.V., 2018. Early Kazanian (Middle Permian) Gastropods. *Paleontological Journal* 52, 796–827.

Mazaev, A.V., 2019. Lower Permian Gastropods of Shakhtau (Asselian–Sakmarian Boundary Beds, Southern Cisuralia). *Paleontological Journal* 53, 1237–1345.

Metcalfe, I., 2011. Tectonic framework and Phanerozoic evolution of Sundaland. *Gondwana Research* 19, 3–21.

Metcalfe, I., 2013. Tectonic evolution of the Malay Peninsula. *Journal of Asian Earth Sciences* 76, 195–213.

Nützel, A., 2014. Larval ecology and morphology in fossil gastropods. *Palaeontology* 57, 479–503.

Nützel, A., 2021. Gastropods as Parasites and Carnivorous Grazers: A Major Guild in Marine Ecosystems. In *The Evolution and Fossil Record of Parasitism: Identification and Macroevolution of Parasites*. De Baets, K., Huntley, J.W., eds, Springer, Cham, 209–229.

Nützel, A. & Bandel, K., 2000. Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 9, 557–569.

Peel, J.S., 1984. Autecology of Silurian gastropods and monoplacophorans. *Special Papers in Palaeontology* 32, 165–182.

Peel, J.S., 2016. Gastropods from the Carboniferous (Namurian) of Congleton Edge, Cheshire, UK. *Papers in Palaeontology* 2, 399–438.

Reed, F.R.C., 1944. Brachiopoda and Mollusca from the Productus limestones of the Salt Range. *Palaeontologia Indica* 23, 1–768.

Sabattini, N., 1980. Gastropods Marinos Carbonicos y permicas de la Sierra de Barreal (Provincia de San Juan). *Ameghiniana* 17, 109–119.

Sabattini, N. & Noirat, S., 1969. Algunos Gastropoda de las superfamilias Euomphalacea, Pleurotomariacea y Platyceratacea del Paleozoico superior de Argentina. *Ameghiniana* 6, 98–118.

Sakagami, S., 1965. Three Carboniferous species of Bryozoa from Khao Noi, central Thailand. *Japanese Journal of Geology and Geography* 36, 143–147.

Sakagami, S., 1969. Fusulinacean fossils from Thailand, Part IV. On some Permian fusulinaceans from peninsular Thailand. In *Geology and Palaeontology of Southeast Asia vol. 6*. Kobayashi, T. & Toriyama, R., eds, University of Tokyo Press, Tokyo, 265–275.

Sakagami, S., 1970. Addition to the Permian Bryozoa from Ko Muk, peninsular Thailand. In *Geology and Palaeontology of Southeast Asia vol. 8*. Kobayashi, T. & Toriyama, R., eds, University of Tokyo Press, Tokyo, 43–68.

Sakagami, S., 1973. Permian Bryozoa from Khao Raen, near Rat Buri, Thailand. In *Geology and Palaeontology of Southeast Asia vol. 12*. Kobayashi, T. & Toriyama, R., eds, University of Tokyo Press, Tokyo, 75–89.

Simões, M. G., Neves, J. P., Taboada, A. C., Pagani, M. A., Varejão, F. G. & Assine, M. L., 2020. Macroinvertebrates of the Capivari marine bed, late Paleozoic glacial Itararé Group, northeast Paraná Basin, Brazil: Paleoenvironmental and paleogeographic implications. *Journal of South American Earth Sciences* 98, 102433.

Sone, M. & Metcalfe, I., 2008. Parallel Tethyan sutures in mainland Southeast Asia: New insights for Palaeo-Tethys closure and implications for the Indosinian orogeny. *Comptes Rendus Geosciences* 340, 166–179.

Stehli, F.G. & Grant, R.E., 1971. Permian brachiopods from Axel Heiberg Island, Canada, and an index of sampling efficiency. *Journal of Paleontology*, 502–521.

Taboada, A.C., Mory, A.J., Shi, G.-R., Haig, D.W. & Pinilla, M.K., 2015. An Early Permian brachiopod–gastropod fauna from the Calytrix Formation, Barbwire Terrace, Canning Basin, Western Australia. Alcheringa: *An Australasian Journal of Palaeontology* 39, 207–223.

Taboada, A.C., Pagani, M.A., Pinilla, M.K., Tortello, F. & Taboada, C.A., 2019. Carboniferous deposits of northern Sierra de Tecka, central-western Patagonia, Argentina: paleontology, biostratigraphy and correlations. *Andean Geology* 46, 629–669.

Ueno, K. & Charoentitirat, T., 2011. Carboniferous and Permian. In *The geology of Thailand*. Ridd, M.F., Barber, A.J. & Crow, M.J., eds, The Geological Society, London, 71–135.

Ueno, K., Miyahigashi, A., Kamata, Y., Kato, M., Charoentitirat, T. & Limruk, S., 2012. Geotectonic implications of Permian and Triassic carbonate successions in the Central Plain of Thailand. *Journal of Asian Earth Sciences* 61, 33–50.

Wang, H.-J. & Xi, Y.H., 1980. Fossil gastropods from late Permian to Early Triassic in West Guizhou Province. In *Late Permain coal-bearing strata, fauna and flora of West Guizhan Province and East Yunnan Province*. Nanjing Institute of Geology and Palaeontology, Academia Sinica, ed, Science Press, Nanjing, 195–232.

Wanner, C., 1922. Die Gastropoden und Lamellibranchiaten der Dyas von Timor. *Palaontologie von Timor* 11, 1–82.

Waterhouse, J.B. & S. Piyasin. 1970. Mid Permian Brachiopods from Khao Phrik, Thailand. *Paleontographica (A: Paläozoologie, Stratigraphie)* 135, 83–197.

Waterhouse, J.B. 1982. An early Permian cool-water fauna from pebbly mudstones in south Thailand. *Geological Magazine* 119, 337–354.

Yanagida, J., 1970. Permian brachiopods from Khao Phrik, near Rat Buri, Thailand. In *Geology and Palaeontology of Southeast Asia vol. 14*. Kobayashi, T. & Toriyama, R., eds, University of Tokyo Press, Tokyo, 7–23.

CHAPTER 5

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Slit-band gastropods (Pleurotomariida) from the Upper Triassic St. Cassian Formation and their diversity dynamics in the Triassic

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Abstract

The St. Cassian Formation, Italy, has yielded the most diverse marine invertebrate fauna known from the Triassic. A quarter of all described Triassic gastropod species has been reported from this formation. Most of the gastropod species from the St. Cassian Formation were erected in the 19th century and many of them are known only from their original figures and descriptions. The failure to study type specimens resulted in many erroneous identifications by subsequent authors. Here, we revise the slit band gastropods (Pleurotomariida) from the St. Cassian Formation—one of the major groups present in this formation. A total of 77 nominate Pleurotomariida species belonging to 29 genera and 11 families are present in the St. Cassian Formation which comprises approximately 14 % of the total nominate gastropod species of that formation. In addition, we revise several taxa that had been wrongly assigned to Pleurotomariida. As other gastropod clades, Pleurotomariida experienced a major extinction at the end-Permian mass extinction event. As in the Late Palaeozoic, their relative abundance in gastropod faunas continued to be 30 % in some Anisian faunas but decreased to 5–10 % afterwards. Their diversification at generic level became interrupted by an extinction event within the Carnian, probably by the Carnian Pluvial Event. As a result of their sluggish recovery compared to the other gastropod groups, their species diversity decreased from 26 % during the Permian to 18 % during the Triassic.

Type specimens of the following genera are studied: *Proteomphalus*, *Rhaphistomella*, *Temnotropis*, *Kittlidiscus*, *Stuorella*, *Schizogonium*, *Wortheniella*, *Bandelium*, *Lancedellia*, *Rinaldoella*, *Pseudowortheniella*, *Paleunema*, *Ampezzalina*, *Bandelastraea*, *Cheilotomona*, *Pseudoscalites*, *Delphinulopsis*, and *Cochlearia*.

Nine new pleurotomariidan genera are erected: *Amplitomaria*, *Pseudoananias*, *Lineacingulum*, *Pressulasphaera*, *Cancellotomaria*, *Acutitomaria*, *Lineaetomaria*, *Nodocingulum*, and *Striacingulum.*

Eight new species are described: *Schizogonium undae*, *Acutitomaria kustatscherae*, *Wortheniella klipsteini*, *Wortheniella paolofedelei*, *Rinaldoella tornata*, *Nodocingulum ernstkittli*, *Nodocingulum*? *turris*, and *Laubella subsulcata*.

Eoworthenia frydai is a new replacement name for *Worthenia rarissima* Barrande.

Key words: Carnian, Gastropoda, St. Cassian, Triassic, Permian, mass extinction, Carnian Pluvial Event

Taxonomic Summary

All Pleurotomariida species from the St. Cassian Formation and their synonyms can be found in the related chresonymy or synonymy lists and are additionally listed in the Appensix S1. Synonyms of the non-pleurotomariidan species discussed in this work can be found in the related synonymy or chresonymy lists. In addition to that, *Guizhouspira* Wang, 1980 (in Wang & Xi) is herein regarded as junior synonym of *Baylea* de Koninck, 1883 and *Schwardtopsis* Bandel, 2007 is regarded as junior synonym of *Delphinulopsis* Laube, 1870.

The following species are used in new combinations (**comb. nov.**), [former combination]:

Proteomphalus canovanus (Kittl, 1899) [*Ptychomphalina canovana*]
Proteomphalus moscardii (Stoppani, 1858–1860) [*Ptychomphalina moscardii*]
Proteomphalus gracilis (Read in Broili, 1907) [*Ptychomphalus gracilis*]
Amplitomaria spuria (Münster, 1841) [*Wortheniella spuria*]
Amplitomaria bilineata (Klipstein, 1844) [*Worthenia*? *bilineata*]

Pseudoananias subgranulata (Münster, 1841) [*Rinaldoella subgranulata*]
Ptychomphalus? *kumbfurensis* (Skwarko, 1967) [*Rhaphistomella*? *kumbfurensis*]
Lineacingulum texturatum (Münster, 1841) [*Laubella texturata*]
Lineacingulum bicingulatum (Klipstein, 1844) [*Pleurotomaria bicingulata*]
Lineacingulum eremita (Koken, 1897) [*Worthenia eremita*]
Rufilla fasciolata (Münster, 1841) [*Gosseletina fasciolata*]
Rufilla distincta (Kittl, 1894) [*Worthenia distincta*]
Rufilla latizonata (Laube, 1868) [*Pleurotomaria latizonata*]
Trochotoma frydai (Kiel & Bandel, 2000) [*Temnotropis frydai*]
Auritoma? *stevniensis* (Hansen, 2019) [*Temnotropis stevniensis*]
Trochotoma (*Placotoma*) *suevica* (Quenstedt, 1881–1884) [*Trochotoma* (*Placostoma*) *suevica*]
Trochotoma fallax (Kittl, 1891) [*Temnotropis fallax*]
Temnotropis fuchsi (Kittl, 1891) [*Gosseletina fuchsi*]
Pressulasphaera pamphilus (d'Orbigny, 1850) [*Pleurotomaria pamphilus*]
Zygites subcancellata (d'Orbigny, 1850) [*Trochus subcancellatus*]
Cancellotomaria subcancellata (d´Orbigny, 1850) [*Pleurotomaria subcancellata*]
Acutitomaria? *paucivoluta* (Yin & Yochelson, 1983a) [*Vistilia*? *paucivoluta*]
Acutitomaria? *elegans* (Yin & Yochelson, 1983a) [*Cheilotomona elegans*]
Lineaetomaria decorata (Münster, 1841) [*Pleurotomaria decorata*]
Euryalox subornatus (d'Orbigny, 1850) [*Trochus subornatus*]
Bathrotomaria plana (Münster, 1844) [*Pleurotomaria plana*]
Kittlidiscus substriatus (Klipstein, 1844) [*Worthenia*? *substriata*]
Vistilia salisburgensis (Schnetzer, 1934) [*Stuorella salisburgensis*]
Stuorella tricarinata (Klipstein, 1844) [*Trochus tricarinatus*]
Triassocirrus russoi (Fucini, 1913) [*Schizogonium russoi*]
Schizogonium? *bicarinatum* (Klipstein, 1844) [*Pleurotomaria bicarinata*]
Wortheniella? *liebeneri* (Kittl, 1891) [*Worthenia liebeneri*]
Wortheniella? *margaritacea* (Laube, 1868) [*Worthenia margaritacea*]
Nodocingulum coronatum (Münster, 1841) [*Rinaldoella coronata*]
Nodocingulum subcoronatum (Münster, 1841) [*Worthenia subcoronata*]
Nodocingulum cirriformis (Laube, 1868) [*Worthenia cirriformis*]
Nodocingulum granulosum (Klipstein, 1844) [*Turbo granulosus*]
Nodocingulum bieberi (Kittl, 1891) [*Worthenia bieberi*]
Nodocingulum johannisaustriae (Klipstein, 1844) [*Rinaldoella johannisaustriae*]
Nodocingulum muensteri (Klipstein, 1844) [*Rinaldoella muensteri*]
Nodocingulum furcatum (Kittl, 1891) [*Worthenia furcata*]
Nodocingulum crenatum (Münster, 1841) [*Rinaldoella crenata*]
Nodocingulum? *subtilis* (Kittl, 1891) [*Worthenia subtilis*]
Nodocingulum pygmaea (Stoppani, 1865) [*Wortheniella pygmaea*]
Nodocingulum rhombifera (Körner, 1937) [*Worthenia rhombifera*]
Striacingulum cancellatocingulatum (Klipstein, 1844) [*Pleurotomaria cancellato-cingulata*]
Striacingulum toulai (Kittl, 1891) [*Worthenia toulai*]
Triassocirrus brandis (Klipstein, 1844) [*Schizogonium*? *brandis*]
Triassocirrus tubifer (Kittl, 1891) [*Coelocentrus tubifer*]
Triassocirrus pichleri (Laube, 1868) [*Coelocentrus pichleri*]
Bandelastraea angulata (Nützel & Senowbari-Daryan, 1999) [*Ampezzalina angulata*]
Bandelastraea lancedelli (Zardini, 1978) [*Paleunema lancedelli*]
Pseudoscalites cochlea (Münster, 1841) [*Pleurotomaria cochlea*]

Lectotypes are designated for the following 106 species [current combination]:

Ptychomphalus gracilis Read, 1907 in Broili [*Proteomphalus gracilis*]
Ptychomphalina canovana Kittl, 1899 [*Proteomphalus canovanus*]

Pleurotomaria spuria Münster, 1841 [*Amplitomaria spuria*]
Pleurotomaria concinna Klipstein, 1844 [*Amplitomaria spuria*]
Turbo bilineatus Klipstein, 1844 [*Amplitomaria bilineata*]
Pleurotomaria subgranulata Münster, 1841 [*Pseudoananias subgranulata*]
Pleurotomaria meyeri Klipstein, 1844 [*Pseudoananias subgranulata*]
Pleurotomaria radians Wissmann, 1841 in Münster [*Rhaphistomella radians*]
Solarium subpunctatum Klipstein, 1844 [*Rhaphistomella radians*]
Euomphalus studeri Klipstein, 1844 [*Rhaphistomella radians*]
Pleurotomaria texturata Münster, 1841 [*Lineacingulum texturatum*]
Pleurotomaria amalthea Klipstein, 1844 [*Lineacingulum texturatum*]
Pleurotomaria bicingulata Klipstein, 1844 [*Lineacingulum bicingulatum*]
Worthenia cassiana Kittl, 1891 [*Lineacingulum bicingulatum*]
Pleurotomaria venusta Münster, 1841 [*Sisenna venusta*]
Pleurotomaria credneri Klipstein, 1844 [*Sisenna venusta*]
Turbo fasciolatus Münster, 1841 [*Rufilla fasciolata*]
Worthenia distincta Kittl, 1894 [*Rufilla distincta*]
Pleurotomaria latizonata Laube, 1868 [*Rufilla latizonata*]
Temnotropis fallax Kittl, 1891 [*Trochotoma fallax*]
Sigaretus carinatus Münster, 1841 [*Temnotropis carinata*]
Sigaretus tenuicinctus Klipstein, 1844 [*Temnotropis carinata*]
Gosseletina fuchsi Kittl, 1891 [*Temnotropis fuchsi*]
Pleurotomaria lineata Klipstein, 1844 [*Pressulasphaera pamphilus*]
Pleurotomaria calypso Kittl, 1894 [*Pressulasphaera pamphilus*]
Delphinula? *cancellata* Klipstein, 1844 [*Zygites subcancellata*]
Pleurotomaria cancellata Münster, 1841 [*Cancellotomaria subcancellata*]
Pleurotomaria bittneri Kittl, 1891 [*Cancellotomaria subcancellata*]
Pleurotomaria cancellata var. *complanata* Klipstein, 1844 [*Cancellotomaria subcancellata*]
Pleurotomaria cancellata var. *elliptica* Klipstein, 1844 [*Cancellotomaria subcancellata*]
Schizostoma costata Münster, 1841 [*Kokenella costata*]
Kokenella klipsteini Kittl, 1891
Kokenella laubei Kittl, 1891
Schizostoma buchii Münster, 1841 [*Kokenella buchi*]
Paleunema costata Zardini, 1978 [*Lancedellia costata*]
Pleurotomaria decorata Münster, 1841 [*Lineaetomaria decorata*]
Worthenia duplicata Kittl, 1891 [*Lineaetomaria decorata*]
Trochus ornatus Klipstein, 1844 [*Euryalox subornatus*]
Pleurotomaria bronni Klipstein, 1844 [*Kittlidiscus bronni*]
Pleurotomaria substriata Klipstein, 1844 [*Kittlidiscus substriatus*]
Schizodiscus planus var. *elevata* Kittl, 1891 [*Kittlidiscus substriatus*]
Trochus subconcavus Münster, 1841 [*Stuorella subconcava*]
Trochus maximilianileuchtenbergensis Klipstein, 1844 [*Stuorella subconcava*]
Trochus tricarinatus Klipstein, 1844 [*Stuorella tricarinata*]
Pleurotomaria scalaris Münster, 1841 [*Schizogonium scalare*]
Schizogonium elevatum Kittl, 1891
Schizogonium tetraptychum Kittl, 1891 [*Schizogonium elevatum*]
Pleurotomaria subcostata Münster, 1841 [*Schizogonium subcostatum*]
Pleurotomaria subdentata Münster, 1841 [*Schizogonium subdentatum*]
Schizostoma serrata Münster, 1841 [*Schizogonium serratum*]
Schizogonium impressum Kittl, 1891
Pleurotomaria bicarinata Klipstein, 1844 [*Schizogonium*? *bicarinatum*]
Schizogonium laubei Kittl, 1891
Worthenia rarissima Kittl, 1891 [*Pseudowortheniella rarissima*]

Worthenia subtilis Kittl, 1891 [*Nodocingulum*? *subtilis*]
Worthenia coralliophila Kittl, 1891 [*Wortheniella coralliophila*]
Pleurotomaria canalifera Münster, 1841 [*Wortheniella canalifera*]
Pleurotomaria subplicata Klipstein, 1844 [*Wortheniella canalifera*]
Pleurotomaria subpunctata Klipstein, 1844 [*Wortheniella canalifera*]
Worthenia liebeneri Kittl, 1891 [*Wortheniella liebeneri*]
Worthenia campensis Zardini, 1978 [*Bandelium campense*]
Pleurotomaria coronata Münster, 1841 [*Nodocingulum coronatum*]
Worthenia coronata var. *bicoronata* Kittl, 1891 [*Nodocingulum coronatum*]
Worthenia coronata var. *depressa* Kittl, 1891 [*Nodocingulum coronatum*]
Pleurotomaria subcoronata Münster, 1841 [*Nodocingulum subcoronatum*]
Worthenia coronata var. *ventricosa* Kittl, 1891 [*Nodocingulum subcoronatum*]
Pleurotomaria granulosa Münster, 1841 [*Nodocingulum granulosum*]
Worthenia bieberi Kittl, 1891 [*Nodocingulum bieberi*]
Ptychomphalus palaeopsis Kittl, 1891 [*Nodocingulum bieberi*]
Pleurotomaria johannisaustriae Klipstein, 1844 [*Nodocingulum johannisaustriae*]
Pleurotomaria gracilis Klipstein, 1844 [*Nodocingulum johannisaustriae*]
Worthenia dregeri Kittl, 1891 [*Nodocingulum johannisaustriae*]
Pleurotomaria münsteri Klipstein, 1844 [*Nodocingulum muensteri*]
Worthenia coronata var. *plicosa* Kittl, 1891 [*Nodocingulum muensteri*]
Worthenia furcata Kittl, 1891 [*Nodocingulum furcatum*]
Pleurotomaria beaumonti Klipstein, 1844 [*Nodocingulum furcatum*]
Pleurotomaria crenata Münster, 1841 [*Nodocingulum crenatum*]
Pleurotomaria? *angulata* Münster, 1841 [*Nodocingulum*? *angulatum*]
Pleurotomaria cancellato-cingulata Klipstein, 1844 [*Striacingulum cancellatocingulatum*]
Worthenia turriculata Kittl, 1891 [*Striacingulum cancellatocingulatum*]
Worthenia toulai Kittl, 1891 [*Striacingulum toulai*]
Pleurotomaria delicata Laube, 1868 [*Laubella delicata*]
Cantantostoma triasica Zittel, 1882 [*Laubella triasica*]
Laubella minor Kittl, 1891
Pleurotomaria nodosa Münster, 1841 [*Paleunema nodosa*]
Pleurotomaria calcar Münster, 1841 [*Ampezzalina calcar*]
Pachypoma damon Laube, 1868 [*Bandelastraea damon*]
Pachypoma endymion Laube, 1868 [*Bandelastraea damon*]
Pleurotomaria brandis Klipstein, 1844 [*Triassocirrus brandis*]
Coelocentrus tubifer Kittl, 1891 [*Triassocirrus tubifer*]
Pleurotomaria pentagonalis Klipstein, 1844 [*Triassocirrus pentagonalis*]
Pleurotomaria blumi Münster, 1841 [*Cheilotomona blumi*]
Pleurotomaria nerei Münster, 1841 [*Cheilotomona blumi*]
Cerithium acutum Münster, 1841 [*Cheilotomona blumi*]
Fusus tripunctatus Münster, 1841 [*Cheilotomona blumi*]
Pleurotomaria tricarinata Klipstein, 1844 [*Cheilotomona blumi*]
Pleurotomaria obtusa Klipstein, 1844 [*Cheilotomona obtusa*]
Pleurotomaria calosoma Laube, 1868 [*Cheilotomona obtusa*]
Trochus tristriatus Münster, 1841 [*Cheilotomona tristriata*]
Trochus acuticarinatus Klipstein, 1844 [*Cheilotomona tristriata*]
Pleurotoma subgranulata Klipstein, 1844 [*Cheilotomona subgranulata*]
Trochus bipunctatus Münster, 1841
Pleurotomaria cochlea Münster, 1841 [*Pseudoscalites cochlea*]
Pseudoscalites elegantissimus Kittl, 1892
Pleurotomaria binodosa Münster, 1841 [*Delphinulopsis binodosa*]
Naticella münsteri Klipstein, 1844 [*Delphinulopsis binodosa*]

Worthenia spuria in Sachariewa-Kowatschewa (1962, pl. 1, figs 1–4) is assigned to *Discotoma incognita* Sachariewa-Kowatschewa, 1962.

Triassocirrus pentagonalis (Klipstein, 1844) and *Nodocingulum*? *angulatum* (Münster, 1841) represent *nomina dubia*.

Introduction

The St. Cassian Formation (Upper Ladinian to Lower Carnian, South Tyrol, N Italy) has yielded the most diverse marine invertebrate fauna known from the Triassic. More than 1400 valid marine metazoan species have been reported of which gastropods are the most diverse group (Roden *et al*. 2020). This gastropod dominance is also present in most Recent marine settings (e.g., Bouchet *et al*. 2002). Pleurotomariida, an ancient order of the class Gastropoda, contribute considerably to the diversity of the St. Cassian fauna and display a high disparity (Figs 98–100 for an overview). Many Triassic pleurotomariidan genera including the type genera of the families Lancedelliidae, Schizogoniidae, Raphistomellidae, Temnotropidae, Kittlidiscidae, Stuorellidae, Wortheniellidae and Zygitidae occur in the St. Cassian Formation. The high diversity of Pleurotomariida in the St. Cassian Formation is in contrast with their absence or low diversity in Recent communities. Pleurotomariida are characterized by an inner nacreous shell layer, a protoconch of the vetigastropod type (less than one whorl), the presence of a slit in the outer lip and a selenizone (slit-band) which is generated by the closure of the slit during the accretionary shell growth. Shell features are commonly exceptionally well preserved in shells from the St. Cassian Formation, which facilitates studying them in great detail. The present study aims to document the St. Cassian Pleurotomariida including type specimens with modern imaging techniques. This provides data for a planned phylogenetic analysis. Another aim is to provide a better understanding of Pleurotomariida diversity across the Palaeozoic–Mesozoic transition as well as their overall dwindling within the Triassic and afterwards which contrasts to the overall expansion of Gastropoda.

The first palaeontological studies on the St. Cassian Formation were published by Münster (1834, 1841). Münster's (1841) first encompassing monograph described 422 invertebrate species from the St. Cassian Formation, amongst them 191 gastropod species. Klipstein's (1843–45) and Laube's (1868, 1870) monographs added a considerable number of gastropod taxa. Kittl (1891, 1892, 1894a) published a comprehensive monograph and revision of the Cassian gastropods. He studied the original material of Münster and Laube and provided more realistic drawings than previous authors. However, the original material of Klipstein (1843–45) which was purchased by the British Museum, London could not be studied by Kittl. The whereabouts of Klipstein's (1843–45) collection has long been unknown until Cleevely (1983, p. 173) mentioned the presence of this collection in the NHMUK, London and Engeser & Taylor (1989) reported the calcareous sponges from that collection. Apart from two type specimens (Nützel 2010; Pieroni *et al*. 2021) no other gastropod material from Klipstein's collection has been studied so far. The present study is the first extensive study of gastropod type material of Klipstein (1843–1845). Gastropods from the St. Cassian Formation representing Pleurotomariida were further studied by Leonardi & Fiscon (1947, 1959), Zardini (1978, 1980, 1985), Bandel (1991, 1993a, 2009), Schwardt (1992), Nützel & Kaim (2014), and Hausmann & Nützel (2015).

The present study revises the Pleurotomariida type specimens of the early Cassian monographs by Münster (1841) and Klipstein (1843–45) housed in Munich (SNSB-BSPG) and London (NHMUK). Most of the species from the St. Cassian Formation are relatively small (commonly few millimetres, mostly less than 20 mm) and due to technical limitations at the time, illustrations and descriptions of studies conducted in the 19th century are commonly not adequate and do not allow for safe identifications. As will be seen, this poor knowledge of the type specimens led to many misidentifications. Nearly all of the type specimens studied herein are documented by modern imaging techniques (micro-photography) for the first time. This provides considerable information about the morphology of the studied species including early ontogenetic shells and ontogenetic change of their shells. Besides the type material of Münster (1841) and Klipstein (1843–45), we studied the Pleurotomariida type specimens and the originals of Laube (1868), Kittl (1891), Bandel (1991), Schwardt (1992), and Zardini (1978, 1980) from the St. Cassian Formation. We also studied originals of Broili (1907) from the Upper Ladinian Pachycardientuffe (Seiser Alm, Italy) and the originals of Böhm (1895) from the Ladinian Marmolada Limestone (Italy), that were attributed to the Cassian pleurotomariidan species. We also studied newly collected specimens to describe the Pleurotomariida species as detailed as possible. In the light of these new data about the type specimens, we discuss the former and current sys-

tematic placement of these species. This is especially important because many of those species are type species of genera. In addition, the composition of many genera and families are modified and their diagnoses are improved.

Abbreviations

GBA	Geologische Bundesanstalt, Vienna, Austria
GPIT	Geologisch-Paläontologisches Institut Tübingen, Germany
MB	Berlin Museum für Naturkunde, Germany
MPRZ	Museo Paleontologico Rinaldo Zardini, Belluno, Italy
NHMUK	Natural History Museum, London, United Kingdom
NHMW	Naturhistorisches Museum Wien, Vienna, Austria
PZO	Naturmuseum Südtirol, Bolzano, Italy
SNSB-BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany

Material and methods

The collections of Münster (1841) from the St. Cassian Formation (Italy), of Broili (1907) from the Upper Ladinian Pachycardientuffe (Seiser Alm, Italy) and of Böhm (1895) from the Ladinian Marmolada Limestone (Italy) are reposited in the Bayerische Staatssammlung für Paläontologie und Geologie (SNSB-BSPG) in Munich.

The studied collections of Laube (1868), Kittl (1891, 1892, 1894a), Bandel (1991), Schwardt (1992) from the St. Cassian Formation are housed in the Naturhistorisches Museum Wien (NHMW) and Geologische Bundesanstalt (GBA) in Vienna. The collection of Klipstein (1843–1845) is reposited in the Natural History Museum in London (NHMUK). The original collection of Zardini (1978, 1980, 1985) is housed in Museo Paleontologico Rinaldo Zardini (herein referred as MPRZ) in Cortina d'Ampezzo.

Newly collected material from the St. Cassian Formation is reposited in the Museum of Nature South Tyrol, Bolzano, Italy (PZO).

We designated lectotypes for a number of taxa proposed in the 19th century. In the case of type series (commonly consisting of specimens that are not conspecific), we chose the specimen resembling the original illustration most closely. In a few cases, if the lot is conspecific (e.g., *Pleurotomaria amalthea* Klipstein), we selected the better-preserved specimen as lectotype instead of the figured specimen. We designated a lectotype even if only a single type specimen is present (potentially monotypic) because it is unsure whether additional material was at hand when the species was erected.

There are various localities of the St. Cassian Formation in South Tyrol and in Belluno, Italy (Roden *et al*. 2020, fig. 1). The location of specimens from the collections of Münster, Klipstein and Laube are usually only indicated as "St. Cassian" on the original labels (Fig. 1). This material comes from the classical localities near the village San Cassiano such as Stuores Meadows (Stuoreswiesen, Prati di Stuores), Pralongia, and Settsass Scharte. Only rarely locality names are written on the historical labels or are mentioned in the monographs.

Kittl (1891, p. 169) summarized the situation of the collection localities as follows: "The most important locality is the area of the Stuoreswiesen [=Stuores Meadows = Prati di Stuores] and the Pralongia-ridge above it. As shown by Laube and further outlined by Mojsisovics, a number of fossiliferous marl beds is exposed at the Stuoreswiesen ... The locality indication "St. Cassian" only, "Stuoresmergel" [Stuores Marls], "surrounding of St. Cassian" always refer to the zone of *Trachyceras aon*, excluding older or younger horizons. In the collections, the paleontological important material (almost always purchased from scientifically untrained collectors) is almost never attributed to specific localities; therefore, I had to be content with "St. Cassian" as locality information in most cases. Only rarely, I could indicate more specific locality information such as Stuores, Set Sass [Settsass Scharte], Prelongei [=Pralongia], Pescol, Valparola (mostly Eisenofengraben) etc. The indication "St. Cassian" therefore refers to the wider surrounding of this village. However, the far more eastwardly situated locality "Seelandalpe" [=Alpe di Specie in the basin of Cortina d'Ampezzo], which has only been exploited in recent years, must be kept separate."

Thus, in the systematic section, we give "St. Cassian Formation" and South Tyrol as for the locality or specimens from historical collections. For new collections, we indicate the exact locations (e.g., Misurina) if available.



FIGURE 1. Examples of the original labels in the studied collections; **A.** A label from Münster's collection in the BSPG, upper two figures are the original drawings of Münster (1841), lower four figures are the original drawings of Kittl (1891), SNSB-BSPG AS VII 1220; **B.** Münster's handwritten label, SNSB-BSPG AS VII 1220; **C.** A label from Laube's collection in the NHMW, NHMW 1858/0009/0014; **D.** A label from Kittl's collection in the NHMW, NHMW 1899/0005/0092; **E.** A standard label in the NHMUK London given for "*Pleurotomaria waterhousi*", NHMUK PI OR 35336; **F.** Klipstein's original label with his handwriting of an unpublished name "*Pleurotomaria waterhousi*" in the NHMUK London, NHMUK PI OR 35336; **G.** Klipstein's original label with an unpublished name "*Pleurotomaria königii*" in the NHMUK London, NHMUK PI OR 35351; **H.** An old label of "*Pleurotomaria königii*" written after the acquirement of Klipstein's collection by the NHMUK London, NHMUK PI OR 35351.

The species and genus diversity graphs were produced with the Triassic gastropod diversity data compiled by A. Nützel during the last years and with the Permian diversity data from the Paleobiology Database (acquired on 19 May 2020). The global Triassic gastropod species diversity list consists of 2177 nominate species and 429 genera at present. Species diversity was calculated as count of species occurrence within each stage (standing diversity, species in bin method). Generic diversity was calculated by using the generic range data (range-through method). Accordingly, genera were assumed to be present in a time interval between their first and last occurrence. The diversity of boundary crossers is also based on the generic range data. Boundary crossers are the genera, ranges of which pass through a stage boundary. Error bars in diversity curves and in bar graph (Fig. 95) are calculated with standard error of a proportion formula. The proportion of number of species/genus extinctions to number of species/genus in a stage is used to calculate the confidence intervals of species/genus diversity (Figs 92–93, 97). The proportion of genera crossing the top boundary of a stage (top boundary crossers) to the total number genera in that stage is used to calculate the confidence interval of boundary crossers diversity (Figs 94, 96). Unnamed species and the species names in open nomenclature are not included in diversity analyses.

The specimens were coated with ammonium chloride before macro- and micro-photography, if not indicated otherwise. The specimens were coated with gold before SEM photography.

In the systematic palaeontology section, the classification scheme proposed by Bouchet *et al*. (2017) is followed.

Synoptic classification

Subclass Vetigastropoda Salvini-Plawen, 1980

Order Pleurotomariida Cox & Knight, 1960

Superfamily Eotomarioidea Wenz, 1938
Family Eotomariidae Wenz, 1938
Genus *Proteomphalus* Gründel, 2011
Genus *Amplitomaria* **gen. nov.**
Genus *Pseudoananias* **gen. nov.**
Family Rhaphistomellidae Bandel, 2009
Genus *Rhaphistomella* Kittl, 1891
Genus *Lineacingulum* **gen. nov.**
Genus *Sisenna* Koken, 1896
Genus *Rufilla* Koken, 1896
Family Temnotropidae Cox, 1960 (in Knight *et al*.)
Genus *Temnotropis* Laube, 1870
?Family Gosseletinidae Wenz, 1938
Genus *Pressulasphaera* **gen. nov.**
Superfamily Pleurotomarioidea Swainson, 1840
Family Zygitidae Cox, 1960 (in Knight *et al*.)
Genus *Zygites* Kittl, 1891
Genus *Cancellotomaria* **gen. nov.**
Genus *Kokenella* Kittl, 1891
Family Lancedelliidae Bandel, 2009
Genus *Lancedellia* Bandel, 1991
Genus *Acutitomaria* **gen. nov.**
Genus *Lineaetomaria* **gen. nov.**
Genus *Euryalox* Cossmann, 1897
Family Kittlidiscidae Cox, 1960 (in Knight *et al*.)
Genus *Kittlidiscus* Haas, 1953
Family Stuorellidae Bandel, 2009
Genus *Stuorella* Kittl, 1891
Family Schizogoniidae Cox, 1960 (in Knight *et al*.)
Genus *Schizogonium* Koken, 1889
Genus *Pseudowortheniella* Bandel, 2009
Family Wortheniellidae Bandel, 2009
Genus *Wortheniella* Schwardt, 1992
Genus *Bandelium* Schwardt, 1992
Genus *Nodocingulum* **gen. nov.**
Genus *Striacingulum* **gen. nov.**
Genus *Rinaldoella* Bandel, 2009
Order Seguenziida
Superfamily Seguenzioidea Verrill, 1884
Family Laubellidae Cox, 1960 (in Knight *et al*.)
Genus *Laubella* Kittl, 1891
Family Eucyclidae Koken, 1896
Genus *Paleunema* Kittl, 1891
Genus *Ampezzalina* Bandel, 1993b
Genus *Triassocirrus* Yin & Yochelson, 1983b
Subclass Caenogastropoda Cox, 1960
Superfamily Orthonematoidea Nützel & Bandel, 2000
Family Goniasmatidae Nützel & Bandel, 2000
Genus *Cheilotomona* Strand, 1928
Genus *Cochlearia* Braun, 1841 (in Münster)
Order Neogastropoda Wenz, 1938
Family Purpurinidae Zittel, 1895

Genus *Pseudoscalites* Kittl, 1892
Subclass Neritimorpha Koken, 1896
Order Cycloneritida Bandel & Frýda, 1999
Superfamily Neritopsoidea Gray, 1847
Family Delphinulopsidae Blodgett, Frýda & Stanley, 2001
Genus *Delphinulopsis* Laube, 1870

Systematic Palaeontology

Class Gastropoda Cuvier, 1795

Subclass Vetigastropoda Salvini-Plawen, 1980

Order Pleurotomariida Cox & Knight, 1960

Superfamily Eotomarioidea Wenz, 1938

Family Eotomariidae Wenz, 1938

Genus *Proteomphalus* Gründel, 2011

Type species. *Pleurotomaria protei* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

Emended diagnosis. Shell biconical, moderately high-spired; suture impressed; selenizone slightly above the suture, at mid-whorl of body whorl, elevated, carina-like, with fine spiral striation and faint lunulae, bordered by bent shell edges, slightly convex; whorl face forming wide, convex ramp above selenizone, concave below selenizone; whorl face ornamented with fine growth lines and faint spiral threads; base convex with moderately wide umbilicus or umbilical chink.

Discussion. Gründel (2011) designated *Scalites protei* Münster as type species of *Proteomphalus* (it must be *Pleurotomaria protei* Münster) and reproduced images that were published by Bandel (2009) as examples (Gründel 2011, pl. 1, figs 11–13). However, Laube (1868) and Bandel (2009) misidentified this species and therefore *Proteomphalus* has a misidentified type species. Bandel's (2009) specimens identified as "*Ptychomphalus protei* (Laube, 1868)" differ from *Pleurotomaria protei* by having a more convex ramp, a higher whorl expansion rate and a lower spire height. Bandel's (2009) and Laube's (1868) specimens represent *Proteomphalus gracilis* (Read, 1907 in Broili) (see below). According to the ICZN Art. 70.3.1, we fix *Pleurotomaria protei* Münster, 1841 as type species of *Proteomphalus*, although Gründel (2011) erected the genus based on the Bandel's (2009) misidentification of the type species. Since *P. gracilis* and *P. protei* are congeneric, the concept of the genus *Proteomphalus* is not changed fundamentally. Nevertheless, we emend Gründel's (2011) generic diagnosis, because the selenizone is now known in greater detail and because an umbilical callus is absent contrary to Gründel's (2011) report. We reject the placement of *Proteomphalus* in Ptychomphalidae and prefer an assignment of *Proteomphalus* to the essentially Palaeozoic Eotomariidae. Ptychomphalids are more low-spired, have an umbilical callus, the selenizone is flush and never forming a carina (e.g., Monari *et al*. 2011). On the other hand, eotomariid genera like the Carboniferous *Tropidostropha* Longstaff, 1912 are much closer to *P. protei* than *Ptychomphalus* (see e.g., Batten 1966). The Triassic genus *Proteomphalus* might be closely related to the Permian genus *Lacunospira* Batten, 1958 but *Lacunospira* is more high-spired and its shape is conical gradate instead of biconical. The Permian genus *Takfaia* Nützel & Ketwetsuriya, 2016 (in Ketwetsuriya *et al*. 2016) is very similar in whorl shape, position of selenizone and somewhat rough whorl face without a regular ornamentation. Unlike *Proteomphalus*, *Takfaia* is widely phaneromphalous, with concave selenizone and lower whorl expansion rate.

We also note that *Proteomphalus* has an inner nacreous shell layer.

Included species. *Ptychomphalina canovana* (Kittl, 1899, pl. 1, fig. 3, refigured here in Fig. 3A–B) and *Ptychomphalina moscardii* (Stoppani, 1858–1860) (Kittl 1899, pl. 1, fig. 5, refigured here in Fig. 3D–E) from the Ladinian Esino Limestone (Italy).

***Proteomphalus protei* (Münster, 1841)**
Fig. 2

*1841	*Pleurotomaria protei*—Münster, p. 112, pl. 12, figs 12a–b.
1850	*Pleurotomaria protei* Münster, 1841—d'Orbigny, p. 195, no. 386.
non 1868	*Scalites protei* Münster sp.—Laube, p. 77, pl. 26, fig. 7.
1891	*Ptychomphalus protei* Laube—Kittl, p. 203, pl. 1, fig. 11–12 (non fig. 13).
1978	*Ptychomphalus protei* (Münster)—Zardini, p. 16, pl. 2, figs 7a–c.
1978	*Ptychomphalina canovana* (Kittl)—Zardini, p. 17, pl. 3, figs 2a–c.
1991	*Ptychomphalus protei* (Laube, 1868)—Bandel, p. 33, pl. 12, fig. 8.
non 2009	*Ptychomphalus protei* (Laube, 1868)—Bandel, pl. 2, figs 23–26.
non 2011	*Proteomphalus protei* (Münster, 1841)—Gründel, pl. 1, figs 11–13.

Material. NHMW 1899/0005/0082/1 (original of Kittl 1891, pl. 1, fig. 11), NHMUK PI OR 35343 from the St. Cassian Formation. Münster's (1841) type specimens could not be found in the BSPG.

Description. Shell broad biconical with spiral angle of 80°–85°; spire imbricated; suture impressed; whorl face above selenizone forming a wide, convex, inclining ramp; whorl face concave just above selenizone; whorl face below selenizone short, steep, slightly facing abapically, distinctly concave; selenizone broad, convex, forming prominent carina, bordered by abaxial projections of shell edges, ornamented with stria-like lunulae (or faint crescentic growth lines) and spiral threads; whorl face above selenizone ornamented with faint spiral threads and bearing prosocyrt growth lines; whorl face below selenizone ornamented with faint spiral threads and with slightly opisthocyrt growth lines; base rounded, with angular outer basal edge and with slightly opisthocyrt growth lines; umbilicus slit-like; aperture broad, subquadrate, as high as wide; outer lip with an angulation, basal lip convex, inner lip straight.

Discussion. The type specimen of *Pleurotomaria protei* Münster, 1841 was lost in the 19th century as it was noted already by Laube (1868). Münster's (1841) illustration is insufficient to establish a clear species identity with subsequent reports of this taxon. This illustration differs from all subsequently published illustrations in having the angulation with the slit-band high above the abapical suture and in being comparatively high-spired. Münster (1841) himself remarked that the lateral view of that species appears too high ("zu hoch gerathen").

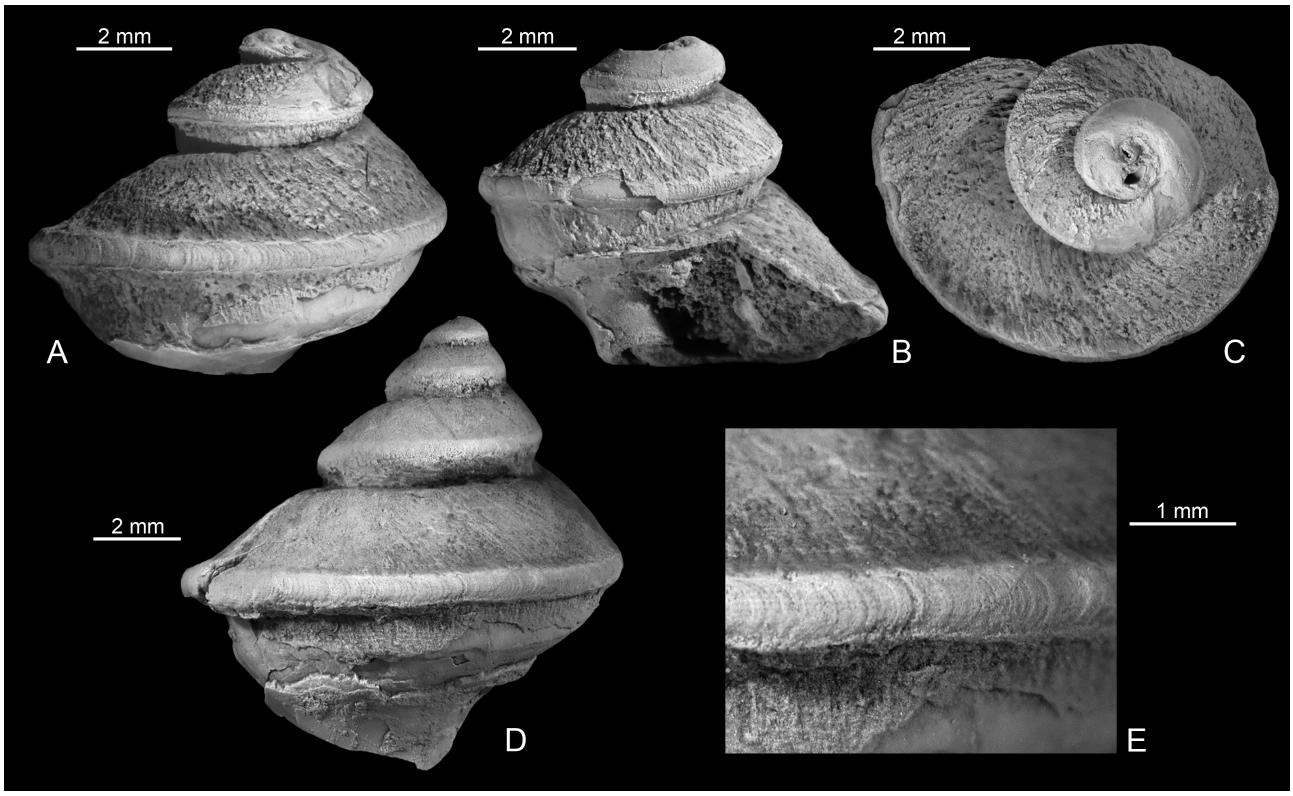

FIGURE 2. *Proteomphalus protei* (Münster, 1841); **A–C.** NHMUK PI OR 35343, St. Cassian Formation; **D–E.** NHMW 1899/0005/0082/1 (original of Kittl 1891, pl. 1, fig. 11), St. Cassian Formation.

Based on our study of the specimens housed in the BSPG, NHMW, NHMUK and MPRZ, we conclude that there are two morphological forms in the St. Cassian Formation. The specimens with relatively higher spire and relatively lower whorl expansion rate are placed into *Pleurotomaria protei* Münster, 1841 and with relatively lower spire and higher whorl expansion rate to *Ptychomphalus gracilis* Read, 1907 (in Broili 1907) herein. Here, we illustrate the original of Kittl (1891, pl. 1 fig. 11) from the St. Cassian Formation and one specimen from Klipstein collection in NHMUK London (Fig. 2). They seem to agree well with Münster's (1841) illustration of *Pleurotomaria protei*. The specimen illustrated as *Proteomphalous canovana* by Zardini (1978, pl. 3, figs 2a–c) is also regarded to represent *P. protei* because there are no significant morphological differences. *Proteomphalous canovanus* (Kittl 1899, pl. 1, fig. 3, refigured here in Fig. 3A–B) and *Proteomphalous moscardii* (Stoppani, 1858–1860) (Kittl 1899, pl. 1, fig. 5, refigured here in Fig. 3D–E) from the Ladinian Esino Limestone (Italy) are probably close relatives of *Proteomphalous protei* and differ by lower expansion rates, smaller apertures, wider umbilici.

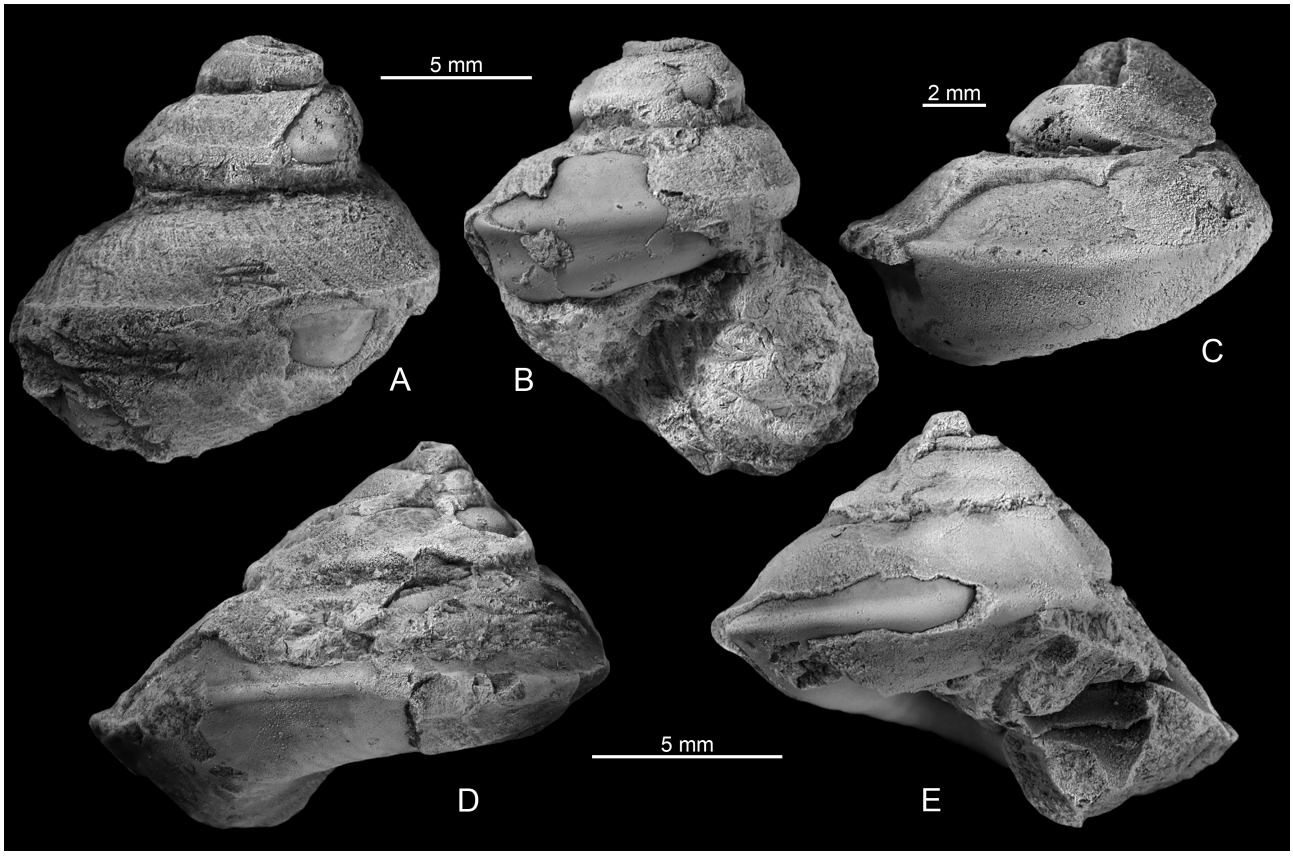

FIGURE 3. A–B. *Proteomphalous canovanus* (Kittl, 1899), lectotype designated herein, NHMW 1969/1089/0000 (original of Kittl 1899, pl. 1, fig. 3), Esino Limestone, Ladinian. **C.** *Proteomphalous* cf. *canovanus* (Kittl, 1899), NHMW 1969/1090/0000 (original of Kittl 1899, pl. 1, fig. 4), Esino Limestone, Ladinian. **D–E.** NHMW 1969/1091/0000 *Proteomphalous moscardii* (Stoppani, 1858–1860) (original of Kittl 1899, pl. 1, fig. 5), Esino Limestone, Ladinian.

Proteomphalus gracilis (Read, 1907 in Broili) comb. nov.

Fig. 4

1868	*Scalites protei* Münster sp.—Laube, p. 77, pl. 26, fig. 7.
1891	*Ptychomphalus protei* Laube—Kittl, p. 203, pl. 1, fig. 13 (non figs 11–12).
*1907	*Ptychomphalus gracilis* Read—Read in Broili, p. 77, pl. 6, fig. 24.
1978	cfr. *Euzone alauna* (Koken)—Zardini, p. 16, pl. 2, figs 8–9.
2009	*Ptychomphalus protei* (Münster, 1841)—Bandel, p. 33, pl. 2, figs 23–26.
2011	*Proteomphalus protei* (Münster, 1841)—Gründel, pl. 1, figs 11–13.

Material. SNSB-BSPG 1903 IX 325 (original of Broili 1907, pl. 6, fig. 24, herein designated as lectotype), 1903 IX 1045 (two specimens, herein designated as paralectotypes) from Pachycardientuffe, Upper Ladinian, Seiser

Alm, Italy. NHMW 1899/0005/0081/1, 1899/0005/0081/2, NHMUK PI OR 35336 from the St. Cassian Formation. MPRZ 2021 1–049 from the St. Cassian Formation, Lower Carnian, Milieres.

Discussion. *Proteomphalus gracilis* differs from *Proteomphalus protei* by having a distinctly larger aperture, a lower spire with a spiral angle of 90°–100° and a lower whorl expansion rate. Both species have the same whorl profile and ornamentation. A specimen representing *P. gracilis* from Zardini's collection (Fig. 4L–P) has a diameter of the initial whorl of 0.3 mm.

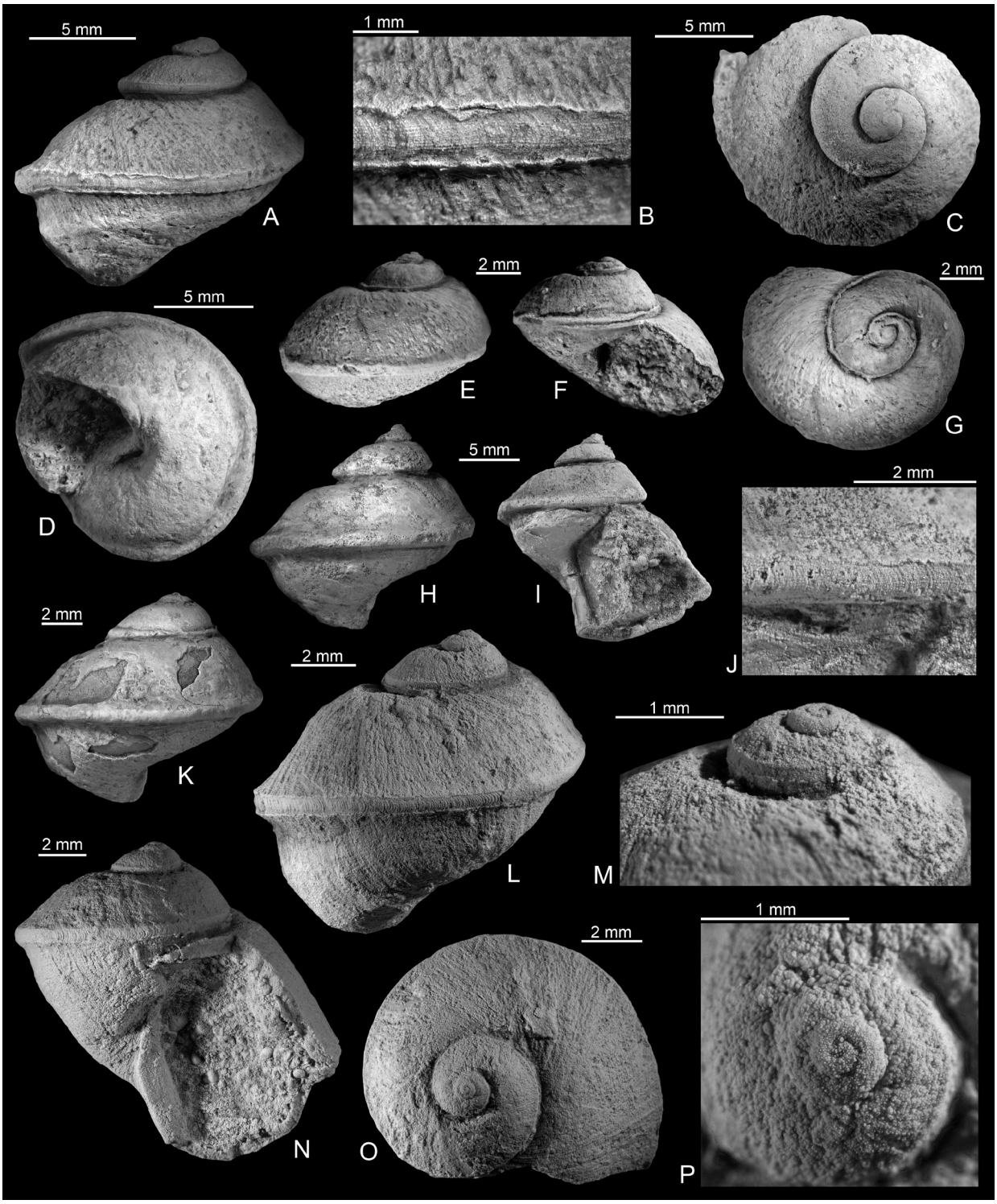

FIGURE 4. *Proteomphalus gracilis* (Read, 1907 in Broili); **A–D.** Lectotype, SNSB-BSPG 1903 IX 325 (original of Broili 1907, pl. 6, fig. 24), Pachycardientuffe, Upper Ladinian, Seiser Alm; **E–G.** NHMUK PI OR 35336, St. Cassian Formation; **H–J.** NHMW 1899/0005/0081/1, St. Cassian Formation; **K.** NHMW 1899/0005/0081/2, St. Cassian Formation; **L–P.** MPRZ 2021 1–049, Milieres, St. Cassian Formation.

The type specimen of *Ptychomphalus gracilis* Read, 1907 (in Broili 1907) from the Pachycardientuffe (refigured here in Fig. 4A–D) agrees well with the specimen illustrated by Laube (1868, pl. 26, fig. 7, as "*Scalites protei* Münster") and Kittl (1891, pl. 1, fig. 13, as "*Ptychomphalus protei*") and other specimens (Fig. 4E–P) from the St. Cassian Formation. Klipstein has also recognized this species and noted the name "*Pleurotomaria waterhousi*" on a handwritten label (Fig. 1D). Since this is an unpublished name, it does not represent a valid species name. The specimens assigned to "cfr. *Euzone alauna* (Koken)" by Zardini (1978, pl. 2, figs 8–9) are regarded to represent *Proteomphalus gracilis*.

Genus *Amplitomaria* gen. nov.
LSID. urn:lsid:zoobank.org:act:A0D34703-3F31-4B85-B1D8-3282F27B0CAC

Type species. *Pleurotomaria spuria* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. From Latin *amplus*, meaning wide, referring the wide shell and the old Roman name of Ampezzo: Amplitium; *-tomaria* referring *Pleurotomaria*: gender feminine.

Diagnosis. Shell globular; first two whorls well rounded, planispirally coiled; selenizone appears at the end of 2nd teleoconch whorl (within 3rd whorl); selenizone concave situated at mid-whorl or slightly above mid-whorl of last whorl, bordered by pronounced spiral cords, ornamented with numerous spiral threads and faint, acute growth lines; whorl face with fine spiral and axial ornament and occasionally with strong axial ribs.

Discussion. The selenizone of *Amplitomaria bilineata* (Klipstein, 1844) appears initially at the same position on whorl face and within the same teleoconch whorl as in *Amplitomaria spuria*. The selenizone gradually shifts downward during ontogeny in *A. bilineata* and is situated at mid-whorl on the last whorl. The selenizone is situated high on the last whorl in *Amplitomaria spuria* (Münster, 1841). Thus, the position of the selenizone on the last whorl varies within *Amplitomaria*. Regarding the high position of the selenizone, *Amplitomaria spuria* (Münster, 1841) resembles the essentially Palaeozoic genera *Glabrocingulum* and *Ananias*, but differs by its more globular shape, its convex whorl face above the selenizone instead of being concave and by the rounded whorl profile below the selenizone without an angulation at the outer edge of the base (see also discussion of *Amplitomaria spuria* below). The early whorls of *Amplitomaria* are somewhat immersed and planispirally coiled which is not the case in *Glabrocingulum* and *Ananias* that have early whorls with a distinctly elevated spire (Karapunar *et al*. in press). The selenizone of *Amplitomaria* is bordered by prominent spiral cords instead of sharp shell edges in *Glabrocingulum* and *Ananias*. Moreover, the selenizone is not ornamented with multiple spiral threads in *Glabrocingulum* and *Ananias*. Regarding the low position of the selenizone, *Amplitomaria bilineata* resembles the Palaeozoic genera *Ptychomphalina* Fischer, 1885 and *Mourlonia* de Koninck, 1883. Like *Amplitomaria*, *Ptychomphalina* has a concave selenizone but in *Ptychomphalina,* the selenizone has distinct lunulae and a sharp axial ornamentation. *Mourlonia* has a convex selenizone which reflects the whorl curvature (Gordon & Yochelson 1987, p. 53). *Amplitomaria bilineata* resembles the Permian species *Bradyospira johnsensis* Batten, 1964 in general whorl shape and having a basal carina but has a wider selenizone and more prominent selenizone borders. *Bradyospira* is a monotypic genus known from few poorly preserved specimens. Further documentation is needed for comparison. The Triassic genus *Proteomphalus* Gründel, 2011 has a very prominent, convex selenizone that is raised from rest of the shell and its whorl face is rough without fine spiral ornament.

Included species. *Amplitomaria spuria* (Münster, 1841) (=*Pleurotomaria concinna* Klipstein, 1844), *Amplitomaria bilineata* (Klipstein, 1844) (=*Ptychomphalus neumayri* Kittl, 1891) from the St. Cassian Formation.

***Amplitomaria spuria* (Münster, 1841) comb. nov.**
Fig. 5

*1841	*Pleurotomaria spuria*—Münster, p. 110, pl. 11, figs 29a–b.
1844	*Pleurotomaria concinna*—Klipstein, p. 164, pl. 10, fig. 20.
1850	*Pleurotomaria spuria*? Münster, 1841—d'Orbigny, p. 195, no. 397.
1850	*Pleurotomaria concinna* Klipstein, 1844—d'Orbigny, p. 195, no. 390.
1868	*Pleurotomaria spuria* Münster—Laube, p. 82, pl. 27, fig. 6.
1891	*Worthenia spuria* Münster sp.—Kittl, p. 191, pl. 3, figs 3–4.
non 1962	*Worthenia spuria* Münster—Sachariewa-Kowatschewa, p. 96, pl. 1, figs 1–4.

1978 *Worthenia münsteri* (Klipstein)—Zardini, p. 20, pl. 5, figs 12a–b (non fig. 13).
1978 *Worthenia spuria* (Münster)—Zardini, p. 20, pl. 6, figs 2a–c.
1980 *Worthenia* sp.—Zardini, p. 3, pl. 1, figs 9a–c.
1991 "*Ptychomphalus*" *neumayri* (Kittl, 1891)—Bandel, pl. 14, fig. 7 (non fig. 8).
1992 *Wortheniella spuria* (Münster, 1841)—Schwardt, p. 30, pl. 1, figs 4–5.
non 2009 *Wortheniella spuria* (Münster, 1841)—Bandel, pl. 6, figs 76–77.

Material. SNSB-BSPG AS VII 1222 (original of Münster 1841, pl. 11, figs 29a–b) from the St. Cassian Formation, herein designated as lectotype. NHMUK PI OR 35333(1) (original of Klipstein 1844, pl. 10, fig. 20) herein designated as lectotype of *Pleurotomaria concinna* Klipstein, 1844 (junior subjective synonym of *Amplitomaria spuria*) from the St. Cassian Formation; MPRZ 2021 1–007, MPRZ 2021 1–023 from Campo, St. Cassian Formation.

Description. Shell turbiniform, low-spired, with gradate spire; apex blunt; lectotype comprises 5.5 whorls, 5.0 mm high, 4.2 mm wide; suture impressed; protoconch 0.2 mm in width, first whorl 0.26 mm in width; early whorls low-spired, planispiral, rounded, lacking axial ribs only having spiral threads; selenizone formed within third whorl; later whorl face angulated at upper edge of selenizone; ramp initially slightly inclined than increasingly steep; ramp in late teleoconch convex at adapical half and concave at abapical half, forming furrow near selenizone; ramp ornamented with regularly spaced, orthocline to slightly prosocyrt axial ribs on convex adapical half and with spiral threads; axial ribs strongest near adapical suture, fading towards selenizone; selenizone concave, ornamented with spiral threads, bordered adapically and abapically by pronounced spiral cords; growth lines within selenizone faint, v-shaped, asymmetrical; whorl face below abapical cord concave, ornamented with spiral threads and 1–2 spiral ribs just above the abapical suture; growth lines on whorl surface prosocyrt above and below selenizone; base rounded, narrowly phaneromphalous; base ornamented with closely spaced spiral ribs and opisthocyrt growth lines, which form opisthocyrt wrinkles near umbilicus; aperture subovate with convex inner and outer lips and rounded basal lip.

Discussion. *Amplitomaria spuria* is characterized by its more or less rounded whorl-face of the last whorl and the pronounced spiral cords bordering the concave selenizone. The concave area between the abapical cord and the whorl base is exaggerated in the original drawing of the type specimen (Münster 1841, pl. 11, fig. 29a). The lectotype of *Pleurotomaria concinna* Klipstein, 1844 (which has been considered to represent a subjective synonym of *Amplitomaria spuria* (Münster, 1841) since Laube (1868)) has a reticulate ornament around the outer basal edge, which is not present or not preserved in the lectotype of *Amplitomaria spuria* (Münster, 1841). Otherwise, both type specimens closely resemble each other so that we maintain the synonymy previously proposed.

Amplitomaria spuria was placed in *Worthenia* by Kittl (1891) but *Worthenia* has a strongly ornamented convex selenizone and more strongly angulated whorls. Schwardt (1992) placed *Pleurotomaria spuria* in *Wortheniella* and illustrated two juvenile specimens that agree well with the comparable growth stages of the lectotype as studied herein. *Amplitomaria spuria* have planispiral, depressed early whorls and a vetigastropod-type protoconch of about one whorl. It was placed in *Wortheniella* mainly based on its planispiral early whorls. However, regarding other characters, it differs considerably from the type species of *Wortheniella* which has a distinctly angulated whorl profile and a convex/angulated selenizone. Moreover, its early teleoconch is ornamented with strong spiral cords/carinations. By contrast the early teleoconch whorls (before the onset of the selenizone) of *Amplitomaria spuria* lacks prominent spiral cords. They are rounded and smooth or ornamented with faint spiral threads. The late whorls are only slightly angulated to almost rounded unlike in most species assigned to *Worthenia*, *Wortheniella* and *Ananias* which have a pronounced and sharp angulation. *Ananias* species have a concave selenizone similar to *A. spuria* but they have distinctly gradate spire with a sharp median angulation and a straight to slightly concave ramp. However, some Permian species assigned to *Ananias* also have a rounded non-gradate whorl profile, for instance *Ananias permianus* Batten, 1989 and *Ananias ootomaria* Batten, 1989 resemble *A. spuria* in this respect and also in ornamentation.

Ananias belaensis Mazaev, 2019 from the Permian of Russia has a similar whorl ornamentation. However, it is not sure whether this species represents *Ananias* because it has a wide selenizone and prominent lunulae, which is untypical for *Ananias* or *Glabrocingulum*. Similar to *Ananias*, *Amplitomaria spuria* has a concave selenizone and rounded early whorls, on which the selenizone appears high on the whorl, but the selenizone of *A. spuria* is formed earlier, within the third whorl (after the third whorl in the Palaeozoic *Glabrocingulum* and *Ananias* species, e.g., Schindel 1982, Karapunar *et al*. in press). Neither *Ananias* nor *Glabrocingulum* species from the Palaeozoic have a planispiral early teleoconch (Karapunar *et al*. in press). *Amplitomaria spuria* differs from Palaeozoic *Glabrocingulum* and *Ananias* species by its prominent spiral cords that border the selenizone.

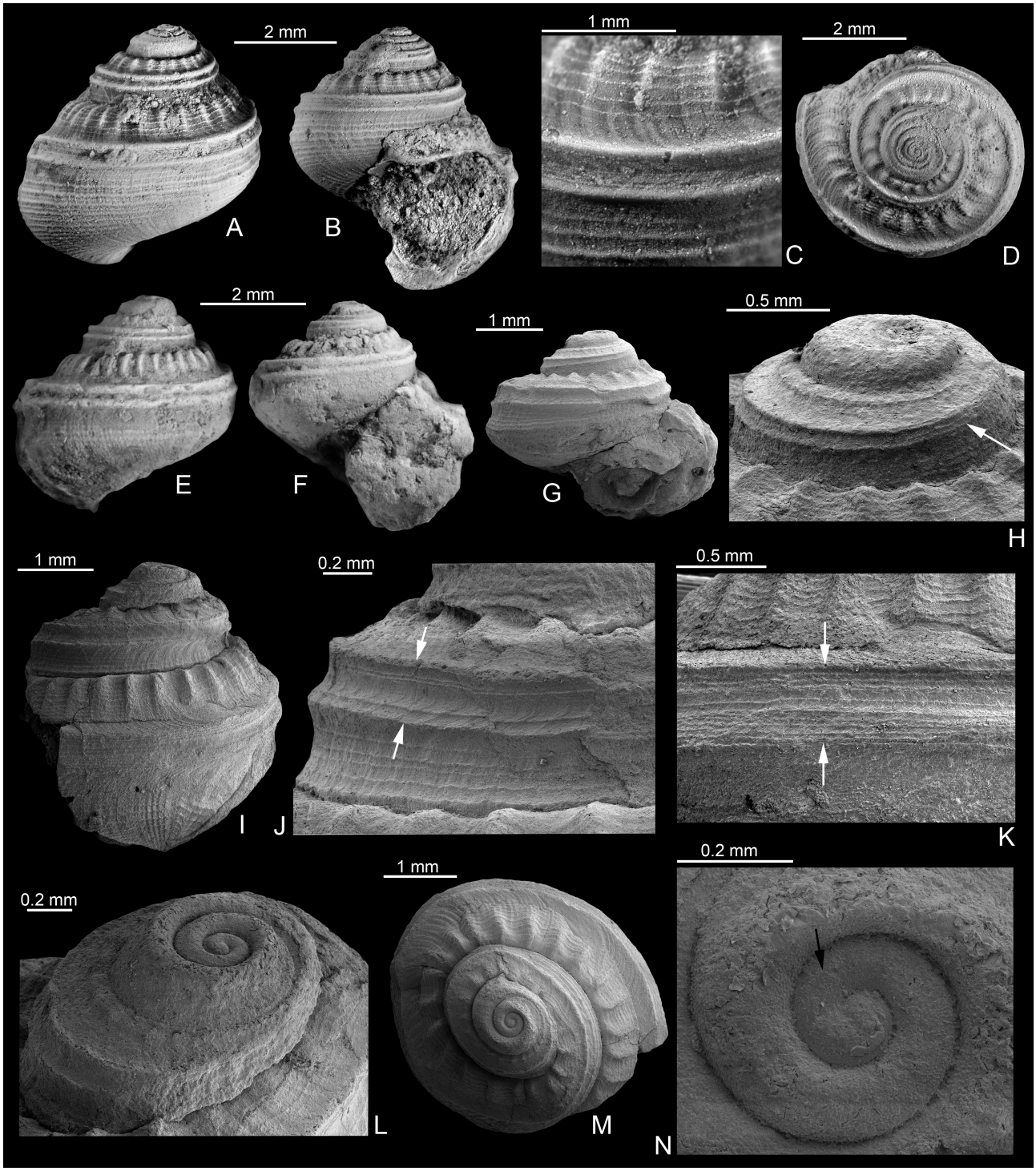

FIGURE 5. *Amplitomaria spuria* (Münster, 1841); **A–D.** Lectotype, SNSB-BSPG AS VII 1222 (original of Münster 1841, pl. 11, figs 29a–b), St. Cassian Formation; **E–F.** Lectotype of *Pleurotomaria concinna* Klipstein, 1844, NHMUK PI OR 35333(1) (original of Klipstein 1844, pl. 10, fig. 20), St. Cassian Formation; **G–H.** MPRZ 2021 1–023, Campo, St. Cassian Formation, SEM image; **H.** early whorls of the specimen in Fig. G, arrow indicates the onset of selenizone; **I–N.** MPRZ 2021 1–007, Campo, St. Cassian Formation, SEM image; white arrows in Fig. J, K indicate selenizone borders, black arrow in Fig. N indicates the protoconch-teleoconch boundary.

Amplitomaria spuria is also similar to the Early Carboniferous genus *Campbellospira* Yoo, 1994. According to Yoo (1994) this genus is characterized by a "planktotrophic" protoconch, i.e. by having two smooth initial whorls that were interpreted as a larval shell of the planktotrophic type as in Caenogastropoda but is unkown in modern and fossil Vetigastropoda. Admittedly, the specimen figured by Yoo (1994, pl. 5, fig. 12, *Campbellospira* sp. B) has

two smooth initial whorls that terminate abruptly but generally the specimens are not illustrated in sufficient detail including apical views to identify this as a protoconch of the planktotrophic type (see also Nützel & Mapes 2001; Nützel & Pan 2005 for a discussion). Moreover, the *Campbellospira* species are characterized by a strong axial ornamentation below the selenizone, which is absent in *A. spuria*.

The specimen illustrated by Sachariewa-Kowatschewa (1962, pl. 1, figs 1–4) and identified as *Worthenia spuria* has a lower spire; it probably represents *Discotoma incognita* Sachariewa-Kowatschewa, 1962.

Bandel (2009, pl. 6, figs 76–77) illustrated a juvenile specimen as *Wortheniella spuria* (Münster, 1841). This specimen could indeed represent *Wortheniella* since it has an immersed protoconch but probably not *A. spuria* because this specimen has an angulated whorl profile and is more high-spired than the earliest preserved whorls of the lectotype which are rather flat. Bandel's (2009) specimen differs in this respect and also regarding the ornamention of the juvenile *A. spuria* specimens.

Amplitomaria bilineata (Klipstein, 1844) comb. nov.

Fig. 6

*1844	*Turbo bilineatus*—Klipstein, p. 159, pl. 10, fig. 12.
1850	*Pleurotomaria bilineata* d'Orb., 1847—d'Orbigny, p. 195, no. 399.
1870	*Turbo fasciolatus* Münster—Laube, p. 21, pl. 31, fig. 10.
1891	*Ptychomphalus neumayri* Kittl n. n.—Kittl, p. 204, pl. 3, fig. 15.
1894a	*Worthenia* (?) *bilineata* Klipst. sp.—Kittl, p. 244.
1978	*Ptychomphalus neumayri* Kittl—Zardini, p., pl. 2, figs 4–6 (non fig. 10).
1991	"*Ptychomphalus*" *neumayri* (Kittl, 1891)—Bandel, pl. 14, fig. 8 (non fig. 7).

Material. NHMUK PI OR 35355(1) (original of Klipstein 1844, pl. 10, fig. 12), from the St. Cassian Formation, herein designated as lectotype; NHMW 1865/0009/0032 from the St. Cassian Formation; MPRZ 2021 1–006 from the St. Cassian Formation near Campo; MPRZ 2021 1–037 from the St. Cassian Formation near Misurina.

Description. Shell turbiniform, low-spired, globular; lectotype comprises 4 preserved whorls; first whorl 0.26 mm in width; first two whorls rounded, planispirally coiled; selenizone appears within 3rd whorl; ramp convex, with prosocline growth lines, and ornamented with weak axial undulations and faint spiral threads; selenizone slightly raised from rest of shell surface, concave, situated somewhat above mid-whorl of last whorl, forming periphery, slightly above abapical suture in spire whorls, bordered by thick spiral cords; suture impressed, just below the abapical cord; whorl surface below selenizone and base ornamented with faint spiral threads; base rounded, with a weak circumumbilical carina, narrowly phaneromphalous; aperture subovate with rounded outer and basal lips and convex inner lip.

Discussion. Kittl (1894a) placed this species tentatively in *Worthenia*. The examination of the type specimens of *Amplitomaria bilineata* showed that *Ptychomphalus neumayri* Kittl, 1891 is a junior synonym. The position of the selenizone at about mid-whorl and the concave shape of the selenizone resembles the Carboniferous *Ptychomphalina*. The thick spiral cords that border the selenizone in *Amplitomaria bilineata* are not present in the type species of *Ptychomphalina* (Knight 1941, pl. 29, fig. 3 and pers. obs.) but are present in *Amplitomaria spuria* (Münster, 1841). The Carboniferous type species of *Ptychomphalina*, *Pleurotomaria striata*, has an ornament of sharp, distinct collabral axial ribs and distinct lunulae on the selenizone; such ornaments are absent in *A. bilineata*. *Amplitomaria bilineata* also resembles the Late Triassic genus *Euzone* Koken, 1897 but *Euzone* has thinner, sharp spiral cords bordering the selenizone and the umbilicus is wider.

The main difference between *Amplitomaria bilineata* and *Amplitomaria spuria* is the position of the selenizone in late ontogeny. Although the selenizone appears at the same position in both species, the selenizone of *A. bilineata* gradually shifts downward and is situated at mid-height of the last whorl while it is situated much higher in *A. spuria*. The position of the selenizone can vary among the members of the same genus (see the discussion of *Kokenella costata*). Moreover, *A. bilineata* lacks strong axial ribs. The specimen figured by Zardini (1978, pl. 2, fig. 10) as *Ptychomphalus neumayri* Kittl is ornamented with orthocline axial ribs above the selenizone unlike the type specimen and probably represents an unnamed new species.

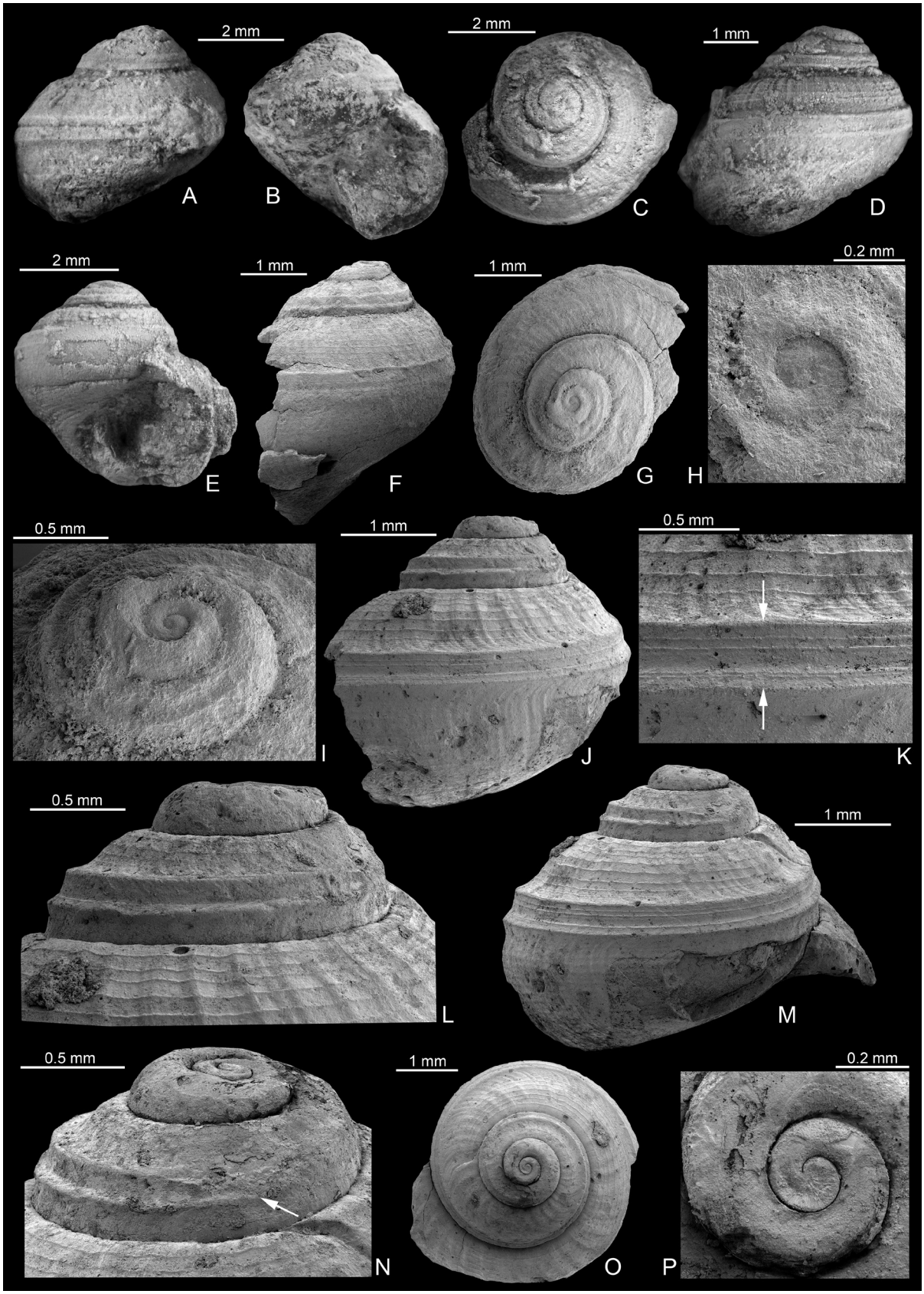

FIGURE 6. *Amplitomaria bilineata* (Klipstein, 1844); **A–C.** Lectotype, NHMUK PI OR 35355(1) (original of Klipstein 1844, pl. 10, fig. 12), St. Cassian Formation; **D–E.** NHMW 1865/0009/0032, St. Cassian Formation; **F–I.** MPRZ 2021 1–006, Campo, St. Cassian Formation, SEM image; **J–P.** MPRZ 2021 1–037, Misurina, St. Cassian Formation, SEM image; arrows in Fig. K indicate selenizone borders; arrow in Fig. N indicates the onset of selenizone.

Genus *Pseudoananias* gen. nov.
LSID. urn:lsid:zoobank.org:act:2761F5A2-D914-49D4-9CF9-2CB4F825A68D

Type species. *Pleurotomaria subgranulata* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. Because it resembles the subgenus *Ananias* Knight, 1945.

Diagnosis. Shell turbiniform; spire moderately elevated, gradate; first whorl planispiral; teleoconch ornamentation of axial and spiral threads and subsutural nodes; selenizone appears at the end of first teleoconch whorl (within second whorl including the protoconch); selenizone flat to slightly convex, ornamented with spiral threads and faint, crescentic growth lines or weak lunulae; selenizone initially wide, comprising approximately 1/3rd of whorl face of early teleoconch whorls, narrower relative to whorl height in later whorls; outer basal edge angulated; base anomphalous.

Discussion. The early ontogenetic whorls of the type species *Pseudoananias subgranulata* (Schwardt 1992, pl. 3, figs 2a–c) (Fig. 7K–O) and the ornamentation of the selenizone are not typical of the Palaeozoic *Worthenia* or *Ananias* (see Karapunar *et al*. in press). Therefore, we erect the new eotomariid genus *Pseudoananias* **gen. nov.** *Manzanospira* Batten, 1989 has a similar type of selenizone, but lacks lunulae on it; the early ontogenetic shell development of *Manzanospira* is unknown.

Pseudoananias **gen. nov.** differs from the wortheniform genera *Wortheniella*, *Sisenna*, *Nodocingulum* **gen. nov.**, and *Lineacingulum* **gen. nov.** in the selenizone characters. The selenizone of *Pseudoananias* **gen. nov.** appears much earlier during ontogeny (within the second teleoconch whorl instead of after 2nd or 3rd whorl) on a convex whorl face (instead of on a whorl carination) and it covers a wider area on whorl face. In addition, the selenizone of *Pseudoananias* **gen. nov.** is not angulated and does not have strong lunulae or nodes. *Ananias* and *Glabrocingulum* have a similar whorl profile. However, the selenizone starts much later, at the end of third whorl (Karapunar *et al*. in press). Moreover, the selenizone of *Ananias* and *Glabrocingulum* lacks clearly visible lunulae, is strongly concave and much narrower than that of *Pseudoananias*. The selenizone covers 1/3rd of the whorl face when it is formed in *Pseudoananias* while it covers 1/5th of the whorl face in *Ananias* when it first appears. The whorl face of *Ananias* and *Glabrocingulum* are covered by both, spiral cords and axial ribs forming a reticulate ornament with nodes at intersections. The whorl face of *Pseudoananias* is covered by spiral threads and has subsutural nodes.

Lineacingulum **gen. nov.** has a narrow shoulder, circumumbilical carina, equally spaced axial threads on its early and late whorl face, a wider, angulated selenizone with v-shaped thread-like lunulae and sinuous growth lines on its ramp. The growth lines of *Lineacingulum* start opisthocline on the shoulder and become prosocline on the wide ramp below the subsutural shoulder. In contrast, the growth lines start prosocline in *Pseudoananias* **gen. nov.** and they somewhat become opisthocline near the selenizone.

The Permian genus *Guizhouspira* Wang, 1980 (in Wang & Xi) differs from *Pseudoananias* by having a narrow subsutural shoulder and a horizontally lying selenizone of which the lower edge represents the whorl periphery. These characters are shared with *Baylea.* Therefore, *Guizhouspira* Wang, 1980 represents undoubtedly a junior synonym of *Baylea*. In *Pseudoananias* **gen. nov.**, the selenizone itself forms the whorl angulation, and not its lower edge as in *Baylea*.

The formation of the selenizone in *Pseudoananias* resembles that of *Worthenia*. The selenizone is formed in both taxa from a wide, u-shaped sinus situated on the convex whorl face. However, unlike in *Worthenia*, the selenizone is formed much earlier in *Pseudoananias* (within the first teleoconch whorl instead of within second teleoconch whorl) and it never develops distinct crescentic lunulae or strong nodes on the selenizone.

Humiliworthenia Yin & Yochelson, 1983a resembles *Pseudoananias* in shape and in being weakly ornamented, mainly by spiral lirae. The ontogenetic development of the selenizone of *Humiliworthenia* is unknown. Therefore, it cannot be differentiated from other wortheniform genera with confidence (e.g., *Wortheniella* Schwardt 1992; Bandel 2009 and herein). The early ontogenetic development of the Palaeozoic genera *Glabrocingulum*, *Ananias,* and *Worthenia* is reported by Karapunar *et al*. (in press) and generally differs from that of Triassic taxa.

***Pseudoananias subgranulata* (Münster 1841) comb. nov.**
Fig. 7

*1841	*Pleurotomaria subgranulata*—Münster, p. 110, pl. 12, figs 2a–b.
1844	*Pleurotomaria meyeri*—Klipstein, p. 162, pl. 10, fig. 16.

1850	*Turbo salinarius* d'Orb., 1847—d'Orbigny, p. 193, no. 336.
1868	*Pleurotomaria subgranulata* Münster—Laube, p. 87, pl. 27, fig. 2.
1891	*Worthenia subgranulata* Münster sp.—Kittl, p. 185, pl. 2, figs 12–15.
1907	*Worthenia subgranulata* Münster sp.—Broili, p. 78, pl. 6, figs 28–29.
non 1909	*Worthenia subgranulata* Münst. sp.—Scalia, p. 302, pl. 9, figs 28–31.
non 1914	*Worthenia subgranulata* Muenst. sp.—Scalia, p. 7, pl. 1, figs 21a–c.
?1959	*Worthenia subgranulata* Münster—Leonardi & Fiscon, p. 15, pl. 1, fig. 19.
1991	*Pseudoschizogonium elevatum* (Kittl, 1891)—Bandel, p. 37, pl. 13, figs 4–5; pl. 17, fig. 3.
1992	*Wortheniella cassiana* (Kittl, 1891)—Schwardt, p. 33, pl. 3, figs 2a–d.
non 1992	*Wortheniella subgranulata* (Münster, 1841)—Schwardt, p. 38, pl. 4, figs 4–5.
non 2009	*Rinaldoella subgranulata* (Münster, 1841)—Bandel, pl. 6, fig. 78–80, 82.

Material. Five type specimens: SNSB-BSPG AS VII 2071 (designated as lectotype herein); AS VII 1212 (original of Münster 1841, pl. 12, fig. 4; paralectotype), AS VII 2072–2073 (2 paralectotypes); (AS VII 2074 found together with the other type material but not conspecific and placed herein to *Nodocingulum coronatum*) from the St. Cassian Formation. NHMW 1899/0005/0042/1 (original of Kittl 1891, pl. 2, fig. 14), NHMW 1899/0005/0042/2 (original of Kittl 1891, pl. 2, fig. 15). GBA 1894/005/0006, 4354, original of Laube 1868 (pl. 27, fig. 2) which is the specimen illustrated by Kittl (1891, pl. 2, fig. 13) from the St. Cassian Formation. NHMUK PI OR 35330(1) (original of Klipstein 1844, pl. 10, fig. 16), herein designated as lectotype of *Pleurotomaria meyeri* from the St. Cassian Formation; PZO 13692 from Settsass, St. Cassian Formation. SNSB-BSPG 1903 IX 331 (original of Broili 1907, pl. 6, fig. 29), 1903 IX 1027 (original of Broili 1907, pl. 6, fig. 28) from Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy.

Description. Shell wortheniform; lectotype comprises about 6 whorls, 5.8 mm high, 5.5 mm wide; first whorl 0.24 mm in width, planispiral; first teleoconch whorl rounded with weak spiral threads; selenizone appears at the end of first teleoconch whorl (within 2nd whorl), initially covers 1/3rd of whorl face; spire gradate with angulated whorl face; angulation at mid-whorl of spire whorls; suture shallow; ramp concave, slightly inclining, almost horizontal near selenizone; whorl face below median angulation concave, parallel to shell axis; selenizone flat to convex, steeply inclined, wide, situated at median angulation; lunulae weak but distinct, neither spiny nor nodular; whorl face above selenizone ornamented with subsutural collabral riblets or elongated nodes, straight prosocline growth lines and spiral threads; whorl face below selenizone ornamented with spiral threads and bearing prosocyrt growth lines; base convex with sharply angulated outer basal edge, with opisthocyrt growth lines, ornamented by spiral cords and circumumbilical wrinkles, anomphalous; aperture as high as wide, with angulated outer lip, convex basal lip and almost straight inner lip; inner lip thickened and curved backwards, forming a narrow umbilical slit.

Discussion. The *Ananias*-like morphology with markedly angulated whorls, the subsutural riblets and the fine spiral striation characterize this species. Münster's (1841) type material is not ideally preserved but shows the mentioned features. The types of Münster and one specimen of Kittl (1891, pl. 2, fig. 15, refigured here in Fig. 7H) have a weakly convex selenizone with closely spaced, relatively weak lunulae. However, the specimens figured by Laube (1868 pl. 27, fig. 2, refigured here in Fig. 7I–J) and Kittl (1891, pl. 2, fig. 13, refigured here in Fig. 7I–J) have a rather flat selenizone with crescentic growth lines and prominent subsutural riblets. The shape of the selenizone and the prominence of subsutural nodes are obviously subject of intraspecific variabilty.

Schwardt (1992) assigned *Pleurotomaria subgranulata* Münster, 1841 to *Wortheniella* based on planispiral early whorls. However, the juvenile specimen illustrated by Schwardt (1992, pl. 4, fig. 4) as *Wortheniella subgranulata* differs from this species by having a distinctly nodular selenizone and strong spiral cords on the base. This specimen does not represent *P. subgranulata*. By contrast, the juvenile specimen illustrated by Schwardt (1992, pl. 3, fig. 2) as *Wortheniella cassiana* (Kittl, 1891) represents *Pseudoananias subgranulata* (Münster, 1841). It has a flat to slightly convex selenizone which is ornamented with spiral striae. Its early whorls are low-spired with a vetigastropod-type protoconch that is slightly immersed as in *Wortheniella*.

Bandel (2009) placed *P. subgranulata* in *Rinaldoella* Bandel, 2009. However, the juvenile specimen which was identified by Bandel (2009, figs 78–80, also the mis-labelled fig. 82) as *R. subgranulata* does not represent this species because it has a distinctly nodular selenizone (as in the specimen figured by Schwardt 1992, pl. 4, fig. 4). Bandel's (2009) specimens represent *Nodocingulum crenatum* (Münster, 1841). Moreover, the type species of *Rinaldoella*, *Wortheniella rinaldoi* Schwardt, 1992, differs from *P. subgranulata* in having a concave selenizone, a distinctly immersed early whorl and continuous sharp axial ribs (Fig. 72).

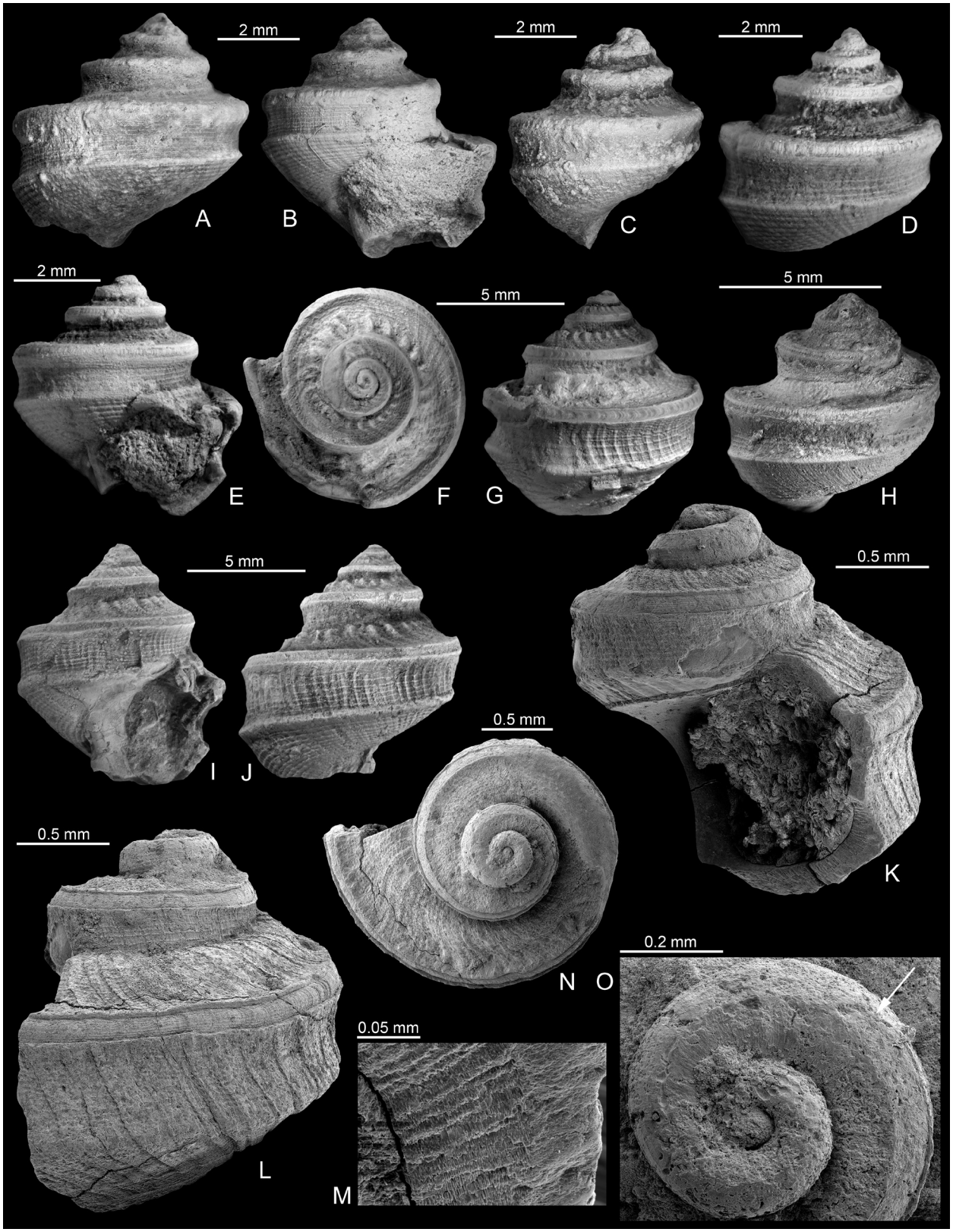

FIGURE 7. *Pseudoananias subgranulata* (Münster 1841); **A–B.** Lectotype, SNSB-BSPG AS VII 2071, St. Cassian Formation; **C.** Paralectotype, SNSB-BSPG AS VII 2073, St. Cassian Formation; **D–E.** Lectotype of *Pleurotomaria meyeri* Klipstein, 1844, NHMUK PI OR 35330(1) (original of Klipstein 1844, pl. 10, fig. 16), St. Cassian Formation; **F–G.** NHMW 1899/0005/0042/1 (original of Kittl 1891, pl. 2, fig. 14); **H.** NHMW 1899/0005/0042/2 (original of Kittl 1891, pl. 2, fig. 15); **I–J.** GBA 1894/005/0006, 4354, original of Laube 1868 (pl. 27, fig. 2) and Kittl (1891, pl. 2, fig. 13), St. Cassian Formation; **K–O.** PZO 13692, Settsass, St. Cassian Formation, SEM image; arrow indicates the onset of selenizone.

Family Rhaphistomellidae Bandel, 2009

Emended diagnosis. Shell rotelliform to low trochiform, with low to moderate spire height; surface smooth or with spiral ornament; growth lines on ramp mostly prosocyrt, opisthocline just below the adapical suture; early whorls with median angulation, from which the selenizone appears; selenizone situated high above mid-whorl on whorl angulation (if present); selenizone flush with surface of whorls or depressed near selenizone borders, angulated or strongly convex, smooth or ornamented with spiral cord(s) and weak lunulae; base phaneromphalous to anomphalous, without callus.

Included genera. *Rhaphistomella* Kittl, 1891, *Lineacingulum* **gen. nov.**, *Sisenna* Koken, 1896 and *Rufilla* Koken, 1896.

Discussion. Bandel (2009) erected the family Rhaphistomellidae based on and containing only *Rhaphistomella*. The similarity of the early teleoconch morphology of *Rhaphistomella radians* and *Sisenna venusta* was noted by Nützel & Kaim (2014) and this is also true of other *Sisenna* species reflecting a similar ontogenetic development in *Sisenna* and *Rhaphistomella*. We studied the type species of *Sisenna* and *Rufilla* from the Carnian–Norian Hallstatt Limestone, Austria, which are housed in the NHMW and GBA, and conclude that the two genera are closely related. *Sisenna* and *Rufilla* have the same growth line pattern (i.e., opisthocline just below the adapical suture then prosocyrt; oblique prosocyrt below selenizone), although the shape of the selenizone differs from each other in both genera (flush and flat in *Rufilla* vs. angulated in *Sisenna*). Based on the similar growth-line pattern, similar morphology of the early whorls, and the position of the selenizone, we place the genera *Rufilla* and *Sisenna* in the family Rhaphistomellidae. *Lineacingulum* **gen. nov.** is also placed within the Rhaphistomellidae based on the growth lines and the similarity of early whorl morphology of *Lineacingulum eremita* (Koken, 1897) to that of *Rhaphistomella radians* (Wissmann in Münster, 1841).

Bandel (2009) assigned the family Rhaphistomellidae to the superfamily Ptychomphaloidea as was maintained by Bouchet *et al*. (2017). Bandel's (2009) proposal to elevate the family Ptychomphalidae to superfamily rank is unjustified because there is no diagnostic character to distinguish Ptychomphaloidea (sensu Bandel 2009) from Eotomarioidea. The Jurassic ptychomphalid genera *Ptychomphalus* and *Angulomphalus* closely resemble *Rhaphistomella* in the rotelliform shape but they have a callus plug in the umbilicus and a different growth line pattern. The family Ptychomphalidae is probably derived from eotomariid genera such as *Liospira* Ulrich & Scofield, 1897, *Trepospira* Ulrich & Scofield, 1897, and *Angyomphalus* Cossmann, 1916, which are similar in the presence of a callus, the position of the selenizone, and in that the selenizone is flush with the surface of the whorls. The family Rhaphistomellidae seems to be closely related to another evolutionary lineage that is represented by the eotomariid genera *Baylea* de Koninck, 1883 and *Biarmeaspira* Mazaev, 2006, which are similar in the position of the selenizone, in having a flush or angulated shape of the selenizone, in the growth lines and in that the spiral ornament is dominant. Phylogenetic analyses are needed to elucidate the relationships of the mentioned genera. At present, Rhaphistomellidae is placed in the superfamily Eotomarioidea.

Genus *Rhaphistomella* Kittl, 1891

Type species. *Pleurotomaria radians* Wissmann in Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

Discussion. *Rhaphistomella* shares some characters with the diverse Palaeozoic genus *Glabrocingulum* Thomas, 1940, e.g., a relatively low spire, the location of the selenizone and a downwards deflection of the last whorl. Both genera were considered to represent synonyms by some authors (Erwin & Pan 1996; Batten 1989; see also Foster *et al*. 2017). However, *Rhaphistomella* differs in having a convex selenizone, in having a lower spire, a deeper suture and in lacking a reticulate ornamentation. Therefore, *Rhaphistomella* and *Glabrocingulum* are not synonymous.

Rhaphistomella? *kumbfurensis* Skwarko, 1967 from the Carnian–Norian Kana Formation of Papua New Guinea lacks the characteristic features of the genus *Rhaphistomella*: deep suture and whorl angulation at the selenizone. *Rhaphistomella*? *kumbfurensis* has a callus, which is not present in the type species *R. radians*. Therefore, it cannot be regarded as *Raphistomella*. It resembles the Jurassic genus *Ptychomphalus* in gross morphology and in having a callus. The earliest record of a possible *Ptychomphalus* is from the Norian of Peru (Ferrari 2015). *Rhaphistomella*? *kumbfurensis* can be better assigned to *Ptychomphalus*.

***Rhaphistomella radians* (Wissmann, 1841 in Münster)**
Fig. 8

*1841	*Pleurotomaria radians*—Wissmann in Münster, p. 112, pl. 12, figs 8a–b.
1844	*Solarium subpunctatum*—Klipstein, p. 201, pl. 14, fig. 9.
1844	*Euomphalus studeri*—Klipstein, p. 201, pl. 14, fig. 10.
1850	*Trochus studeri* d'Orb, 1847—d'Orbigny, p. 190, no. 283.
1850	*Trochus bianor* d'Orb, 1847—d'Orbigny, p. 191, no. 287.
1850	*Pleurotomaria radians* Wissmann, Münster, 1841—d'Orbigny, p. 195, no. 381.
1868	*Pleurotomaria radians* Wissmann—Laube, p. 78, pl. 26, fig. 9.
1882	*Pleurotomaria* (*Cryptaenia*) *radians* Wissm.—Zittel, p. 181, fig. 221.
1891	*Rhaphistomella radians* Wissmann sp.—Kittl, p. 202, pl. 1, figs 15–17.
1894a	*Euomphalus* (?) *studeri* Klipst. sp.—Kittl, p. 245.
1907	*Rhaphistomella radians* Wissm. sp.—Broili, p. 80, pl. 6, fig. 36.
1978	*Rhaphistomella radians* (Wissmann)—Zardini, p. 17, pl. 3, figs 3a–c.
1991	*Rhaphistomella radians* (Wissmann, 1841)—Bandel, p. 31, pl. 11, figs 7–8, pl. 12, figs 1–2.
1991	*Gosseletina fasciolata*—Bandel, p. 34, pl. 12, fig. 4 (the same specimen figured in pl. 12, fig. 2) (non fig. 5–7).
2009	*Rhaphistomella radians* (Wissmann, 1841)—Bandel, pl. 2, fig. 27.
2011	*Proteomphalus protei* (Münster, 1841)—Gründel, pl. 1, figs 14–15.
2012	*Rhaphistomella radians* (Wissmann, 1841)—Urlichs, figs 3.7–3.8.
2014	*Rhaphistomella radians*—Hausmann & Nützel, fig. 5B.
2014	*Rhaphistomella radians* (Wissmann in zu Münster 1841)—Nützel & Kaim, p. 412, figs 4s–t.

Material. SNSB-BSPG AS VII 1224 (original of Münster 1841, pl. 12, figs 8a–b) herein designated as lectotype, AS VII 1444 (61 paralectotypes) from the St. Cassian Formation. SNSB-BSPG 1903 IX 341 (original of Broili 1907, pl. 6, fig. 36) from Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMUK PI OR 35826 (original of Klipstein 1844, pl. 14, fig. 9), herein designated as lectotype of *Solarium subpunctatum* Klipstein; NHMUK PI OR 35828(1), (original of Klipstein 1844, pl. 14, fig. 10), herein designated as lectotype of *Euomphalus studeri* Klipstein from the St. Cassian Formation. PZO 13701, PZO 13705 from St. Cassian Formation.

Description. Shell rotelliform, low-spired; lectotype comprises 5.5 whorls, 7.7 mm high, 9.6 mm wide; whorl face of early teleoconch almost straight, evenly sloping at an angle of 60° with axis (spiral angle 120°); protoconch consisting of slightly less than one whorl, smooth with a diameter of 0.28 mm; diameter of initial whorl 0.3–0.4 mm; earliest teleoconch whorl angulated at mid-whorl of whorl face; angulation moves downward with growth until a suprasutural position is reached; later teleoconch whorls with pronounced angulation emerging at abapical suture; angulation well above mid-whorl in body whorl, formed at adapical edge of selenizone; whorl face below selenizone straight, vertical, with evenly rounded transition to base; abapical border of selenizone formed by faint suture; last whorl deflected downward so that angulation situated at mid-height of whorl face; suture deep; straight, oblique ramp between subsutural nodular spiral cord and peripheral angulation; whorl face just after the protoconch ornamented with faint spiral threads; later whorl face ornamented with subsutural spiral cord composed of spirally elongated nodes, shell otherwise smooth; subsutural nodes appear on fourth whorl and tend to become weaker on last whorl; selenizone convex, forming whorl angulation at adapical border of selenizone at periphery, raised slightly above sutural ramp; selenizone occasionally separated from ramp by a furrow; selenizone starts seemingly after third whorl; asymmetric growth lines on selenizone culminating at its adapical edge that forms angulation of whorls; growth lines orthocline to slightly opisthocline between adapical suture to subsutural spiral cord, prosocyrt on ramp and prosocyrt below the selenizone; whorl face below selenizone flat; base rounded, convex, phaneromphalous, with slightly opisthocyrt growth lines, ornamented with radial wrinkles on circumumbilical region; aperture as wide as high, with angulated outer lip, rounded basal lip and straight columellar lip.

Discussion. *Rhaphistomella radians* is one of the most abundant and best-studied gastropods of the St. Cassian Formation. Fürsich & Wendt (1977) found it was by far the most abundant species in basin assemblages such as the *Rhaphistomella radians*/*Palaeonucula strigilata* association. These authors interpreted the species as an algal dweller which is of course speculative. Münster's (1841) original illustration is not realistic, but the species has been well documented subsequently (e.g., Kittl 1891; Bandel 1991, 2009). The lectotype designated herein is a well-preserved specimen that was labeled as the one illustrated by Münster (1841) (the type material consists of more than 60 conspecific specimens). This specimen was also illustrated by Bandel (1991 pl. 11, fig. 7) and is documented here in much greater detail. Bandel (1991) also reported a thick inner nacreous layer for *Rhaphistomella radians*.

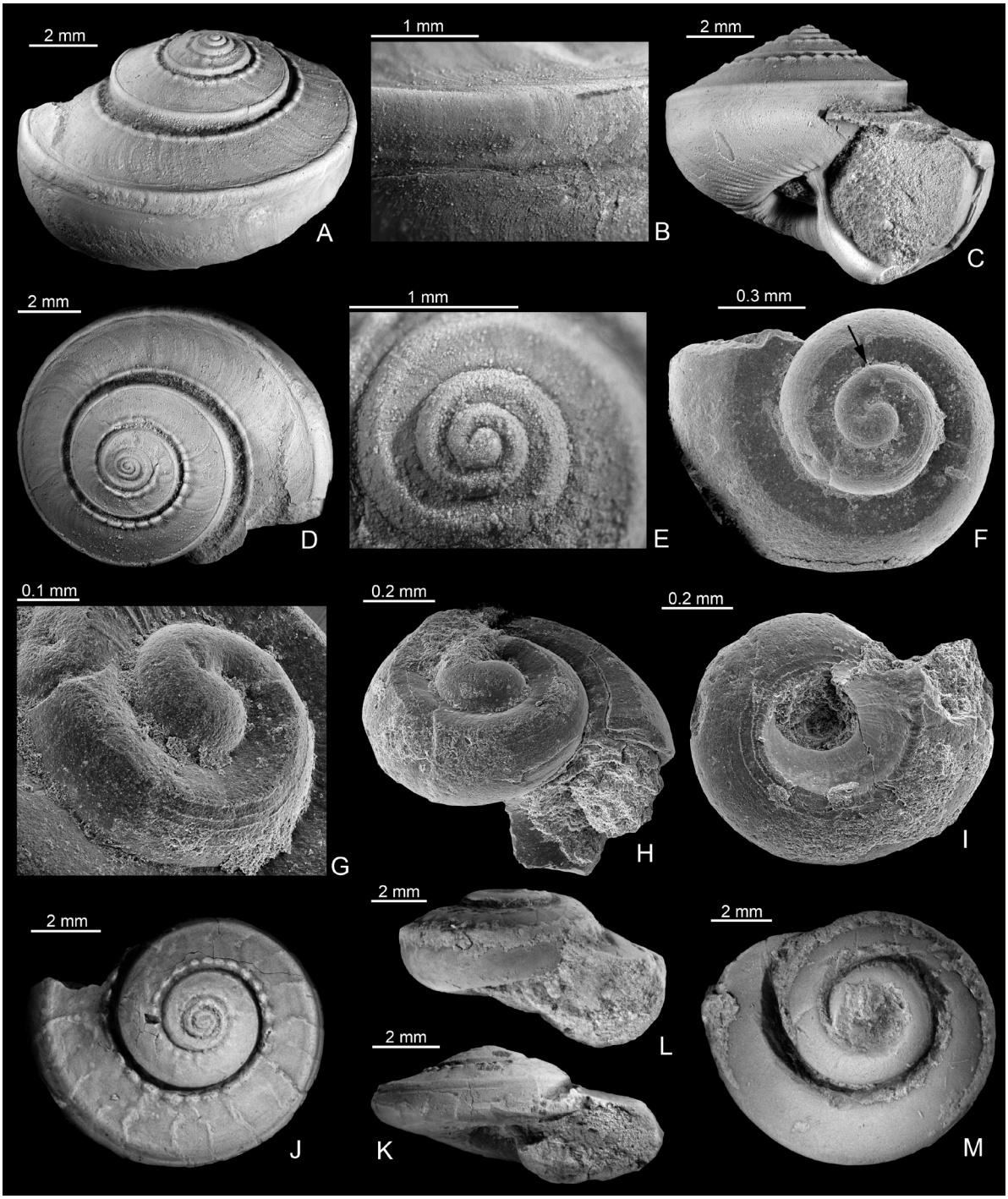

FIGURE 8. *Rhaphistomella radians* (Wissmann, 1841 in Münster); **A–E.** Lectotype, SNSB-BSPG AS VII 1224 (original of Münster 1841, pl. 12, figs 8a–b), St. Cassian Formation; **F–G.** PZO 13701, St. Cassian Formation, SEM image, arrow indicates the protoconch-teleoconch boundary; **H–I.** PZO 13705, St. Cassian Formation, SEM image; **J–K.** Lectotype of *Solarium subpunctatum* Klipstein, 1844, NHMUK PI OR 35826 (original of Klipstein 1844, pl. 14, fig. 9); **L–M.** Lectotype of *Euomphalus studeri* Klipstein, 1844, NHMUK PI OR 35828(1), (original of Klipstein 1844, pl. 14, fig. 10).

The middle part of the selenizone is occasionally concave. *Rhaphistomella radians* specimens commonly show healed shell fractures. The species was obviously exposed to considerable predatory pressure (also see discussion on *Cheilotomona blumi* below).

The lectotype of *Solarium subpunctatum* Klipstein, 1844 (NHMUK PI OR 35826; Fig. 8J–K) is a crushed specimen and the lectotype of *Euomphalus studeri* Klipstein, 1844 (NHMUK PI OR 35828(1), Fig. 8L–M) represents an inner mould; both belong to *Rhaphistomella radians*.

Genus *Lineacingulum* gen. nov.
LSID. urn:lsid:zoobank.org:act:4DE231A3-C0AE-4041-AFD6-F645F84B2DB0

Type species. *Pleurotomaria texturata* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. From Latin *linea*, meaning thread, string; Latin *cingulum*, meaning band, belt; referring thread-like ornamentation on whorl face and selenizone; gender neuter.

Diagnosis. Shell broadly conical, wortheniform; spire gradate; whorls with pronounced angulation at mid-whorl of spire whorls and broad concave ramp; angulation at middle of selenizone or above; selenizone broad with asymmetric, fine lunulae; teleoconch ornamented with axial and spiral threads; early whorls trochiform, not depressed, poorly ornamented or smooth, base with circumumbilical carina.

Discussion. *Lineacingulum* **gen. nov.** differs from other wortheniform genera (e.g., *Worthenia*, *Wortheniella*, *Humiliworthenia*) in its sinuous growth lines on the ramp, narrow shoulder, relatively wide selenizone, fine lunulae on selenizone and in the presence of a circumumbilical carina. It differs from *Worthenia* in forming the selenizone from a v-shaped notch, and in having v-shaped lunulae and spiral threads on the selenizone instead of a knobby, convex selenizone. *Wortheniella* differs in having immersed early whorls with strong spiral cords and in the presence of subsutural nodes. *Humiliworthenia* is largely smooth without distinct lunulae and with subsutural nodes. *Ananias* has a concave, smooth and narrow selenizone without angulation in early whorl, so selenizone is formed from convex whorl face. *Sisenna* has similar growth lines and a narrow shoulder but differs in having a carina on the early teleoconch, a narrower selenizone and its whorl face lacks pronounced, equally spaced axial threads instead *Sisenna* has a dominant spiral ornament.

Included species. *Lineacingulum texturatum* (Münster, 1841) (=*Pleurotomaria amalthea* Klipstein, 1844), *Lineacingulum bicingulatum* (Klipstein, 1844) (= *Worthenia cassiana* Kittl, 1891) from the St. Cassian Formation; *Worthenia eremita* Koken, 1897 from the Hallstatt Limestone.

***Lineacingulum texturatum* (Münster, 1841) comb. nov.**
Fig. 9

*1841	*Pleurotomaria texturata*—Münster, p. 110, pl. 12, figs 1a–b.
1844	*Pleurotomaria amalthea*—Klipstein, p. 169, pl. 10, figs 19a–b.
1850	*Pleurotomaria texturata* Münster, 1841—d'Orbigny, p. 195, no. 383.
?1868	*Pleurotomaria texturata* Münster sp.—Laube, p. 79, pl. 26, fig. 11.
1891	*Worthenia texturata* Münster sp.—Kittl, p. 193, pl. 3, figs 10–11.
non 1914	*Worthenia* cfr. *texturata* Muenst. sp.—Scalia, p. 8, pl. 1, fig. 32.
non 1978	*Worthenia texturata* (Münster)—Zardini, p. 21, pl. 6, figs 7–8.
non 1985	*Worthenia texturata* (Münster)—Zardini, pl. 6, fig. 7.
1991	*Laubella texturata* (Münster, 1841)—Bandel, p. 44, pl. 15, fig. 5 (non pl. 15, figs 6–7).

Material. SNSB-BSPG AS VII 1220 (original of Münster 1841, pl. 12, figs 1a–b), herein designated as lectotype from the St. Cassian Formation (SNSB-BSPG AS VII 1221 found in the same box of AS VII 1220 but is not conspecific, probably representing *Nodocingulum muensteri*. Münster might have mixed the two species). NHMUK PI OR 35334(1), designated as lectotype of *Pleurotomaria amalthea* Klipstein herein; NHMUK PI OR 35334(2) (original of Klipstein 1844, pl. 10, figs 19a–b) designated as paralectotype herein, from the St. Cassian Formation.

Description. Shell trochiform; lectotype comprises about 6 whorls, 7.4 mm high, 6.6 mm wide; spire gradate with angulated whorl face; suture moderately deep; early whorls convex, smooth or poorly ornamented, trochiform, not depressed; whorl face concave between subsutural spiral cord and median angulation, concave and parallel to shell axis between median angulation and abapical suture; selenizone broad, with mid-angulation, ornamented with thread-like lunulae, bordered by spiral threads, situated at median angulation of whorl face; lunulae v-shaped, thread-like; whorl face ornamented with collabral and spiral threads, forming a weak cancellate pattern; collabral threads opisthocline between adapical suture and subsutural spiral cord, oblique prosocyrt to prosocline between subsutural spiral cord and selenizone, prosocyrt below selenizone; base convex with rounded outer basal edge and circumumbilical carina, forming a pseudo-umbilicus; base ornamented with opisthocyrt growth lines and weak spiral threads; aperture as wide as high with angulated outer lip, angulato-convex basal lip and convex columellar lip.

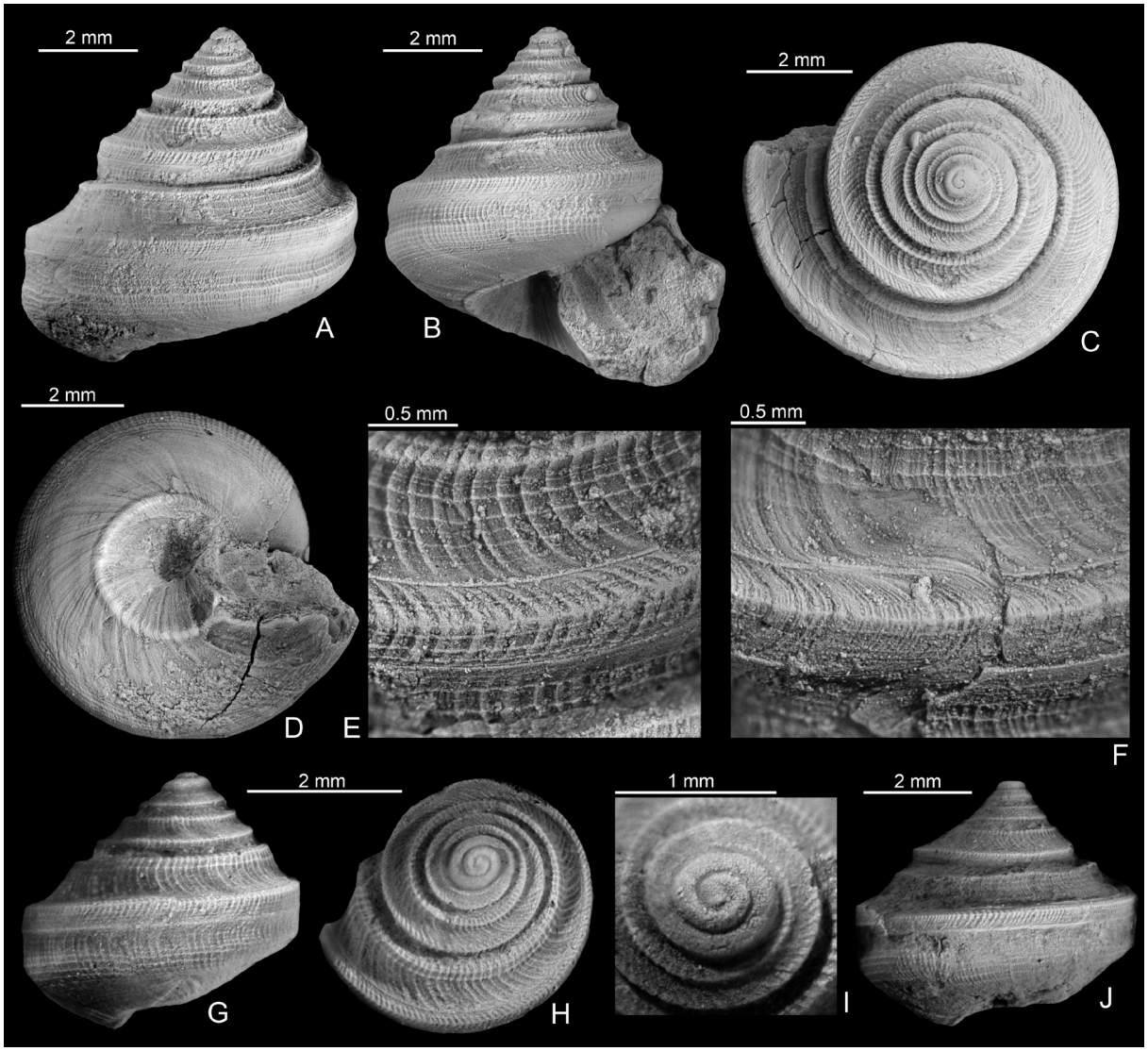

FIGURE 9. *Lineacingulum texturatum* (Münster, 1841); **A–F.** Lectotype, SNSB-BSPG AS VII 1220 (original of Münster 1841, pl. 12, figs 1a–b), St. Cassian Formation; **G–I.** Lectotype, *Pleurotomaria amalthea* Klipstein, 1844, NHMUK PI OR 35334(1), St. Cassian Formation; **J.** Paralectotype of *Pleurotomaria amalthea*, NHMUK PI OR 35334(2) (original of Klipstein 1844, pl. 10, figs 19a–b), St. Cassian Formation.

Discussion. Bandel (1991), who previously studied Münster's (1841) type material, placed this species in *Laubella* Kittl, 1891; however, the species assigned to *Laubella* including its type species are much smaller, lack a median angulation and their selenizone is located subsuturally. The specimen assigned to *Laubella texturata* by Bandel (1991, pl. 15, figs 6–7; refigured here in Fig. 73C) represents *Laubella delicata* (Laube, 1868) (= *Laubella bella* Bandel, 1991) (the lectotype is refigured here in Fig. 73A). The specimens figured by Zardini (1978, pl. 6, figs 7–8) as *Worthenia texturata* also represent *Laubella delicata*. The specimen figured by Laube (1868, p. 79, pl. 26, fig. 11) as *L. texturatum* does not match this species and is of doubtful identity.

Lineacingulum texturatum differs from *Lineacingulum bicingulatum* (Klipstein, 1844) (= *Worthenia cassiana* Kittl, 1891) in having spiral threads, a higher spire and a rounded outer basal edge rather than an angular one. The type specimen of *Pleurotomaria bicingulata* Klipstein, 1844 figured by Klipstein (1844, pl. 10, fig. 10, NHMUK PI OR 35331(1) (Fig. 10A–C) is herein designated as lectotype of this species (=*Lineacingulum bicingulatum*). The type specimen of *Worthenia cassiana* Kittl, 1891 figured by Kittl (1891, pl. 3, fig. 7, NHMW 1899/0005/0072/2) (Fig. 10D–E) is designated herein as lectotype of this species which represents a junior synonym of *Lineacingulum bicingulatum*.

The lectotype of *Lineacingulum texturatum* has a repaired shell fracture (Fig. 9F).

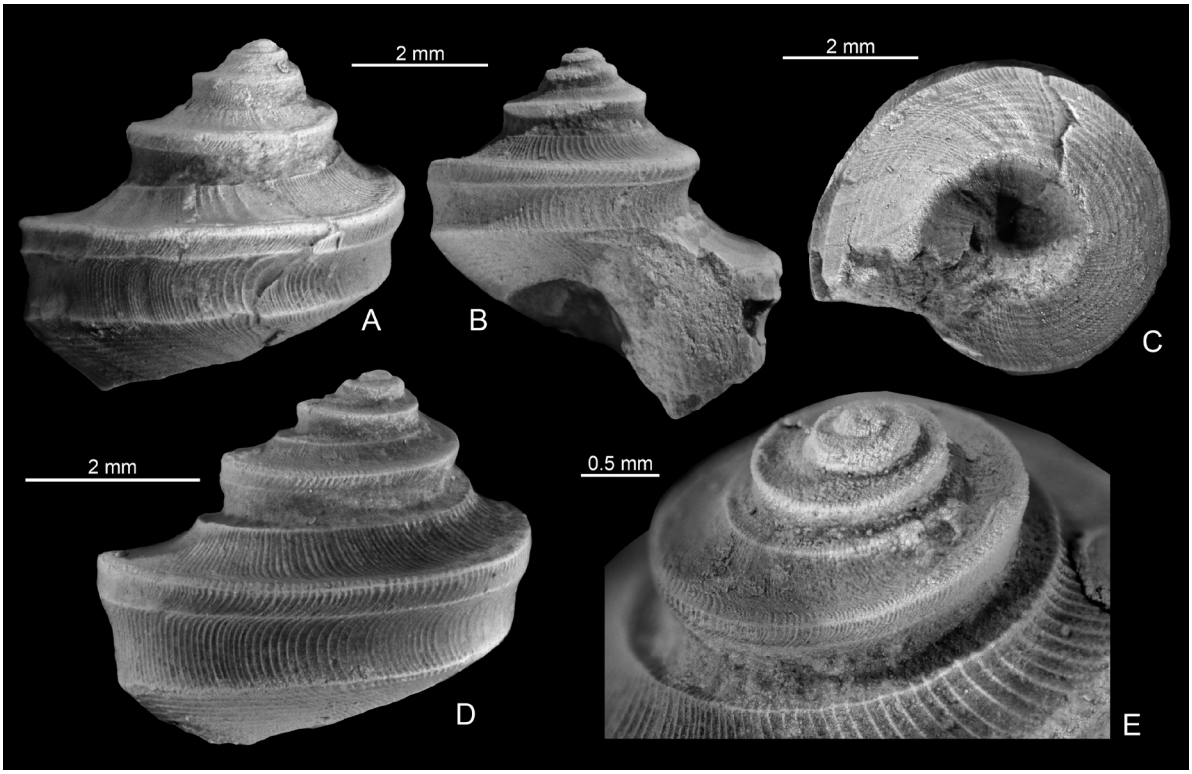

FIGURE 10. *Lineacingulum bicingulatum* (Klipstein, 1844); **A–C.** Lectotype, NHMUK PI OR 35331(1) (original of Klipstein 1844, pl. 10, fig. 10), St. Cassian Formation; **D–E.** Lectotype of *Worthenia cassiana* Kittl, 1891, NHMW 1899/0005/0072/2 (original of Kittl 1891, pl. 3, fig. 7), St. Cassian Formation.

Genus *Sisenna* Koken, 1896

Type species. *Pleurotomaria turbinata* Hörnes, 1855, Hallstatt Limestone, Carnian, Hallstatt, Austria; subsequent designation by Cossmann (1897).

Sisenna venusta (Münster, 1841)

Fig. 11

*1841	*Pleurotomaria venusta*—Münster, p. 113, pl. 12, figs 13a–b.
1844	*Pleurotomaria credneri*—Klipstein, p. 163, pl. 10, fig. 17.
1850	*Trochus salus* d'Orb., 1847—d'Orbigny, p. 192, no. 312.
1850	*Turbo credneri* d'Orb., 1847—d'Orbigny, p. 193, no. 337.
1868	*Pleurotomaria venusta* Münster—Laube, p. 87, pl. 28, fig. 4.
1891	*Worthenia venusta* Münster sp.—Kittl, p. 190, pl. 3, figs 1–2.
non 1962	*Worthenia venusta* Münster—Sachariewa-Kowatschewa, p. 95, pl. 3, figs 11–12; pl. 4, fig. 10; pl. 9, fig. 8.
1978	*Worthenia venusta* (Münster)—Zardini, p. 21, pl. 6, fig. 6 (non fig. 12); pl. 39, figs 8a–c.
1978	*Worthenia* sp.—Zardini, p. 19, pl. 4, fig. 7.
1980	*Worthenia* sp.—Zardini, p. 3, pl. 1, figs 9a–c.
1985	*Worthenia venusta* Klipstein—Zardini, p. 11, pl. 4, figs 4a–c.
1992	*Wortheniella venusta* (Münster, 1841)—Schwardt, p. 32, pl. 2, figs 2–3.
2009	*Sisenna venusta* (Münster, 1841)—Bandel, pl. 4, fig. 60, pl. 5, figs 61–62.

Material. SNSB-BSPG AS VII 1215 (original of Münster 1841, pl. 12, figs 13a–b), herein designated as lectotype from the St. Cassian Formation. NHMUK PI OR 35360(1) (original of Klipstein 1844, pl. 10, fig. 17), herein designated as lectotype of *Pleurotomaria credneri* Klipstein, 1844 from the St. Cassian Formation. PZO 13700, PZO 13704 from the St. Cassian Formation; MPRZ 2021 1–008, MPRZ 2021 1–017, MPRZ 2021 1–025 from Campo, St. Cassian Formation.

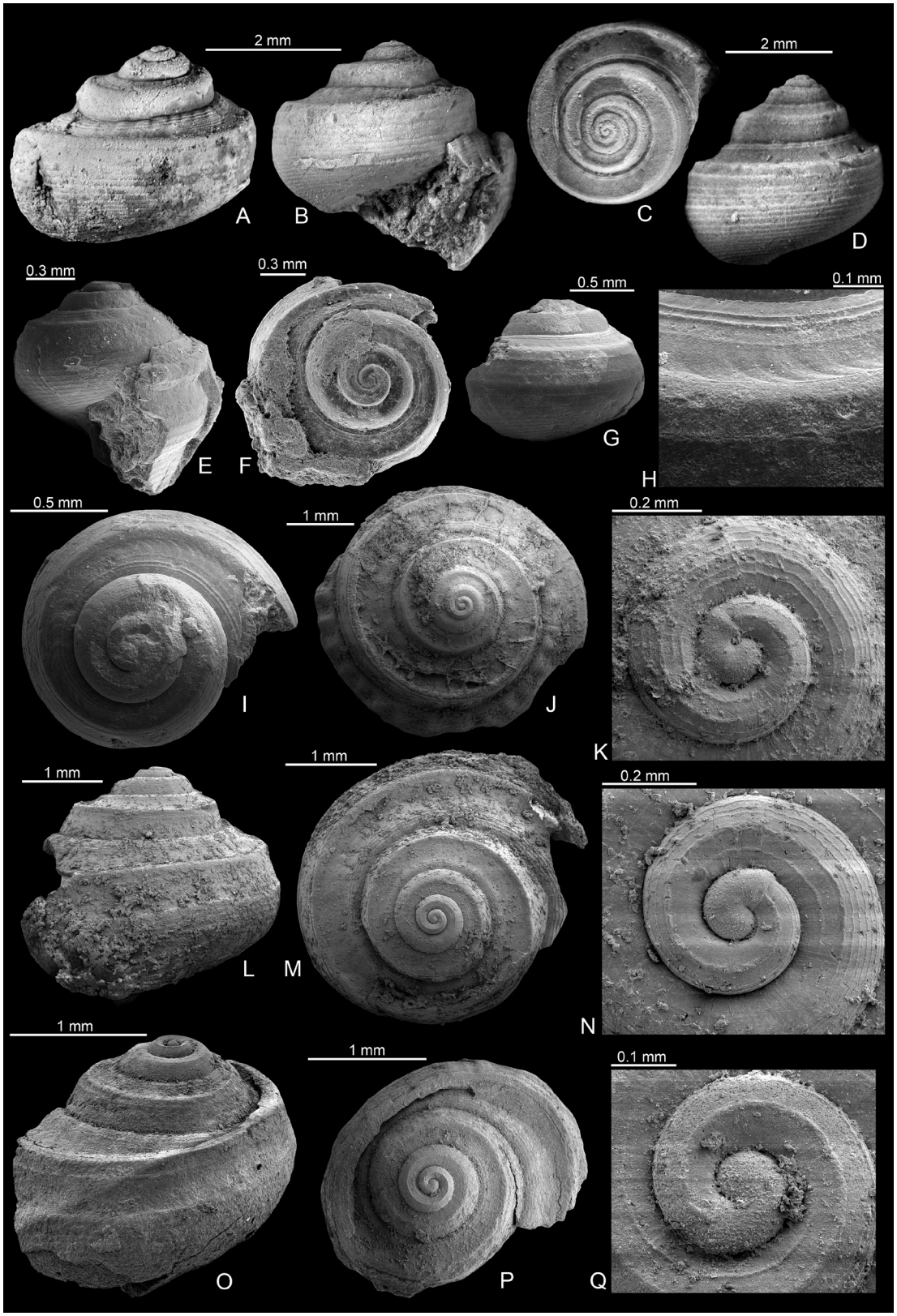

FIGURE 11. *Sisenna venusta* (Münster, 1841); **A–B.** Lectotype, SNSB-BSPG AS VII 1215 (original of Münster 1841, pl. 12, figs 13a–b), St. Cassian Formation; **C–D.** Lectotype of *Pleurotomaria credneri* Klipstein, 1844, NHMUK PI OR 35360(1) (original of Klipstein 1844, pl. 10, fig. 17), St. Cassian Formation; **E–F.** PZO 13700, St. Cassian Formation, SEM image; **G–I.** PZO 13704, St. Cassian Formation, SEM image; **J–K.** MPRZ 2021 1–025, Campo, St. Cassian Formation, SEM image; **L–N.** MPRZ 2021 1–008, Campo, St. Cassian Formation, SEM image; **O–Q.** MPRZ 2021 1–017, Campo, St. Cassian Formation, SEM image.

Description. Shell wortheniform, broad, low-spired; spire gradate; lectotype comprises 5 whorls, 3.4 mm high (basal lip not preserved), 3.6 mm wide; protoconch pitted, consisting of less than one whorl, 0.18 mm wide; first whorl diameter 0.25; first 1.5 whorls planispiral but not depressed; suture slightly incised; early teleoconch just after protoconch ornamented with spiral threads; early teleoconch whorls rounded, convex with an slight angulation at adapical spiral thread at about mid-whorl of whorl face; angulation shifts in abapical direction with growth; angulation high on body whorl, at about adapical fourth of whorl height; ramp slightly concave, weakly inclined; whorl face slightly convex below angulation, vertical to very steeply sloping; selenizone convex, encompassing whorl angulation, slightly elevated, not bordered by spiral cords; ramp ornamented with subsutural axial wrinkles or wavy ribs in late whorls and regularly spaced, fine spiral cords; lateral whorl face and base ornamented with imbricated, low spiral cords; transition from whorl face to base evenly rounded; base convex, narrowly phaneromphalous.

Discussion. Münster's (1841) type specimen is well-preserved. The early teleoconch of *Sisenna venusta* was documented by Bandel (1991, 2009) and Schwardt (1992). The early whorls of well-preserved specimens are figured herein (Fig. 11). Bandel (2009) reported a pitted protoconch of less than one whorl of the vetigastropod type for this species which is also documented herein (Fig. 11K, 11N). The early whorls are not depressed as in *Wortheniella* as can also be seen in the specimen illustrated by Schwardt (1992). Nevertheless, *S. venusta* was placed in *Wortheniella* that was primarily characterized as having depressed, immersed early whorls. Some members of *Sisenna* have a convex, evenly rounded whorl face in the early teleoconch and develop a whorl angulation in later whorls (e.g., the Early Jurassic *Sisenna canalis,* see Nützel & Gründel 2015). However, the whorl angulation of *Sisenna venusta* starts immediately after the protoconch (Schwardt 1992, pl. 2, figs 2–3; see Fig. 11J, K, M, N, P, Q) as is also the case in the Carnian *Sisenna turbinata* Koken, 1897. The growth lines cannot be seen in the lectotype but are visible in another specimen (see Fig. 11G–I). It has opisthocline growth lines just below the suture as is typical of *Sisenna*. The selenizone is not as sharply angular as in several other members of *Sisenna*. The specimens illustrated by Kittl (1891, pl. 3, figs 1, 2) are more slender and the ramp is more inclined, which is regarded as intraspecific variation. Examination of the type specimens of *Pleurotomaria credneri* Klipstein, 1844 confirmed that this taxon is a junior synonym of *S. venusta*. The only other *Sisenna* species known from the St. Cassian Formation is *Sisenna ampezzana* Leonardi & Fiscon, 1947 (Fig. 12), which differs from *Sisenna venusta* in ornamentation and its higher spired early whorls.

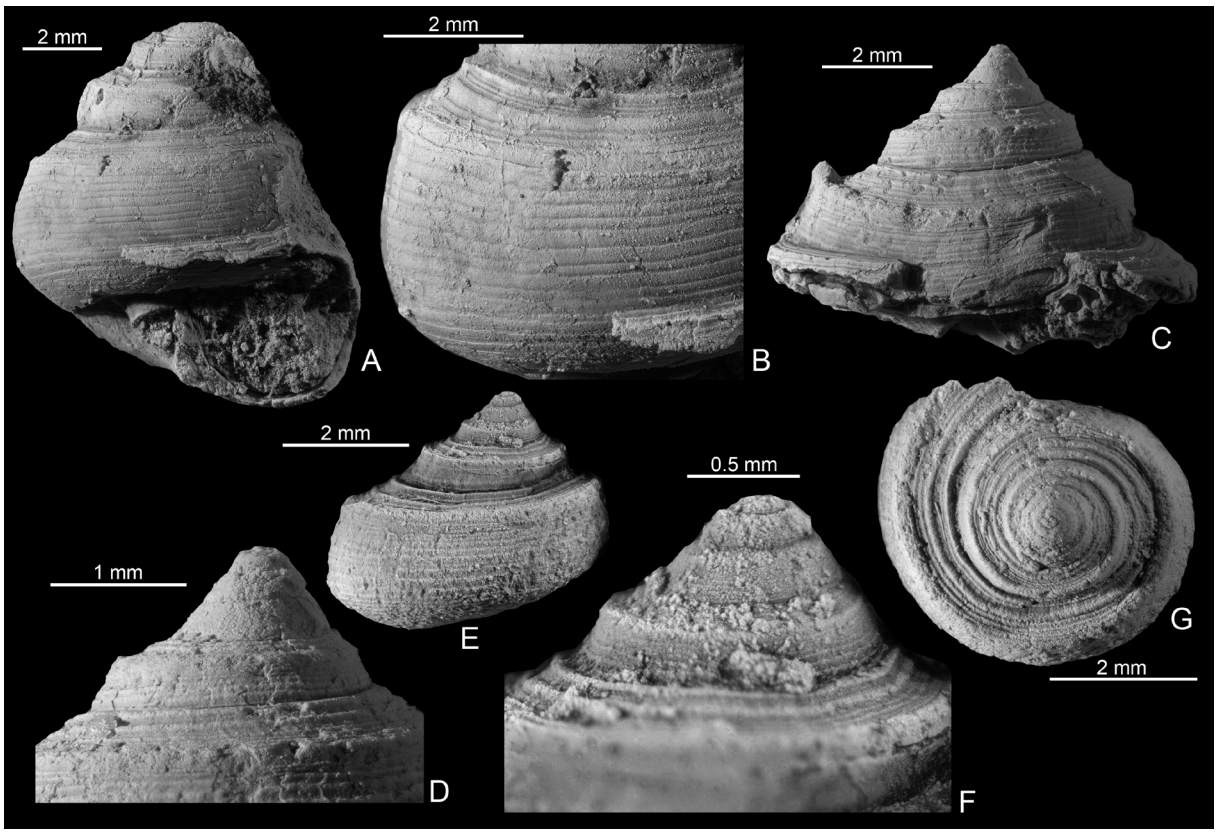

FIGURE 12. *Sisenna ampezzana* Leonardi & Fiscon, 1947; **A–B.** PZO 13681, Rumerlo Misurina mix, St. Cassian Formation; **C–D.** MPRZ 2021 1–045, Rumerlo, St. Cassian Formation; **E–G.** PZO 13684, Rumerlo Misurina mix, St. Cassian Formation.

Genus *Rufilla* Koken, 1896

Type species. *Rufilla densecincta* Koken, 1896, Hallstatt Limestone, Carnian, Lower Rötelstein (Bad Aussee), Austria; subsequent designation by Cossmann (1897, p. 140).

***Rufilla fasciolata* (Münster, 1841) comb. nov.**
Fig. 13

*1841	*Turbo fasciolatus*—Münster, p. 114, pl. 12, figs 21a–b.
1850	*Trochus fasciolatus* d'Orb., 1847—d'Orbigny, p. 190, no. 263.
non 1870	*Turbo fasciolatus* Münster—Laube, p. 21, pl. 31, fig. 10.
1891	*Gosseletina fasciolata* Münster sp.—Kittl, p. 41, pl. 1, fig. 25 (non figs 23–24).
?1908	*Gosseletina fasciolata* (Münster, 1841)—Häberle, p. 457, pl. 2, figs 6a–b.
non 1991	*Gosseletina fasciolata* (Münster, 1841)—Bandel, p. 34, pl. 12, fig. 4. [*Rhaphistomella radians* (Münster, 1841)].
non 1991	*Gosseletina fasciolata* (Münster, 1841)—Bandel, p. 34, pl. 12, figs 5–7.
2009	*Gosseletina fasciolata* (Münster, 1841)—Bandel, pl. 4, figs 58–59.

Material. SNSB-BSPG AS VII 1593 (original of Münster 1841, pl. 12, figs 21a–b), herein designated as lectotype from the St. Cassian Formation. GBA 1868/008/0002, 4339, one specimen labeled as *Pleurotomaria calypso* from Laube's collection from the St. Cassian Formation. MPRZ 2021 1–048 from Misurina Landslide, St. Cassian Formation, Italy.

Description. Shell bulbous, turbiniform with low spire; lectotype comprises 5 whorls, 5.8 mm high, 5.7 mm wide; initial whorls elevated, low-spired, without visible ornament; first whorl diameter 0.3 mm; suture abutting; whorls embrace at periphery at mid-whorl; whorl face convex, ornamented with sharp spiral cords separated by concave grooves; interspaces much wider than spiral cords; whorl face above selenizone and whorl face between selenizone and abapical suture ornamented with about 4–5 spiral cords; selenizone flush with shell surface, flat, with faint crescentic growth lines (Fig. 13G); selenizone situated almost at middle of whorl face of spire whorls, somewhat closer to abapical suture but rather high on fully exposed last whorl; base convex with even transition to whorl face, ornamented with around 22 spiral cords, narrowly phaneromphalous; aperture tear-shaped, slightly higher than wide; with convex outer lip, rounded basal lip and convex inner lip.

Discussion. The lectotype is well-preserved and shows a fine but distinct ornament of spiral cords that is, however, absent on the selenizone. *Rufilla fasciolata* resembles species of the genus *Gosseletina* and was previously placed in that genus. The Carboniferous type species of *Gosseletina*, *Pleurotomaria callosa* de Koninck, 1843, is entirely smooth. However, several species with spiral ornament were placed in *Gosseletina*, for instance the Carboniferous species *G. portlockiana* (de Koninck, 1843) (see Batten 1966) and the Permian species *G. permianus* Batten, 1989. The type species of *Gosseletina* has a thick inductura generating an umbilical callus (Knight 1941), both is obviously absent in *R. fasciolata*. Many Palaeozoic species without an inductura were also placed in *Gosseletina*. Kittl (1891) discussed the issue and concluded that a callus may be present or absent in the case of *Gosseletina*. These differences raise doubts as to whether *G. fasciolata* should be placed in the genus *Gosseletina*. Here we place this species in the genus *Rufilla*, based on the position and morphology of the selenizone (i.e., flush with whorl surface), whorl shape and surface ornamentation. The Late Triassic type species of *Rufilla* from the Hallstatt Limestone seems to have an ornament of pronounced (but weaker than the spiral cords) thread-like growth lines that is absent in *R. facsiolata*. Whether the mentioned spirally ornamented Palaeozoic taxa that have been placed in *Gosseletina* also do belong to *Rufilla* needs to be investigated.

The specimens assigned to *Gosseletina fasciolata* (Münster, 1841) by Kittl (1891, pl. 1, figs 23–24) and by Bandel (1991, pl. 12, figs 5, 6) lack a prominent spiral ornament. The lack of spiral ornament of Kittl's (1891) and Bandel's (1991) material cannot be explained with the state of preservation because the growth lines are well-preserved in their specimens. These specimens are not conspecific with the lectotype of *Rufilla fasciolata* and are assigned to *Rufilla latizonata* (Laube, 1868).

The specimen illustrated by Bandel (2009, figs 58–59) as *Gosseletina fasciolata* seems to have a swelling or tooth on the inner lip of the aperture. It needs to be examined whether such a tooth is really present in this species.

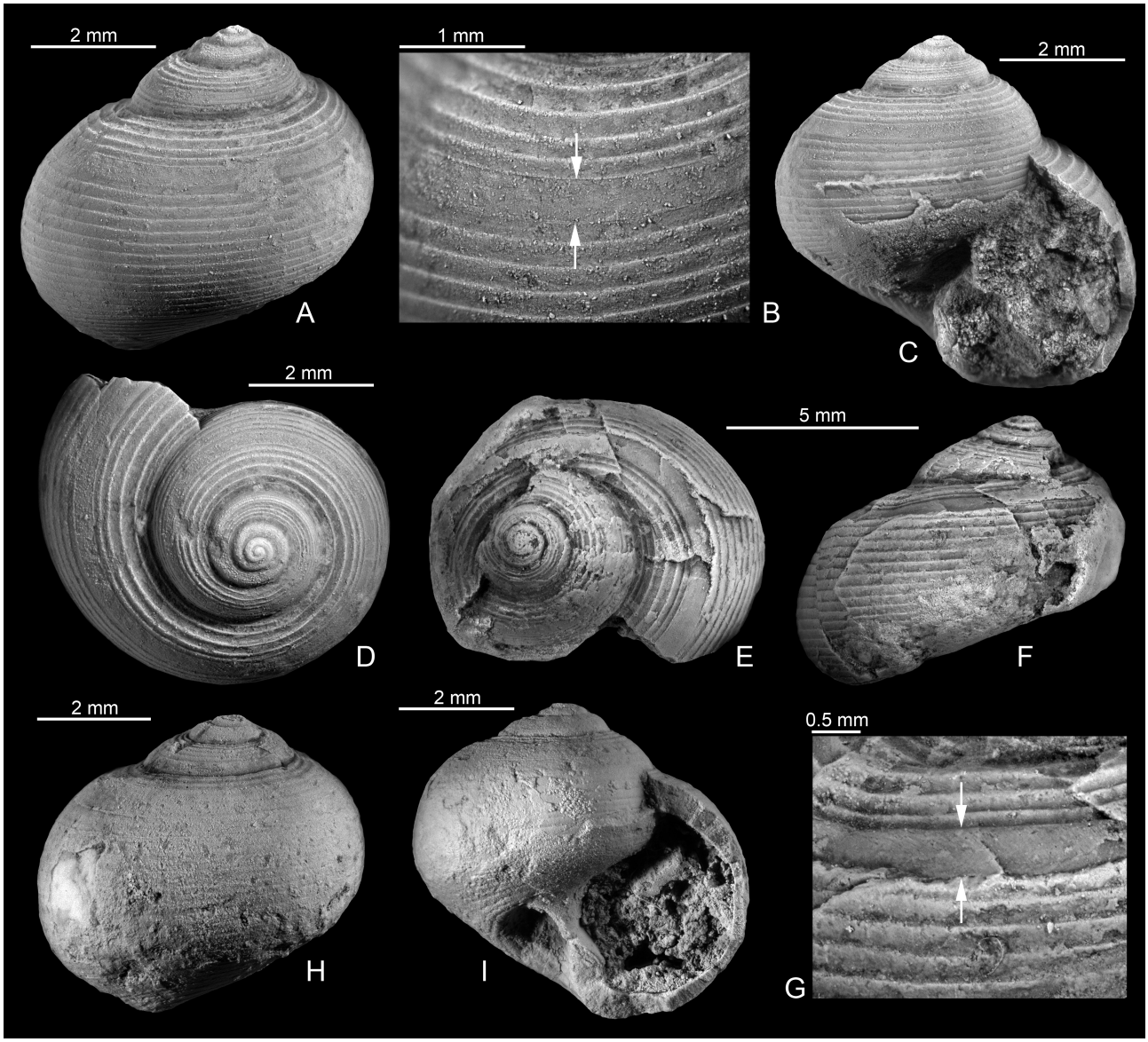

FIGURE 13. *Rufilla fasciolata* (Münster, 1841); **A–D.** Lectotype, SNSB-BSPG AS VII 1593 (original of Münster 1841, pl. 12, figs 21a–b); arrows indicate selenizone borders, St. Cassian Formation; **E–G.** GBA 1868/008/0002, 4339, one specimen from Laube's collection, arrows indicate selenizone borders, St. Cassian Formation; **H–I.** MPRZ 2021 1–048 Misurina Landslide, St. Cassian Formation.

***Rufilla distincta* (Kittl, 1894) comb. nov.**
Fig. 14

*1894a *Worthenia distincta* n. f.—Kittl, pl. 8, fig. 1.

Material. NHMW 1899/0005/0075 (original of Kittl 1894a, pl. 8, fig. 1), from the St. Cassian Formation, Carnian, South Tyrol (Italy) is herein designated as lectotype.

Discussion. The lectotype of *Worthenia distincta* Kittl, 1894 from the St. Cassian Formation (Kittl 1894a, pl. 8, fig. 1) is figured here (Fig. 14). We place this species in *Rufilla* because its whorls are rounded and lack distinct angulations as would be typical for *Worthenia*. *Rufilla distincta* (Kittl, 1894a) is slightly higher spired and is ornamented with nodular cords on the whorl surface and selenizone.

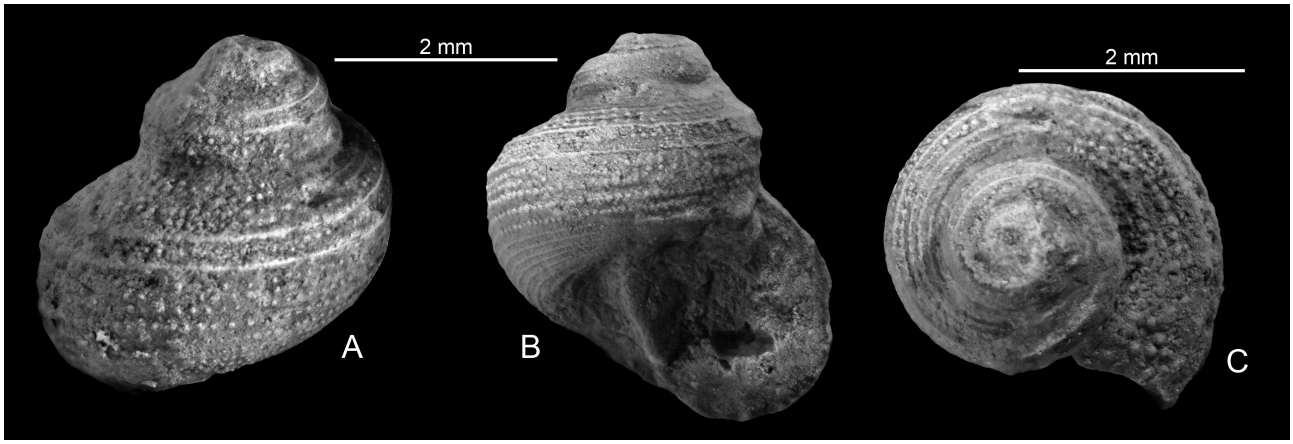

FIGURE 14. *Rufilla distincta* (Kittl, 1894); **A–C.** Lectotype, NHMW 1899/0005/0075 (original of Kittl 1894a, pl. 8, fig. 1), St. Cassian Formation.

***Rufilla latizonata* (Laube, 1868) comb. nov.**
Fig. 15

*1868 *Pleurotomaria latizonata* Laube—Laube, p. 57, pl. 26, fig. 8.
1891 *Gosseletina fasciolata* Münster sp.—Kittl, p. 41, pl. 1, figs 23–24 (non fig. 25).
1991 *Gosseletina fasciolata* (Münster, 1841)—Bandel, p. 34, pl. 12, figs 5–7 (non fig. 4).

Material. NHMW 1899/0005/0097 (original of Kittl 1891, pl. 1, fig. 23), NHMW 1990/0638/0000 (original of Bandel 1991, pl. 12, figs 5–6) from the St. Cassian Formation, Carnian, South Tyrol (Italy).

Description. Shell bulbous, turbiniform with low spire; with 5 visible whorls, first whorls not seen; suture incised; whorls embrace at periphery at mid-whorl; whorl face convex, smooth with prosocline growth lines above selenizone; selenizone flush with shell surface, flat, bordered by weak spiral lirae; selenizone with faint crescentic growth lines only; selenizone situated almost at middle of whorl face, somewhat closer to abapical suture; transition from whorl face to base evenly convex; base rounded, largely smooth, but ornamented with spiral cords near circum-umbilical region, narrowly phaneromphalous; aperture tear-drop-shaped, slightly higher than wide; with convex outer lip, rounded basal lip and convex inner lip; inner lip slightly reflected.

Discussion. Kittl (1891) regarded the absence of spiral ribs in the type material of *Rufilla latizonata* as a preservational artefact and regarded *Rufilla latizonata* to be conspecific with *Rufilla fasciolata*. As a result, the original material of Kittl (1891), housed in the NHMW, which Kittl assigned to *Gosseletina fasciolata* is composed of mixed *Rufilla fasciolata* and *Rufilla latizonata* specimens. In that mixed lot, *Rufilla latizonata* specimens are generally larger in size, which might be a character of this species. Here we figure the specimen illustrated by Bandel (1991, pl. 12, figs 5–6) to show that the lack of spiral ornament is not a preservational artefact (see also the discussion on *Rufilla fasciolata* above).

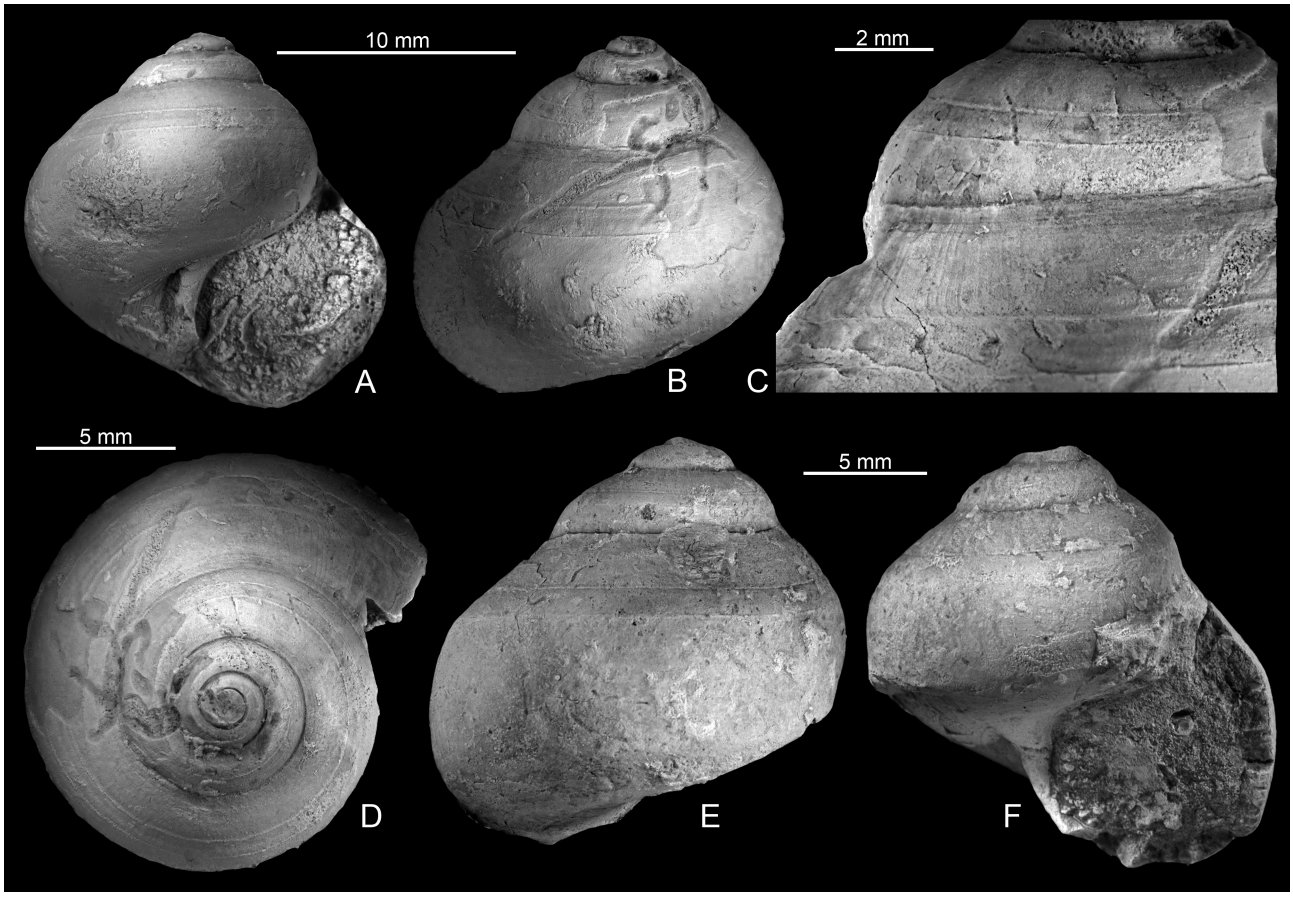

FIGURE 15. *Rufilla latizonata* (Laube, 1868); **A–D.** NHMW 1990/0638/0000 (original of Bandel 1991, pl. 12, figs 5–6), St. Cassian Formation; **E–F.** NHMW 1899/0005/0097 (original of Kittl 1891, pl. 1, fig. 23), St. Cassian Formation.

Family Temnotropidae Cox, 1960 (in Knight et al.)

Genus *Temnotropis* Laube, 1870

Type species. *Sigaretus carinatus* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; designated by Diener (1926, p. 31).

Discussion. Laube (1870, p. 42) and Koken (1889, p. 365) proposed that Haliotidae arose from Pleurotomarioidea via forms like *Temnotropis* but retained this genus in pleurotomariidans. Similarly, based on the presence of an ear-shaped aperture and nacre, Temnotropidae were placed in Haliotioidea by Bandel (1991, 2009). Kiel & Bandel (2000) assigned a Cretaceous species from Spain to *Temnotropis*. Accordingly, this occurrence would bridge the stratigraphic gap between *Temnotropis* and the first occurrence of *Haliotis* and would corroborate previous ideas stating a close relation between Temnotropidae and Haliotidae. However, the Cretaceous *Temnotropis frydai* Kiel & Bandel, 2000 belongs probably to *Trochotoma. Trochotoma* is a diverse genus that existed from the Late Triassic to the Early Cretaceous (Ferrari *et al*. 2015). The low-spired *Trochotoma* species (e.g., *Trochotoma* (*Placotoma*) *tornatilis* Phillips, 1829 from the Oxfordian) has a similar early teleoconch and selenizone like the specimen reported by Kiel & Bandel (2000). A good example is the early shell of *Trochotoma* (*Placotoma*) *suevica* (Quenstedt, 1881–1884) from the Kimmeridgian of S Germany figured by Gründel *et al*. (2017, pl. 4, fig. 1) who erroneously spelled the genus *Placostoma* [not *Plocostoma* Gemmellaro, 1889]. *Temnotropis stevniensis* Hansen, 2019 from the Cretaceous of Denmark does not represent *Temnotropis* because of its low position of the selenizone and in lacking a lateral whorl face. As also discussed by Hansen (2019), it probably represents a scissurellid genus. Herein, we tentatively assign it to *Auritoma* Szabó *et al*., 2019. The generic attribution of *Temnotropis costellata* Gemmellaro, 1889 and *Temnotropis transitoria* Gemmellaro, 1889 from the Permian of Italy is doubtful. Therefore, the reliable record of *Temnotropis* is restricted to the Triassic according to the present state of knowledge. It is more likely that Haliotidae

is derived from Trochotomidae, the members of which develop a trema (a hole formed by the expansion of the shell slit) and an oblique aperture and are found throughout the Jurassic and Late Triassic (see Ferrari *et al*. 2015 for a list of trochotomids). The presence of a trema in trochotomids could be an argument that trochotomoids gave rise to haliotids which have a row of tremata. Oblique apertures and high expansion rates are also seen in some members of *Rhineoderma* from the Carboniferous. These characters alone cannot be used for inferring phylogeny. They might reflect a similar ecology and be result of convergence. Temnotropidae seems to be closely related to the family Trochotomidae, but further phylogenetic analyses are needed. The presence of a continuous selenizone rather than a row of tremata suggests that Temnotropidae should be placed in Eotomarioidea. Temnotropids probably evolved from eotomarioids (such as *Plocostoma* Gemmellaro, 1889) by increasing whorl expansion rate and obliquity of the aperture.

Temnotropis fallax Kittl, 1891 (the original of Kittl 1891, pl. 5, figs 18–19, NHMW 1899/0005/0026 designated as lectotype herein and refigured here in Fig. 16A–C) is herein placed in *Trochotoma* Eudes-Deslongchamps, 1843 due to whorl morphology (e.g., oblique aperture, whorl profile, thickened outer basal edge). *Trochotoma fallax* (Kittl, 1891) lacks a trema but tremata are not present in all Trochotomidae (Ferrari *et al*. 2015). Tremata are formed during the last stage of ontogeny and are therefore not present in juvenile shells or in specimens in which the last whorl is broken off. *Trochotoma* differs from *Temnotropis* by the presence a prominent bulge at the transition to the base, a funnel-shaped base and it has more whorls.

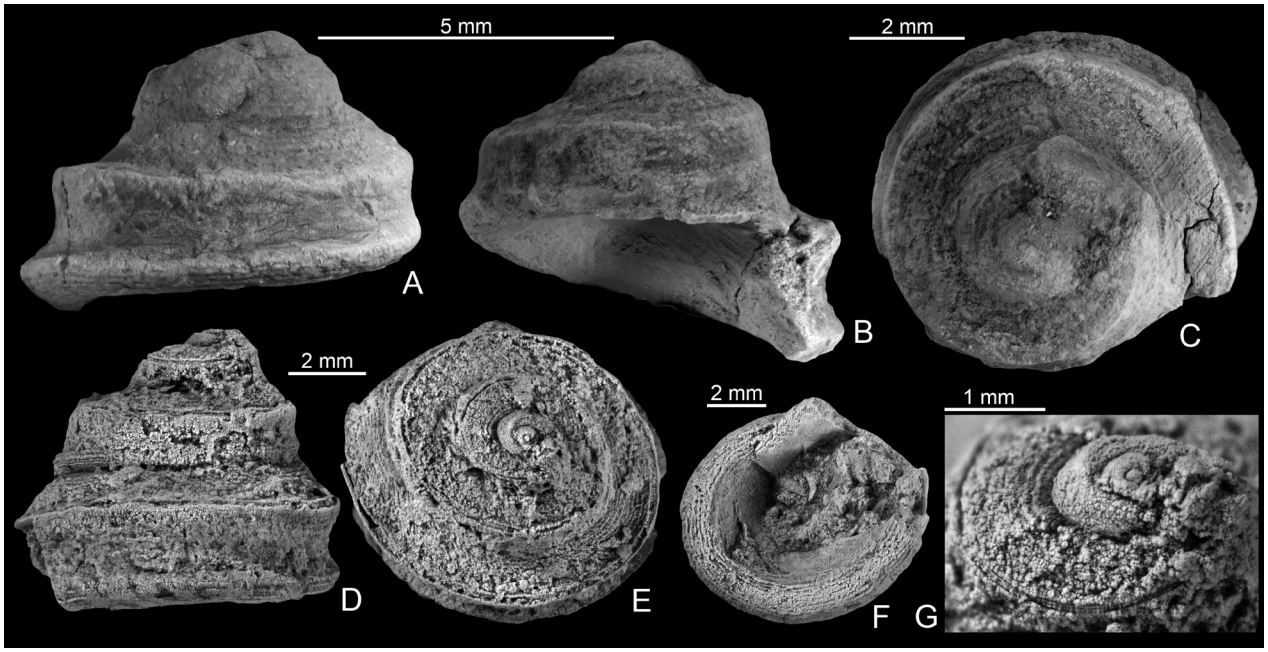

FIGURE 16. *Trochotoma fallax* (Kittl, 1891); **A–C.** Lectotype, NHMW 1899/0005/0026 (original of Kittl 1891, pl. 5, figs 18–19), St. Cassian Formation; **D–G.** NHMW 1899/0005/0025/3 (original of Bandel 1991, pl. 14, fig. 6), St. Cassian Formation.

Temnotropis carinata (Münster, 1841)

Fig. 17

*1841	*Sigaretus carinatus*—Münster, p. 93, pl. 9, figs 16a–b.
1844	*Sigaretus tenuicinctus*—Klipstein, p. 204, pl. 14, figs 20a–b.
1850	*Stomatia carinata* d'Orb., 1847—d'Orbigny, p. 194, no. 376.
1870	*Temnotropis carinata* Münster—Laube, p. 42, pl. 35, fig. 5.
1891	*Temnotropis carinata* Münster sp.—Kittl, p. 179, pl. 6, figs 6, 9–10.
1907	*Temnotropis carinata* Münster sp.—Broili, p. 77, pl. 7, fig. 1.
non 1962	*Temnotropis carinata* Münster—Sachariewa-Kowatschewa, p. 98, pl. 2, figs 4–5.
?1973	*Temnotropis carinata* (Münster, 1841)—Kollarova-Andrusova & Kochanova, p. 197, pl. 10A, fig. 11.
non 1978	*Temnotropis carinata* (Münster)—Zardini, p. 17, pl. 2, figs 12a–d.
1991	*Temnotropis carinata* (Münster, 1841)—Bandel, p. 38.
non 2009	*Temnotropis carinata*—Bandel, pl. 8, fig. 107.
2015	*Temnotropis bicarinata*—Hausmann & Nützel, figs 5D1–2.

Material. SNSB-BSPG AS VII 1803 (original of Münster 1841, pl. 9, figs 16a–b), herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG 1903 IX 324 (original of Broili 1907, pl. 7, fig. 1) from Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMUK PI OR 35842(1), type specimen figured by Klipstein (1844, pl. 14, fig. 20), designated herein as lectotype of *Sigaretus tenuicinctus* Klipstein from the St. Cassian Formation.

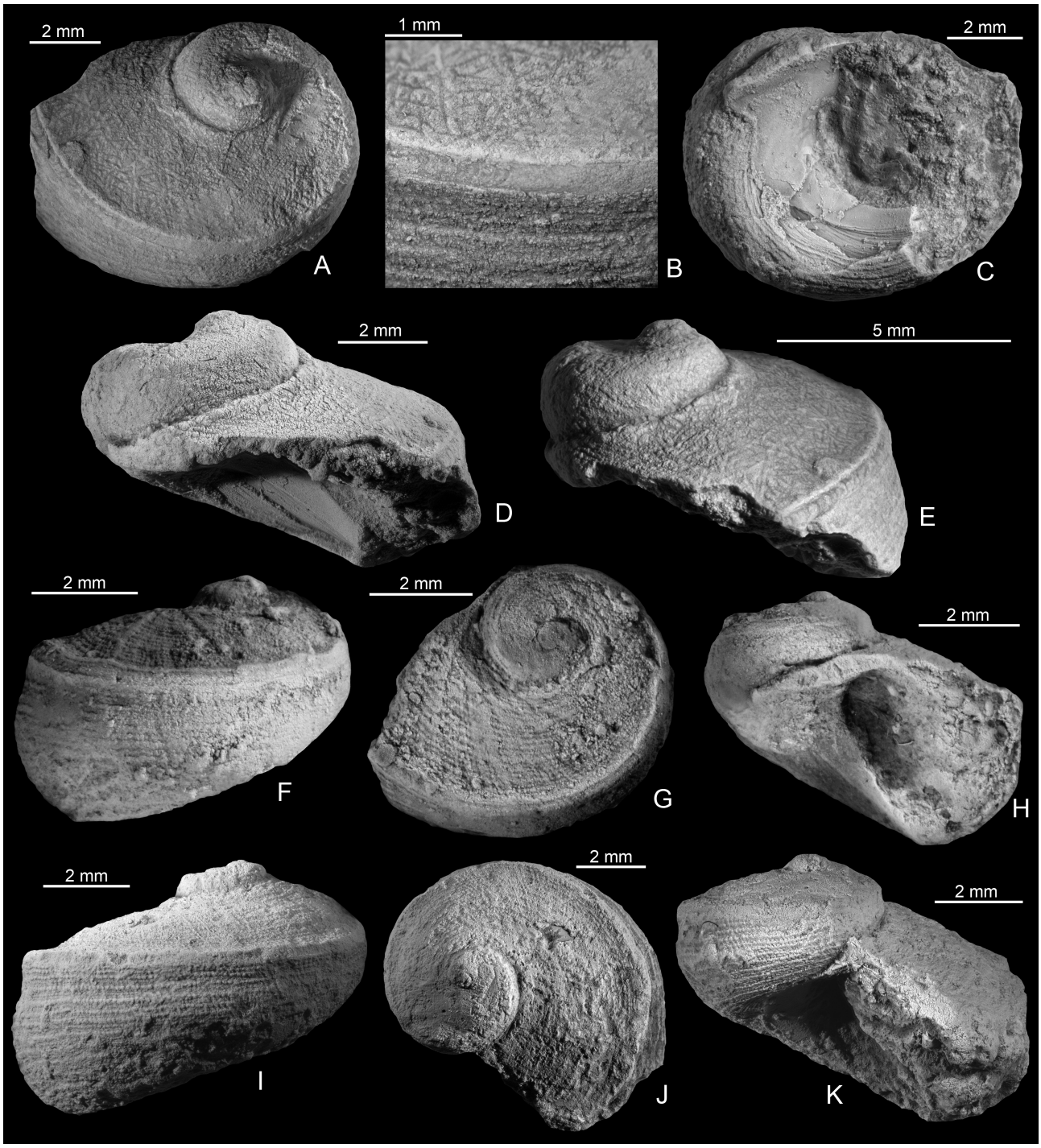

FIGURE 17. *Temnotropis carinata* (Münster, 1841); **A–E.** Lectotype, SNSB-BSPG AS VII 1803 (original of Münster 1841, pl. 9, figs 16a–b), St. Cassian Formation; **F–H.** Lectotype of *Sigaretus tenuicinctus* Klipstein, 1844, NHMUK PI OR 35842(1) (original of Klipstein 1844, pl. 14, fig. 20), St. Cassian Formation; **I–K.** SNSB-BSPG 1903 IX 324 (original of Broili 1907, pl. 7, fig. 1), Pachycardientuffe, Upper Ladinian, Seiser Alm.

Description. Shell auriform with rapidly enlarging whorls; lectotype comprises about 2.5 whorls, 6.2 mm high (basal lip not preserved), 9.2 mm wide; spire low; whorl face between suture and selenizone convex in early whorls; in later whorls, wide, slightly convex ramp develops, bordered by the upper edge of selenizone that angulates whorl

face; ramp slightly concave near adapical suture and near elevated selenizone; whorl face between suture and selenizone ornamented with dense pattern of spiral threads and furrows; growth lines prosocline; abapical whorl face concave just below selenizone then convex, ornamented with spiral lirae and prosocyrt growth lines; selenizone elevated, flat, with stria-like lunulae, bordered by projecting shell margins; base convex, ornamented with spiral lirae and opisthocyrt growth lines, anomphalous; umbilical region completely covered by callus; aperture broad, ovate, oblique; inner lip with inductura.

Discussion. The lectotype is well-preserved but the shell surface is somewhat corroded so that the spiral ornament was probably more pronounced originally. The outer lip of the aperture is broken off and the inner lip is slightly crushed. *Temnotropis carinata* has a higher spire than was generally assumed by previous authors. The lectotype of *Sigaretus tenuicinctus* Klipstein (Fig. 17F–H), a younger synonym of *Temnotropis carinata*, and the specimen figured by Broili (1907, pl. 7, fig. 1) (Fig. 17I–K) give a better impression about the shell shape of *Temnotropis carinata*.

Bandel (1991, pl. 14, figs 3–4) assigned a specimen to *Temnotropis fallax*, then assigned the same specimen to *Temnotropis carinata* (Bandel 2009, pl. 8, fig. 107). We studied this specimen (NHMW 1899/0005/0025/1). It represents *Temnotropis fallax* as initially correctly identified by Bandel (1991). Bandel (1991) figured three specimens, all with the same inventory number (NHMW 1899/0005/0025/1). The other specimens are renumbered as following: NHMW 1899/0005/0025/2 is the original of Bandel (1991, pl. 14, fig. 5); NHMW 1899/0005/0025/3 is the original of Bandel (1991, pl. 14, fig. 6). The latter one (NHMW 1899/0005/0025/3) is figured here in Fig. 16D–G and represents *Temnotropis fallax* as previously identified by Bandel (1991). NHMW 1899/0005/0025/2 (Bandel 1991, pl. 14, fig. 5) is herein assigned to *Nodocingulum cirriformis* (Laube, 1868).

The specimen assigned to *Temnotropis carinata* by Zardini (1978, pl. 2, fig. 12) probably represents *Nodocingulum granulosum*. The specimen figured by Sachariewa-Kowatschewa (1962, pl. 2, figs 4–5) has a reticulate ornament and does therefore not represent *Temnotropis carinata*. *Temnotropis bicarinata* Laube, 1870 (see Fig. 18) differs from *Temnotropis carinata* by having an angulated outer basal edge, which is situated more distant from the shell axis and the lateral whorl face inclines less steeply.

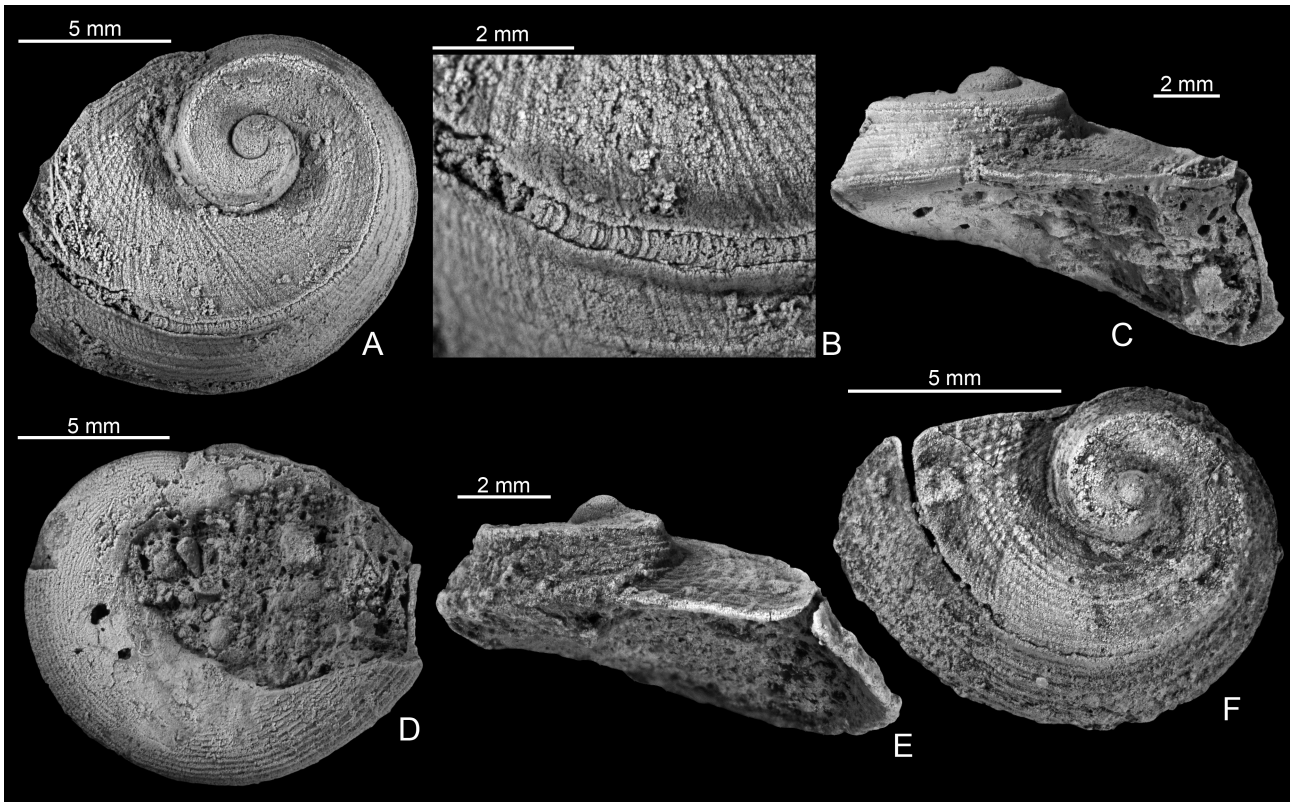

FIGURE 18. *Temnotropis bicarinata* Laube, 1870; **A–D.** NHMW 1899/0005/0024/2, St. Cassian Formation; **E–F.** NHMW 1899/0005/0024/1 (original of Bandel 1991, pl. 13, fig. 6–7), St. Cassian Formation.

***Temnotropis fuchsi* (Kittl, 1891) comb. nov.**
Fig. 19

*1891	*Gosseletina fuchsi* n. f.—Kittl, p. 206, pl. 1, fig. 22.
1978	*Gosseletina fuchsi* (Kittl)—Zardini, p. 56, pl. 40, figs 2a–d.
1991	*Euzone calypso* (Laube, 1868)—Bandel, p. 36, pl. 13, figs 1–2 (non fig. 3).

Material. NHMW 1899/0005/0100, original of Kittl (1891, pl. 1, fig. 22), herein designated as lectotype, from the St. Cassian Formation.

Discussion. *Gosseletina fuchsi* Kittl, 1891 (lectotype figured here in Fig. 19) is similar to *Temnotropis carinata* in ornamentation, early whorl morphology, growth lines and aperture morphology but differs in having more whorls, a less oblique aperture and in lacking an elevated selenizone. *Gosseletina fuchsi* does certainly not belong to *Gosseletina* (as was proposed by Kittl 1891) and is herein placed in *Temnotropis*. *Temnotropis fuchsi* (Kittl, 1891) has a much narrower, concave selenizone unlike the selenizone of *Gosseletina* which is wide and flush with the surface of the whorls to slightly convex (e.g., Batten 1966). On the ramp, the growth lines are sinuous in *Gosseletina* while they are straight prosocline in *Temnotropis fuchsi*. Moreover, *Temnotropis fuchsi* has more rapidly expanding whorls and its early whorls are identical to that of *Temnotropis carinata*.

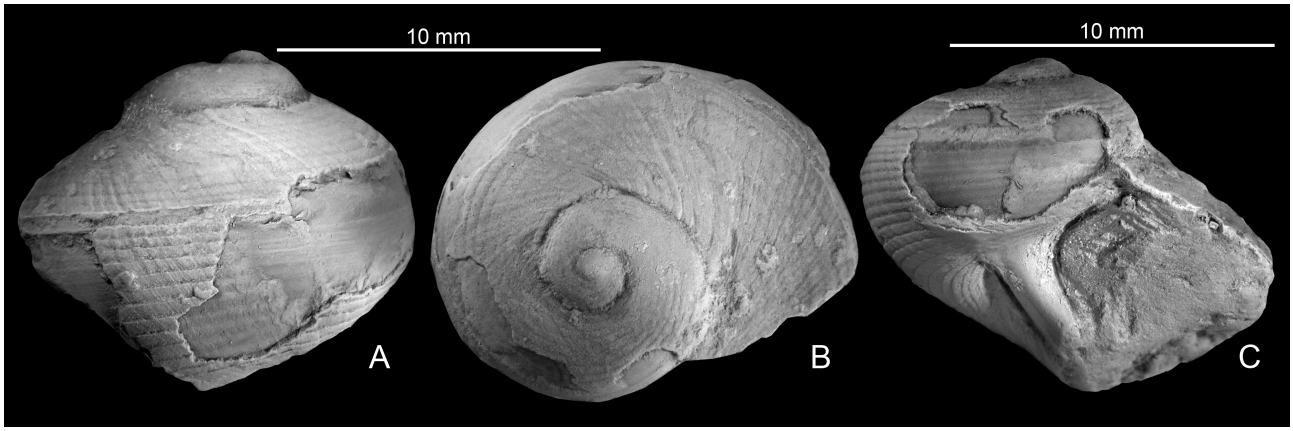

FIGURE 19. *Temnotropis fuchsi* (Kittl, 1891); **A–C.** Lectotype, NHMW 1899/0005/0100 (original of Kittl 1891, pl. 1, fig. 22), St. Cassian Formation.

Bandel (1991) illustrated two specimens and assigned them to *Euzone calypso* Laube. The first specimen (Bandel 1991, pl. 13, figs 1–2) was previously figured by Zardini (1978, pl. 40, figs 2a–d) and identified as *Temnotropis fuchsi*. Zardini's original species assignment is correct. The species identification as *Euzone calypso* of the other specimen illustrated by Bandel (1991, pl. 13, fig. 3) is correct but that species is now considered to represent a junior synonym of *Pressulasphaera lineata* (Klipstein) (see below). Although the illustration of *Pressulasphaera lineata* by Bandel (1991, pl. 13, fig. 3) is of low quality, it can be differentiated from *Temnotropis fuchsi* (Kittl, 1891) by its much lower whorl expansion rate. Neither *Temnotropis fuchsi* nor *Pressulasphaera lineata* represent *Euzone*, which has a wider, raised selenizone that is situated on mid-whorl and ornamented by prominent lunulae.

?Family Gosseletinidae Wenz, 1938

Genus *Pressulasphaera* gen. nov.
LSID. urn:lsid:zoobank.org:act:ADC59E93-C5A7-4BDF-996A-0BF57D1916EB

Type species. *Pleurotomaria pamphilus* d'Orbigny, 1850 (=*Pleurotomaria lineata* Klipstein, 1844 non Goldfuss), St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. Latin *pressula*, meaning compressed; Latin *sphaera*, meaning globe; gender feminine.

Diagnosis. Shell low-spired turbiniform; whorls elliptical in outline; whorl face convex, ornamented with spiral

cords; selenizone situated near abapical suture and above mid-whorl on last whorl, narrow, convex, ornamented with median spiral cord; anomphalous.

Discussion. *Pressulasphaera* **gen. nov.** resembles the Jurassic genus *Cryptaenia* Eudes-Deslongchamps, 1864 in shell shape and the position of the selenizone. However, members of *Cryptaenia* have an umbilical callus and a wider selenizone without a spiral ornamentation (e.g., Gründel 2011). In the other callus-bearing Jurassic genus *Ptychomphalus* Agassiz, 1837, the selenizone is covered by the succeeding whorls and can only be seen on the last whorl and the selenizone is situated on the whorl angulation. The Jurassic subgenus *Placotoma* Ferrari *et al*. 2015 (replacement name for *Discotoma*) has a lower spired, broader shell, a much narrower and concave selenizone bordered by raised shell edges, a wide umbilicus, an oblique aperture and a prominent bulge at the transition to base. The Permian genus *Plocostoma* Gemmellaro, 1889 has a narrow selenizone but with a deep groove on the inner lip and forms an angulation where the selenizone is situated (Knight 1941, p. 262). The Palaeozoic genus *Gosseletina* Fischer, 1885 has a globular shell with wider selenizone. The Devonian genus *Agniesella* Cossmann, 1909 resembles *Pressulasphaera* **gen. nov.** in whorl shape and position of the selenizone, but the selenizone of *Agniesella* is covered by subsequent whorls and its base is phaneromphalous. *Pressulasphaera* **gen. nov.** does not belong to Ptychomphalidae because its selenizone is not flush with the whorl surface. It is tentatively placed in the family Gosseletinidae because the selenizone is situated high on the whorl.

Zardini (1978) figured two specimens from the St. Cassian Formation which probably represent an undescribed species that might belong to *Pressulasphaera* **gen. nov.** (Zardini 1978, pl. 10, fig. 2 as transitional morph between "*Pleurotomaria costifer* (Koken) and *Pleurotomaria bittneri* (Kittl)"; pl. 40, fig. 9: "*Pleurotomaria bittneri* (Kittl)").

Pressulasphaera pamphilus (d'Orbigny, 1850) comb. nov.

Fig. 20

1844	*Pleurotomaria lineata*—Klipstein, p. 170, pl. 11, figs 3a–b [non *Pleurotomaria lineata* Goldfuss, 1844].
*1850	*Pleurotomaria pamphilus* d'Orb., 1847—d'Orbigny, p. 194, no. 377.
1868	*Pleurotomaria calypso* Laube—Laube, p. 58, pl. 28, fig. 2.
1891	*Gosseletina calypso* Laube sp.—Kittl, p. 206, pl. 1, fig. 18.
1894a	*Pleurotomaria lineata* Klipst.—Kittl, p. 245.
1991	*Euzone calypso* (Laube, 1868)—Bandel, p. 36, pl. 13, fig. 3 (non figs 1–2).

Material. NHMUK PI OR 35327 (original of Klipstein 1844, pl. 11, fig. 3), herein designated as lectotype of *Pleurotomaria lineata* Klipstein from the St. Cassian Formation. GBA 1868/008/0001, 4339, original of Laube (1868, pl. 28, fig. 2), herein designated as lectotype of *Pleurotomaria calypso* from the St. Cassian Formation. GBA 1894/005/0001, 4337, original of Kittl (1891, pl. 1, fig. 18) from the St. Cassian Formation.

Description. Shell low-spired turbiniform, wider than high, comprising five whorls; first whorl 0.28 mm in width; first whorls convex, low trochopiral: later whorl face convex, ornamented by closely spaced spiral cords, grooves between spiral cords and prosocyrt growth lines above and below selenizone; selenizone narrow, convex, situated near abapical suture and above mid-whorl on last whorl, ornamented by median spiral cord and weakly arched growth lines, bordered by indistinct spiral cords; mid-whorl represents periphery, where whorls embrace; base convex, anomphalous, ornamented by spiral cords; outer lip rounded, basal lip convex, inner lip convex, oblique.

Discussion. D'Orbigny (1850) replaced *Pleurotomaria lineata* Klipstein, 1844 with *Pleurotomaria pamphilus* because *P. lineata* is allegedly a junior homonym of *Pleurotomaria lineata* Goldfuss, 1844 which was assigned by d'Orbigny to the publication year 1843. However according to Quenstedt (1963, p. 18) the publication date is 1844, second half of that year (Goldfuss, p. 67, pl. 183, fig. 12). According to the publication dates given by Urlichs (2017), Klipstein's work was published in three parts, all gastropods were published in the second delivery in 1844. Hence both taxa were seemingly published in 1844 and priority is unclear. Usually, the work of Klipstein is given as 1843 which seems to be wrong.

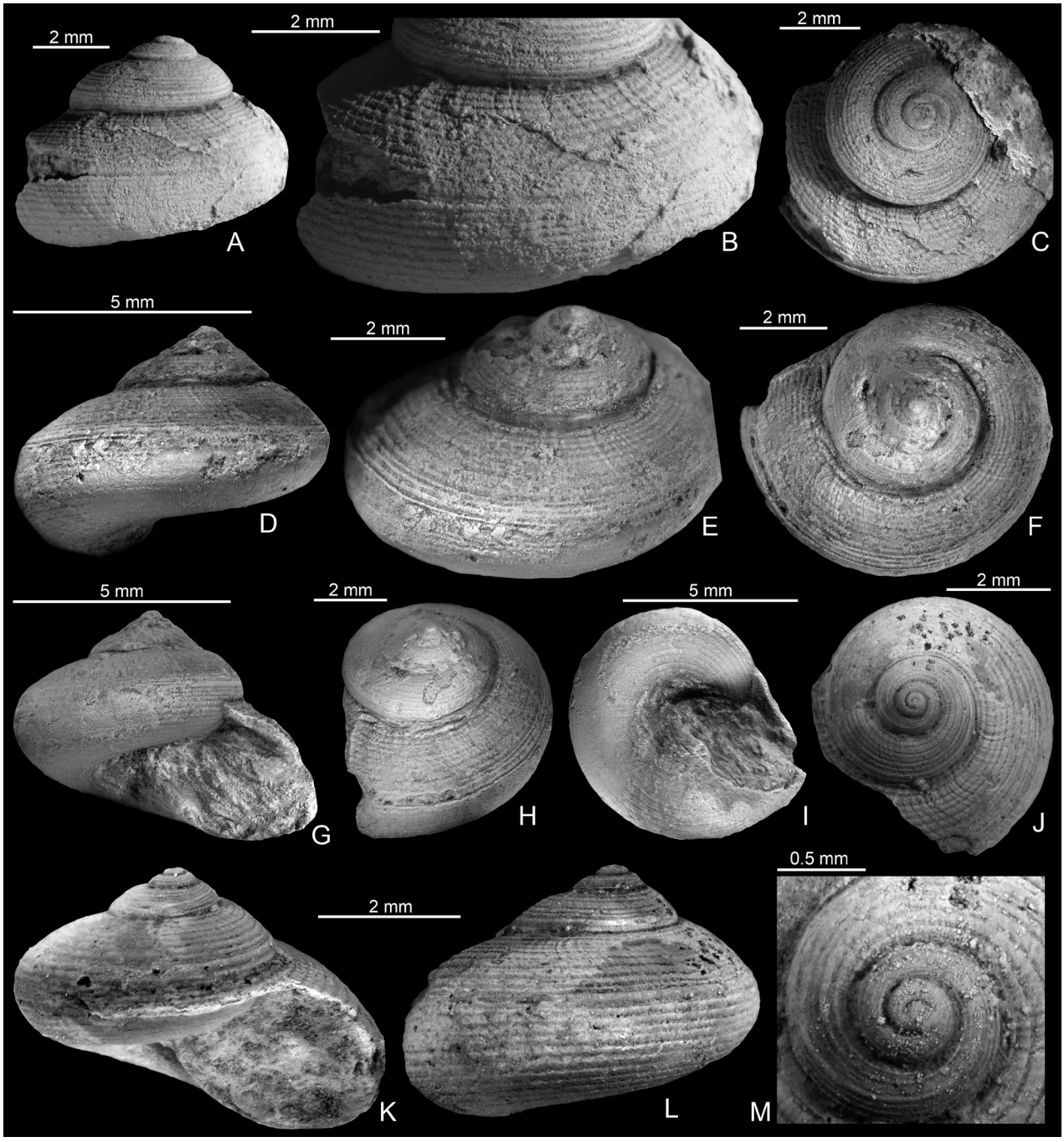

FIGURE 20. *Pressulasphaera pamphilus* (d'Orbigny, 1850); **A–C.** Lectotype, NHMUK PI OR 35327 (original of Klipstein 1844, pl. 11, fig. 3), St. Cassian Formation; **D–I.** GBA 1894/005/0001, 4337, original of Kittl (1891, pl. 1, fig. 18), St. Cassian Formation; **J–M.** Lectotype of *Pleurotomaria calypso* Laube, 1868 GBA 1868/008/0001, 4339, original of Laube (1868, pl. 28, fig. 2), St. Cassian Formation.

Superfamily Pleurotomarioidea Swainson, 1840

Family Zygitidae Cox, 1960 (in Knight et al.)

Genus *Zygites* Kittl, 1891

Type species. *Pleurotomaria delphinula* Laube, 1868 (= *Trochus subcancellatus* d'Orbigny, 1850; nom. nov. pro *Delphinula*? *cancellata* Klipstein, 1844), St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

***Zygites subcancellata* (d'Orbigny, 1850) comb. nov.**
Fig. 21

1844	*Delphinula*? *cancellata*—Klipstein, p. 203, pl. 15, fig. 15 [non *Delphinula cancellata* Gray, 1828; non *Delphinula cancellata* Kiener, 1838].
*1850	*Trochus subcancellatus* d'Orb, 1847—d'Orbigny, p. 190, no. 280.
1868	*Pleurotomaria delphinula* Laube—Laube, p. 56, pl. 27, fig. 9.
1891	*Zygites delphinula* Laube sp.—Kittl, p. 200, text-fig. 1, pl. 1, fig. 1.
1991	*Zygites delphinula* (Laube, 1868)—Bandel, p. 11, pl. 1, figs 7–8.
non 2009	*Zygites delphinula* (Laube, 1868)—Bandel, pl. 1, fig. 1.

Material. NHMUK PI OR 35833(1), figured type specimen of Klipstein (1844, pl. 15, fig. 15), herein designated as lectotype, from the St. Cassian Formation. NHMW 1899/0005/0087/1, original of Bandel (1991, pl. 1, fig. 7); NHMW 1899/0005/0088, original of Kittl (1891, text-fig. 1) from the St. Cassian Formation.

Description. Shell turbiniform, elliptical, low-spired with blunt apex; lectotype comprises 5 whorls; suture impressed; whorls well-rounded; protoconch of vetigastropod-type, consisting of less than one whorl; first three whorls planispirally coiled, fourth and fifth whorls trochospirally coiled; teleoconch ornamented with intersecting sharp, narrow, equally prominent axial ribs and spiral cords, forming cancellate pattern; whorl face above selenizone convex, ornamented with prosocyrt fold-like axial ribs (in addition to cancellate ornament); selenizone concave, depressed, formed within second whorl at mid-whorl face, high above mid-height of the whorl, gradually shifting abapically during ontogeny, situated just above abapical suture in spire whorls, at mid-height of whorl on last whorl; selenizone bordered by spiral cords, ornamented with prominent, regularly spaced, sharp lunulae; slit depth 1/8 of last whorl; base with a circumumbilical carina, otherwise rounded, widely phaneromphalous; ornament of base cancellate, of same type as on whorl face, with prominent nodes on the circumubilical carina; aperture subcircular, as wide as high, with rounded outer and basal lip, inner lip forms rounded corner where it meets base.

Discussion. D'Orbigny (1850) proposed a replacement name because he placed *Delphinula*? *cancellata* Klipstein into *Trochus* and assumed that it would have become a secondary homonym of *Trochus cancellatus* Münster, 1844 (in Goldfuss). *Delphinula*? *cancellata* Klipstein, 1844 is an invalid name anyhow because it is preoccupied by *Delphinula cancellata* Gray, 1828 and *Delphinula cancellata* Kiener, 1838.

Laube (1868) placed *Delphinula*? *cancellata* Klipstein (=*Zygites subcancellata* (d'Orbigny, 1850)) in *Pleurotomaria* and proposed *Pleurotomaria delphinula* as a replacement name without explaining the reason for this replacement. Laube could not assign *Delphinula*? *cancellata* Klipstein to *Pleurotomaria* because it would be a secondary homonym of *Pleurotomaria cancellata* Phillips, 1841. Laube could not assign *Trochus subcancellatus* d'Orbigny, 1850 (=*Delphinula*? *cancellata* Klipstein) to *Pleurotomaria* because *Pleurotomaria subcancellata* d'Orbigny, 1850 (=*Cancellotomaria subcancellata*) was preoccuppied. Kittl (1891) erected the genus *Zygites* and used Laube's (1868) replacement species name *Zygites delphinula* (Laube) for its type species (by monotypy) although *Trochus subcancellatus* d'Orbigny was available. The oldest available name for this species is *Trochus subcancellatus* d'Orbigny, 1850.

The specimen figured by Bandel (2009, pl. 1, fig. 1) as "*Zygites delphinula* (Laube, 1868)" (= *Zygites subcancellata*) represents *Nodocingulum coronatum* (Münster, 1841).

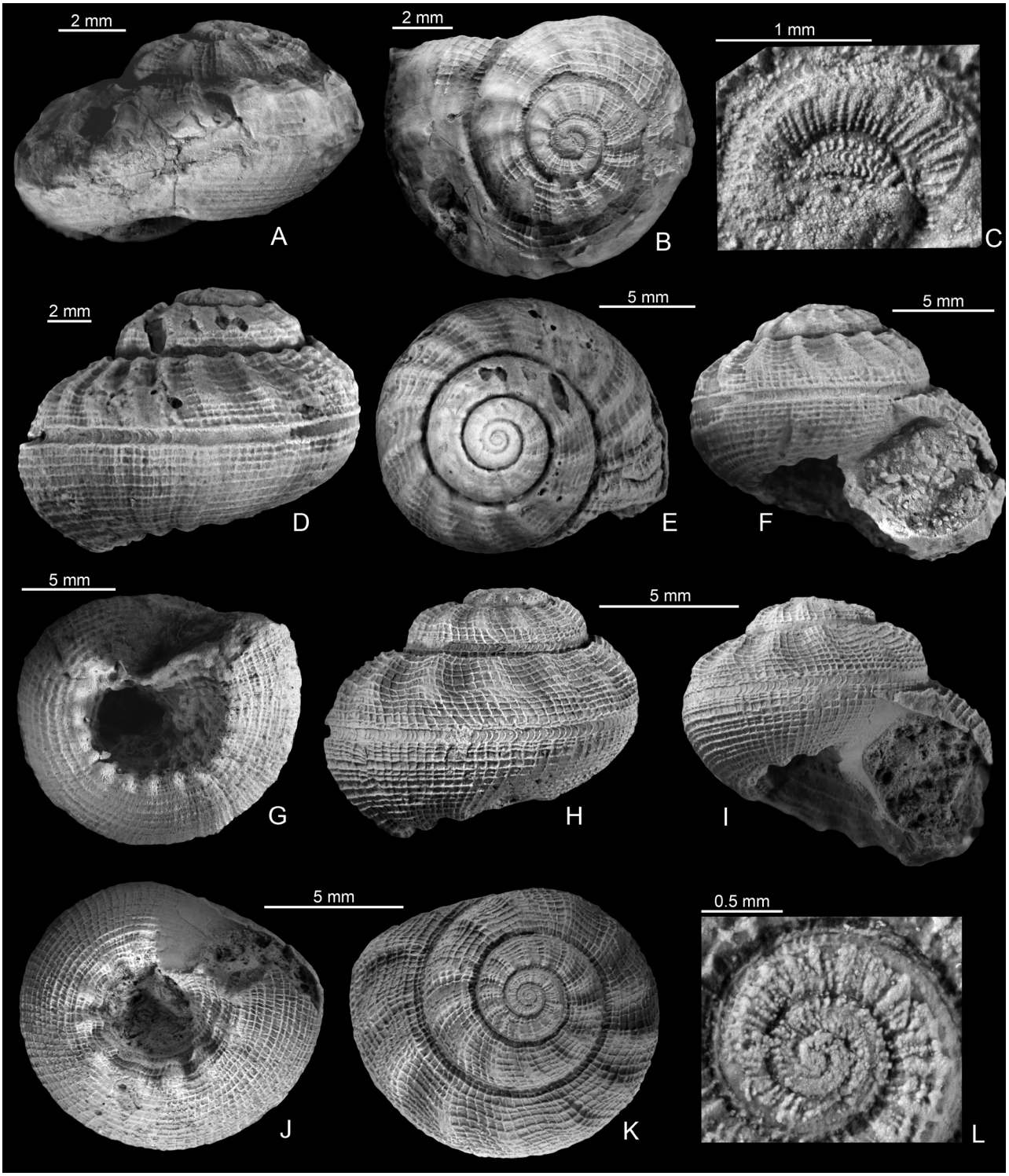

FIGURE 21. *Zygites subcancellata* (d'Orbigny, 1850); **A–C.** Lectotype, NHMUK PI OR 35833(1), original of Klipstein (1844, pl. 15, fig. 15), St. Cassian Formation; **D–G.** NHMW 1899/0005/0088, original of Kittl (1891, text-fig. 1), St. Cassian Formation; **H–L.** NHMW 1899/0005/0087/1, original of Bandel (1991, pl. 1, fig. 7), St. Cassian Formation.

Genus *Cancellotomaria* gen. nov.
LSID. urn:lsid:zoobank.org:act:A7B06D3E-FB57-4A61-8C95-8149555D2959

Type species. *Pleurotomaria subcancellata* d'Orbigny, 1850 (replacement name for *Pleurotomaria cancellata* Münster, 1841), St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. From Latin *cancello*, meaning arranged in lattice, *-tomaria* referring *Pleurotomaria*; referring a slit-band gastropod with cancellate ornament; gender feminine.

Diagnosis. Shell turbiniform, cyrtoconoid, with low-spired early whorls resulting in blunt apex; early teleoconch whorls with subsutural ramp, later whorls evenly rounded; whorls ornamented with numerous spiral and axial threads of the same strength forming a regular network without pronounced nodular intersections; selenizone above mid-whorl, narrow, with sharp lunulae; base flatly convex, narrowly phaneromphalous.

Discussion. *Trochotomaria* Conti & Fischer, 1981 (type species *T. tricarinata* Conti & Fischer, 1981, junior synonym of *T. somhegyensis* (Szabó, 1980) from the Middle Jurassic) has a similar reticulate ornament but the axial ornament is more pronounced, it has a conical shape and is not or only very slightly cyrtoconoid, the selenizone is situated low on the whorl (at least in the type species), the whorls are lower and less convex than in *Cancellotomaria* **gen. nov.** An emended diagnosis for *Trochotomaria* was provided by Szabó *et al*. (2019) who also reported several Jurassic species from Sicily. It is well possible that *Trochotomaria* is a junior synonym of *Eymarella* Cossmann, 1897; but this needs further study.

The type species of *Cancellotomaria* **gen. nov.**, *Pleurotomaria subcancellata* d'Orbigny, 1850, was placed in the Triassic genus *Euryalox* Cossmann, 1897 by Yin & Yochelson (1983a). Indeed, *Euryalox* resembles *Cancellotomaria* **gen. nov.** in the turbiniform shape, in having convex whorls and a reticulate ornament. However, in *Euryalox* the spiral cords are distinctly stronger than the axial ribs, the selenizone is generally wider, the umbilicus is much wider, and *Euraylox* species are rather large, commonly several centimeters. In the type species of *Euryalox*, *Sagana juvavica* Koken, 1896, the spiral cords are more prominent than the axial threads and axial threads pass over the spiral cords. In *Cancellotomaria subcancellata* axial and spiral ribs are equally prominent and the axial ribs do not pass over the spiral cords at intersections. *Euryalox applanatus* Nützel, Kaim & Grădinaru, 2018 from the Anisian of Romania has a narrow selenizone that is ornamented with a median spiral cord, a character which is only known from members of Palaeozoic Portlockiellidae, Phymatopleuridae and Mesozoic Pleurotomariidae but not from other *Euryalox* species. The meaning of this character remains to be discussed but is seems that *Euryalox applanatus* shows an affinity to Pleurotomariidae and might represent a new genus within Pleurotomariidae.

Cancellotomaria subcancellata (d'Orbigny, 1850) also resembles Jurassic species representing *Pleurotomaria*. The similarity between *Cancellotomaria subcancellata* and the early teleoconch of *Pleurotomaria amalthei* Quenstedt, 1857 (Nützel & Gründel 2015, pl. 1, figs G–H; pl. 2, figs A–C) is striking. However, *Pleurotomaria* species are much larger and develop a whorl angulation in later whorls, the selenizone placed below the angulation and have strong ribs or nodes on the angulation and often also on the peribasal angulation (Monari & Gatto 2013). Strong ribs or nodes and relatively large size are also shared by many members of Pleurotomariidae but not by *Cancellotomaria subcancellata*. Therefore, *Cancellotomaria subcancellata* is probably not a member of Pleurotomariidae.

Bandel (1991, 2009) placed *Cancellotomaria subcancellata* (d'Orbigny, 1850) in the genus *Dictyotomaria* Knight, 1945 which has a Carboniferous type species. He assigned *Dictyotomaria* to the family Zygitidae. The family Zygitidae was erected by Cox (in Knight *et al*. 1960) based on the genus *Zygites* Kittl, 1891, which might be closely related to *Cancellotomaria subcancellata* but it is not closely related to the Palaeozoic *Dictyotomaria*. The type species of *Dictyotomaria* (Sturgeon 1964, pl. 121, figs 6–9 for the lectotype; Knight 1945, pl. 79, figs 3a–b) possesses a wider selenizone which is located at or below mid-whorl and is bordered by distinct spiral cords (vertically (outward) projecting selenizone borders), unlike that of *Cancellotomaria subcancellata* (d'Orbigny, 1850). Moreover, *Dictyotomaria* has an almost vertical outer face and the selenizone is situated on this vertical portion and it has a rounded angulation towards the base (Knight 1945, Sturgeon 1964)—both are not the case in *Cancellotomaria subcancellata*.

We agree with Bandel (2009) that *Cancellotomaria subcancellata* is similar to the members of Zygitidae in ornamentation of whorls and the selenizone but differs in prominence of the ornamentation above and below the selenizone, trochospiral coiling of the early whorls and the position of the selenizone in later whorls. Hence, we place the new genus in Zygitidae. *Zygites* differs from the new genus by having a wider umbilicus and wavy axial ribs in addition to its cancellate fine ornamentation.

***Cancellotomaria subcancellata* (d´Orbigny, 1850) comb. nov.**
Fig. 22

1841	*Pleurotomaria cancellata*—Münster, p. 113, pl. 12, figs 16a–b [non *Pleurotomaria cancellata* Phillips, 1841].
1844	*Pleurotomaria cancellata* Münster varietas *complanata* nobis—Klipstein, p. 169, pl. 11, figs 2a–c.
1844	*Pleurotomaria cancellata* Münster varietas *elliptica* nobis—Klipstein, p. 168, pl. 10, figs 31a–b.
*1850	*Pleurotomaria subcancellata* d'Orb., 1847—d'Orbigny, p. 195, no. 396.
1868	*Pleurotomaria subcancellata* d'Orbigny—Laube, p. 80, pl. 27, fig. 1.
1891	*Pleurotomaria subcancellata* d'Orbigny—Kittl, p. 199, pl. 1, figs 20–21.
1891	*Pleurotomaria bittneri* Kittl n. f.—Kittl, p. 200, pl. 1, figs 19.
?1914	*Pleurotomaria subcancellata* d'Orb—Arthaber, p. 190.
1959	*Pleurotomaria bittneri* Kittl n. var. *alta*—Leonardi & Fiscon, pl. 1, figs 2a–b.
non 1962	*Pleurotomaria subcancellata* Münster—Sachariewa-Kowatschewa, p. 99, pl. 2, figs 12–13.
1978	*Pleurotomaria subcancellata* (Orbigny)—Zardini, p. 18, pl. 3, fig. 11; pl. 40, figs 10a–b.
1978	*Pleurotomaria subcancellata* n. f. *depressa*—Zardini, p. 18, pl. 4, fig. 1a–b.
1983a	*Euryalox subcancellata* (d'Orbigny)—Yin & Yochelson, p. 182, figs 7B–D.
1991	*Dictyotomaria subcancellata* (d´Orbigny, 1849)—Bandel, p. 7, pl. 1, figs 1–6; pl. 2, figs 3–4, 8.
2009	*Dictyotomaria subcancellata* (d´Orbigny, 1849)—Bandel, pl. 1, figs 2, 4–5 (non pl. 1, fig. 3).

Material. SNSB-BSPG AS VII 1213 (original of Münster 1841, pl. 12, figs 16a–b), herein designated as lectotype; AS VII 1214 herein designated as paralectotype from the St. Cassian Formation. NHMW 1899/0005/0094, original of Kittl (1891, pl. 1, figs 20–21) from the St. Cassian Formation. GBA 1894/005/0003, original of Kittl (1891, pl. 1, fig. 19), herein designated as lectotype of *Pleurotomaria bittneri* Kittl from the St. Cassian Formation. NHMUK PI OR 35328(1), original of Klipstein (1844, pl. 11, fig. 2), herein designated as lectotype of *Pleurotomaria cancellata* var. *complanata* Klipstein from the St. Cassian Formation. NHMUK PI OR 35329(1), original of Klipstein (1844, pl. 10, fig. 31), herein designated as lectotype of *Pleurotomaria cancellata* var. *elliptica* Klipstein from the St. Cassian Formation.

Description. Shell turbiniform, cyrtoconoid with blunt apex due to very low-spired first two to three whorls; lectotype comprises 5 whorls, 4.6 mm high, 5.4 mm wide; suture impressed; protoconch consisting of one planispiral whorl, smooth, diameter of 0.3 mm; whorl face convex, with gently inclined subsutural ramp and steeply inclined below ramp in early teleoconch whorls but more or less evenly rounded in later whorls; selenizone concave, depressed, situated below mid-whorl and somewhat above suture in early spire whorls and at mid-whorl in later whorls; selenizone bordered by spiral cords for the most part, with prominent, sharp lunulae; teleoconch ornamented with intersecting sharp, narrow axial ribs and spiral cords of about equal strength, forming a cancellate pattern; cancellate pattern below selenizone slightly finer; interspaces between axial ribs much wider than ribs; base nearly flat, convex, narrowly phaneromphalous; umbilicus encircled by an edge; base covered with numerous axial ribs and spiral cords forming cancellate ornament similar to that of whorl face; aperture slightly wider than high with convex outer and inner lip and with nearly flat basal lip.

Discussion. The lectotype designated here is well-preserved but slightly compressed axially so the last whorl seems to have a subsutural angulation, which is actually result of the deformation. *Cancellotomaria subcancellata* has a u-shaped sinus at the beginning of the teleoconch which develops rapidly into a selenizone (Bandel 1991, pl. 1, figs 3–4). The selenizone of *Cancellotomaria subcancellata* is located on the mid-whorl face of spire whorls and above mid-height of the body whorl; it is ornamented with prominent, sharp lunulae.

Klipstein (1844) mentioned two variations of *Pleurotomaria cancellata* Münster, 1841 (=*Cancellotomaria subcancellata*). Laube (1868) placed these two variations in *Pleurotomaria subcancellata* d'Orbigny (=*Cancellotomaria*). This treatment was followed by Kittl (1891), who also erected *Pleurotomaria bittneri* Kittl, 1891. This species agrees in all aspects with *Cancellotomaria subcancellata* and represents a deformed specimen of this species. This is also true for *Pleurotomaria cancellata* var. *elliptica* (Klipstein 1844, pl. 10, fig. 31a; its lectotype is figured here in Fig. 22H–I); it is slightly broader than the lectotype of *Cancellotomaria subcancellata*.

The specimen identified as *Pleurotomaria bittneri* Kittl by Zardini (1978, pl. 40, figs 9a–b) is not conspecific with *Cancellotomaria subcancellata*; it differs in having a finer ornamentation, in being more low-spired and in having the selenizone slightly above the abapical suture.

The specimen described as *Pleurotomaria bittneri* Kittl n. var. *alta* by Leonardi & Fiscon (1959, pl. 1, figs 2a–b) and the specimen described as *Pleurotomaria subcancellata* n. f. *depressa* by Zardini (1978, pl. 4, fig. 1) differ from *Cancellotomaria subcancellata* in having a more conical shell shape and an almost straight whorl face; at present we interpret this as intraspecific variability.

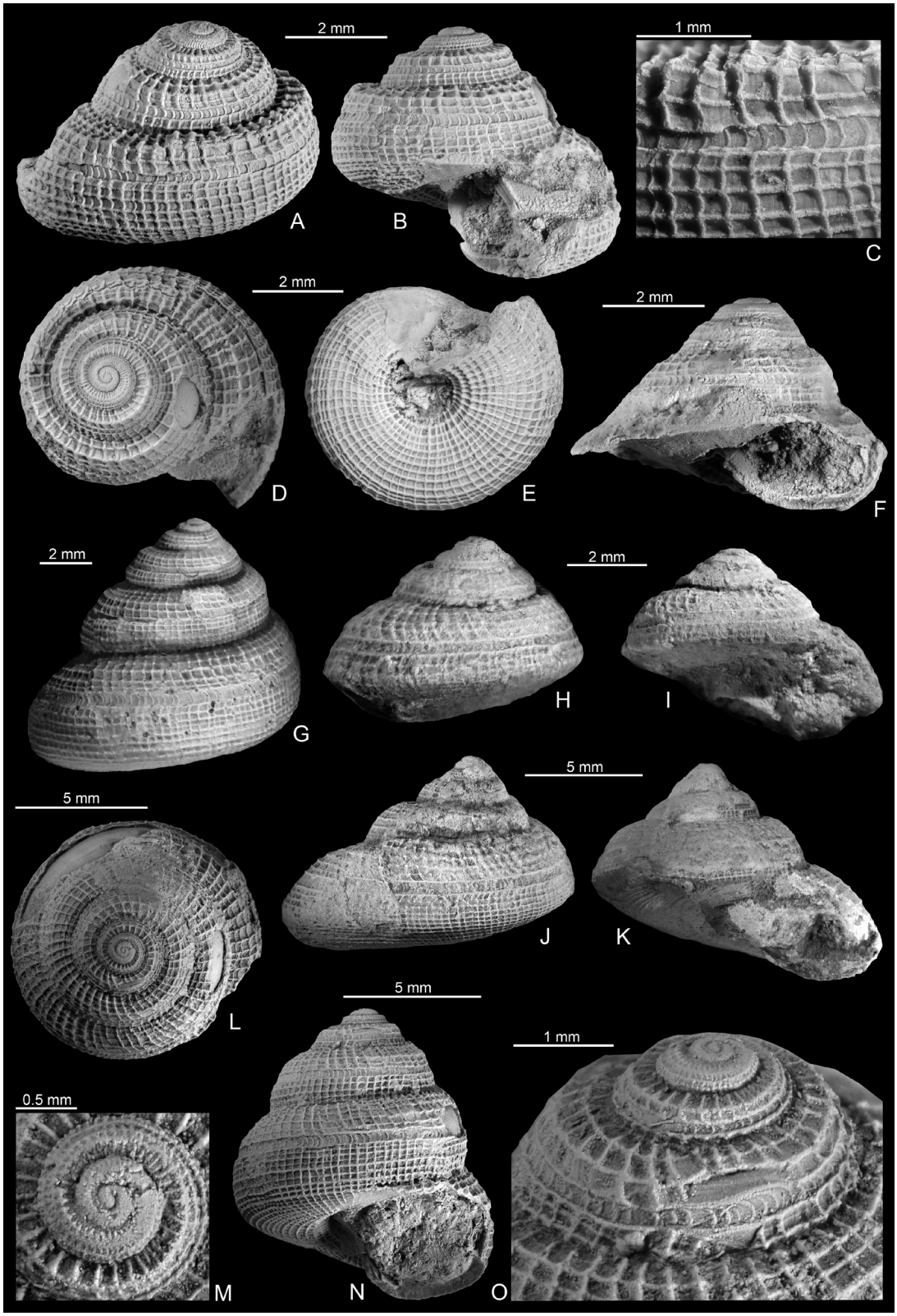

FIGURE 22. *Cancellotomaria subcancellata* (d´Orbigny, 1850); **A–E.** Lectotype, SNSB-BSPG AS VII 1213 (original of Münster 1841, pl. 12, figs 16a–b), St. Cassian Formation; **F.** Paralectotype, SNSB-BSPG AS VII 1214, St. Cassian Formation; **G.** Lectotype of *Pleurotomaria cancellata* var. *complanata* Klipstein, 1844, NHMUK PI OR 35328(1), original of Klipstein (1844, pl. 11, fig. 2), St. Cassian Formation; **H–I.** Lectotype of *Pleurotomaria cancellata* var. *elliptica* Klipstein, 1844, NHMUK PI OR 35329(1), original of Klipstein (1844, pl. 10, fig. 31), St. Cassian Formation; **J–K.** Lectotype of *Pleurotomaria bittneri* Kittl, 1891, GBA 1894/005/0003, original of Kittl (1891, pl. 1, fig. 19), St. Cassian Formation; **L–O.** NHMW 1899/0005/0094, original of Kittl (1891, pl. 1, figs 20–21), St. Cassian Formation.

The specimen figured by Sachariewa-Kowatschewa (1962, pl. 2, figs 12–13) as *Pleurotomaria subcancellata* Münster has a whorl angulation above the selenizone and the selenizone is situated low on the whorl. Therefore, this specimen does not represent *Cancellotomaria subcancellata* but rather resembles *Borestus*.

The specimen assigned to *Dictyotomaria subcancellata* by Bandel, 2009 (pl. 1, fig. 3) has an angulated whorl profile and the selenizone is situated at the angulation; it also differs in shell ornamentation and clearly does not represent *Cancellotomaria subcancellata*. Bandel's (2009) specimen probably represents *Nodocingulum granulosum* (Klipstein, 1844).

Genus *Kokenella* Kittl, 1891

Type species. *Porcellia fischeri* Hörnes, 1855, Hallstatt Limestone, Norian, Sandling near Bad Aussee, Austria; original designation.

Kokenella costata (Münster, 1841)

Fig. 23

*1841	*Schizostoma costata*—Münster, p. 106, pl. 11, fig. 6.
1850	*Porcellia costata* d'Orb., 1847—d'Orbigny, p. 195, no. 402.
1868	*Porcellia costata* Münster sp.—Laube, p. 91, pl. 28, fig. 10.
1891	*Kokenella costata* Münster sp.—Kittl, p. 177, pl. 1, figs 30–32.
1962	*Kokenella costata* Münster—Sachariewa-Kowatschewa, p. 96, pl. 1, figs 6–8, 15–18.
1978	*Kokenella costata* (Münster)—Zardini, p. 17, pl. 3, figs 7–8.
1991	*Kokenella costata* (Münster, 1841)—Bandel, p. 9, pl. 2, figs 1, 2, 5–7.
1999	*Kokenella costata* (Münster 1841)—Nützel & Senowbari-Daryan, p. 96, pl. 1, figs 1–4.
2009	*Kokenella costata* (Münster, 1841)—Bandel, pl. 1, figs 9–12.

Material. SNSB-BSPG AS VII 1495 (original of Münster 1841, pl. 11, fig. 6), herein designated as lectotype from the St. Cassian Formation. PZO 13706 from the St. Cassian Formation.

Description. Shell discoidal, dextral; whorls rounded, embracing flank of preceding whorls; lectotype has a diameter of 9.1 mm, 3.9 mm high; upper and lower umbilici of about same depth; whorl surface above and below selenizone ornamented with fine but sharp, somewhat oblique and curved axial/radial threads and numerous spiral threads forming cancellate pattern; axial threads slightly stronger than spiral threads; upper and lower side of whorls also ornamented with regular, broad, wavy axial (radial) ribs; selenizone concave, situated at periphery somewhat above mid-whorl, encompassing about 14 % of whorl height, ornamented with prominent, sharp lunulae; selenizone bordered by spiral threads; aperture oval; mid-height of aperture situated slightly below mid-height of preceding whorl.

Discussion. The lectotype is sufficiently well-preserved to characterize this species. This species has been identified correctly by most of the authors. Bandel (1991, 2009) reported the early whorls including the protoconch which is of the vetigastropod type consisting of one whorl. The early whorls are planispiral and thus Kittl (1891) and Bandel (1993a, 2009) excluded *Kokenella* from the family Porcelliidae because *Porcellia* has elevated early whorls. Bandel (2009) placed *Kokenella* in the family Zygitidae based on cancellate ornaments shared with *Zygites* and *Cancellotomaria subcancellata*. Bandel (1991) differentiated *Kokenella* from the Early Jurassic *Talantodiscus* Fischer, 1885 based on the position of the selenizone which is situated at mid-whorl face in *Kokenella* but is decentral in *Talantodiscus*. However, in some species representing *Kokenella*, the selenizone is situated at the adapical portion of the whorl (e.g., *Kokenella klipsteini* Kittl, 1891 (lectotype figured here in Fig. 24A–B), *Kokenella laubei* Kittl, 1891 (lectotype figured here in Fig. 24C–D), and *Kokenella chlathrata* Kutassy, 1937. Therefore, *Talantodiscus* and *Kokenella* cannot be separated unequivocally based on this character. In *Talantodiscus*, the selenizone is not covered by subsequent whorls and *Talantodiscus* is seeminly lacking the characteristic cancellate pattern of *Kokenella* (see Fischer & Weber 1997, fig. 5, pl. 29, figs 7, 8). In addition, the early teleoconch whorls of *Talantodiscus* is distinctly elevated and trochospiral (Monari & Gatto 2013, fig. 13). Due to morphological continuity between *Talantodiscus* and *Pleurotomaria*, Monari & Gatto (2013) suggested to consider *Talantodiscus* as synonym of *Pleurotomaria*. Based on the well-documented early teleoconchs of *Porcellia* and *Kokenella* (Bandel 1991, 1993a), we agree that *Kokenella* is not closely related to *Porcellia*.

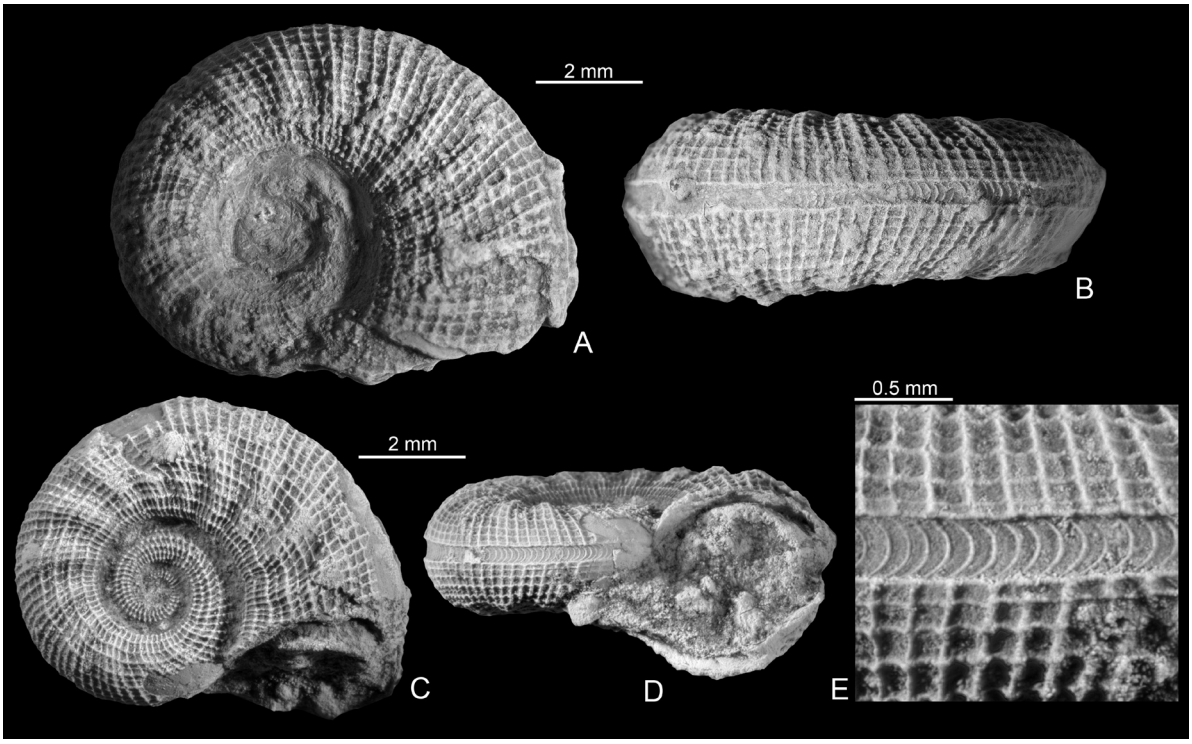

FIGURE 23. *Kokenella costata* (Münster, 1841); **A–B.** Lectotype, SNSB-BSPG AS VII 1495 (original of Münster 1841, pl. 11, fig. 6), St. Cassian Formation; **C–E.** PZO 13706, St. Cassian Formation.

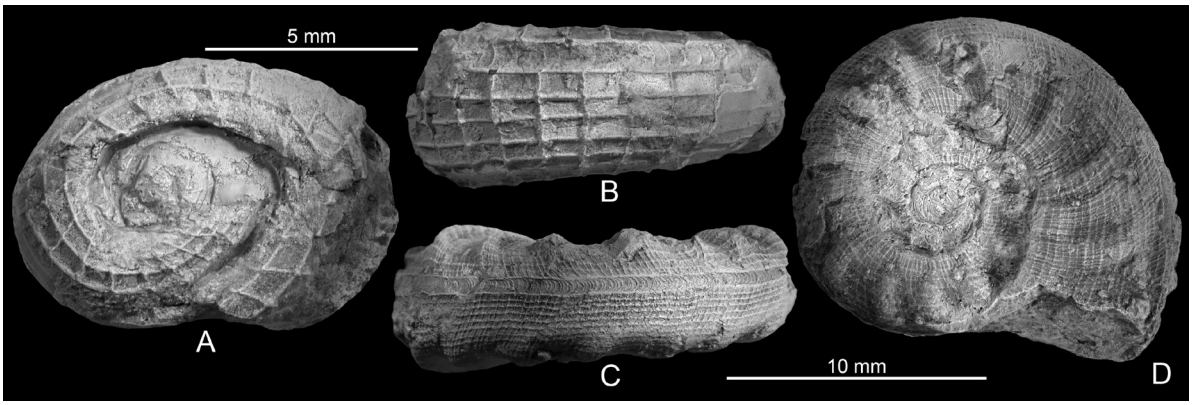

FIGURE 24. A–B. *Kokenella klipsteini* Kittl, 1891, NHMW 1899/0005/0021 (original of Kittl 1891, pl. 1, fig. 34) is designated as lectotype herein, St. Cassian Formation; **C–D.** *Kokenella laubei* Kittl, 1891, NHMW 1899/0005/0018 (original of Kittl 1891, pl. 1, fig. 33) is designated as lectotype herein, St. Cassian Formation.

Kokenella buchi (Münster, 1841)

Fig. 25

*1841	*Schizostoma buchii*—Münster, p. 105, pl. 11, figs 5a–d.
1850	*Porcellia buchii* d'Orb., 1847—d'Orbigny, p. 195, no. 401.
1891	*Kokenella buchi* Münster sp.—Kittl, p. 178, pl. 1, fig. 29.
1978	*Kokenella buchi* (Münster)—Zardini, p. 17, pl. 3, figs 9–10, 14.
?1985	*Kokenella buchi* (Münster)—Zardini, pl. 6, fig. 3.

Material. SNSB-BSPG AS VII 1494 (original of Münster 1841, pl. 11, figs 5a–d), herein designated as lectotype from the St. Cassian Formation.

Description. Shell discoidal, planispirally and dextrally coiled; lectotype has a diameter of 9.0 mm, 3.2 mm

high; lower umbilicus is deeper than the upper umbilicus; whorls rounded with convex periphery; whorl surface above and below selenizone ornamented with fine but sharp axial ribs and spiral cords, forming regular mesh-work pattern; axial ribs prosocline above and opisthocline below selenizone; axial ribs somewhat stronger and more widely spaced than spiral cords; axial ribs curving backward near selenizone; selenizone depressed, bordered by spiral cords, situated at mid-whorl, encompassing about 17 % of whorl height; lunulae sharp, prominent but weaker than axial ribs on whorl face; aperture ovate; mid-height of aperture situated slightly below mid-height of preceding whorl.

Discussion. *Kokenella buchi* differs from *Kokenella costata* in lacking broad axial (radial), wavy folds on the upper and lower side of the whorls, in having a slightly wider selenizone, more widely spaced axial ribs and fewer spiral ribs.

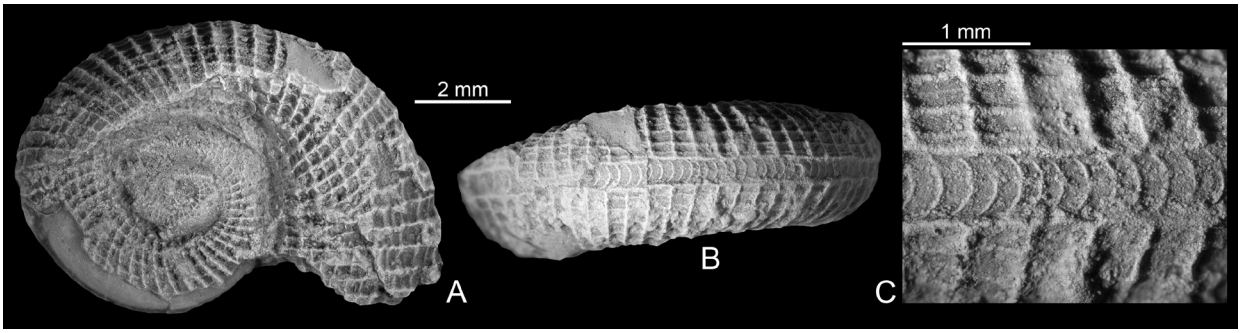

FIGURE 25. *Kokenella buchi* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1494 (original of Münster 1841, pl. 11, figs 5a–d), St. Cassian Formation.

Family Lancedelliidae Bandel, 2009

Genus *Lancedellia* Bandel, 1991

Type species. *Paleunema costata* Zardini, 1978, St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

Emended diagnosis. Shell trochiform, higher than wide; ornamented with widely spaced strong collabral ribs and spiral carina at the transition to base; selenizone narrow, sunken, situated high on the whorls, above mid-whorl; lunulae absent; base anomphalous, with axial and collabral ornament.

Discussion. Bandel (1991) erected new genus *Lancedellia* and included *Paleunema costata* Zardini, 1978 as the only species (type by monotypy). However, his description of *Lancedellia costata* as well as the diagnosis were based on another specimen that is not part of Zardini's (1978) type series of three specimens (Zardini 1978, table p. 10) and that represents a different species (see below). Hence, *Lancedellia* has a misidentified type species. In accordance with ICZN article 70.3.1., we fix *Paleunema costata* Zardini, 1978 as type species of *Lancedellia*. Bandel (1991) proposed that the specimen figured by Zardini (1978, pl. 13, fig. 5a, b) is the holotype. However, Zardini (1978) did not designate a holotype. We designate herein the specimen figured by Zardini (1978, p. 30, pl. 13, fig. 5) as lectotype and the other specimen figured by Zardini (1978, p. 30, pl. 13, fig. 4a–c) as paralectotype. Both specimens are undoubtedly conspecific and come from Misurina which is therefore the type locality of the type species. Bandel (1991, pl. 17, figs 5–8) designated a newly gathered specimen as paratype. This is an invalid action because types (lectotype or paralectotypes) can only be selected from Zardini's (1978) type series. This specimen (Bandel 1991, pl. 17, figs 5–8) is here designated as holotype of *Acutitomaria kustatscherae* **sp. nov.** (see below).

***Lancedellia costata* (Zardini, 1978)**
Fig. 26

1978	*Paleunema costata* n. sp.—Zardini, p. 30, pl. 13, figs 4–5.
non 1991	*Lancedellia costata* (Zardini, 1978)—Bandel, p. 47, pl. 17, figs 5–8.
non 2009	*Lancedellia costata* (Zardini, 1978)—Bandel, p. 9, pl. 2, figs 19–22.

Material. MPRZ 1263 M-Z (original of Zardini 1978, pl. 13, fig. 5) from Misurina, St. Cassian Formation, reposited in Cortina Museum is herein designated as lectotype. MPRZ 1262 M-Z (original of Zardini 1978, pl. 13, fig. 4) from Misurina, St. Cassian Formation, reposited in Cortina Museum is herein designated as paralectotype. MPRZ 3348 S-Z from Alpe di Specie (Seelandalpe), St. Cassian Formation, reposited in Cortina Museum. NHMW 1899/0005/0079 from the St. Cassian Formation.

Discussion. *Lancedellia costata* is a small trochiform gastropod with gradate spire, a narrow selenizone at mid-whorl face of spire whorls. The periphery is formed by a strong spiral cord low on the whorls and it has an ornament of relatively few axial ribs; the base has an ornament of few strong spiral cords. It is clear that *Lancedellia costata* (Zardini, 1978) is not conspecific with the specimens illustrated and described by Bandel (1991, 2009) as *L. costata*. Bandel's (1991, 2009) specimens represent *Acutitomaria kustatscherae* **sp. nov.** as described below. Our knowledge of *Lancedellia* is limited to Zardini's (1978) figures and the specimens figured herein (Fig. 26) which do not show the early whorls in detail. Hence, *Lancedellia* cannot be compared with other genera regarding these characters such as *Rinaldoella* Bandel, 2009 and *Lineaetomaria* **gen. nov.** Although the knowledge on *Lancedellia* is limited, we maintain Lancedelliidae Bandel, 2009 and include those genera with strong axial ribs in the early teleoconch before the onset of selenizone i.e., *Lineaetomaria* **gen. nov.**, *Euryalox* Cossmann, 1897 and *Acutitomaria* **gen. nov.**

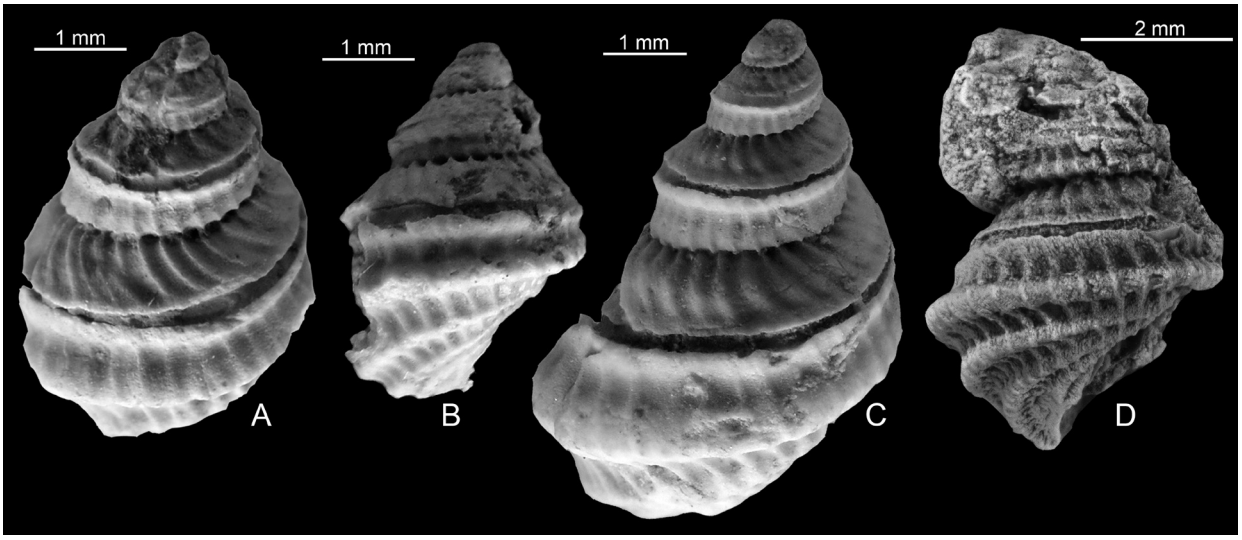

FIGURE 26. *Lancedellia costata* (Zardini, 1978); **A.** Lectotype, MPRZ 1263 M-Z (original of Zardini 1978, pl. 13, fig. 5), Misurina, St. Cassian Formation; **B.** Paralectotype, MPRZ 1262 M-Z (original of Zardini 1978, pl. 13, fig. 4) Misurina, St. Cassian Formation; **C.** MPRZ 3348 S-Z, Alpe di Specie (Seelandalpe), St. Cassian Formation; **D.** NHMW 1899/0005/0079, St. Cassian Formation.

Genus *Acutitomaria* gen. nov.
LSID. urn:lsid:zoobank.org:act:824B1A50-01B9-48E2-8CBC-4314B79E3202

Type species. *Acutitomaria kustatscherae* **sp. nov.**, Late Triassic, Early Carnian, St. Cassian Formation, Alpe di Specie (Seelandalpe), South Tyrol, N Italy.

Derivation of name. *Acuti-* Latin for acute, because of the turreted shape,—*tomaria*, for the iconic genus *Pleurotomaria*, the slit-band snails.

Diagnosis. Shell high-spired, with convex whorls; early whorls low-spired to planispiral including protoconch of the vetigastropod type of about one whorl; early teleoconch whorls ornamented with regularly spaced axial threads separated by wide interspaces; selenizone appearing late on teleoconch from u-shaped sinus, wide, situated at periphery at about mid-whorl of spire whorls; selenizone bordered by sharp, outward projecting shell edges; mature whorls ornamented with axial and few spiral threads.

Discussion. *Acutitomaria* resembles *Pseudomurchisonia* Koken, 1896 that was erected by Koken (1896) for high-spired slit-band gastropods in which the slit develops late and is rather broad. However, the generic composition of *Pseudomurchisonia* is not homogenous. *Pseudomurchisonia woehrmanni* Koken, 1896 from the Late Triassic Hallstatt Limestone forms the selenizone within the fifth whorl very high on the whorl face and remains in this

position during ontogeny (well above mid whorl of body whorl). In contrast, the type species of *Pseudomurchisonia, P. insinueta* Koken, 1896 from the Late Triassic Hallstatt Limestone of Austria, develops the selenizone very late during ontogeny (onset unclear because the early shell is broken off but probably after 7th whorl) above mid-whorl and shifts to mid-whorl later. The selenizone of *P. insinueta* Koken, 1896 is much narrower and lacks lunulae. *Pseudomurchisonia woehrmanni* Koken, 1896 shares the same shape and ornamentation in early whorls prior to the onset of the selenizone and has a similar selenizone formation as *Acutitomaria kustatscherae* **sp. nov.** (pers. obs.). Hence *Pseudomurchisonia woehrmanni* might be congeneric with *Acutitomaria kustatscherae* **sp. nov.**

According to the morphology of its type species, *Pseudomurchisonia* differs from *Acutitomaria* by having the selenizone and periphery low on the whorls of mature whorls, by lacking spiral threads on its whorl face and its selenizone is flush with the whorl surface and bordered by spiral lirae instead of sharp, vertically (outward) projecting shell edges. Moreover, the selenizone of *Pseudomurchisonia* is not distinctly concave as in *Acutitomaria*. *Pseudomurchisonia* was placed tentatively in the caenogastropod family Purpurinidae by Wenz (1938, p. 526) who erroneously considered *P. woehrmanni* to represent the type species. However, examination of the type material of *P. woehrmanni* (Geologische Bundesanstalt Vienna) and the figure of the type species given by Koken (1896, 1897) showed that it is a high-spired pleurotomarioid with the selenizone situated at the periphery. The protoconch and earliest teleoconch of the type species *P. insinueta* are unknown.

The Triassic *Murchsisonia*-like gastropod genera *Vistilia* Koken, 1896 and *Trypanocochlea* Tomlin, 1931 differ in having a convex selenizone. *Cheilotomona* has a strongly angulated periphery, its early whorls are not planispiral but heliciform and smooth (see below); its selenizone lacks distinct lunulae.

Vistilia? *paucivoluta* Yin & Yochelson, 1983a and *Cheilotomona elegans* Yin & Yochelson, 1983a might also belong to *Acutitomaria* **gen. nov.** but further study of these taxa is needed to corroborate this.

There are two Permian species that resemble *Acutitomaria kustatscherae* **sp. nov.** in spire height, whorl morphology and position of the selenizone: *Apachella exaggerata* Batten, 1989 and *Altotomaria reticulata* Ketwetsuriya *et al*., 2020. However, the early whorls prior to the onset of the selenizone of these two species do not have an axial ornament; therefore, they are not considered congeneric.

***Acutitomaria kustatscherae* sp. nov.**

Fig. 27

LSID. urn:lsid:zoobank.org:act:451F40E6-3DCC-410D-88EF-5EF68D03B033

1991	*Lancedellia costata* (Zardini, 1978)—Bandel, p. 47, pl. 17, figs 5–8.
2009	*Lancedellia costata* (Zardini, 1978)—Bandel, p. 9, pl. 2, figs 19–22.

Derivation of name. In honor of the palaeobotanist Evelyn Kustatscher for her research on the paleontology of South Tyrol and her help during field work in that area.

Holotype. NHMW 1990/0642/0000.

Paratype. MPRZ 2021 1–050.

Type locality, age, formation. Alpe di Specie (Seelandalpe), South Tyrol, Italy, Early Carnian, St. Cassian Formation.

Material. NHMW 1990/0642/0000 (original of Bandel 1991, pl.17, figs 5–8), holotype, Alpe di Specie (Seelandalpe), St. Cassian Formation. MPRZ 2021 1–050, paratype, Misurina, St. Cassian Formation.

Description. Shell high-spired, holotype consists of eight whorls, first two whorls including vetigastropod-type protoconch of less than one whorl rounded and planispirally coiled; first two teleoconch whorls ornamented with regularly spaced, parallel, prosocyrt axial threads; two spiral threads appear within the second teleoconch whorl, a third, subsutural spiral thread starts within the 3rd whorl, gradually shifting downwards, situated at middle of sutural ramp on last whorl; axial threads sharp, lamella-like, not changing in strength throughout ontogeny, losing their regular, parallel arrangement within 4th whorl, where they start to form subsutural scales; subsutural scales periodically formed by amalgamation of two axial threads just below adapical suture; selenizone develops late, after fourth teleoconch whorl, formed directly above the middle spiral thread at periphery as a result of transformation of u-shaped sinus into a slit (Bandel 1991, pl. 17, fig. 8), selenizone concave, ornamented by sharp lunulae, bordered by sharp, vertically (outward) projecting, undulating shell edges; selenizone terminates in a trema on last whorl; whorl face overall convex, slightly angulated at borders of selenizone; base convex, ornamented with sharp axial threads and one spiral thread.

Discussion. The holotype from the Seeland Alpe (Alpe di Specie) is the same specimen that was figured and described by Bandel (1991, pl. 17, figs 5–8) as *Lancedellia costata* (Zardini, 1978). However, *Acutitomaria kustatscherae* **sp. nov.** differs from *Lancedellia costata* by being more slender, by having a much wider selenizone (0.14 vs. 0.08 of height of whorl face), a rounded whorl profile whereas *L. costata* has step-like whorl profile with a vertical lower whorl face and a steep ramp. The whorl periphery of *Acutitomaria kustatscherae* **sp. nov.** is formed by the lower edge of the selenizone at about mid-whorl. However, in *Lancedellia costata* the periphery is formed by a much more prominent suprasutural cord. *Lancedellia costata* has fewer axial ribs that are more distant to each other and lacks spiral cords or threads on the ramp.

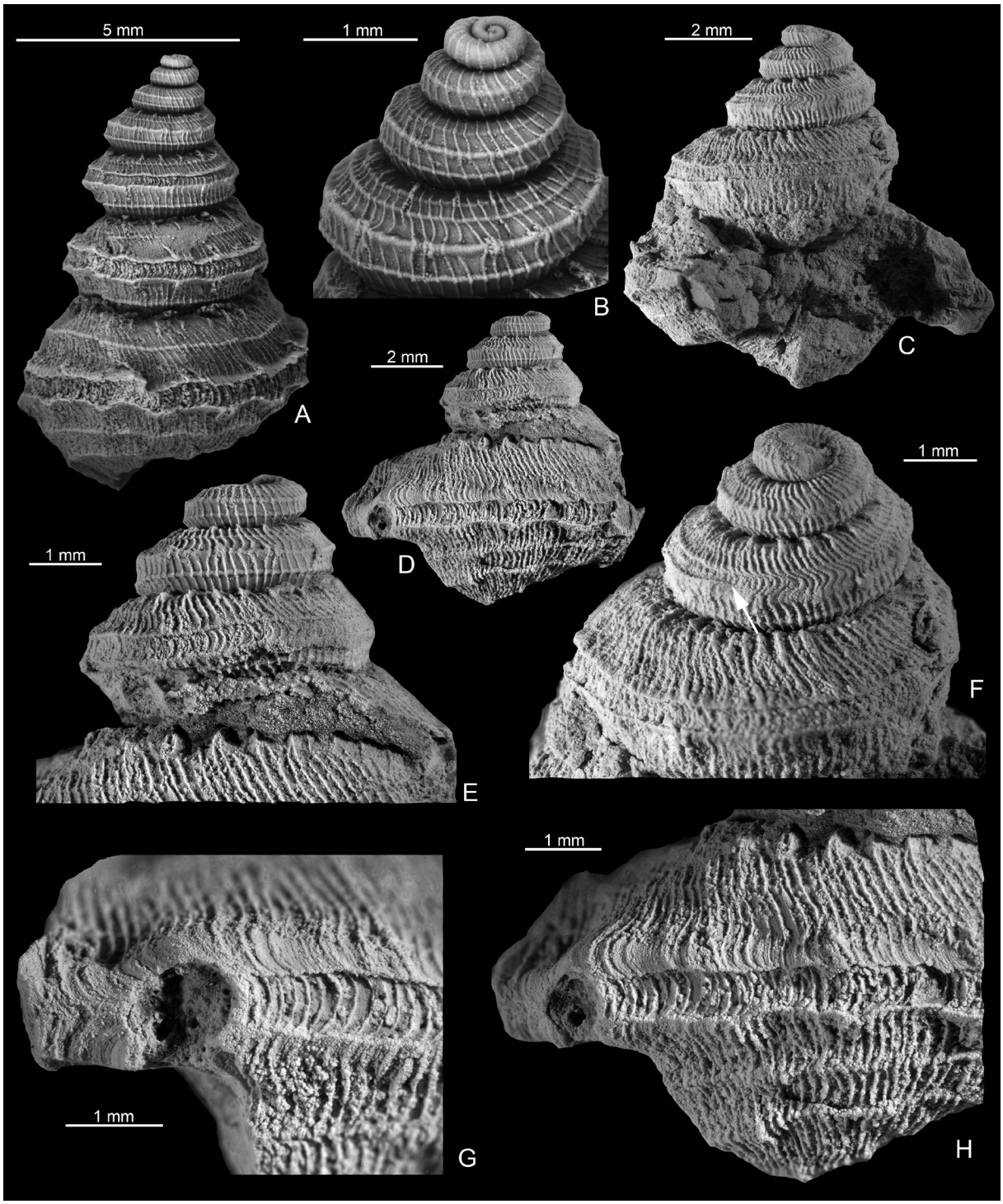

FIGURE 27. *Acutitomaria kustatscherae* **sp. nov. A–B.** Holotype, NHMW 1990/0642/0000 (original of Bandel 1991, pl.17, figs 5–8), Alpe di Specie (Seelandalpe), St. Cassian Formation. **C–H.** Paratype, MPRZ 2021 1–050, Misurina, St. Cassian Formation, arrow indicates the onset of selenizone.

Genus *Lineaetomaria* gen. nov.
LSID. urn:lsid:zoobank.org:act:355AB0E9-7CB5-4002-AAA3-43D43ACCC1D6

Type species. *Pleurotomaria decorata* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. From Latin *linea* (pl. *lineae*), meaning thread, string; *-tomaria* referring the genus *Pleurotomaria*; referring a slit-band gastropod with multiple axial threads; gender feminine.

Diagnosis. Shell trochiform, early teleoconch whorls ornamented with axial riblets; later teleoconch whorl ornamented with prominent spiral cords and oblique straight axial riblets that pass over spiral cords; selenizone situated high above mid-whorl on whorl angulation, very narrow, concave, with fine, regularly spaced lunulae; anomphalous.

Discussion. The formation and position of the selenizone, the presence of axial riblets before the onset of the selenizone and the type of reticulate ornamentation (spiral ribs pass over the axial ribs) in later whorls are similar to other lancedelliid taxa (e.g., *Euryalox juvavica*, *Acutitomaria kustatscherae* **sp. nov.**); therefore, the new genus is placed at present in the family Lancedelliidae. In contrast to *Euryalox* and *Acutitomaria* **gen. nov.**, the selenizone is much narrower in *Lineaetomaria* **gen. nov.** and *Lancedellia* and is situated higher on the whorl throughout its entire ontogeny.

***Lineaetomaria decorata* (Münster, 1841) comb. nov.**
Fig. 28

*1841	*Pleurotomaria decorata*—Münster, p. 112, pl. 12 fig. 11.
1850	*Pleurotomaria triton* d'Orb., 1847—d'Orbigny, p. 195, no. 385.
1868	*Pleurotomaria triton* d'Orbigny—Laube, p. 79, pl. 26, fig. 10.
1891	*Worthenia triton* Orbigny sp.—Kittl, p. 198, pl. 3, figs 17–18.
1891	*Worthenia duplicata* Kittl n. f.—Kittl, p. 198, pl. 3, fig. 19.

Material. SNSB-BSPG AS VII 1592 (original of Münster 1841, pl. 12, fig. 11), herein designated as lectotype from the St. Cassian Formation. GBA 1894/005/0005, original of Laube (1868, pl. 26, fig. 10) which is refigured by Kittl (1891, pl. 3, fig. 19) and herein designated as lectotype of *Worthenia duplicata* Kittl from the St. Cassian Formation. NHMW 1884/0001/0143/1 from the St. Cassian Formation. PZO 13690 from Stuores, St. Cassian Formation.

Description. Shell littoriniform; lectotype comprises about 2 preserved teleoconch whorls, 3.3 mm high, 3.0 mm wide; largest specimen comprises 5 whorls; spire gradate with angulated whorl face; protoconch less than one whorl, 0.2 mm wide, distinctly elevated, without visible ornament; teleoconch just after protoconch is without visible ornament, axial ribs start after 1.3 whorls; first two whorls convex; in third whorl, whorl face becomes angulated, selenizone appears gradually from sinus on whorl angulation, spiral cords and nodes appear; ramp slightly concave, ornamented with straight prosocline axial riblets and two spiral cords, one situated subsuturally, the other bordering selenizone; whorl face below selenizone slightly concave, ornamented with orthocline to straight prosocline axial riblets and two spiral cords: one bordering abapical edge of selenizone, other situated at mid-whorl representing periphery; axial riblets pass over spiral cords, forming short, axially elongated nodes at intersections with spiral cords; selenizone depressed, narrow, concave, situated at an angulation high above mid-whorl of body whorl, bordered by spiral cords; lunulae fine, thread-like, regularly spaced, more crowded than the axial riblets on whorl face; suture moderately deep, situated on the first basal spiral cord distant from the peripheral cord; base convex, ornamented with spiral cords and slightly opisthocyrt riblets, anomphalous; aperture as wide as high with angulated outer lip, rounded basal lip and convex columellar lip.

Discussion. *Pleurotomaria decorata* Münster, 1841 was replaced with the name *Pleurotomaria triton* by d'Orbigny (1849) in order to avoid secondary homonymy, because d'Orbigny placed *Trochus decoratus* (Hehl in Zieten, 1830, p. 46) within the genus *Pleurotomaria*. Münster's (1841) name was not a primary homonym when erected and is therefore available.

Lancedellia costata (Zardini, 1978) differs from *Lineatomaria decorata* in having a higher spire, lower whorl expansion rate and more prominent and fewer basal ribs.

Pleurotomaria minima Wanner, 1942 from the Permian of Timor resembles *Lineatomaria decorata* in whorl morphology, surface ornamentation and position of the selenizone but differs in having a much wider selenizone. *Pleurotomaria minima* Wanner, 1942 might represent the oldest representative of Lancedelliidae.

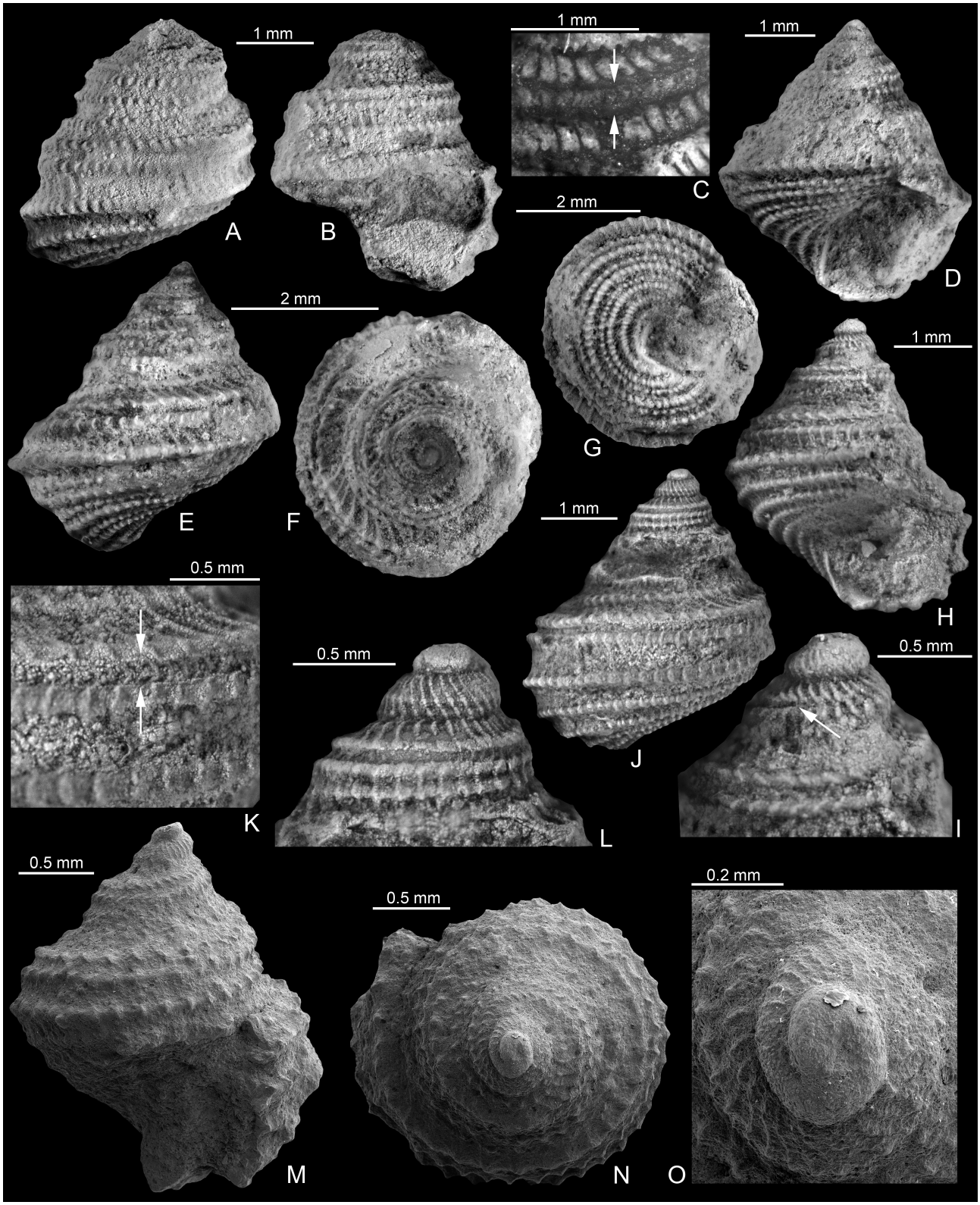

FIGURE 28. *Lineaetomaria decorata* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1592 (original of Münster 1841, pl. 12, fig. 11), St. Cassian Formation, arrows in Fig. C indicate selenizone borders; **D–G.** Lectotype of *Worthenia duplicata* Kittl, 1891, GBA 1894/005/0005, original of Laube (1868, pl. 26, fig. 10) and Kittl (1891, pl. 3, fig. 19), St. Cassian Formation; **H–L.** NHMW 1884/0001/0143/1, St. Cassian Formation, arrow in Fig. I indicates the onset of selenizone, arrows in Fig. K indicate selenizone borders; **M–O.** PZO 13690, Stuores, St. Cassian Formation, SEM image.

Genus *Euryalox* Cossmann, 1897
[nom. nov. pro *Sagana* Koken, 1896 non *Sagana* Walker, 1855 (Lepidoptera)]

Type species. *Pleurotomaria juvavica* Koken, 1894, Hallstatt Limestone, Anisian (Illyrian), Schreieralm (Hallstatt), Austria; subsequent designation by Cossmann (1897, p. 140).

***Euryalox subornatus* (d'Orbigny, 1850) comb. nov.**
Fig. 29

1844	*Trochus ornatus*—Klipstein, p. 147, pl. 9, fig. 9 [non *Trochus ornatus* Lamarck, 1804].
*1850	*Trochus subornatus* d'Orb., 1847—d'Orbigny, p. 190, no. 264.
1852	*Trochus splendidus*—Giebel, p. 533, no. 2797.
1894a	*Trochus* (?) *ornatus* Klipst. sp.—Kittl, p. 249.

Material. NHMUK PI OR 35312(1), original of Klipstein (1844, pl. 9, fig. 9), herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG 1964 XVII 194 from the St. Cassian Formation.

Description. Shell trochiform; lectotype comprising five whorls, initial whorls broken off; whorls with two angulations, one at abapical edge of selenizone, other forming outer basal edge; whorl face between angulations parallel to spire axis; whorl face ornamented with equally spaced axial riblets and three somewhat more prominent spiral cords; two spiral cords situated on whorl angulations, one bordering adapical edge of selenizone; selenizone formed late during ontogeny after second preserved whorl from u-shaped sinus between the two spiral cords; selenizone situated at mid-whorl face, above mid-height of last whorl, ornamented with regularly spaced lunulae which are as strong as axial riblets; suture impressed, situated between outer basal edge and first spiral cord on the base; base ornamented with four spiral cords and axial riblets, innermost spiral cord forming pseudoumbilicus, interspace between spiral ribs concave; aperture broken.

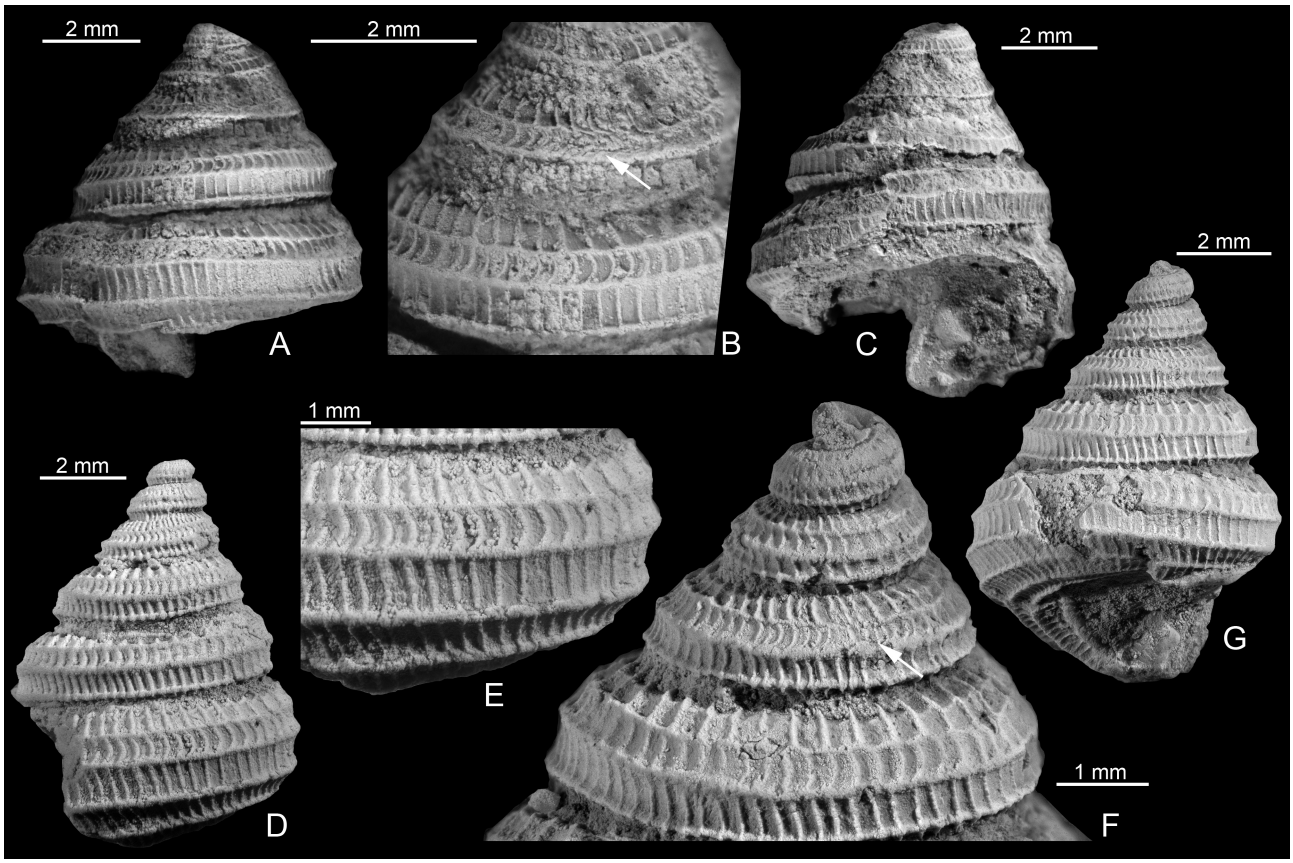

FIGURE 29. *Euryalox subornatus* (d'Orbigny, 1850); **A–C.** Lectotype, NHMUK PI OR 35312(1), original of Klipstein (1844, pl. 9, fig. 9), St. Cassian Formation, arrow indicates the onset of selenizone; **D–G.** SNSB-BSPG 1964 XVII 194, St. Cassian Formation, arrow indicates the onset of selenizone.

Discussion. Kittl (1891) suggested to use *Trochus splendidus* Giebel, 1852 for this species, if it belongs to *Trochus*. However, *Trochus subornatus* d'Orbigny, 1850 is the oldest available name. *Euryalox subornatus* (d'Orbigny, 1850) is higher-spired compared to the other members of the genus but shows the same type of selenizone development and surface ornamentation. Another species showing a similar selenizone development is *Acutitomaria kustatscherae* **sp. nov.** However, in *A. kustatscherae*, the ornamentation and the spiral ridges bordering the selenizone are sharply projecting.

Family Kittlidiscidae Cox, 1960 (in Knight et al.)

Genus *Kittlidiscus* Haas, 1953

[nom. nov. pro *Schizodiscus* Kittl, 1891, non Clarke, 1888 in Hall & Clarke]

Type species. *Pleurotomaria plana* Klipstein, 1844 (= *Pleurotomaria bronni* Klipstein, 1844), St. Cassian Formation, Carnian, South Tyrol, Italy; subsequent designation by Woodward (1892).

Discussion. *Kittlidiscus* is a poorly documented genus and only known from the St. Cassian Formation. Bandel (1991, p. 37–38; 2009, p. 15) claimed that *Kittlidiscus* lacks a nacreous shell layer and selenizone and proposed to include it within Caenogastropoda. However, Bandel (1991, 2009) did not document the shell microstructure; therefore, it is uncertain whether an inner nacreous layer is absent in *Kittlidiscus*. Here we document the selenizone and therefore keep Kittlidiscidae within the superfamily Pleurotomarioidea.

Kittlidiscus bronni (Klipstein, 1844)

Fig. 30

*1844	*Pleurotomaria bronnii*—Klipstein, p. 161, pl. 10, figs 14a–c.
1844	*Pleurotomaria plana*—Klipstein, p. 170, pl. 14, figs 30a–b.
1850	*Pleurotomaria subplana* d'Orb., 1847—d'Orbigny, p. 194, no. 378.
1850	*Turbo bronnii* d'Orb., 1847—d'Orbigny, p. 193, no. 334.
1868	*Solarium planum* Laube—Laube, p. 45, pl. 25, fig. 10.
1891	*Schizodiscus planus* Klipstein sp.—Kittl, p. 212, text-fig. 2.
non 1978	cfr. *Kittlidiscus bronni* (Klipstein)—Zardini, p. 25, pl. 9, figs 3–5.
1978	*Schizodiscus* cfr. *planus* (Klipstein)—Zardini, p. 25, pl. 9, figs 21a–c.
2009	*Kittlidiscus planus* (Klipstein, 1843)—Bandel, pl. 4, figs 55–57.

Material. NHMUK PI OR 35325(1), original of Klipstein (1844, pl. 10, fig. 14) herein designated as lectotype of *Pleurotomaria bronni* Klipstein from the St. Cassian Formation. NHMW 1865/0001/0062, original of Laube (1868, pl. 25, fig. 10) from the St. Cassian Formation. NHMW 1899/0005/0089, original of Kittl (1891, text-fig. 2) from the St. Cassian Formation.

Description. Shell low trochiform to lenticular, up to five teleoconch whorls visible; whorl face angulated below suture; angulation delimiting narrow, gently sloping sutural shelf; whorl face below sutural shelf slightly concave, moderately inclining, angulated at transition to selenizone; whorl face ornamented by widely spaced prosocline, straight to prosocyrt axial ribs, and occasionally by spiral cords, if present forming reticulate ornament with axial ribs; axial ribs more prominent on whorl face; selenizone wide, broadly concave, occupies whole lateral whorl face, parallel to shell axis, ornamented by regularly spaced asymmetric, bow-shaped lunulae; selenizone bordered by two prominent carinae, both forming whorl angulations; lower edge of selenizone represents the outer basal edge; base convex, broadly phaneromphalous, funnel-shaped, ornamented with irregularly spaced, prominent spiral ribs and fine axial threads; axial threads pass over the spiral ribs; circumumbilical carina present.

Discussion. The type material of *Pleurotomaria plana* Klipstein, 1844 was not found in the NHMUK London but we found the type material of *Pleurotomaria bronnii* Klipstein, 1844. Judging from the drawings and text provided by Klipstein (1844), these two names represent synonyms as was also pointed out by Kittl (1891) who synonymized them under the name *Schizodiscus planus*. D'Orbigny (1850) proposed a replacement name for *Pleurotomaria plana* Klipstein because he thought that the name was pre-occupied by *Pleurotomaria plana* Münster (in Goldfuss 1844, p. 76, pl. 187, fig. 4). Both taxa were proposed in the same year and priority cannot be resolved.

Therefore, we use the first available synonym which is *Pleurotomaria bronni*. *Pleurotomaria plana* Münster, 1844, probably represents *Bathrotomaria*.

The early whorls of *Kittlidiscus bronni* are generally not well preserved but preserved parts show a single peripheral keel before the onset of the selenizone. The selenizone appears just above the peripheral keel so that the peripheral keel represents the lower border of the selenizone. The upper border of the selenizone shifts abaxially within a half whorl (Bandel 2009, pl. 4, fig. 57).

Kittl's specimen (1891, p. 212, text-fig. 2 as "*Schizodiscus planus*"; refigured here in Fig. 30D–F) is ornamented with spiral ribs in contrast to the original specimen figured by Laube (1868, pl. 25, fig. 10; refigured here in Fig. 30G–I). At present, this difference is regarded as an intraspecific variation.

The specimens figured by Zardini (1978, pl. 9, figs 3–5) as *Kittlidiscus bronni* have nodes on the circumumbilical carina, which are absent in *Kittlidiscus planus* and it does not possess a selenizone; therefore, these specimens are not conspecific. These specimens represent *Faloriella cortinense* Bandel, 1992 as already indicated by Bandel (1992, p. 42).

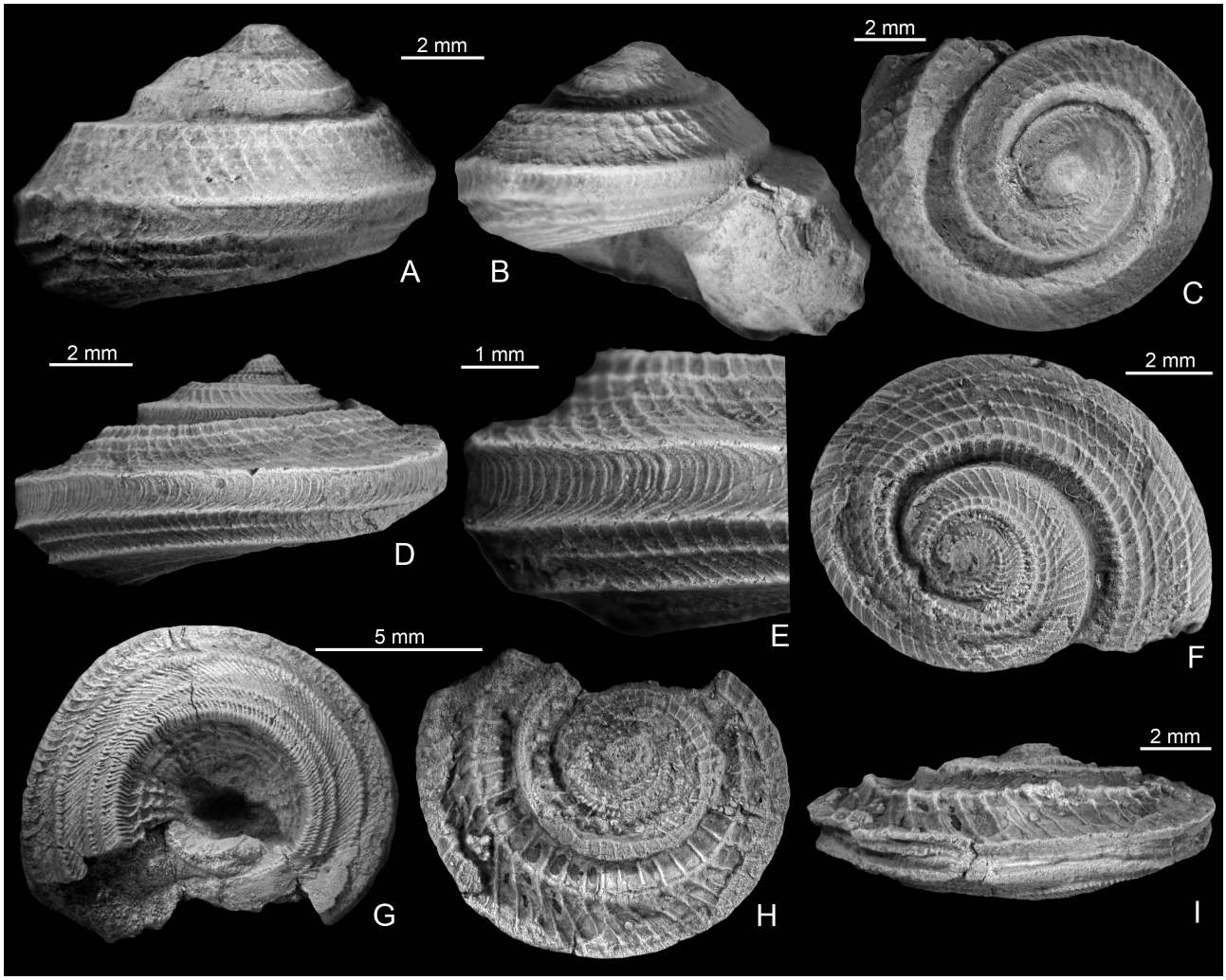

FIGURE 30. *Kittlidiscus bronni* (Klipstein, 1844); **A–C.** Lectotype, NHMUK PI OR 35325(1), original of Klipstein (1844, pl. 10, fig. 14), St. Cassian Formation; **D–F.** NHMW 1899/0005/0089, original of Kittl (1891, text-fig. 2), St. Cassian Formation; **G–I.** NHMW 1865/0001/0062, original of Laube (1868, pl. 25, fig. 10), St. Cassian Formation.

***Kittlidiscus substriatus* (Klipstein, 1844) comb. nov.**
Fig. 31

*1844	*Pleurotomaria substriata*—Klipstein, p. 162, pl. 10, figs 15a–c.
1850	*Turbo substriatus* d'Orb., 1847—d'Orbigny, p. 193, no. 335.

1891 *Schizodiscus planus* var. *elevata* Kittl—Kittl, p. 212, text-fig. 3.
1894a *Worthenia* (?) *substriata* Klipst. sp.—Kittl, p. 244.
non 1991 *Pseudoschizogonium elevatum* (Kittl, 1891) n. sp.—Bandel, p. 37, pl. 13, figs 4–5; pl. 17, fig. 3.
non 2009 *Pseudoschizogonium elevatum* (Kittl, 1891)—Bandel, pl. 3, figs 42–45; pl. 4, figs 46–49.
non 2015 *Pseudoschizogonium elevatum*—Hausmann & Nützel, figs 5C1–2.

Material. NHMUK PI OR 35326(1), original of Klipstein (1844, pl. 10, fig. 15) herein designated as lectotype of *Pleurotomaria substriata* from the St. Cassian Formation. NHMW 1899/0005/0092, original of Kittl (1891, text-fig. 3) herein designated as lectotype of *Schizodiscus planus* var. *elevata* Kittl from the St. Cassian Formation.

Description. Shell low-spired trochiform, up to four teleoconch whorls preserved; whorl face with very narrow sutural shelf; suture incised; whorl face below sutural shelf concave, inclined at an angle of approximately 30°–40°, angulated at transition to selenizone; whorl face ornamented with equally spaced axial and spiral ribs, which form reticulate ornament, axial ribs straight prosocyrt; selenizone wide, concave, occupies whole lateral whorl face, lies parallel to shell axis, ornamented by regularly spaced asymmetric lunulae; zenith of lunulae adapically situated; selenizone bordered by two prominent carinae, both form whorl angulations; whorl face below selenizone very narrow, facing abapically, ornamented with axial threads, which are as fine as lunulae but less frequent than lunulae; base convex, broadly phaneromphalous, ornamented with regularly spaced, prominent spiral ribs and fine axial threads; interspace between spiral ribs concave, axial threads pass over spiral ribs; circumumbilical carina present.

Discussion. Bandel (1991, 2009) attributed several specimens to *Kittlidiscus elevatus*, which he assigned to genus *Pseudoschizogonium*. The specimen originally figured by Bandel (1991, pl. 13, figs 4–5; pl. 17, fig. 3) represents *Pseudoananias subgranulata* (Münster, 1841), while the original of Bandel (2009, pl. 3, figs 42–45; pl. 4, figs 46–47) represents *Nodocingulum coronatum* (Münster, 1841) and the specimen figured in Bandel (2009, pl. 4, figs 48–49) represents *Bandelastraea* (see discussion on *Nodocingulum muensteri* below). Hausmann & Nützel (2015, figs 5C1–2) figured one specimen and assigned it to *Pseudoschizogonium elevatum*, which represents *Nodocingulum granulosum* (Klipstein, 1844).

Kittlidiscus substriatus resembles *Kittlidiscus bronni* in ornamentation and general whorl profile. *K. substriatus* differs from *K. bronni* in having a distinctly higher spire, narrower and more deeply concave ramp below sutural shelf.

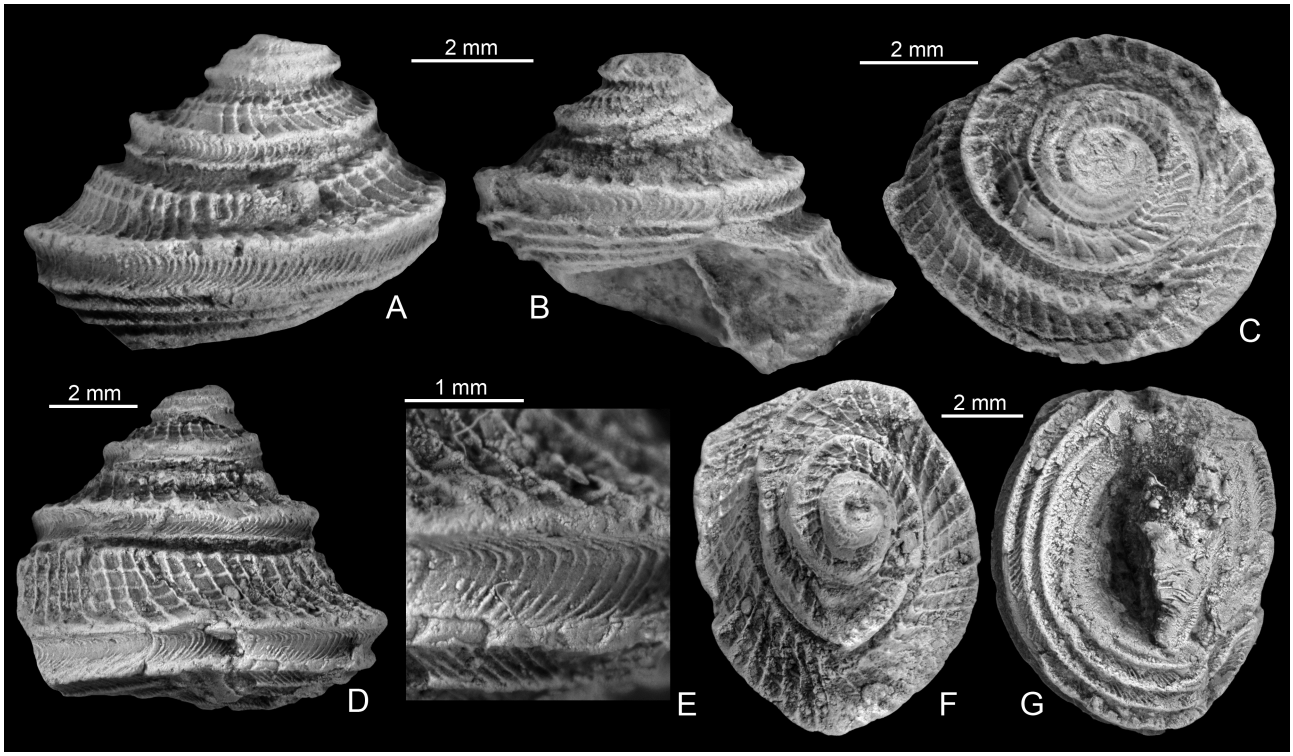

FIGURE 31. *Kittlidiscus substriatus* (Klipstein, 1844); **A–C.** Lectotype, NHMUK PI OR 35326(1), original of Klipstein (1844, pl. 10, fig. 15), St. Cassian Formation; **D–G.** Lectotype of *Schizodiscus elevata* Kittl, 1891, NHMW 1899/0005/0092, original of Kittl (1891, text-fig. 3), St. Cassian Formation.

Family Stuorellidae Bandel, 2009

Discussion. Stuorellidae are composed of *Stuorella* Kittl, 1891 and *Codinella* Kittl, 1899, both with a Triassic type species, and *Ramusotomaria* Szabó *et al*. 2019, with a type species from Early Jurassic (Toarcian). In addition, one *Stuorella* specimen was reported from Cretaceous deposits of Spain (Kiel & Bandel 2000).

When Bandel (2009) introduced the family Stuorellidae, he put the emphasis on the general shell shape. The same general shell shape can be exhibited by members of distant families due to convergence in morphology (e.g., wortheniform shells present in the eotomariid *Ananias*, the phymatopleurid *Worthenia* and the raphistomellid *Sisenna*). Bandel (2009) compared *Stuorella* with the Permian *Glyptotomaria* Knight, 1945 and Jurassic *Pyrgotrochus* Fischer, 1885. *Stuorella* is very similar to the Carboniferous genus *Glyptotomaria* Knight, 1945 in whorl and selenizone morphology. The early ontogenetic development of *Glyptotomaria* is not well known but it is without doubt closely related to *Dictyotomaria* and therefore represents Phymatopleuridae (Karapunar *et al*. in press). Members of Phymatopleuridae Batten, 1956 form the selenizone earlier during ontogeny (within the second or third whorl) and their selenizone is ornamented with distinct lunulae.

The selenizone starts much earlier in *Pyrgotrochus* than in *Stuorella.* The early ontogenetic development of *Pyrgotrochus* is shared by other members of the family Pleurotomariidae (i.e., selenizone formation from a u-shaped sinus within the first or second whorl and the selenizone is ornamented with distinct lunulae; e.g., Monari *et al*. 2017). The ornamentation of the whorl face of late whorls and late selenizone of *Pyrgotrochus* is also shared by other Pleurotomariidae. The general shell shape of *Glyptotomaria*, *Stuorella* and *Pyrgotrochus* is an example of convergence in shell morphology in three different families (see also Karapunar *et al*. in press).

The selenizone of members of the family Stuorellidae appears very late (after the 4th whorl). This character unites *Stuorella* and *Codinella* apart from their high number of whorls and conical shell shape. *Ramusotomaria* Szabó *et al*. 2019 shares the general shell shape with *Stuorella* and *Codinella* but this might be as a result of convergence as well (see above). *Ramusotomaria* resembles the Triassic genus *Tahua* Begg & Grant-Mackie, 2003 in overall shell morphology, whorl profile, growth lines, position of selenizone and absence of lunulae. Therefore, *Ramusotomaria* might represent a younger synonym of *Tahua* and hence belong to the family Pleurotomariidae. The early ontogenetic development of *Ramusotomaria* needs to be documented to better understand its relationship to other taxa and to understand which family it belongs to.

The type material of *Stuorella salisburgensis* Schnetzer, 1934 from the Anisian of Austria is reposited in the BSPG (SNSB-BSPG AS XXXIV 557) and studied by the authors. It is removed from the *Stuorella* due to its angulated whorl profile and its convex selenizone and is herein placed to *Vistilia* Koken, 1896.

Genus *Stuorella* Kittl, 1891

Type species. *Trochus subconcavus* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; by monoytpy.

Remarks. The genus *Stuorella* is characterized by its conical, trochiform, occasionally cyrto- to coeloconoid shape, very low whorls, a narrow selenizone and a flat to concave base. The ornamentation of whorls and selenizone are used herein to differentiate *Stuorella* species from the St. Cassian Formation. Having a cyrtoconoid to coeloconoid shape (e.g., Bandel 1991, pl. 9, figs 7–8) is regarded herein as result of intraspecific variation. Here, we report *S. subconcava*, *S. tricarinata*, and *S. tofanae*. In addition, *Stuorella costalaricensis* Leonardi & Fiscon, 1959 (Zardini 1978, pl. 7, figs 1–2) has been reported from the St. Cassian Formation.

***Stuorella subconcava* (Münster, 1841)**
Fig. 32

*1841	*Trochus subconcavus*—Münster, p. 107, pl. 11, figs 13a–b.
1844	*Trochus maximiliani leuchtenbergensis*—Klipstein, p. 147, pl. 9, figs 8a–b.
1850	*Trochus subconcavus* Münster, 1841—d'Orbigny, p. 189, no. 241.
1850	*Trochus maximiliani leuchtenbergensis* Klipstein, 1844—d'Orbigny, p. 190, no. 267.

1870 *Trochus subconcavus* Münster—Laube, p. 32, pl. 33, fig. 6.
1891 *Stuorella subconcava* Münster sp.—Kittl, p. 210, pl. 4, figs 2–4.
1959 *Stuorella subconcava* (Münster)—Leonardi & Fiscon, p. 11, pl. 1, figs 12a–b.
?1962 *Stuorella subconcava* Münster—Sachariewa-Kowatschewa, p. 101, pl. 3, figs 14; pl. 4, 14–15.
non 1978 *Stuorella subconcava* (Münster)—Zardini, p. 22, pl. 7, figs 3–4; pl. 40, fig. 11.
1991 *Stuorella subconcava* (Münster, 1841)—Bandel, p. 26, pl. 10, fig. 1 (non pl. 9, figs 7–8; pl. 10, figs 2–5, 7).
non 2009 *Stuorella subconcava* (Münster, 1841)—Bandel, pl. 1, figs 13–15; pl. 2, figs 16–18.

Material. SNSB-BSPG AS VII 1226 (original of Münster 1841, pl. 11, figs 13a–b), herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG AS VII 1227 (a poorly preserved *Stuorella* specimen from the Münster collection) from the St. Cassian Formation. NHMW 1899/0005/0109/1, 1899/0005/0109/2 from the St. Cassian Formation. NHMUK PI OR 35290(1), original of Klipstein (1844, pl. 19, fig. 8), herein designated as lectotype of *Trochus maximilianileuchtenbergensis* Klipstein, 1844 from the St. Cassian Formation.

Description. Shell conical, slightly coeloconoid; lectotype comprises 8 preserved teleoconch whorls, 8.6 mm high, 8.2 mm wide; whorls very low, slowly increasing in height, slightly subimbricate; suture slightly incised; whorls ornamented with regularly spaced orthocline, fold-like axial ribs and spiral threads; narrow whorl face below selenizone bearing short axial ribs so that this zone appears as convex bulge; whorl face above selenizone slightly convex; selenizone depressed, bordered by vertical (outward) projections of shell, ornamented with regularly spaced, spirally elongated, strong nodes, which are less frequent than axial ribs; selenizone narrow, width about 14 % of whorl height, situated just below mid-whorl so that adapical edge of selenizone represents mid-height of whorl face; base concave with angular transition to whorl-face, smooth, narrowly phaneromphalous; aperture subtrapezoidal.

Discussion. The lectotype is well-preserved although covered with fine sedimentary crusts. The identity of this characteristic species is beyond doubt. We also illustrate one specimen from the NHMW collection (Fig. 32C–D) which is better preserved and shows the ornamentation in great detail. The lectotype has been figured by Bandel (1991, pl. 10, fig. 1) but this illustration is of poor quality. The specimens illustrated by Bandel (2009, pl. 1, figs 14–15; pl. 2, figs 16–17) as *Stuorella subconcava* are weakly ornamented and lack the strong ribs and nodes on the selenizone. They certainly do not represent *S. subconcava* but might belong to *Stuorella tofanae* Leonardi & Fiscon, 1947.

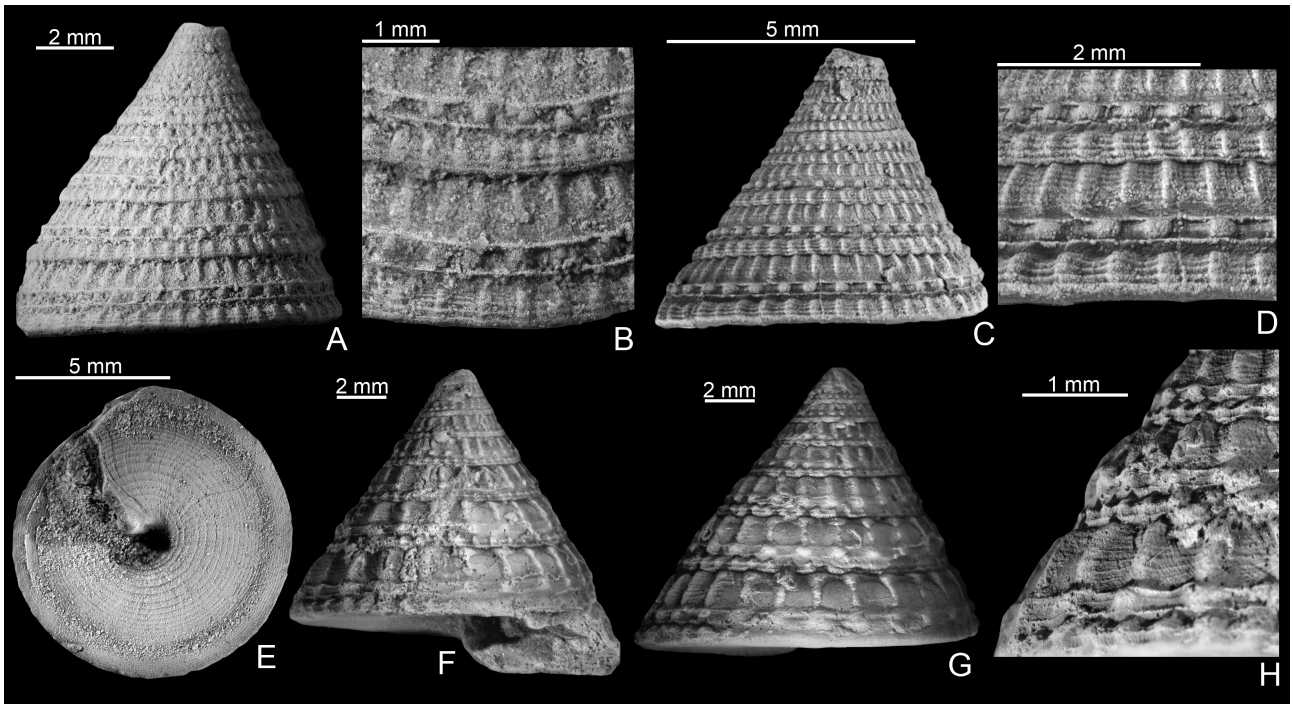

FIGURE 32. *Stuorella subconcava* (Münster, 1841); **A–B.** Lectotype, SNSB-BSPG AS VII 1226 (original of Münster 1841, pl. 11, figs 13a–b), St. Cassian Formation; **C–D.** NHMW 1899/0005/0109/1, St. Cassian Formation; **E.** NHMW 1899/0005/0109/2, St. Cassian Formation; **F–H.** Lectotype of *Trochus maximiliani leuchtenbergensis* Klipstein, 1844, NHMUK PI OR 35290(1), original of Klipstein (1844, pl. 19, fig. 8), St. Cassian Formation.

The specimens assigned to *Stuorella subconcava* by Zardini (1978, pl. 7, figs 3–4; pl. 40, figs 11a–b) and by Bandel (1991, pl. 9, figs 7–8) lack prominent knobs on the selenizone. Thus, these specimens are misidentified. They represent *Stuorella tricarinata* (Klipstein, 1844).

The juvenile specimen illustrated as "cfr. *Stuorella tofanae* (Leonardi-Fiscon)" by Zardini (1978, pl. 6, fig. 18) was later placed in *Stuorella subconcava* by Bandel (1991, pl. 10, fig. 2). This juvenile specimen and other juvenile specimens that were placed in *Stuorella subconcava* by Bandel (1991, pl. 10, figs 3–5, 7; 2009, pl. 1, fig. 13) have irregular and less prominent axial ribs than the lectotype of *Stuorella subconcava.* Therefore, Bandel's (1991) species identification of these juvenile specimens is doubtful.

Stuorella tricarinata (Klipstein, 1844) comb. nov.

Fig. 33

*1844	*Trochus tricarinatus*—Klipstein, p. 148, pl. 9, figs 10a–c.
1978	*Stuorella subconcava* (Münster)—Zardini, p. 22, pl. 7, figs 3–4; pl. 40, fig. 11.
1991	*Stuorella subconcava* (Münster, 1841)—Bandel, p. 26, pl. 9, figs 7–8 (non pl. 10, figs 1–5, 7).

Material. NHMUK PI OR 35291(1), original of Klipstein (1844, pl. 9, fig. 10), herein designated as lectotype of *Trochus tricarinatus* Klipstein from the St. Cassian Formation. NHMW 2019/0177/0019 Carnian Raibl Formation, Seiser Alm, Italy. NHMW 1990/0833/0000/1 from St. Cassian Formation. MPRZ 2021 1–046, PZO 13682 from Misurina, St. Cassian Formation.

Description. Shell conical; lectotype comprises five preserved teleoconch whorls; whorls very low and slowly increasing in height, slightly subimbricate; suture incised; whorl face above selenizone convex, ornamented with regularly spaced subsutural knobs, spiral threads and oblique prosocyrt collabral threads; spiral and collabral threads of equal strength, forming a reticulate pattern; selenizone depressed, bordered by vertical (outward) shell projections, ornamented with thread-like lunulae; selenizone width about 18 % of whorl height, situated just below mid-whorl so that adapical edge of selenizone represents mid-height of whorl face; whorl face below selenizone ornamented with prosocyrt collabral threads and spiral threads, spiral groove just below selenizone and prominent rounded basal carina, representing whorl periphery; base flatly concave, with faint spiral bands, narrowly phaneromphalous; aperture subtrapezoidal.

Discussion. *Trochus tricarinatus* Klipstein, 1844 was considered to represent a synonym of *Ziziphinus semipunctatus* (Braun in Münster, 1841, p. 107, pl. 11, fig. 15) by Giebel (1852) and Kittl (1894a). However, the study of Klipstein's (1844) type material does not corroborate this synonymization.

In the lectotype (Fig. 33A–D), the collabral threads are more prominent and the whorl profile is more gradate than in other specimens that are regarded as conspecific (Zardini 1978, pl. 7, figs 3–4, pl. 40, fig. 11; Bandel 1991, pl. 9, figs 7–8). Unlike *Stuorella subconcava*, *S. tricarinata* (Klipstein, 1844) develops prominent subsutural knobs rather than axially elongated ribs and it lacks nodes on the selenizone.

Stuorella tofanae Leonardi & Fiscon, 1947

Fig. 34

*1947	*Stuorella* n. sp. *tofanae*—Leonardi & Fiscon, p. 45, pl. 1, figs 6–7.
1959	*Stuorella* n. sp. *tofanae*—Leonardi & Fiscon, p. 12, pl. 1, figs 13–14.
1978	*Stuorella tofanae* (Leonardi & Fiscon)—Zardini, p. 22, pl. 6, figs 15–17.
1978	cfr. *Stuorella tofanae* (Leonardi & Fiscon)—Zardini, p. 22, pl. 6, fig. 18.
1978	*Stuorella antecedens* (Kittl)—Zardini, p. 22, pl. 7, fig. 5.
1991	*Stuorella subconcava* (Münster, 1841)—Bandel, p. 26, pl. 10, figs 2–5, 7 (non pl. 9, figs 7–8; pl. 10, fig. 1).
1991	*Stuorella toffanae* Leonardi & Fiscon, 1959—Bandel, p. 26, pl. 10, fig. 6.
1991	*Stuorella costalaricensis* Zardini, 1978—Bandel, p. 27, pl. 10, fig. 8, pl. 11, figs 1–4 [non *Stuorella costalaricensis* Leonardi & Fiscon, 1947].
2009	*Stuorella subconcava* (Münster, 1841)—Bandel 2009, pl. 1, figs 13–15; pl. 2, figs 16–17, 18.

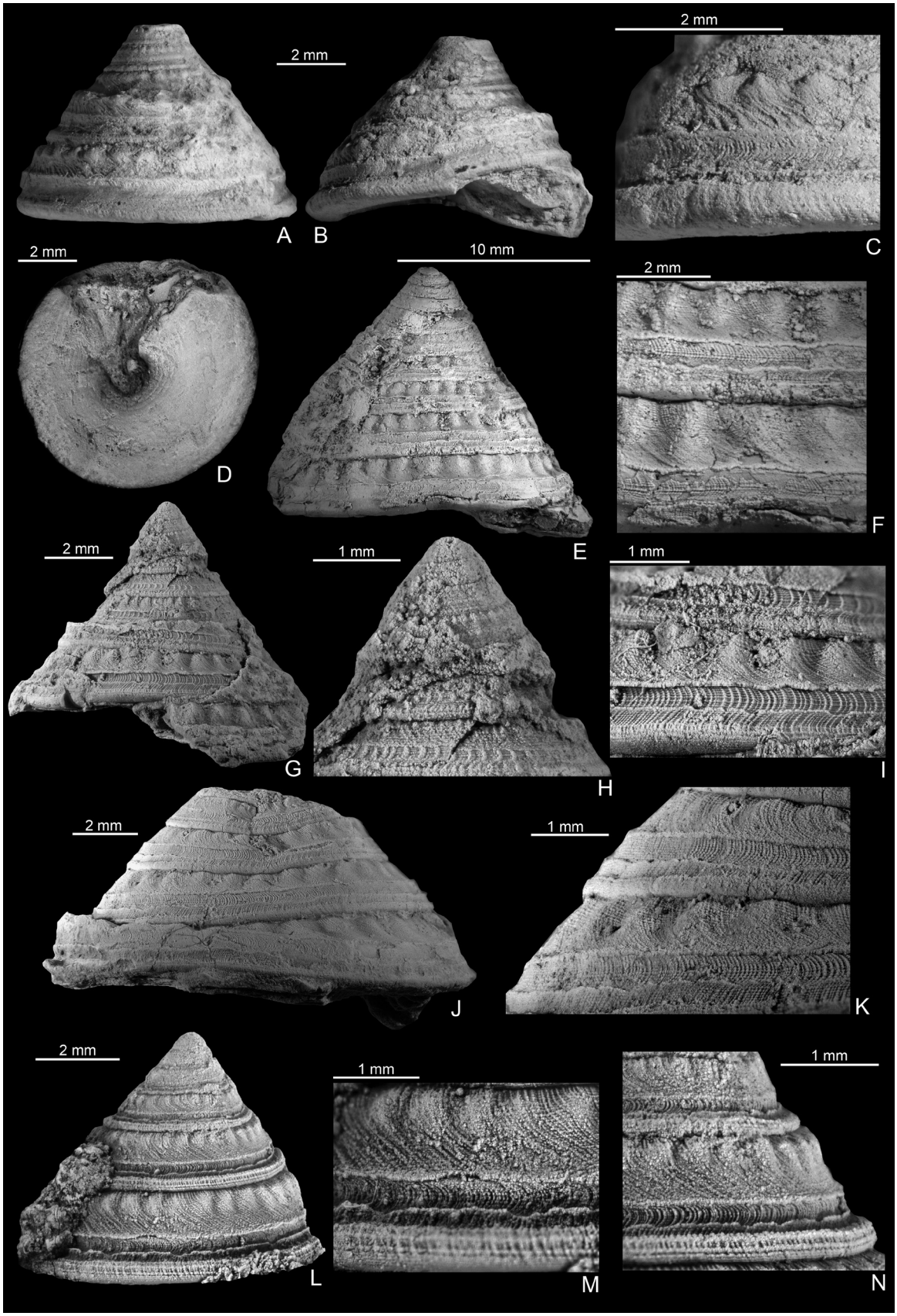

FIGURE 33. *Stuorella tricarinata* (Klipstein, 1844); **A–D.** Lectotype, NHMUK PI OR 35291(1), original of Klipstein (1844, pl. 9, fig. 10), St. Cassian Formation; **E–F.** NHMW 1990/0833/0000/1, St. Cassian Formation; **G–I.** PZO 13682 from Misurina, St. Cassian Formation; **J–K.** MPRZ 2021 1–046, Misurina, St. Cassian Formation; **L–N.** NHMW 2019/0177/0019 Carnian Raibl Formation, Seiser Alm, Italy.

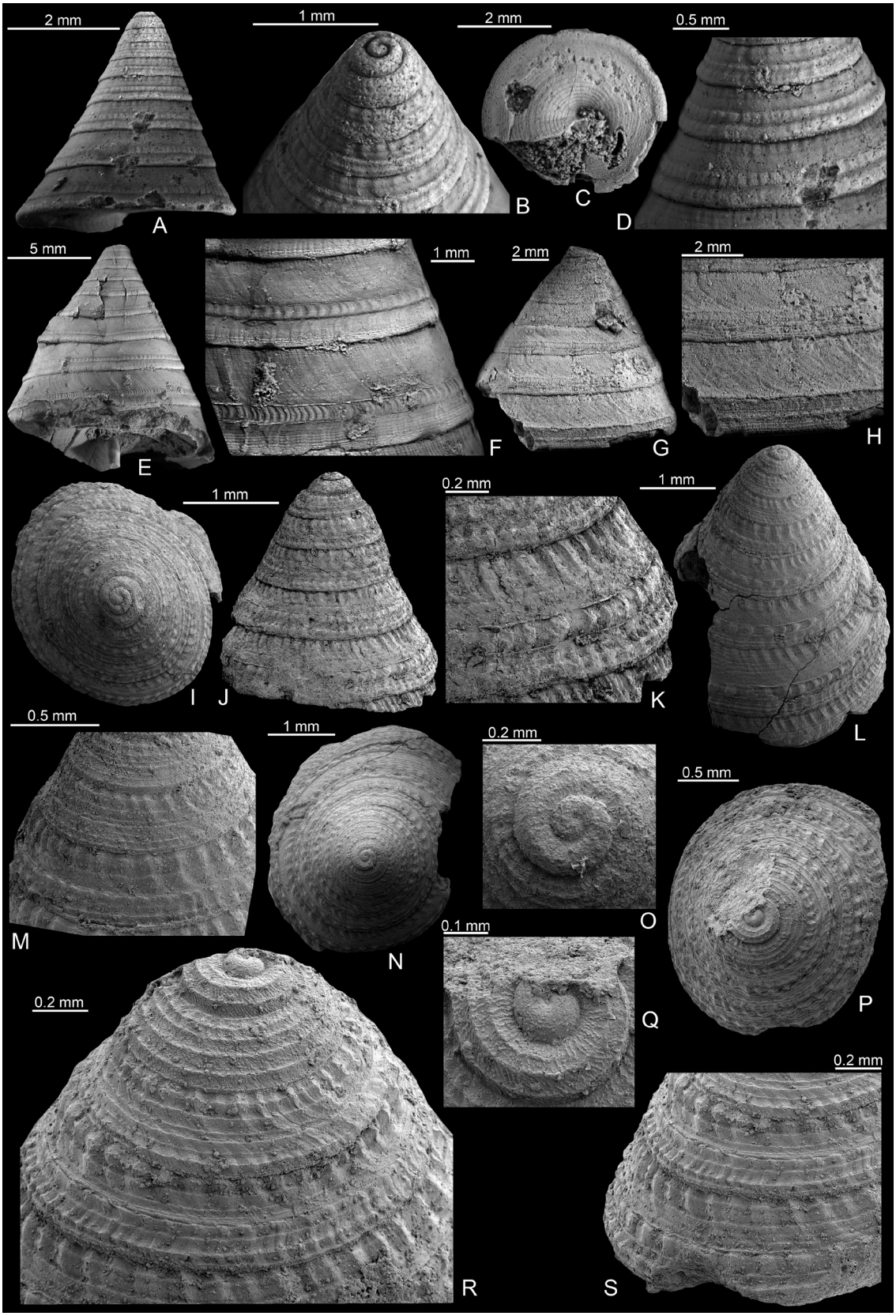

FIGURE 34. *Stuorella tofanae* Leonardi & Fiscon, 1947; **A–D.** NHMW 1990/0633/0000 (original of Bandel 1991, pl. 10, fig. 8; pl. 11, figs 2–3), Alpe di Specie (Seelandalpe), St. Cassian Formation; **E–F.** NHMW 1990/0634/0000 (original of Bandel 1991, pl. 11, fig. 4), Alpe di Specie (Seelandalpe), St. Cassian Formation; **G–H.** MPRZ 2021 1–047 Rumerlo, St. Cassian Formation; **I–K.** MPRZ 2021 1–002, Campo, St. Cassian Formation, SEM image; **L–O.** MPRZ 2021 1–026, Campo, St. Cassian Formation, SEM image; **P–S.** MPRZ 2021 1–020, Campo, St. Cassian Formation, SEM image.

Material. NHMW 1990/0633/0000 (original of Bandel 1991, pl. 10, fig. 8; pl. 11, figs 2–3), NHMW 1990/0634/0000 (original of Bandel 1991, pl. 11, fig. 4) from Alpe di Specie (Seelandalpe), St. Cassian Formation. MPRZ 2021 1–047 from Rumerlo; MPRZ 2021 1–002, MPRZ 2021 1–020, MPRZ 2021 1–026 from Campo, St. Cassian Formation.

Description. Shell conical; largest specimen with ten preserved teleoconch whorls; whorls very low and slowly increasing in height, slightly subimbricate; early spire (first 8 whorls) slightly coeloconoid (with concave sides), spire of adult whorls with straight sides; suture incised; protoconch pitted; first whorl 0.22 mm in width, almost planispiral to low trochospiral; first teleoconch whorl with three axial cords and axial irregular ornament; axial cords increase to four in second whorl and decrease in strength; third whorl with six less strong spiral cords, weak axially elongated subsutural nodes and sinuous growth lines: i.e., prosocline on upper half and opisthocline on lower half; selenizone appears at transition from 4th to 5th whorl; selenizone situated just below mid-height, adapical edge of selenizone representing mid-whorl, selenizone ornamented with irregularly spaced weak nodes or wide weak lunulae, occasionally with spiral striae; selenizone bordered by narrow shell edges or grooves; selenizone width about 15 % of whorl height; whorl face above selenizone flat to slightly convex, ornamented with irregularly spaced axially elongated, very weak subsutural nodes in early ontogenetic whorls, with oblique prosocyrt growth lines and spiral threads in late whorls; whorl face below selenizone slightly convex, ornamented with spiral threads and showing prosocyrt growth lines; transition to base with rounded basal carina, representing whorl periphery; base flatly concave, with faint spiral bands and thin spiral grooves between bands, narrowly phaneromphalous; aperture subtrapezoidal.

Discussion. *Stuorella tofanae* displays a characteristic reduction of the ornament with weakly ornamented late whorls. The distinction of *Stuorella tofanae* Leonardi & Fiscon, 1947 from *Stuorella costalaricensis* Leonardi & Fiscon, 1947 is unclear. Judging from the figure of its holotype (Leonardi & Fiscon 1947, p. 46, pl. 1, fig. 8; 1959, pl. 1, fig. 15; Zardini 1978, pl. 7, fig. 2) and an additional specimen figured by Zardini (1978, pl. 7, fig. 1), it can be said that *Stuorella costalaricensis* tends to form an angulation at the adapical edge of the selenizone and does not form weak nodes or wide lunulae on its selenizone. *Stuorella costalaricensis* develops a somewhat gradate whorl profile and is ornamented only with growth lines on its whorl face and selenizone.

Family Schizogoniidae Cox, 1960 (in Knight et al.)

Remarks. Bandel (2009) elevated the family Schizogoniidae Cox, 1960 (in Knight *et al*.) to superfamily rank—an action that needs corroboration by phylogenetic analyses.

Genus *Schizogonium* Koken, 1889

Type species. *Pleurotomaria scalaris* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; subsequent designation by Diener (1926).

Discussion. *Schizogonium* is only known from the Triassic and most species are known from the St. Cassian Formation, except of *Schizogonium pentagonum* Pan, 1974 from the Middle Triassic of China (Yu *et al*. 1974; Stiller 2001). *Schizogonium russoi* Fucini, 1913 from the Early Jurassic of Sicily does not represent *Schizogonium* but might belong to *Triassocirrus*. *Schizogonium* is a highly characteristic type of slit-band gastropod and is placed in the family Schizogoniidae together with *Pseudowortheniella* Bandel, 2009. Batten (1972, p. 32) proposed that the family Schizogoniidae evolved from the Late Palaeozoic genus *Worthenia*. We do not agree with this opinion, since the early ontogeny and the adult shell morphology of the two groups differ distinctly from each other. The early teleoconch of *Worthenia* is trochospiral (in most species), rounded, its surface is smooth or ornamented with reticulate ornament and it forms a relatively wider selenizone (Karapunar *et al*. in press). The early teleoconch of both members of Schizogoniidae, *Schizogonium* and *Pseudowortheniella*, is planispirally coiled and ornamented with prominent axial ribs. The selenizone is much narrower and situated high on the whorl in schizogoniids. Moreover, *Worthenia* lacks spines on the outer basal edge. However, *Worthenia* and Schizogoniidae share the presence of two whorl angulations (one at the selenizone, one at transition to the base) and the nodular ornamentation of the selenizone.

The only genus that has a strong axial ornamentation before the selenizone starts and a similar position and or-

namentation of the selenizone is the genus *Bandelium* Schwardt, 1992 (family Wortheniellidae Bandel, 2009) from the St. Cassian Formation. It is possible that the family Schizogoniidae has evolved from Wortheniellidae via forms like *Bandelium*.

Schizogonium scalare (Münster, 1841)

Fig. 35

*1841	*Pleurotomaria scalaris*—Münster, p. 109, pl. 11, figs 27a–b.
1850	*Trochus subscalaris* d'Orb., 1847—d'Orbigny, p. 191, no. 288.
1868	*Pleurotomaria scalaris* Münster—Laube, p. 88, pl. 28, fig. 6.
1891	*Schizogonium scalare* Münster sp.—Kittl, p. 215, pl. 5, figs 10–14.
1907	*Schizogonium subcostatum* (Münster)—Broili, p. 81, pl. 6, fig. 38 (non fig. 37).
non 1914	*Schizogonium scalare* Muenst. sp.—Scalia, p. 11, pl. 1, figs 36a–c.
non 1959	*Schizogonium scalare* Münster—Leonardi & Fiscon, p. 10, pl. 1, figs 7a–b.
?1978	*Schizogonium serratum* (Münster)—Zardini, p. 26, pl. 9, figs 9 (non pl. 9, figs 6–8; pl. 7, fig. 10).
1978	*Schizogonium subcostatum* (Münster)—Zardini, p. 10, pl. 9, figs 11, 14 (non pl. 8, fig. 20).
1978	*Schizogonium scalare* (Münster)—Zardini, p. 25, pl. 9, figs 15–16.
1978	*Schizogonium elevatum* (Münster)—Zardini, p. 26, pl. 9, fig. 17.
non 1991	*Schizogonium scalare* Münster—Bandel, p. 14, pl. 3, figs 1–8.
?1991	*Schizogonium elevatum* Kittl—Bandel, p. 22, pl. 9, fig. 3 (non figs 2, 4–6).
non 2009	*Schizogonium scalare* (Münster, 1841)—Bandel, pl. 3, figs 32–33.

Material. Münster's (1841) type specimens from the St. Cassian Formation: SNSB-BSPG AS VII 1660 (original of Münster (1841, pl. 11, figs 27a–b), herein designated as lectotype; AS VII 1661 and AS VII 2067 herein designated as paralectotypes from the St. Cassian Formation. SNSB-BSPG 1903 IX 1040 (original of Broili 1907, pl. 6, fig. 38) from Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMW 1899/0005/0136/1 (original of Kittl 1891, pl. 5, fig. 12), 1899/0005/0136/2 (original of Kittl 1891, pl. 5, fig. 14) from the St. Cassian Formation.

Description. Shell turbiniform, low-spired; lectotype 8.5 mm high, 9.2 mm wide; spire gradate; whorl face with mid-angulation (median carina) and peripheral carina; whorl face flat at ramp, with angulation at median position, concave between median carina and peripheral carina; area below median carina concave and steeply inclined in early whorls, concave parallel to shell axis in last whorl; peripheral carina consists of abapically inclined strong spines, 13–22 per whorl; peripheral carina at transition to base; selenizone (obscured by preservation) situated at median carina; base convex with a spiral basal groove just below peripheral carina, with narrow umbilical chink half covered by inner lip; base bearing opisthocyrt growth lines; aperture as high as wide, subcircular, with angular outer lip, convex basal and inner lips.

Discussion. Both type specimens are not very well preserved but show the characteristic morphology of the genus *Schizogonium*. Both match Münster's (1841) original illustration. The specimen figured here in Fig. 35E–G is probably the one illustrated by Münster (1841). It is the better preserved one and we designate it as lectotype herewith. Both specimens show the characteristic relatively high whorls which is also obvious from Münster's (1841) illustration. The specimens illustrated as *Schizogonium scalare* by Bandel (1991, 2009) and Leonardi & Fiscon (1959) are assigned herein to *Schizogonium subcostatum* (Münster, 1841) (see below). The specimen illustrated as *Schizogonium elevatum* by Zardini (1978, pl. 9, fig. 17) was re-illustrated by Bandel (1991, pl. 9, fig. 3) and forms a spine bearing prominent peripheral carina, which is not present in *S. elevatum.* This specimen probably represents *S. scalare*.

Schizogonium scalare differs from *Schizogonium impressum* (Kittl 1891, pl. 5, fig. 8) (Fig. 40) in having a higher spire and a much narrower umbilicus; it differs from *Schizogonium elevatum* in having prominent spines and a slit-like umbilicus.

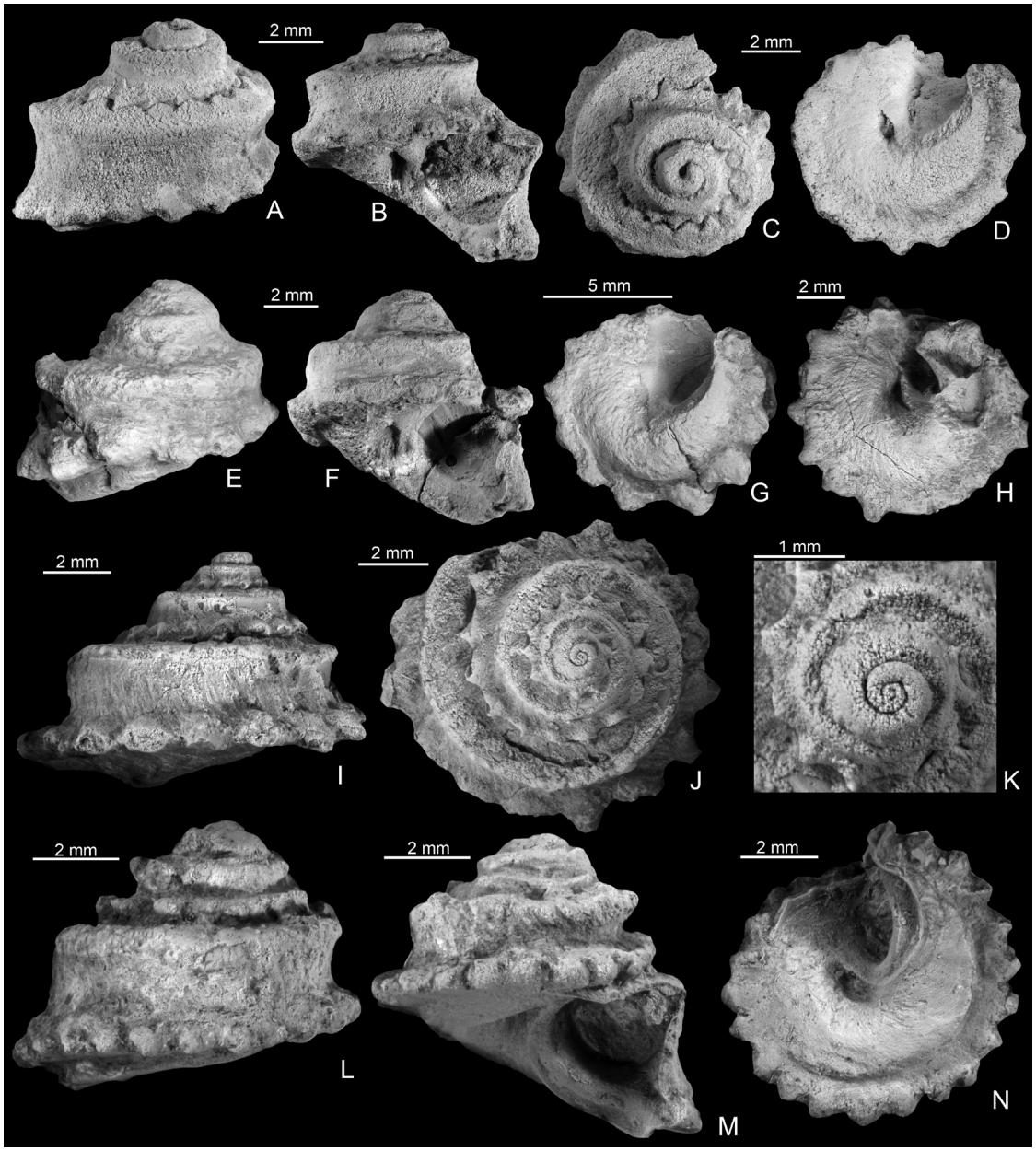

FIGURE 35. *Schizogonium scalare* (Münster, 1841); **A–D.** Paralectotype, SNSB-BSPG AS VII 1661, St. Cassian Formation; **E–G.** Lectotype, SNSB-BSPG AS VII 1660 (original of Münster 1841, pl. 11, figs 27a–b), St. Cassian Formation; **H–K.** NHMW 1899/0005/0136/2 (original of Kittl 1891, pl. 5, fig. 14), St. Cassian Formation; **L–N.** NHMW 1899/0005/0136/1 (original of Kittl 1891, pl. 5, fig. 12), St. Cassian Formation.

Schizogonium elevatum Kittl, 1891

Fig. 36

*1891	*Schizogonium elevatum* Kittl n. f.—Kittl, p. 217, pl. 5, fig. 15, 17.
1891	*Schizogonium tetraptychum* Kittl n. f.—Kittl, p. 218, pl. 5, fig. 16.
non 1978	*Schizogonium elevatum* (Münster)—Zardini, p. 26, pl. 9, fig. 17.
?1991	*Schizogonium elevatum* Kittl—Bandel, p. 22, pl. 9, figs 2, 4–6 (non fig. 3).

Material. NHMW 1899/0005/0138/1 (original of Kittl 1891, pl. 5, fig. 17), herein designated as lectotype of *Schizogonium elevatum* from the St. Cassian Formation. NHMW 1899/0005/0139 (original of Kittl 1891, pl. 5, fig. 16), herein designated as lectotype of *Schizogonium tetraptychum* from the St. Cassian Formation. NHMW 1899/0005/0137/1 from the St. Cassian Formation.

Description. Shell turbiniform, with moderate spire height; lectotype 5.8 mm high, 5.8 mm wide; spire gradate; whorl face with mid-angulation (median carina) and peripheral carina; ramp concave facing adapically in the early teleoconch, then becoming flat and perpendicular to shell axis or slightly inclined; lateral whorl face concave, steeply inclined in the early teleoconch whorls, than lies parallel to shell axis; slit narrow, situated at median carina, slit depth approximately 0.22 of one whorl; peripheral carina situated at transition to base, forming weak spines; base slightly convex, with basal groove just below peripheral carina and with opisthocyrt growth lines, anomphalous; aperture slightly wider than high, subovate, with angular outer lip, convex basal and inner lips; inner and basal lips thickened; short canal (groove) present where basal lip and outer lip meet.

Discussion. Kittl (1891) erected two species, *S. elevatum* and *S. tetraptychum*. Accordingly, *S. tetraptychum* differs from *S. elevatum* in having two spiral keels on the base. He probably referred the peripheral keel as the first spiral keel and the bulge on the base as the second keel which is formed due to the groove just below the peripheral keel. The same groove is present in the lectotype of *S. elevatum* as is the bulge on the base. *Schizogonium elevatum* and *S. tetraptychum* do not differ from each other in any morphological aspect and are therefore regarded to be conspecific. The juvenile specimen illustrated by Bandel (1991, pl. 9, figs 2, 4–6) as *Schizogonium elevatum* bears prominent spines on the peripheral carina. Similar spines are also present in the early shell of the lectotype of *S. elevatum* (refigured here in Fig. 36A–C) but they are not as prominent as in the specimen illustrated by Bandel (1991). Therefore, the assignment of the specimen illustrated by Bandel (1991) is doubtful.

Schizogonium elevatum differs from *S. scalare* in having a lower whorl expansion rate and much weaker spines.

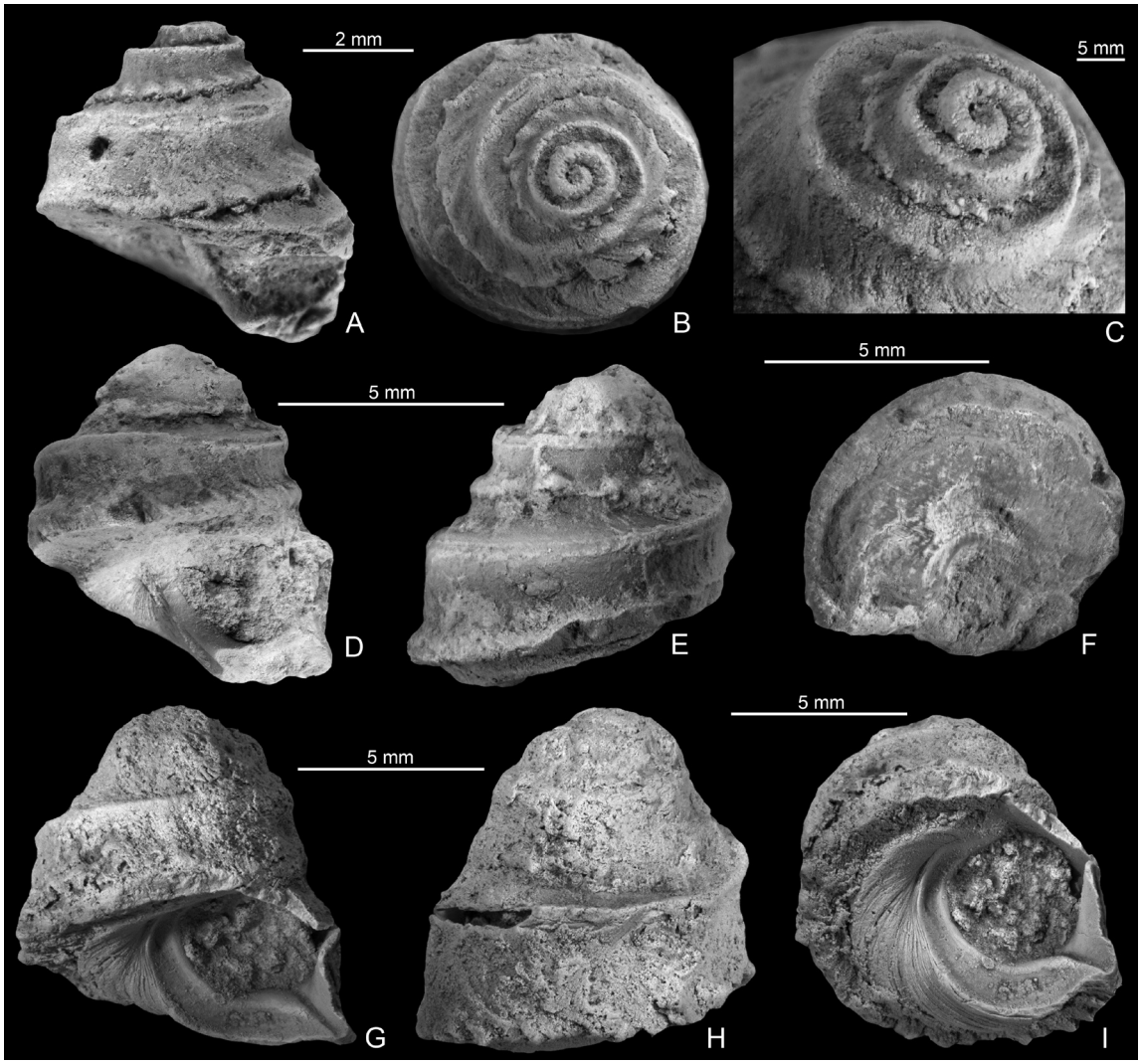

FIGURE 36. *Schizogonium elevatum* Kittl, 1891; **A–C.** Lectotype, NHMW 1899/0005/0138/1 (original of Kittl 1891, pl. 5, fig. 17), St. Cassian Formation; **D–F.** Lectotype of *Schizogonium tetraptychum* Kittl, 1891, NHMW 1899/0005/0139 (original of Kittl 1891, pl. 5, fig. 16), St. Cassian Formation; **G–I.** NHMW 1899/0005/0137/1, St. Cassian Formation.

***Schizogonium subcostatum* (Münster, 1841)**
Fig. 37

*1841	*Pleurotomaria subcostata*—Münster, p. 111, pl. 12, figs 3a–b.
1850	*Trochus timeus* d'Orb., 1847—d'Orbigny, p. 190, no. 269.
non 1868	*Pleurotomaria subcostata* Münster—Laube, p. 88, pl. 26, fig. 12.
1891	*Schizogonium subcostatum* Münster sp.—Kittl, p. 216, pl. 5, figs 5–6.
non 1895	*Schizogonium subcostatum* Münst. sp.—Böhm, p. 222, pl. 9, fig. 7.
1907	*Schizogonium subcostatum* (Münster)—Broili, p. 81, pl. 6, fig. 37 (non fig. 38).
non 1914	*Schizogonium subcostatum* Muenst. sp.—Scalia, p. 12, pl. 1, figs 37a–b.
1959	*Schizogonium scalare* Münster—Leonardi & Fiscon, p. 10, pl. 1, figs 7a–b.
?1959	*Schizogonium subcostatum* Münster—Leonardi & Fiscon, p. 10, pl. 1, figs 9a–b.
1978	*Schizogonium subcostatum* (Münster)—Zardini, p. 26, pl. 8, figs 20a–c (non pl. 9, figs 11, 14).
?1978	*Schizogonium serratum* (Münster)—Zardini, p. 26, pl. 9, figs 6 (non pl. 9, figs 7–9; pl. 7, fig. 10).
1978	*Schizogonium impressum* (Kittl)—Zardini, p. 25, pl. 9, figs 13a–d.
1991	*Schizogonium scalare* Münster—Bandel, p. 14, pl. 3, figs 1–2, ?3–8.
1991	*Schizogonium subcostatum* Münster—Bandel, p. 15, pl. 4, figs 1–5.
2009	*Schizogonium scalare* (Münster, 1841)—Bandel, pl. 3, figs 32–33.

Material. SNSB-BSPG AS VII 1516 (original of Münster 1841, pl. 12, figs 3a–b), herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG 1903 IX 340 (original of Broili 1907, pl. 6, fig. 37), SNSB-BSPG 1903 IX 1050 (additional material of Broili (1907), 2 specimens) from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMW 1899/0005/0129 (original of Kittl, 1891, pl. 5, fig. 6), NHMW 1990/0648/0000/1, NHMW 1990/0648/0000/2 from the St. Cassian Formation. PZO 13686, PZO 13687 from Misurina, St. Cassian Formation.

Description. Shell with low, gradate spire; lectotype 4.3 mm high, 6.0 mm wide; first whorl diameter 0.22 mm; first two whorls rounded, planispirally coiled, with widely spaced, prominent axial ribs and spiral threads; subsequent whorls with two prominent angulations; upper angulation (median carina) high on whorl face, bordering concave, almost horizontal ramp; lower angulation forming periphery, emerging from abapical suture; whorl face between median carina and peripheral carina concave and steeply inclined; peripheral carina pointing abapically, with short notches (broken off spines), situated at mid-height of body whorl; selenizone convex, situated at median carina; base convex, narrowly phaneromphalous, ornamented with opisthocyrt undulations formed by growth lines; aperture as high as wide, subovate, with angular outer lip, convex basal and inner lips.

Discussion. *Schizogonium subcostatum* differs from *Schizogonium scalare* in being lower spired and in having the peripheral keel at mid-whorl whereas in *Schizogonium scalare* the peripheral keel is positioned low on the whorl. *Schizogonium subcostatum* differs from *S. serratum* and *S. ampezzanum* in having a narrower, chink-like umbilicus and a higher spire. Bandel (1991, pl. 4, figs 3–5) figured a juvenile specimen with strong axial ribs on the early teleoconch (not preserved in Münster's (1841) type specimen) which he identified as *S. subcostatum*. Bandel's (1991) specimen agrees well in shape with the lectotype of *S. subcostatum*. Therefore, we assume that *S. subcostatum* has this type of early teleoconch morphology. Bandel (1991, pl. 3, fig. 1–2) figured the same specimen (also figured by Bandel 1991, pl. 4, figs 3–5) and misidentified it as *S. scalare*. This juvenile specimen and the other juvenile specimens identified as *Schizogonium scalare* by Bandel (1991, pl. 3, figs 3–8) share the same teleoconch morphology and ornamentation. They differ from *S. scalare* Münster, 1841 in having the peripheral ridge at mid-whorl (instead of below mid-whorl) and in having axial ridges on the base, which are typical characters of *S. subcostatum*. The juvenile specimens figured by Bandel (1991, pl. 3, figs 1–8) also have the same teleoconch morphology and ornamentation as the paratype of *S. ampezzanum* (Bandel 1991, pl. 7, figs 5, 6, 8; pl. 8, fig. 2). The only difference is the presence of spiral ornament on the base of the paratype of *S. ampezzanum* (visible on Bandel's illustrated paratype), which is identified as *S. subdentatum* herein.

The specimen identified as *Schizogonium scalare* by Leonardi & Fiscon (1959, pl. 1, figs 7a–b) was later re-figured by Bandel as *Schizogonium subcostatum* (1991, pl. 4, fig. 1). We agree with Bandel's identification because the peripheral carina is positioned at mid-whorl of the body whorl in this specimen.

The specimen assigned to *Schizogonium subcostatum* by Böhm (1895, pl. 9, fig. 7) has a higher spire and a wider umbilicus and is not conspecific with the lectotype.

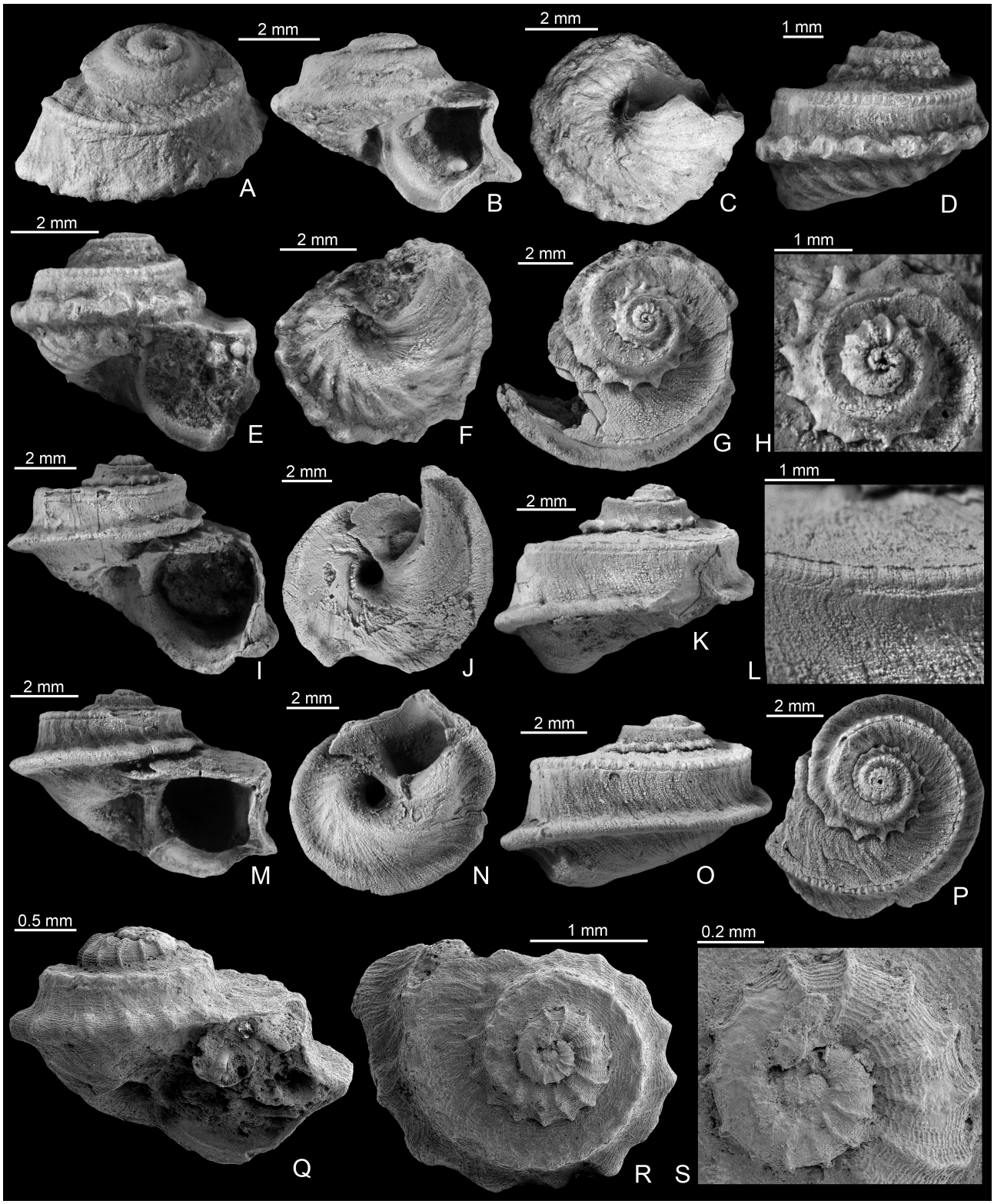

FIGURE 37. *Schizogonium subcostatum* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1516 (original of Münster 1841, pl. 12, figs 3a–b), St. Cassian Formation; **D–F.** NHMW 1899/0005/0129 (original of Kittl, 1891, pl. 5, fig. 6), St. Cassian Formation; **G–L.** NHMW 1990/0648/0000/1, St. Cassian Formation; **M–P.** NHMW 1990/0648/0000/2, St. Cassian Formation; **Q–S.** PZO 13686, Misurina, St. Cassian Formation, SEM image.

The specimen assigned to *Schizogonium subcostatum* Münster by Leonardi & Fiscon (1959, pl. 1 figs 9a–b) has a slightly wider shell and might belong to *S. impressum* Kittl, 1891.

The specimen figured as *Schizogonium impressum* by Zardini (1978, pl. 9, figs 13a–d) agrees well with *S. subcostatum* in the position of the peripheral carina and general shell morphology and belongs to this species.

Additional *S. subcostatum* specimens that are housed in the NHMW do not develop spines on the peripheral carina in late teleoconch whorls (figured here in Fig. 37G–P). Presence or disappearance of spines in the later teleoconch is considered as intraspecific variation herein because the specimens are identical in all other aspects (whorl morphology, early ontogeny, position of peripheral keel etc.). This variation further supports the relationship between *Schizogonium* and non-spine-bearing *Pseudowortheniella*.

The identity of the specimen illustrated as *Schizogonium subcostatum* by Laube (1868) is discussed in the discussion part of *Schizogonium serratum* (see below).

Schizogonium subdentatum (Münster, 1841)

Fig. 38

*1841	*Pleurotomaria subdentata*—Münster, p. 111, pl. 12, figs 5a–c.
1850	*Trochus subdentatum* d'Orb., 1847—d'Orbigny, p. 190, no. 271.
1870	*Delphinula subdentata* Münster—Laube, p. 28, pl. 32, fig. 13.
1891	*Schizogonium subdentatum* Münster sp.—Kittl, p. 215, pl. 5, figs 3–4.
non 1980	*Schizogonium subdentatum* (Münster)—Zardini, p. 6, pl. 2, fig. 12.
non 1991	*Schizogonium subdentatum* (Münster, 1841)—Bandel, p. 19, pl. 6, figs 7–8, pl. 7, figs 1–3.
1991	*Schizogonium ampezzanum* n. sp.—Bandel, p. 20, pl. 7, figs 5, 6, 8; pl. 8, fig. 2 (non pl. 7, fig. 4, 7).

Material. SNSB-BSPG AS VII 1662 (original of Münster 1841, pl. 12, figs 5a–c), herein designated as lectotype from the St. Cassian Formation.

Description. Shell rather low-spired, gradate, with low whorls; lectotype 3.3 mm high, 4.9 mm wide; whorl face with angulation at mid-whorl (median carina) and peripheral carina; whorl face with flatly concave subsutural shelf, angulated at median carina, concave and steeply inclined between median carina and peripheral carina at transition to base; peripheral carina inclined abapically, with spines (broken off, eroded); selenizone (obscured by preservation) situated at median carina; base convex, anomphalous, ornamented with two strong spiral cords and with opisthocyrt growth lines; aperture slightly wider than high with angular outer and basal lips, convex inner lip.

Discussion. The lectotype is a rather worn, strongly encrusted specimen. Its lower whorls and spire separate it from *S. scalare*. The presence of two spiral cords on the base separates it from all other *Schizogonium* species treated herein.

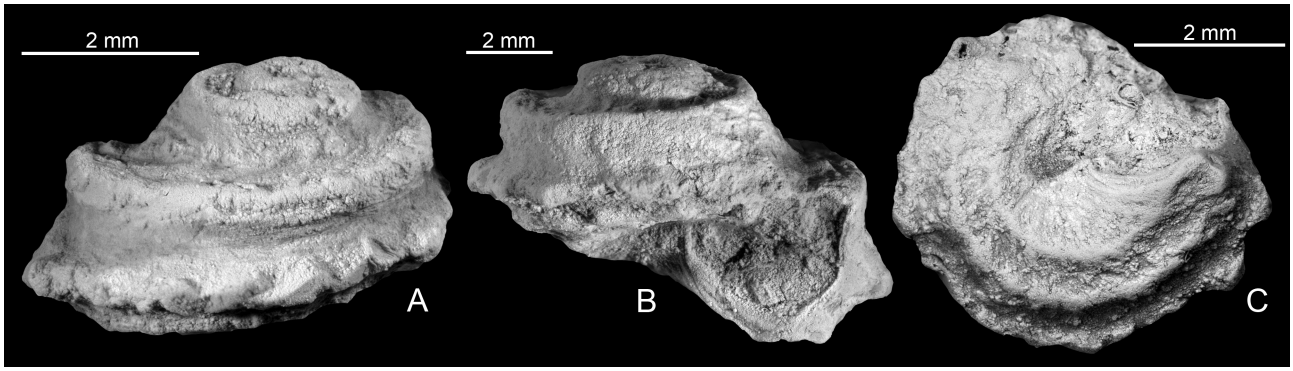

FIGURE 38. *Schizogonium subdentatum* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1662 (original of Münster 1841, pl. 12, figs 5a–c), St. Cassian Formation.

The juvenile specimen figured as *Schizogonium subdentatum* by Zardini (1980, pl. 2, fig. 12) does not bear two spiral cords on its base and is therefore not considered as conspecific.

The specimens identified as *Schizogonium subdentatum* by Bandel (1991, pl. 6, figs 7–8, pl. 7, figs 1–3) represent *S. undae* **sp. nov.** (see below).

The paratype of *S. ampezzanum* (Bandel 1991, pl. 7, figs 5, 6, 8; pl. 8, fig. 2) differs from its holotype in the ornamentation of the early shell. The paratype of *S. ampezzanum* has fewer transverse ribs on the first teleoconch whorl (11 vs. 25) and is ornamented with axial folds on the base. This specimen is herein considered to represent *S. subdentatum*. The base of the paratype of *Schizogonium ampezzanum* (Bandel 1991, pl. 7, figs 5, 6, 8; pl. 8, fig. 2)

is ornamented with a spiral cord and axial ribs. The axial ribs/folds are somewhat strengthened along a weak spiral angulation lying parallel to the spiral cord. Thus, the paratype does not form two distinct spiral cords. The specimen figured by Kittl (1891, pl. 5, fig. 3) also shows a strengthening of axial ribs along two spiral angulations rather than having two distinct spiral cords. Obviously *Schizogonium subdentatum* has either two distinct spiral cords (as in the lectotype) or two spiral angulations. This is regarded as intraspecific variability.

Schizogonium serratum (Münster, 1841)

Fig. 39

*1841	*Schizostoma serrata*—Münster, p. 106, pl. 11, figs 7a–b.
1850	*Trochus serratus* d'Orb., 1847—d'Orbigny, p. 191, no. 290.
non 1868	*Pleurotomaria subcostata* Münster—Laube, p. 88, pl. 26, fig. 12.
1891	*Schizogonium serratum* Münster sp.—Kittl, p. 214, pl. 5, fig. 2 (non fig. 1).
non 1978	*Schizogonium serratum* (Münster)—Zardini, p. 26, pl. 9, figs 6–9; pl. 7, fig. 10.
non 1980	cfr. *Schizogonium serratum* Muenster—Zardini, p. 4, pl. 2, fig. 4.
non 1980	*Schizogonium serratum* Muenster f. giovanile—Zardini, p. 5, pl. 2, figs 5, 13–14.
non 1985	*Schizogonium serratum* (Münster)—Zardini, pl. 6, fig. 5.
1991	*Schizogonium serratum* (Münster, 1841)—Bandel, p. 18, pl. 5, fig. 6–8 (non pl. 5, figs 2, 4–5).
non 2009	*Schizogonium serratum* (Münster, 1841)—Bandel, pl. 3, figs 34–35.

Material. SNSB-BSPG AS VII 1225 (original of Münster 1841, pl. 11, figs 7a–b), herein designated as lectotype from the St. Cassian Formation. NHMW 1899/0005/0125/1 from the St. Cassian Formation.

Description. Shell flat with low, gradate spire; lectotype comprises 4 whorls, 4.7 mm high, 10.0 mm wide; first two whorls of teleoconch with closely and regularly spaced axial ribs; selenizone starts after second whorl; whorl face of teleoconch with two pronounced carinations; upper carina situated on whorl face, closer to the adapical suture than to the abapical one; upper carina forms the the most adapical part of the whorls where selenizone lies; lower carination forms pronounced spiny crest representing periphery (peripheral carina) of whorls, situated low on the last whorl and directly above the abapical suture in spire whorls with its spines resting on succeeding whorl; whorl face between adapical suture and selenizone concave, facing adapically in early teleoconch, later becoming flat, perpendicular to shell axis; whorl face between selenizone and peripheral carina concave, steeply inclined; lectotype has about 24 spines per whorl on peripheral carina; selenizone convex, narrow, having regularly spaced nodes; selenizone bordered by sharp crests; whorl face between adapical suture and selenizone with prosocline/prosocyrt growth lines and very thin collabral threads; whorl face below selenizone with prosocline/prosocyrt growth lines and numerous collabral threads; base convex with abrupt transition to peripheral crest; base ornamented with regular, crescentic, sickle-shaped radial folds and spiral threads, and with opisthocyrt growth lines; umbilicus wide; aperture ovate, somewhat wider than high with rounded lips.

Discussion. The lectotype designated here was previously illustrated by Kittl (1891, pl. 5, fig. 2) and by Bandel (1991, pl. 5, figs 6–8). Bandel (1991) considered it to represent the holotype. These illustrations are of sub-optimal quality despite the good preservation of this specimen. Laube (1868) erroneously considered *Schizogonium serratum* (Münster, 1841) to represent a synonym of *Schizogonium subcostatum* (Münster, 1841), accordingly they represent different growth stages. By contrast, Kittl (1891) kept both species separate and placed the original of Laube (1868, pl. 26, fig. 12) in *S. serratum*. The specimen figured as *Schizogonium subcostatum* by Laube (1868, pl. 26, fig. 12) is figured here (NHMW 1858/0009/0014/1 Fig. 40E–G). It has a much more elevated spire than *S. serratum* and has a vertical lateral whorl face. Laube's figured specimen, in our opinion, represents *S. impressum* Kittl, 1891 (the original of Kittl 1891, pl. 5, fig. 8, NHMW 1899/0005/0134, is figured here in Fig. 40A–D and designated as lectotype of *Schizogonium impressum* herein).

The specimen figured by Kittl (1891, pl. 5, fig. 1, NHMW 1899/0005/0127) as *Schizogonium serratum* Münster (figured here in Fig. 41) lacks peripheral spines and represents *Schizogonium tamarinum* Bandel, 1991. The specimens figured as *Schizogonium serratum* by Zardini (1978, pl. 7, fig. 10; 1980, pl. 2, figs 4–5, 13–14) also represents *S. tamarinum*. The specimen assigned to *Schizogonium serratum* by Zardini (1985, pl. 6, fig. 5) has much more prominent axial ribs on the early whorls and a steep lateral whorl face; therefore, it does not represent *S. serratum*.

Schizogonium serratum differs from *Schizogonium ampezzanum* Bandel, 1991 in having a higher spire, in

lacking a median spiral cord on the base and in the position of the peripheral spines, which are situated at mid-whorl in *S. serratum* but at the abapical portion of the whorls in *S. ampezzanum*. Both taxa share the same early teleoconch morphology and whorl face.

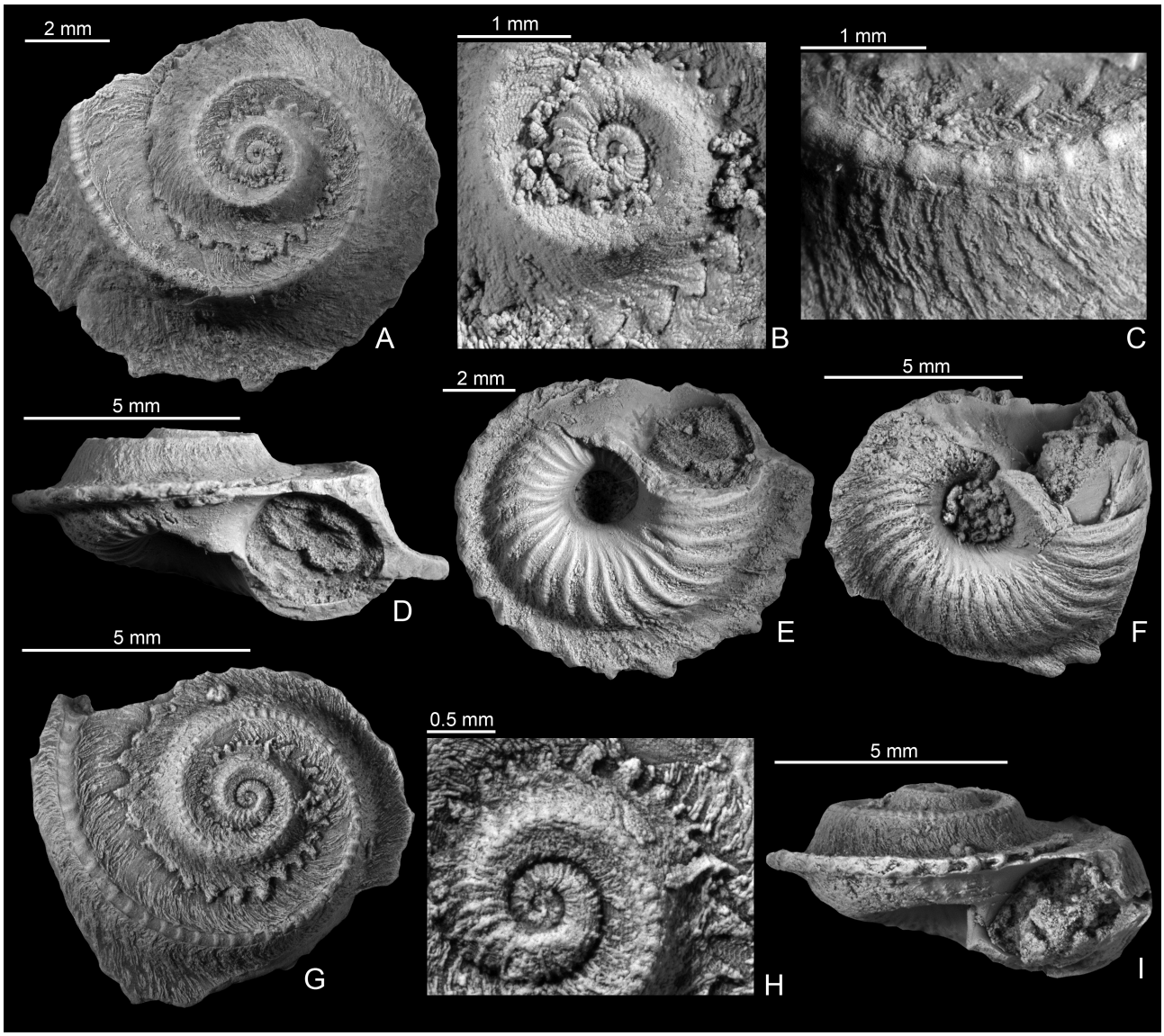

FIGURE 39. *Schizogonium serratum* (Münster, 1841); **A–E.** Lectotype, SNSB-BSPG AS VII 1225 (original of Münster 1841, pl. 11, figs 7a–b), St. Cassian Formation; **F–I.** NHMW 1899/0005/0125/1, St. Cassian Formation.

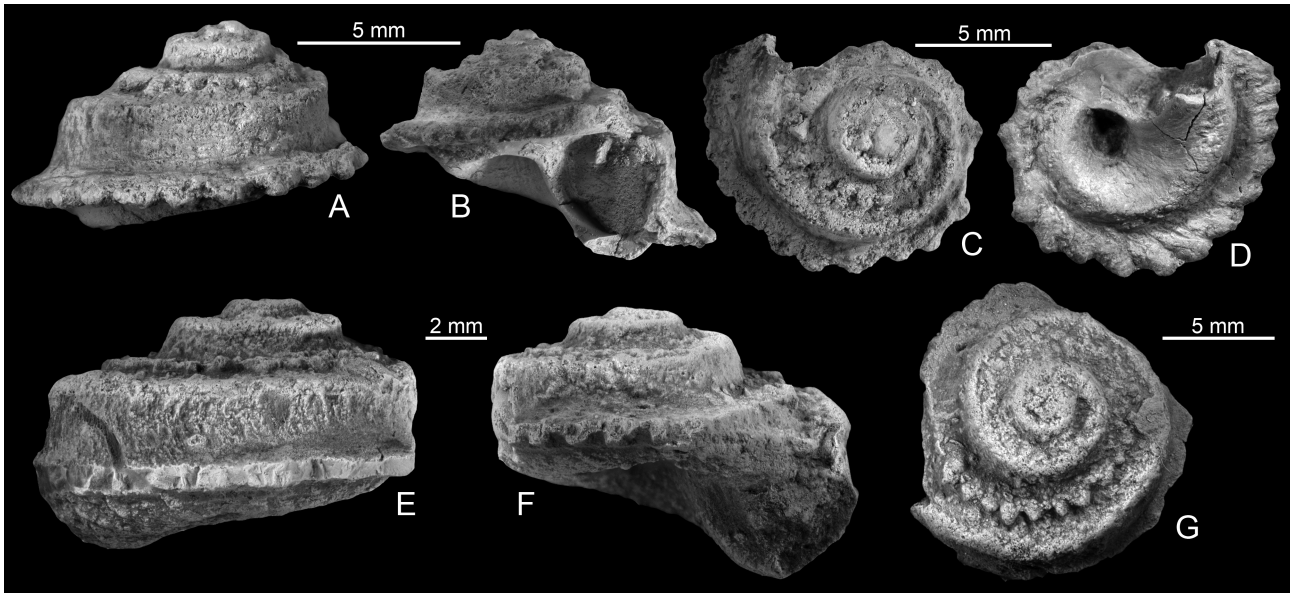

FIGURE 40. *Schizogonium impressum* Kittl, 1891; **A–D.** Lectotype, NHMW 1899/0005/0134 (original of Kittl 1891, pl. 5, fig. 8), St. Cassian Formation; **E–G.** NHMW 1858/0009/0014/1 (original of Laube 1868, pl. 26, fig. 12), St. Cassian Formation.

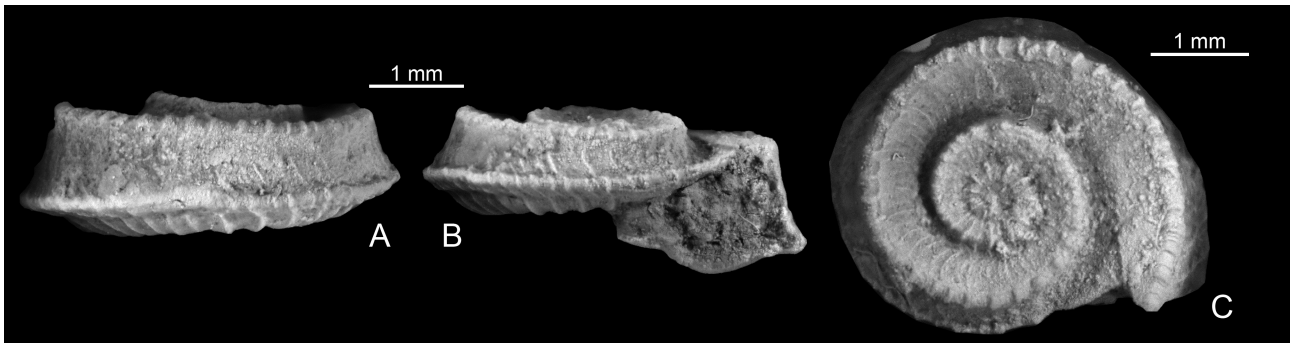

FIGURE 41. *Schizogonium tamarinum* Bandel, 1991; **A–C.** NHMW 1899/0005/0127 (original of Kittl 1891, pl. 5, fig. 1), St. Cassian Formation.

Schizogonium ampezzanum Bandel, 1991

Fig. 42

*1991	*Schizogonium ampezzanum* n. sp.—Bandel, p. 20, pl. 7, figs 4, 7 (non pl. 7, figs 5, 6, 8; pl. 8, fig. 2).
1991	*Schizogonium serratum* (Münster, 1841)—Bandel, p. 18, pl. 5, figs 2, 4–5 (non figs 6–8).
2009	*Schizogonium serratum* (Münster, 1841)—Bandel, pl. 3, figs 34–35.
non 2009	*Schizogonium ampezzanum* Bandel, 1991—Bandel, pl. 3, figs 39–41.

Material. NHMW 1990/0626/0000 (original of Bandel 1991, pl. 7, figs 4, 7), holotype, and NHMW 1990/0619/0000 (original of Bandel 1991, pl. 5, figs 2, 4–5) from the St. Cassian Formation.

Description. Shell with low, gradate spire; protoconch consists of about one whorl (vetigastropod-type); first two whorls of teleoconch ornamented with closely and regularly spaced axial ribs (approximately 25 on first teleoconch whorl) and spiral threads; selenizone starts after second whorl; whorl face of teleoconch with two pronounced carinations; adapical carina bearing selenizone; peripheral carina forms flat spines, situated low on last whorl, directly above abapical suture with its spines resting on preceding whorl; whorl face between adapical suture and selenizone flat, horizontal (perpendicular to shell axis); lateral whorl face concave, steeply inclined; selenizone convex, narrow, ornamented with regularly spaced nodes and spiral threads; selenizone bordered by shell edges; whorl face between adapical suture and selenizone with prosocline/prosocyrt growth lines and very thin collabral threads; whorl face below selenizone with prosocline/prosocyrt growth lines and numerous short collabral threads

and widely spaced, thin spiral threads; base convex with a median spiral carina; base ornamented with flickering spiral threads and with opisthocyrt growth lines; umbilicus wide.

Discussion. *Schizogonium ampezzanum* and *S. serratum* share the same whorl face morphology and ornamentation, but *S. ampezzanum* differs in the presence of a median spiral cord on its base and in having a higher spire. The paratype of *S. ampezzanum* (Bandel 1991, pl. 7, figs 5, 6, 8; pl. 8, fig. 2) is placed in *S. subdentatum* in the present study (see discussion of *S. subdentatum*). The specimens assigned to *Schizogonium serratum* by Bandel (1991, pl. 5, figs 2, 4–5; 2009, pl. 3, figs 34–35) have a distinctly elevated spire and differ from the type specimen of *S. serratum* in this respect. Those specimens are identified as *Schizogonium ampezzanum* Bandel, 1991. The specimen figured by Bandel (1991, pl. 5, figs 2, 4–5) is a juvenile specimen and is figured here (Fig. 42F–I). It has a distinctly elevated spire and its base is ornamented with a median spiral cord; this specimen represents *S. ampezzanum*. However, Bandel's specimen has weak, sickle-shaped folds, which are not present in the holotype of *S. ampezzanum*. It is possible that the weakly developed sickle-shaped folds disappear in later growth stages in *S. ampezzanum*. The basal ornament of the figured specimen (Bandel 2009, pl. 3, figs 34–35) is unknown and this specimen needs further documentation.

The juvenile specimen assigned to *S. ampezzanum* by Bandel (2009, pl. 3, figs 39–41) differs from the holotype of *S. ampezzanum* in having fewer transverse ribs on the first teleoconch whorl (11 vs. 25), and therefore does not belong to *S. ampezzanum*.

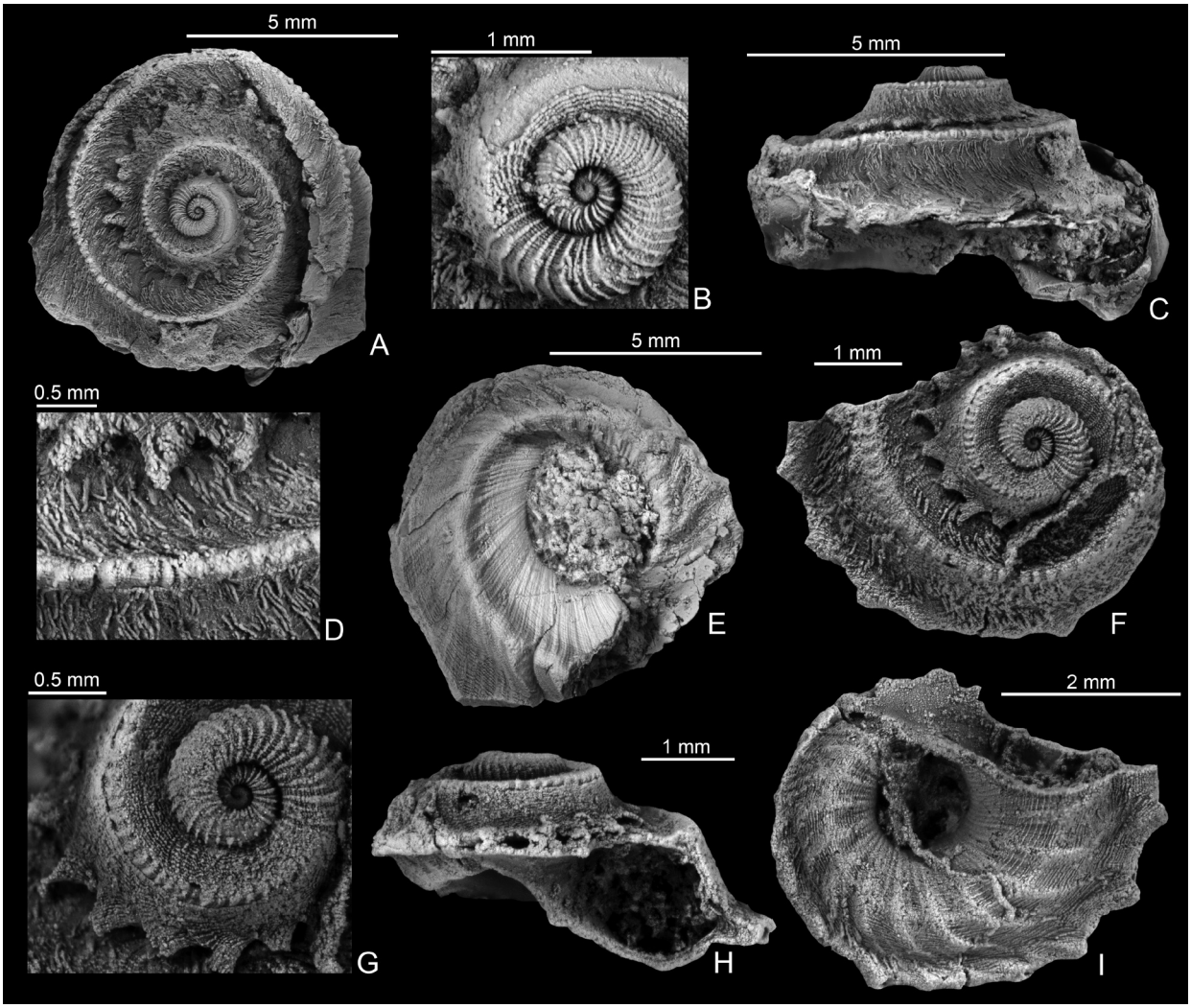

FIGURE 42. *Schizogonium ampezzanum* Bandel, 1991; **A–E.** Holotype, NHMW 1990/0626/0000 (original of Bandel 1991, pl. 7, figs 4, 7), St. Cassian Formation; **F–I.** NHMW 1990/0619/0000 (original of Bandel 1991, pl. 5, figs 2, 4–5), St. Cassian Formation.

***Schizogonium undae* sp. nov.**
Fig. 43
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1978 *Schizogonium serratum* (Münster)—Zardini, p. 26, pl. 9, figs 7–8 (non pl. 9, figs 6, 9; pl. 7, fig. 10).
1991 *Schizogonium gracilis* (Münster, 1841)—Bandel, p. 16, pl. 4, figs 7–8, pl. 5, figs 1, 3.
1991 *Schizogonium subdentatum* (Münster, 1841)—Bandel, p. 19, pl. 6, figs 7–8, pl. 7, figs 1–3.

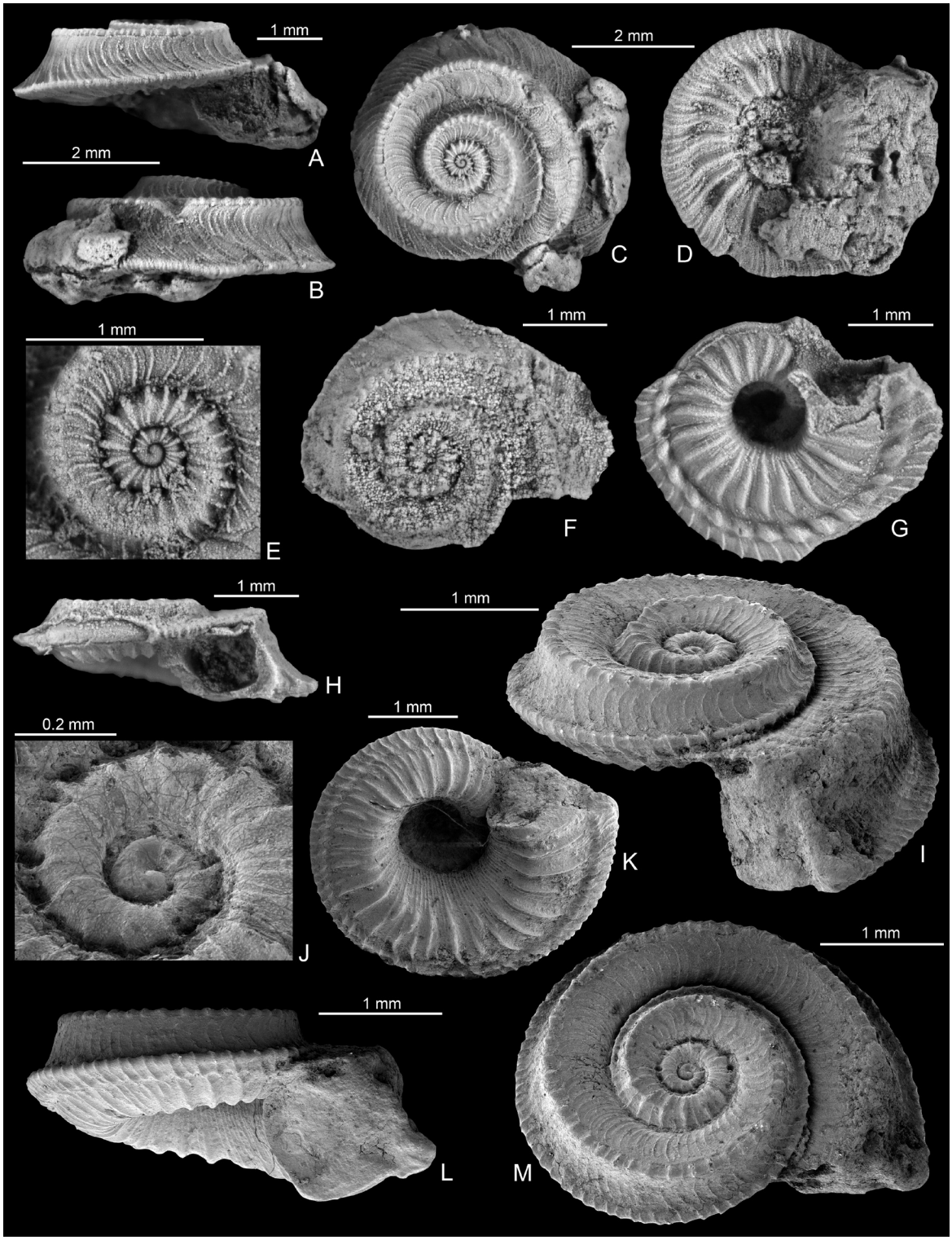

FIGURE 43. *Schizogonium undae* **sp. nov.**; **A–E.** Holotype, NHMW 1990/0624/0003/1, Alpe di Specie (Seeland Alpe), St. Cassian Formation; **F–H.** Paratype, NHMW 1990/0624/0003/2, Alpe di Specie (Seeland Alpe), St. Cassian Formation; **I–M.** MB.Ga.4291, St. Cassian Formation, SEM image.

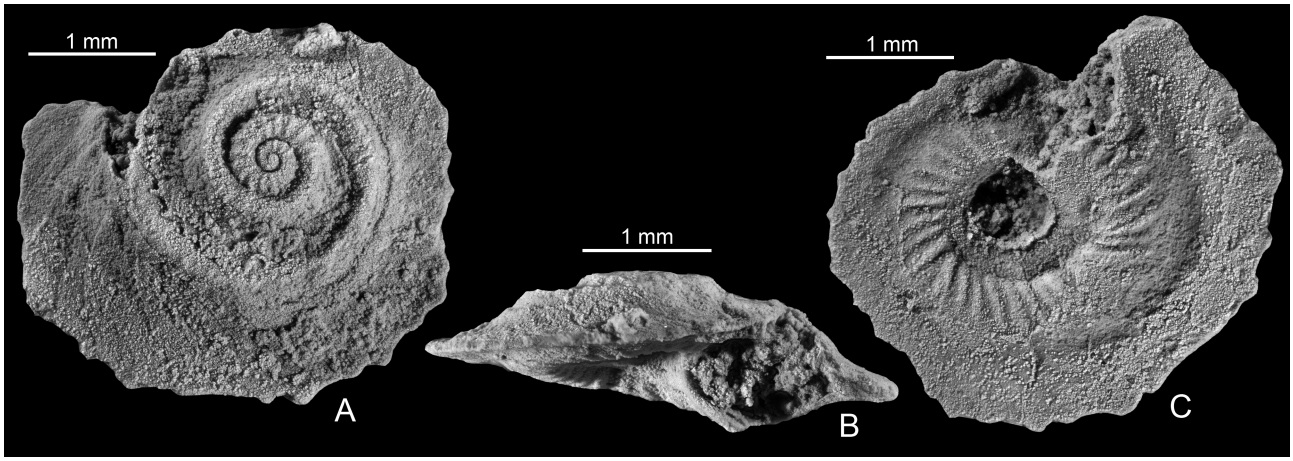

FIGURE 44. *Schizogonium lamellosum* Bandel, 1991; **A–C.** MPRZ 2021 1–056, Campo, St. Cassian Formation.

Derivation of name. From Latin *undae*, waves; due to its resemblance to water ripples made by a water drop.

Holotype. NHMW 1990/0624/0003/1.

Paratype. NHMW 1990/0624/0003/2.

Type locality, age, formation. Alpe di Specie (Seeland Alpe), N Italy, Early Carnian, St. Cassian Formation.

Material. NHMW 1990/0624/0003/1 (holotype) and 1990/0624/0003/2 (paratype) from Alpe di Specie (Seeland Alpe), St. Cassian Formation; MB.Ga.4291 from the St. Cassian Formation.

Description. Shell with flat spire, consisting of at least 4.5 whorls; protoconch of less than one whorl (vetigastropod-type); first two whorls of teleoconch ornamented with irregularly spaced axial ribs of variable strength (approximately 16 in the first teleoconch whorl); selenizone starts after the second whorl; whorl face of teleoconch with two pronounced carinations; selenizone situated on upper carina; peripheral carina situated low on last whorl, directly above abapical suture in preceding whorls; whorl face between adapical suture and selenizone concave, facing adapically in the early teleoconch then horizontal (perpendicular to shell axis) in last whorl; lateral whorl face concave, steeply inclined; selenizone convex, narrow, ornamented with irregularly spaced, short nodes; selenizone bordered by sharp edges; whorl face between adapical suture and selenizone with widely spaced prosocyrt, collabral threads; lateral whorl face ornamented with widely spaced, oblique prosocyrt axial threads; base convex, ornamented with axial folds; in some specimens an additional spiral band with nodes is present between peripheral carina and base; umbilicus wide.

Discussion. This species was identified as *Schizogonium gracilis* (Münster, 1841) by Bandel (1991). However, the identity of *Schizostoma gracilis* Münster, 1841 is doubtful. The type material of *Schizostoma gracilis* is missing at the BSPG as was already indicated by Kittl (1891). Münster (1841) illustrated *Schizostoma gracilis* with a rectangular whorl profile lacking a crest and a selenizone situated on the upper whorl face and also lacking an angulation on the upper whorl face. In these respects, it differs from *Schizogonium gracilis* (Münster, 1841) sensu Bandel (1991). However, it is unclear how accurate Münster's (1841) illustration is—if it is fairly accurate, this species does not belong to *Schizostoma* and Bandel's (1991) material does not represent "*Schizostoma*" *gracilis*. Kittl (1891) already noted that the identity of this species is doubtful and placed it tentatively in *Euomphalus*.

Schizogonium tamarinum Bandel, 1991 has a narrower whorl face between the adapical suture and the selenizone, a much narrower lateral whorl face (whorl face between selenizone and peripheral keel), its peripheral keel is at mid-whorl (Bandel 1991, pl. 8, fig. 6) rather than being below mid-whorl, its early teleoconch whorls are ornamented with regular, prominent axial ribs and its base is ornamented with orthocline ribs rather than being wavy. *Schizogonium subnodosum* Zardini, 1978 has a much wider lateral whorl face; it is probably conspecific with *Schizogonium lamellosum* Bandel, 1991 (Fig. 44). The holotype (Bandel 1991, pl. 6, figs 1–2, 4) and the paratype (Bandel 1991, pl. 6, figs 3, 5) of *S. lamellosum* are not conspecific. At comparable growth stages, the paratype (Bandel 1991, pl. 6, figs 3, 5) has strong axial ribs, its selenizone is farther away from the adapical suture, and its peripheral carina forms short spines which are absent in the holotype. The paratype (Bandel 1991, pl. 6, figs 3, 5) resembles *Schizogonium subcostatum* (Münster, 1841) and might belong to that species.

***Schizogonium*? *bicarinatum* (Klipstein, 1844) comb. nov.**
Fig. 45

*1844	*Pleurotomaria bicarinata*—Klipstein, p. 172, pl. 14, figs 32a–b.
1894a	*Pleurotomaria*? *bicarinata* Klipst.—Kittl, p. 245.

Material. NHMUK PI OR 35337(1), original of Klipstein (1844, pl. 14, fig. 32), herein designated as lectotype of *Pleurotomaria bicarinata* Klipstein from the St. Cassian Formation.

Discussion. The type lot of *Pleurotomaria bicarinata* Klipstein, 1844 consists of two specimens that are not conspecific. The specimen resembling the original figures of Klipstein (1844, pl. 14, fig. 32a–b) is selected as the lectotype. The lectotype is a poorly preserved specimen with a spine/node bearing peripheral carina and an angular transition from whorl face to base. Among the Cassian gastropods, one species shows a similar morphology: *Trochus zardinii* Leonardi & Fiscon, 1947 (Leonardi & Fiscon 1947, p. 47, pl. 1, fig. 11a–d; 1959, pl. 2, fig. 16; Zardini 1978, pl. 12, figs 1–2), which, however, differs in having a circumumbilical carina and a slightly higher spire. At present we tentatively assign *Pleurotomaria bicarinata* to *Schizogonium* due to the spine bearing peripheral carina and the morphology of its base. If it represents a *Schizogonium*, then its selenizone is situated subsuturally. No *Schizogonium* specimen similar to the lectotype has ever been reported from the St. Cassian Formation; therefore, it is considered as a distinct species. *Schizogonium laubei* Kittl, 1891 (the original of Kittl 1891, pl. 5, fig. 7, NHMW 1899/0005/0132, is figured here in Fig. 46 and is designated as lectotype of *Schizogonium laubei* herein) has a similar subsutural selenizone, but it has very prominent spines.

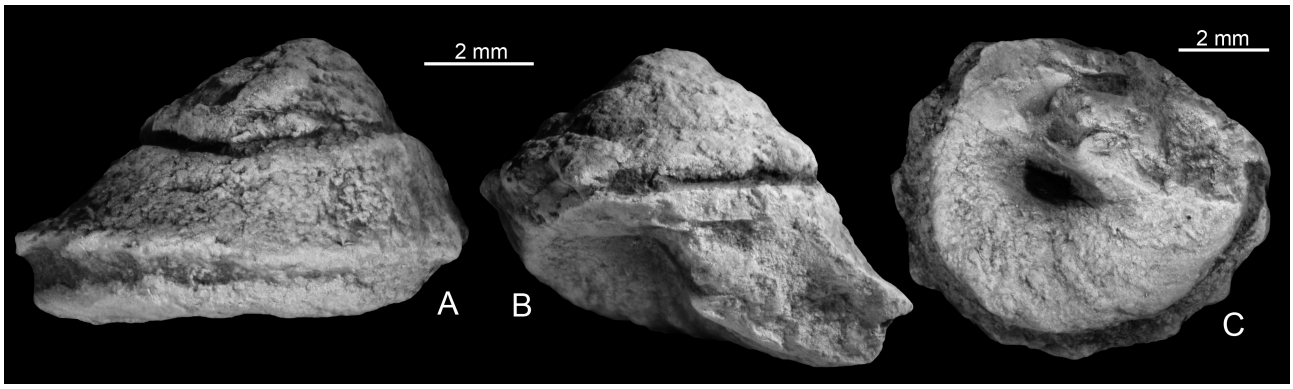

FIGURE 45. *Schizogonium*? *bicarinatum* (Klipstein, 1844); **A–C.** Lectotype, NHMUK PI OR 35337(1), original of Klipstein (1844, pl. 14, fig. 32), St. Cassian Formation.

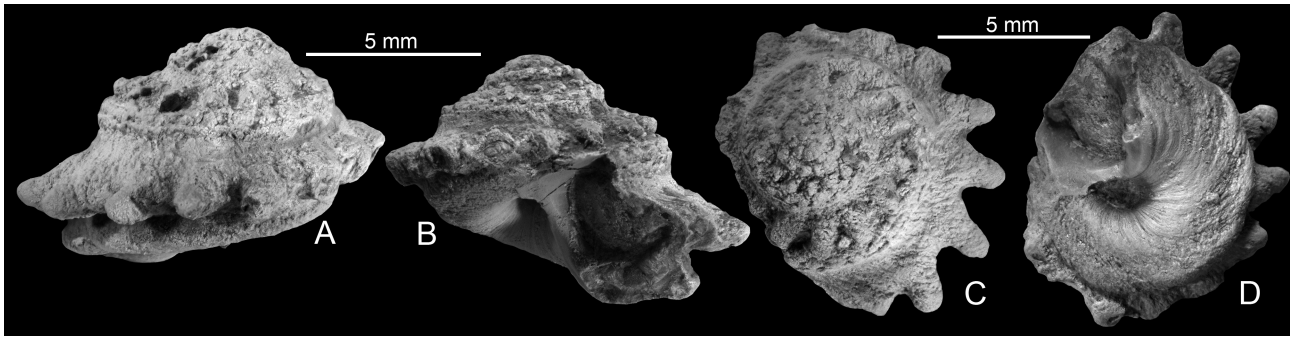

FIGURE 46. *Schizogonium laubei* Kittl, 1891; **A–D.** Lectotype, NHMW 1899/0005/0132 (original of Kittl 1891, pl. 5, fig. 7), St. Cassian Formation.

Genus *Pseudowortheniella* Bandel, 2009

Type species. *Worthenia rarissima* Kittl, 1891, St. Cassian Formation, Carnian, South Tyrol, Italy; original designation.

Discussion. Bandel (2009) stated that *Pseudowortheniella* and *Schizogonium* are closely related, but nevertheless

he erected a family, Pseudowortheniellidae and differentiated it from Schizogoniidae by the absence of spines. Not all *Schizogonium* species develop prominent spines, and some even lose them during ontogeny (Fig. 37G–P). We agree with Bandel (2009) that they are closely related and place *Pseudowortheniella* in family Schizogoniidae. Thus, Pseudowortheniellidae falls into the synonymy of Schizogoniidae.

Pseudowortheniella rarissima (Kittl, 1891)

Fig. 47

*1891	*Worthenia rarissima* Kittl n. f.—Kittl, p. 193, pl. 3, figs 8–9.
1959	*Worthenia rarissima* Kittl—Leonardi & Fiscon, p. 16, pl. 1 figs 21a–b.
1978	*Worthenia rarissima* (Kittl)—Zardini, p. 20, pl. 5, figs 11, 14; pl. 6, fig. 1.
non 1978	*Worthenia rarissima* (Kittl) f. juvenile—Zardini, p. 20, pl. 5, figs 15–16.
1978	*Worthenia costata* (Garavello-Spaetti)—Zardini, p. 19, pl. 4, fig. 14; pl. 5, fig. 4.
non 1980	*Worthenia rarissima* (Kittl) f. giovanile—Zardini, p. 3, pl. 1, figs 7a–c.
1985	*Worthenia misurinensis* n. sp.—Zardini, p. 9, pl. 3, figs 3a–c.
1992	*Wortheniella rarissima* (Kittl)—Schwardt, p. 29, pl. 1, figs 1–3.
2009	*Pseudowortheniella rarissima* (Kittl, 1891)—Bandel, pl. 4, figs 50–54.

Material. NHMW 1899/0006/0011 (original of Kittl 1891, pl. 3, figs 8–9) herein designated as lectotype and NHMW 1899/0006/0010/1 from the St. Cassian Formation.

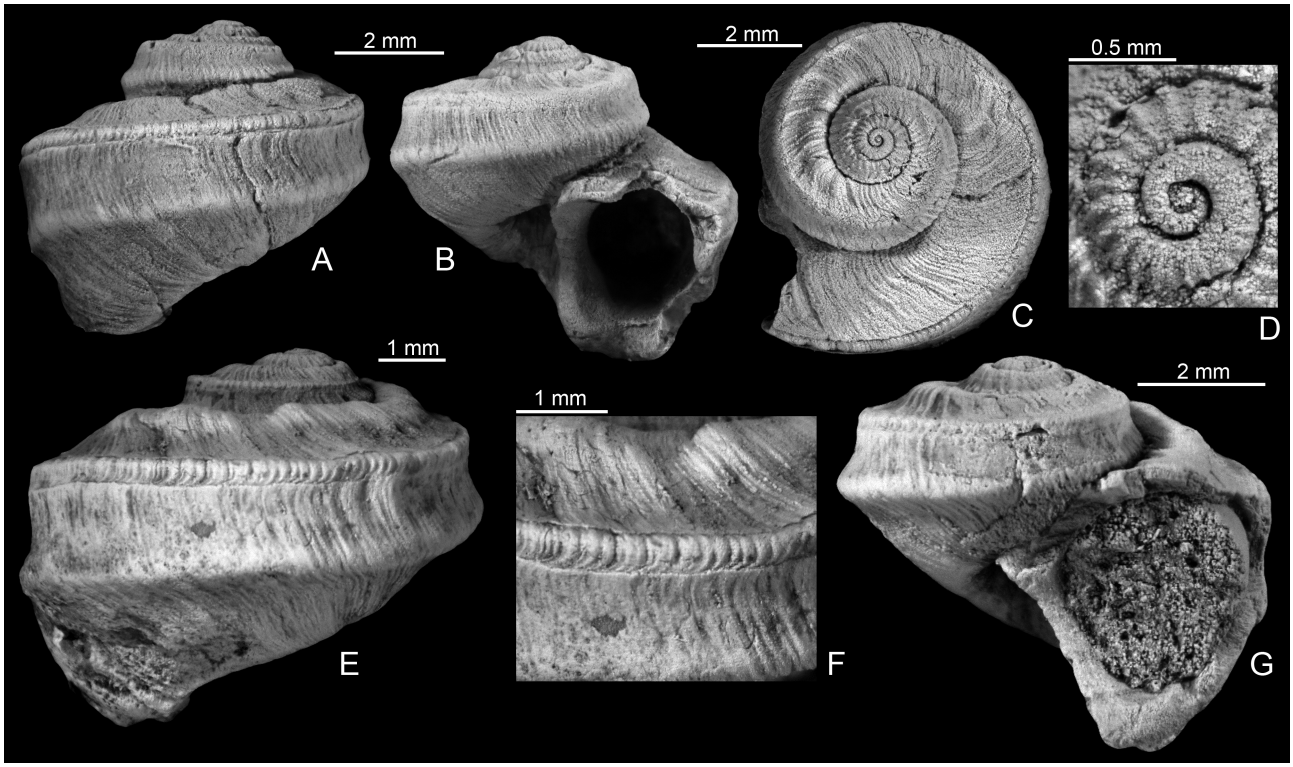

FIGURE 47. *Pseudowortheniella rarissima* (Kittl, 1891); **A–D.** Lectotype, NHMW 1899/0006/0011 (original of Kittl 1891, pl. 3, figs 8–9), St. Cassian Formation; **E–G.** NHMW 1899/0006/0010/1, St. Cassian Formation.

Description. Shell low-spired with blunt apex and angular whorls; lectotype comprises five whorls; protoconch coarsely recrystallized, first whorl with diameter of 0.25 mm; early whorls planispiral; early whorl face of teleoconch convex, ornamented with spiral threads and prominent axial ribs; selenizone onset at the end of third whorl, at mid-whorl; whorl face becomes angular after onset of selenizone; selenizone at whorl angulation, convex with rough lunulae, bordered by sharp, slightly upward bent shell edges; shell angulation at adapical part of selenizone; suture impressed, just below the outer basal edge; whorl face with subsutural furrow and bulge followed by slightly inclining, concave ramp between bulge and selenizone at angulation; ramp ornamented with fine spiral threads and with prosocline rough growth lines; whorl face below selenizone steeply inclined in fourth whorl, then subparallel to

shell axis in last whorl, ornamented with fine spiral threads and with oblique prosocline rough growth lines; growth lines turn backwards near selenizone; outer basal edge rounded and prominent; base rounded, convex, ornamented in same style as whorl face, phaneromphalous.

Discussion. *Pseudowortheniella rarissima* specimens were generally correctly identified by subsequent authors. The last whorl of the specimen figured by Kittl (1891, pl. 3, figs 8–9, lectotype figured here in Fig. 47A–D) is slightly deflected downwards. The two specimens identified as *Worthenia rarissima* by Zardini (1978, pl. 5, figs 15–16) represent *Rinaldomphalus cassianus* Bandel, 1993b.

Worthenia rarissima Barrande, 1903 (in Perner 1903 pl. 62, figs 11–14; Perner 1907, p. 65) is a junior homonym of *Worthenia rarissima* Kittl, 1891. Frýda (1998) introduced *Eoworthenia* with the type species *Worthenia rarissima* Barrande, 1903. Since the species name is preoccupied, we replace the name *Worthenia rarissima* Barrande, 1903 with *Eoworthenia frydai* nom. nov. herein.

Family Wortheniellidae Bandel, 2009

Emended diagnosis. Shell gradate trochiform with angulated teleoconch whorls; protoconch of vetigastropod type comprising less than one whorl, immersed or on same level with early planispiral teleoconch whorl; spire height moderate to low; selenizone at mid-whorl, at whorl angulation, onset after 2nd whorl; selenizone ornamented with nodes, spines or v-shaped lunulae, occassionally with one or two spiral carinae, sunken concave and un-ornamented in *Bandelium*; early whorl face ornamented with prominent spiral ribs/carinae or reticulate ornament or strong axial ribs, whorl face may have micro-ornament of tiny pustules.

Included genera. *Wortheniella* Schwardt, 1992; *Bandelium* Schwardt, 1992; *Rinaldoella* Bandel, 2009; *Nodocingulum* **gen. nov.**; *Striacingulum* **gen. nov.**

Discussion. Although some species are removed from *Wortheniella* herein and thus also from Wortheniellidae (e.g., *Amplitomaria spuria* (Münster, 1841), *Lineacingulum texturatum* (Münster, 1841)), the diagnosis of Wortheniellidae as given by Bandel (2009) remains essentially unchanged. The oblique orientation of the protoconch was included in the family diagnosis by Bandel (2009) but this feature is not present in all species included. Bandel (2009) reported also "an outer layer with complex crossed acicular structure and inner nacre"—features that are also present in many other Pleurotomariida.

Previously, most wortheniform species with a selenizone located on a median whorl angulation were assigned to *Worthenia* (e.g., Kittl 1891; Yin & Yochelson 1983a; see also Pieroni 2019). Yin & Yochelson (1983a) erected the wortheniform *Humiliworthenia* as a subgenus of *Worthenia* and assigned several Triassic species to *Humiliworthenia* that do not possess a nodose selenizone and have a largely smooth shell. It is uncertain whether the subgenus *Humiliworthenia* is closely related to the Palaeozoic genus *Worthenia* or to the Triassic *Wortheniella* because its early ontogeny is unknown. Several Triassic species that were assigned to *Worthenia* differ from Late Palaeozoic members of *Worthenia* in early ontogeny. The type species of *Worthenia*, *Worthenia tabulata* (Conrad, 1835), has rounded, largely smooth, elevated early teleoconch whorls and the slit is developed from a u-shaped sinus on the convex whorl face (Karapunar *et al*. in press). The whorl angulation, where the selenizone is situated, is formed during later ontogeny. In contrast, the studied Triassic wortheniform species (trochiform Pleurotomariida with selenizone situated at whorl angulation) develop a whorl angulation before the onset of the selenizone and the selenizone appears at the angulation from a v-shaped notch/sinus. None of the studied Triassic species that were previously assigned to *Worthenia* show early ontogenetic teleoconch whorls similar to those of the type species of *Worthenia* from the Carboniferous. Therefore, their assignments to *Worthenia* are rejected. It is not sure whether the Permian species that have been assigned to *Worthenia* really represent this genus, because their early ontogeny is unknown. Some might belong to other Triassic wortheniform genera (e.g., *Nodocingulum* **gen. nov.**, *Wortheniella*).

When Schwardt (1992) erected the genus *Wortheniella*, she separated it from *Worthenia* based on planispiral or depressed coiling of the early whorls. However, Schwardt (1992) did not show that the 'main character' of *Wortheniella* or the *Wortheniella*-group (i.e. planispiral early whorls) was different from similar Late Palaeozoic forms such as *Worthenia*. The claim that the planispiral early whorls of *Wortheniella* are unlike those of Palaeozoic forms was not substantiated by study of Palaeozoic material or citing literature that reports this feature. Ontogenetic change from planispiral coiling of the first whorls to higher-spired in later ones is a widespread feature that is also present in other Triassic genera of Pleurotomariida (e.g., *Sisenna*, *Zygites*, *Schizogonium*). Batten (1966, 1972) reported

planispiral and trochospiral coiling within the individuals of the same *Borestus* species from the Carboniferous and regarded planispiral coiling as insignificant at the generic level (Batten, 1972). Planispiral coiling of the early whorls is common among several members of the largely Palaeozoic Phymatopleuridae (i.e., *Borestus, Dictyotomaria, Discotomaria, Callitomaria*). In addition to forming a depressed "nest" by slightly changing the coiling direction around the protoconch (as was also described by Bandel 2009), *Wortheniella* species differ from *Worthenia* also in having prominent spiral cords in the early teleoconch. Another genus sharing these characters is *Platyworthenia* Chronic, 1952 from the Permian of the U.S.A., which was regarded as a junior synonym of *Worthenia* by Knight *et al*. (1960). *Platyworthenia* might represent the oldest available name and might be substituted for *Wortheniella* (Nützel & Senowbari-Daryan, 1999) but this genus needs to be studied more closely to corroborate this.

Wortheniellidae seem to be more closely related to Pleurotomarioidea (e.g., family Phymatopleuridae) than to Eotomarioidea (e.g., family Eotomariidae) because Wortheniellidae share characters regarding the selenizone (i.e., ornamentation, morphology etc.) with members of Pleurotomarioidea (e.g., *Worthenia*, *Phymatopleura*). However, it cannot be discarded with certainty that Wortheniellidae derived from the eotomarioid family Rhaphistomellidae considering the shared characters between *Wortheniella*, *Sisenna* and *Rhaphistomella*: angulated whorl profile, subsutural nodes, selenizone on whorl angulation. The significance of these morphological characters should be tested with phylogenetic methods, then they can be evaluated with more confidence. The evolutionary relationships discussed in this paper and in previous papers are expert opinions and will be subject of planned phylogenetic analyses.

Wortheniellidae might have given rise to Schizogoniidae via forms like *Bandelium*, which shares the following characters with schizogoniids: strong axial ribs before onset of selenizone and nodular selenizone which is situated high on the whorl face. In *Bandelium ruedigeri* (Schwardt, 1992) and *Bandelium campense* (Zardini, 1980), the selenizone is formed near the adapical suture and shifts abapically during ontogeny and the early teleoconch is ornamented with strong spiral cords. It is noteworthy that *Bandelium*, *Rinaldoella,* some species of *Wortheniella*, *Nodocingulum* **gen. nov.** and *Schizogonium* have a micro-ornament of tiny pustules on the teleoconch. These tiny pustules can only be seen with the aid of SEM and need excellent preservation. Their function or phylogenetic significance is unknown.

The ornamentation of the selenizone and other selenizone characters are usually highly conserved at generic level in Pleurotomariida. This reflects the fact that such characters were commonly used for the diagnoses of genera. In many cases, the same type of selenizone is present in genera of the same family of the order Pleurotomariida (e.g., *Kokenella* and *Zygites*; *Glyptotomaria* and *Dictyotomaria*; *Pleurotomaria* and *Obornella*) as also previously noted by Batten (1967). However, the ornamentation of the selenizone seems to be highly variable between the species of wortheniellid genera (e.g., *Nodocingulum granulosum* with thread-like lunulae, *Nodocingulum cirriformis* with short spines formed by notches, *Nodocingulum coronatum* with nodes). The type species of *Wortheniella*, *Wortheniella coralliophila* (Kittl, 1891) (lectotype figured here in Fig. 48A–C), is ornamented with strong spiral carinae or cords before the onset of the selenizone and its protoconch is immersed (Schwardt 1992, pl. 7, figs 1–2; also see Fig. 48I–S). *Wortheniella canalifera* (Münster, 1841) has a similar early teleoconch morphology. While the selenizone has one spiral carina in *W. coralliophila* and *W. canalifera*, the selenizone of *Wortheniella tenera* Schwardt, 1992 has two carinae. Similar to *W. tenera*, *Striacingulum toulai* (Kittl, 1891, figured here in Fig. 70) is ornamented with strong spiral cords in the early ontogeny and develops two spiral carinae on its selenizone; but unlike the above discussed *Wortheniella* species its whorl face is ornamented with strong axial ribs and additional two spiral carinae/crests in later whorls. *Nodocingulum furcatum* (Kittl, 1891, figured here in Fig. 64A–B; = *Pleurotomaria beaumonti* Klipstein, 1844, figured here in Fig. 64E–G) shows a bicarinate selenizone as well. However, unlike *Striacingulum toulai* and *Striacingulum cancellatocingulatum*, whorl face of *N. furcatum* lacks a narrow shoulder formed by a subsutural carina and a strong spiral carina on its lateral whorl face.

Species of *Nodocingulum* **gen. nov.** generally do not have an immersed protoconch, but immersed protoconchs were found in some specimens (e.g., Fig. 60G–K, 63Q–T). They are generally relatively low-spired compared to members of other wortheniellid genera, and they form prominent spines, nodes or prominent lunulae on the selenizone. The selenizone of *Nodocingulum* is situated on a whorl angulation and develops from a v-shaped notch.

The type species of *Rinaldoella* Bandel, 2009, *Wortheniella rinaldoi* Schwardt, 1992, has a concave selenizone lacking any nodes or spines (Fig. 72). Its protoconch is immersed and it has prominent spiral cords in the early teleoconch. The other species included in *Rinaldoella* by Bandel (2009) do not share the same early teleoconch

morphology; therefore, they do not belong to *Rinaldoella*. The early shell of *Rinaldoella* has three thick spiral cords before the onset of the selenizone and abruptly develops a u-shaped slit. *Nodocingulum joannisaustriae* (Klipstein, 1844) and *Nodocingulum muensteri* (Klipstein, 1844) develop a reticulate ornament and an angulation instead of strong spiral cords in the early teleoconch unlike *Wortheniella* and *Rinaldoella*. They also show the characteristic selenizone formation of *Nodocingulum* i.e., a gradual slit formation from a v-shaped sinus on the whorl angulation; therefore, *Pleurotomaria muensteri* Klipstein and *Pleurotomaria johannisaustriae* Klipstein are removed from *Rinaldoella* and are placed in *Nodocingulum*. *Nodocingulum*? *subtilis* (Kittl, 1891) (specimen figured by Kittl 1891, pl. 3, fig. 14, NHMW 1899/0007/0005, herein designated as lectotype of *Worthenia subtilis* Kittl, figured here in Fig. 68) is similar to *Rinaldoella rinaldoi* regarding its later teleoconch ornament, but *Nodocingulum*? *subtilis* has spines in the early teleoconch and has a higher whorl expansion rate. *Rinaldoella* is characterized by a strong spiral ornamentation on its early and late whorls. Its type species *R. rinaldoi* has long been known only from a single specimen, which has a concave, sunken selenizone unlike in any other wortheniellid genus. A new *R. rinaldoi* specimen from Zardini's collection is figured herein (Fig. 72).

Genus *Wortheniella* Schwardt, 1992

Type species. *Worthenia coralliophila* Kittl, 1891, St. Cassian Formation, Carnian, South Tyrol, Italy; original designation.

Emended diagnosis. Shell gradate trochiform with angulated teleoconch whorls; protoconch comprising less than one whorl, immersed or on same level with early planispiral teleoconch whorl; spire height moderate; first teleoconch whorls ornamented with prominent spiral ribs/carinae; selenizone on whorl angulation at mid-whorl, onset after 3rd whorl; selenizone smooth or with v-shaped crest-like lunulae, with one or two spiral carinae; whorl face largely smooth, ornamented with subsutural nodes, occasionally with spiral threads or cords.

Discussion. According to the original diagnosis given by Schwardt (1992), the genus comprises species with a gradate spire having one or two angulations, planispiral early whorls, a selenizone situated at mid-whorl, and a spiral ornamentation. The species composition of the genus was modified by Bandel (2009) and is further revised herein. As discussed above in detail, planispiral early whorls are not a distinguishing character alone and having an angulation at mid-whorl is shared by many other wortheniform genera. In addition to the planispiral early whorls and the two angulations it can be added that the first two whorls are ornamented with spiral cords/angulations and small pustules; the selenizone has one or two carinae and faint, crest-like lunulae, the whorl surface is largely smooth, with subsutural nodes and spiral cords or threads, axial ornament is absent or faint.

Wortheniella coralliophila (Kittl, 1891)

Fig. 48

*1891	*Worthenia coralliophila* Kittl n. f.—Kittl, p. 189, pl. 2, fig. 27.
1907	*Worthenia coronata* var. *plicosa* Kittl—Broili, p. 77, pl. 6, fig. 26.
1978	*Wortheniella coralliophila*—Zardini, p. 19, pl. 4, figs 8–9.
1992	*Wortheniella coralliophila* (Kittl, 1891)—Schwardt, p. 46, pl. 7, figs 1–2.
2009	*Wortheniella coralliophila* (Kittl, 1891)—Bandel, pl. 5, figs 66–70.
2009	*Wortheniella subpunctata* (Laube, 1868)—Bandel, pl. 5, figs 71–73 (non fig. 74).
non 2014	*Wortheniella coralliophila* (Kittl 1891)—Nützel & Kaim, p. 409, figs 4a–b.

Material. NHMW 1899/0006/0008 (original of Kittl, 1891, pl. 2, fig. 27) herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG 1903 IX 327 (original of Broili 1907, pl. 6, fig. 26), 1903 IX 1037 from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. PZO 13685 from Prato Piazza, St. Cassian Formation. MPRZ 2021 1–031, MPRZ 2021 1–038 from Misurina, St. Cassian Formation.

Description. Shell trochiform to conical, with weakly gradate whorl profile; first two whorls planispiral with nested, immersed protoconch; later whorls dextral trochospiral; protoconch 0.18 mm wide, ornamented with minute tubercles, some of which irregularly arranged in spiral lines; first teleoconch whorl with two spiral cords, which become whorl angulations in second teleoconch whorl, gradually shifting downward as coiling turns from planispiral to trochospiral; first two teleoconch whorls ornamented additionally with spiral threads and small pustules;

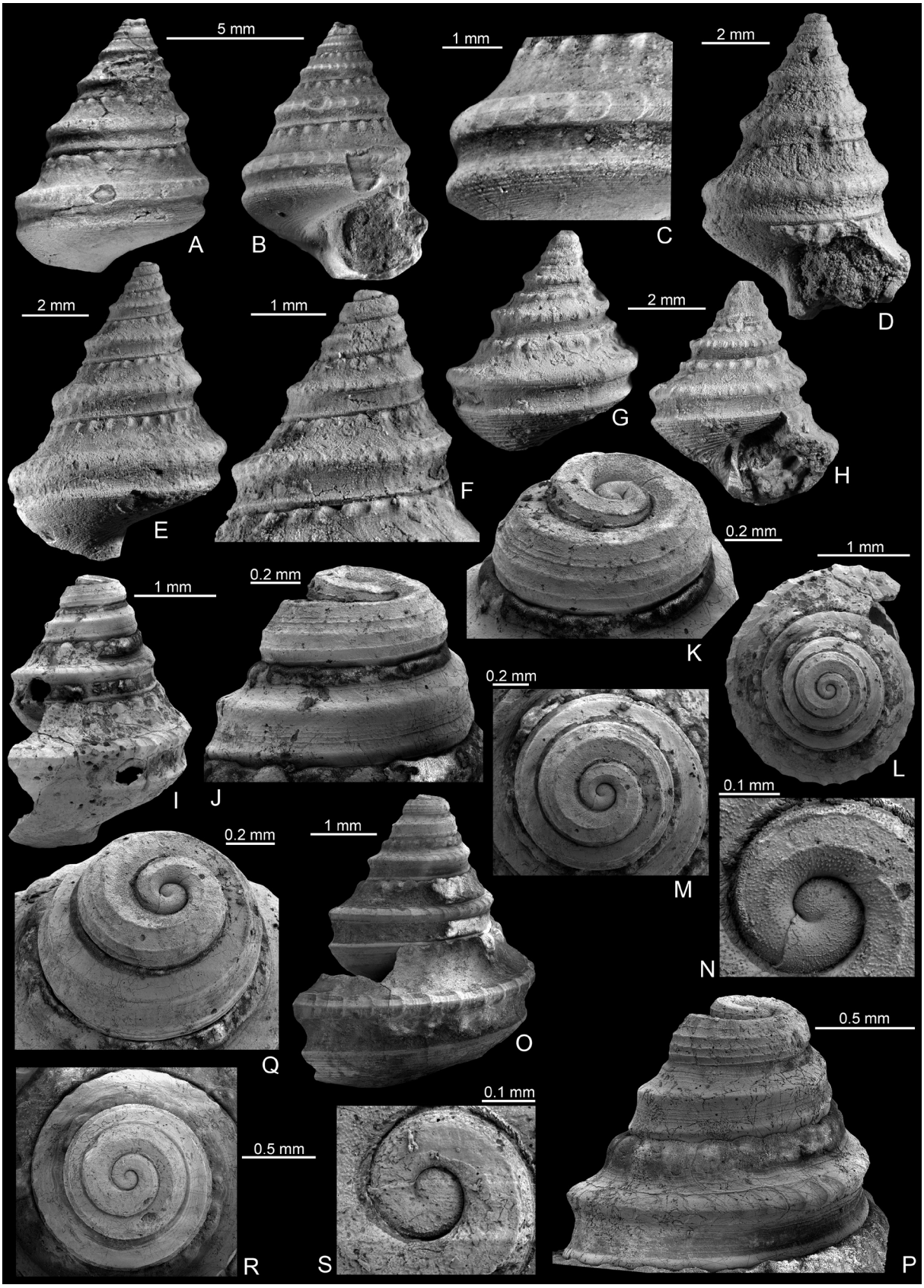

FIGURE 48. *Wortheniella coralliophila* (Kittl, 1891); **A–C.** Lectotype, NHMW 1899/0006/0008 (original of Kittl, 1891, pl. 2, fig. 27), St. Cassian Formation; **D–F.** PZO 13685, Prato Piazza, St. Cassian Formation; **G–H.** SNSB-BSPG 1903 IX 327 (original of Broili 1907, pl. 6, fig. 26), Pachycardientuffe, Upper Ladinian, Seiser Alm; **I–N.** MPRZ 2021 1–031, Misurina, St. Cassian Formation, SEM image; **O–S.** MPRZ 2021 1–038, Misurina, St. Cassian Formation, SEM image.

subsutural nodes and selenizone appear at transition from 3rd whorl to 4th whorl; ramp steeply inclining, concave, ornamented with prominent subsutural nodes, faint spiral threads and bearing prosocyrt growth lines; selenizone strongly convex with median angulation, situated at median carina, relatively wide covering 18 % of whorl face, ornamented with regularly spaced, crest-like lunulae, bordered by spiral cords; lateral whorl face narrower than ramp, only slightly wider than half width of whorl ramp, concave, lying subparallel to shell axis, ornamented with faint spiral threads and bearing prosocyrt growth lines; transition to base with angulated outer basal edge; base anomphalous, convex, ornamented with spiral threads and cords and with opisthocyrt growth lines; aperture subrounded, as wide as high.

Discussion. The specimen assigned to *Wortheniella coralliophila* by Nützel & Kaim (2014, p. 409, figs 4a–b) is assigned to *Wortheniella klipsteini* **sp. nov.** (see discussion below).

Wortheniella canalifera (Münster, 1841)

Fig. 49

*1841	*Pleurotomaria canalifera*—Münster, p. 111, pl. 12, fig. 4.
1844	*Pleurotomaria subplicata*—Klipstein, p. 167, pl. 10, fig. 27.
1844	*Pleurotomaria subpunctata*—Klipstein, p. 167, pl. 10, fig. 28.
1850	*Trochus mineus* d'Orb., 1847—d'Orbigny, p. 190, no. 270.
1850	*Turbo subpunctatus* d'Orb., 1847—d'Orbigny, p. 192, no. 327.
1850	*Pleurotomaria subplicata* Klipstein, 1844—d'Orbigny, p. 195, no. 392.
1868	*Pleurotomaria canalifera* Münster—Laube, p. 81, pl. 27, fig. 4.
non 1868	*Pleurotomaria subpunctata* Klipstein—Laube, p. 59, pl. 28, fig. 5 [non *Pleurotomaria subpunctata* Klipstein, 1844 = *Wortheniella canalifera* (Münster, 1841)].
1870	*Turbo silenus* Laube—Laube, p. 24, pl. 32, fig. 5.
1891	*Worthenia canalifera* Münster sp.—Kittl, p. 188, pl. 2, figs 23–26.
1891	*Worthenia subplicata* Klipstein sp.—Kittl, p. 191.
1907	*Worthenia canalifera* (Münster)—Broili, p. 80, pl. 6, fig. 32.
non 1914	*Worthenia canalifera* Muenst. sp.—Scalia, p. 9, pl. 1, figs 33a–c.
?1959	*Worthenia* cfr. *canalifera* Münster—Leonardi & Fiscon, p. 15, pl. 1, fig. 20.
non 1978	*Worthenia canalifera* f. typica (Münster)—Zardini, p. 19, pl. 5, fig. 1–2.
non 1978	*Worthenia* cfr. *canalifera* (Münster) n. f. *faloriae*—Zardini, p. 19, pl. 5, fig. 3.
non 1986	*Worthenia* cf. *canalifera* Münster, 1843—Batten & Stokes, p. 6, fig. 4.
1992	*Wortheniella canalifera* (Münster, 1841)—Schwardt, p. 46, pl. 8, fig. 3 {non fig. 2).

Material. SNSB-BSPG AS VII 1223 (original of Münster 1841, pl. 12, fig. 4) herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG 1903 IX 338 (original of Broili 1907, pl. 6, fig. 32), 1903 IX 1035 (additional material of Broili 1907: 3 specimens) from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. SNSB-BSPG 1964 XVII 196 from the St. Cassian Formation. NHMUK PI OR 35346(1), original of Klipstein (1844, pl. 10, fig. 27) from the St. Cassian Formation, herein designated as lectotype of *Pleurotomaria subplicata* Klipstein. NHMUK PI OR 35363(1), original of Klipstein (1844, pl. 10, fig. 28) from the St. Cassian Formation, herein designated as lectotype of *Pleurotomaria subpunctata* Klipstein.

Description. Shell trochiform; lectotype comprises about 6 whorls (early whorls are encrusted), 10.1 mm high, 6.9 mm wide; spire gradate with angulated whorl face; suture slightly incised; ramp concave, steeply inclined, with prosocline/prosocyrt growth lines; selenizone smooth, broad, with angulation (in the middle of the selenizone or near its adapical border) forming median angulation of whorl face, without visible lunulae but with u-shaped growth lines; whorl face ornamented with small subsutural nodes; whorl face below selenizone concave, lying parallel to shell axis, with prosocyrt growth lines; base rounded, convex with angulated outer basal edge, with umbilical chink, ornamented with fine spiral cords and with opisthocyrt growth lines; aperture slightly higher than wide, with angulated outer lip, rounded basal lip and slightly convex inner lip.

Discussion. Laube (1868) considered *Pleurotomaria concava* Münster, 1841 (Münster 1841, pl. 12, fig. 7) to represent a synonym of *Wortheniella canalifera*. As already reported by Laube (1868) and Kittl (1891), the type material of *Pleurotomaria concava* is not present at the BSPG. Therefore, Laube's (1868) synonymization can neither be confirmed nor rejected.

The specimens assigned to *Worthenia canalifera* by Zardini (1978, pl. 5, figs 2–3) and to *Worthenia* sp. (Zardini

1978, pl. 6, fig. 3) are not pleurotomariidan gastropods but probably represent *Eunema badiotica* (Kittl 1891, pl. 2, fig. 35; Hausmann *et al*. 2021, fig. 5). The specimen figured by Zardini (1978, pl. 5, fig. 1) as *Worthenia canalifera* has a narrower ramp and lateral whorl face. This specimen represents *Wortheniella klipsteini* **sp. nov.**

We have examined the specimens assigned to *Wortheniella subpunctata* (Laube, 1868) by Schwardt (1992) including the figured specimen (Schwardt 1992, pl. 8, fig. 1), which are housed in the NHMW, and identify them as *Wortheniella klipsteini* **sp. nov.** (see also discussion of *Nodocingulum*? *turris* **sp. nov.**).

The late teleoconch whorls of *Wortheniella canalifera* differ from that of *Wortheniella coralliophila* (Kittl, 1891) in having a more convex base, a wider lateral whorl face, a less pronounced median carina where the selenizone is situated, lacking nodes on the selenizone and in having more and less prominent subsutural nodes.

Worthenia cf. *canalifera* as illustrated by Batten & Stokes (1986, fig. 4) from the Smithian (Early Triassic) of the Sinbad Limestone (Utah, U.S.A.) certainly does not represent this species; its spiral ribs are much stronger and it has a much stouter shape. Batten & Stokes (1986) mentioned that their specimen probably represents a new species and we agree with this view.

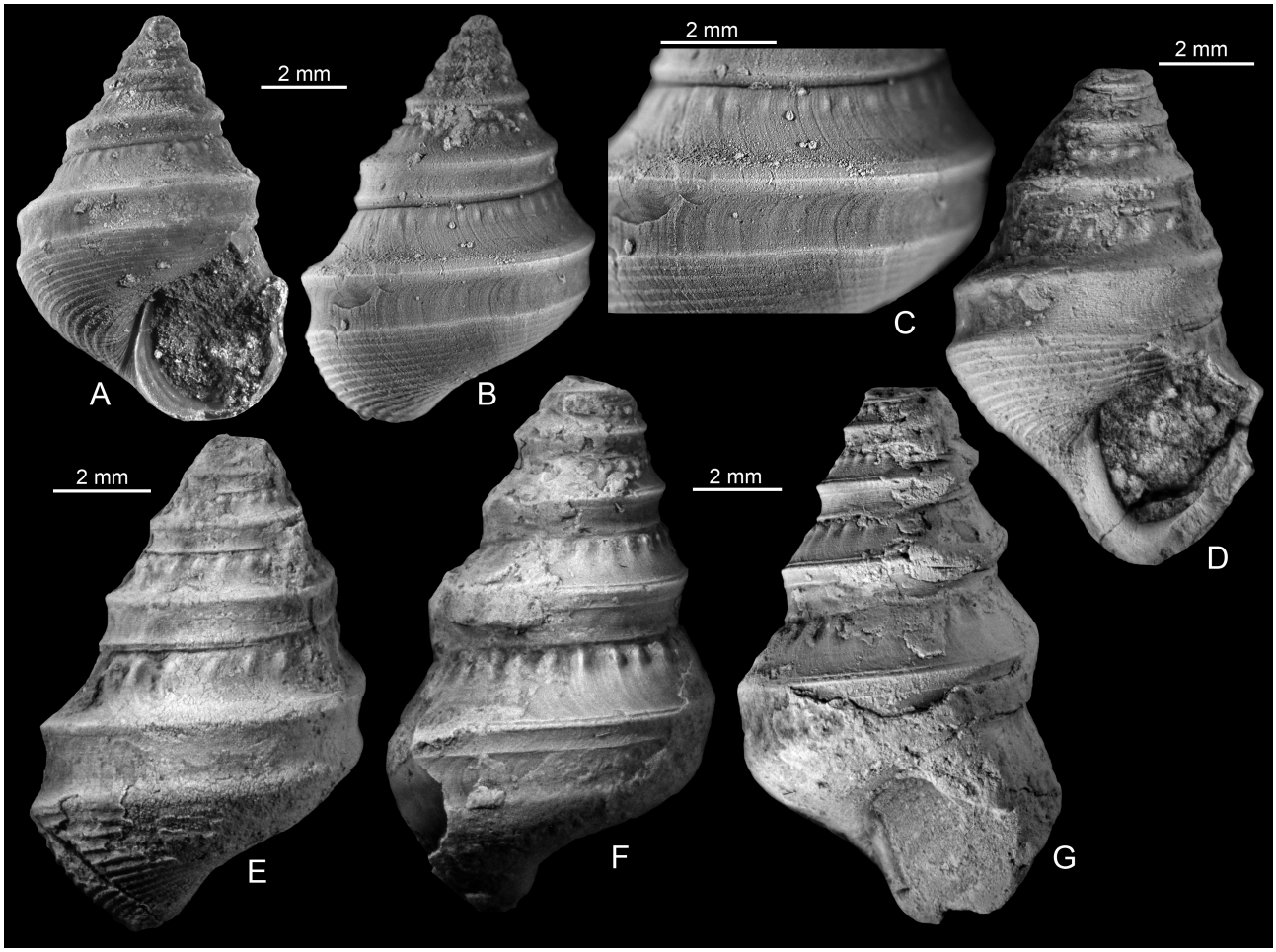

FIGURE 49. *Wortheniella canalifera* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1223 (original of Münster 1841, pl. 12, fig. 4), St. Cassian Formation; **D–E.** Lectotype of *Pleurotomaria subpunctata* Klipstein, 1844, NHMUK PI OR 35363(1), original of Klipstein (1844, pl. 10, fig. 28), St. Cassian Formation; **F–G.** Lectotype of *Pleurotomaria subplicata* Klipstein, 1844, NHMUK PI OR 35346(1), original of Klipstein (1844, pl. 10, fig. 27), St. Cassian Formation.

***Wortheniella klipsteini* sp. nov.**

Fig. 50

LSID. urn:lsid:zoobank.org:act:5B9065B8-F66F-4F80-9A04-9384B9AF01EF

1978 *Worthenia canalifera* f. typica (Münster)—Zardini, p. 19, pl. 5, fig. 1 (non fig. 2).
1978 *Worthenia venusta* (Münster)—Zardini, p. 21, pl. 6, fig. 12 (non pl. 6, fig. 6; pl. 39, fig. 8).

1978 forma di passaggio tra *Worthenia coralliophila* (Kittl) e *Worthenia subgranulata* (Laube)—Zardini, p. 21, pl. 6, figs 4a–b.
1992 *Wortheniella canalifera* (Münster, 1841)—Schwardt, p. 46, pl. 8, fig. 2 (non fig. 3).
?1992 *Wortheniella subpunctata* (Laube, 1868)—Schwardt, p. 48, pl. 8, fig. 1.
2014 *Wortheniella coralliophila* (Kittl 1891)—Nützel & Kaim, p. 409, figs 4a–b.
2014 *Wortheniella* cf. *canalifera* (zu Münster 1841)—Nützel & Kaim, p. 409, figs 4c, 4d–h.

Derivation of name. After August von Klipstein, who recognized this species but did not publish its name.

Holotype. NHMUK PI OR 35351.

Type locality, age, formation. Italy, South Tyrol, Late Triassic, Early Carnian, St. Cassian Formation.

Material. NHMUK PI OR 35351, holotype from the St. Cassian Formation. MPRZ 2021 1–018, MPRZ 2021 1–027 from Campo, St. Cassian Formation.

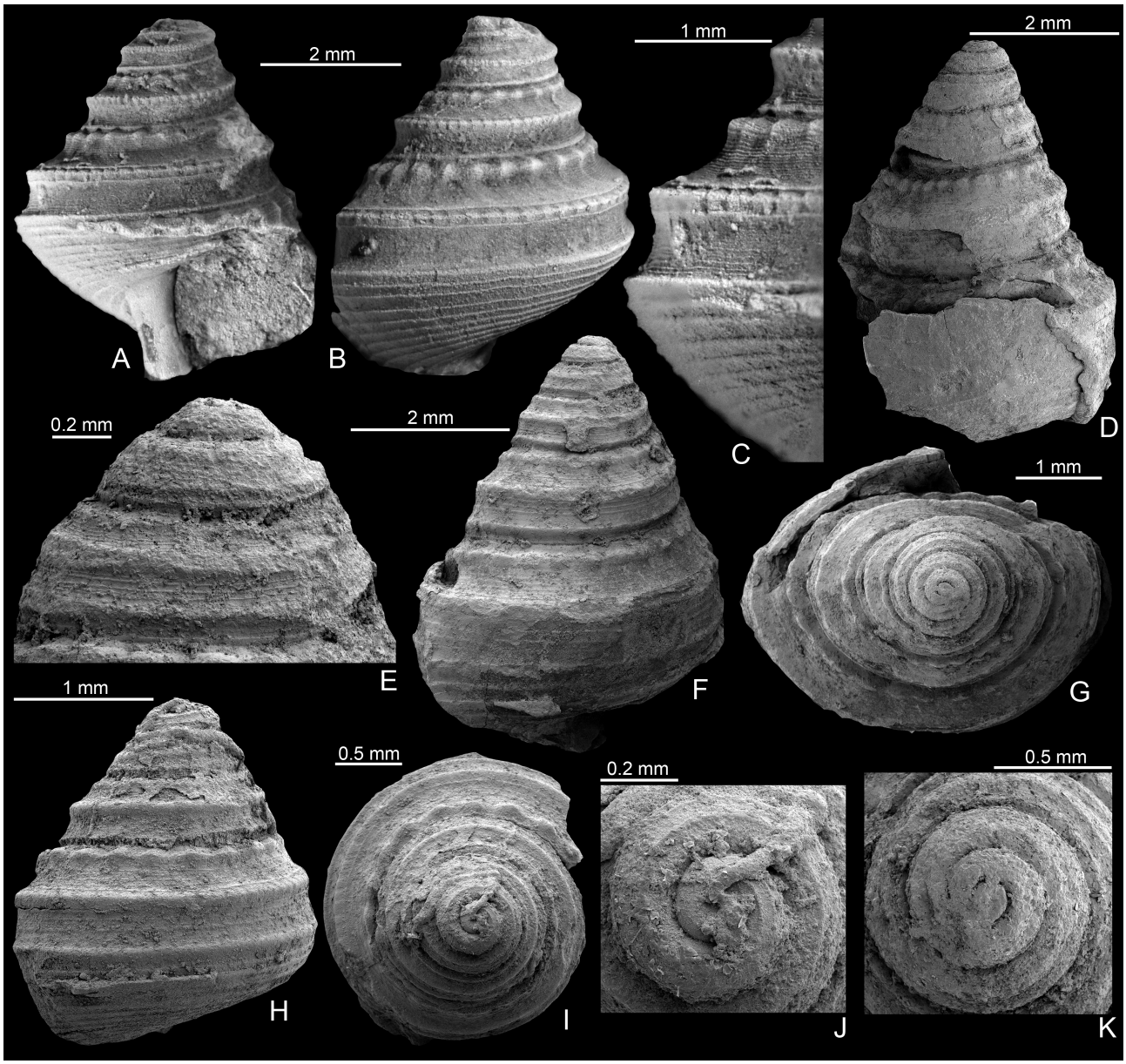

FIGURE 50. *Wortheniella klipsteini* **sp. nov.**; **A–C.** Holotype, NHMUK PI OR 35351, St. Cassian Formation; **D–G.** MPRZ 2021 1–027, Campo, St. Cassian Formation, SEM image; **H–K.** MPRZ 2021 1–018, Campo, St. Cassian Formation, SEM image.

Description. Shell trochiform, with gradate whorl profile and angulated whorl face; holotype comprising 4 whorls, early whorls broken off; suture shallow, incised; ramp concave, steeply inclined, with prosocline growth

lines; ramp ornamented with a row of subsutural nodes and fine, regularly spaced spiral threads; selenizone angular, situated at median angulation, ornamented with imbricated v-shaped lunulae, bordered by simple shell edges; whorl face below selenizone concave, lying subparallel to shell axis, ornamented with fine regularly spaced spiral threads; sharp outer basal edge represents whorl periphery; base convex, ornamented with spiral cords and bearing opisthocyrt growth lines, anomphalous; aperture broken off, with slightly convex inner lip.

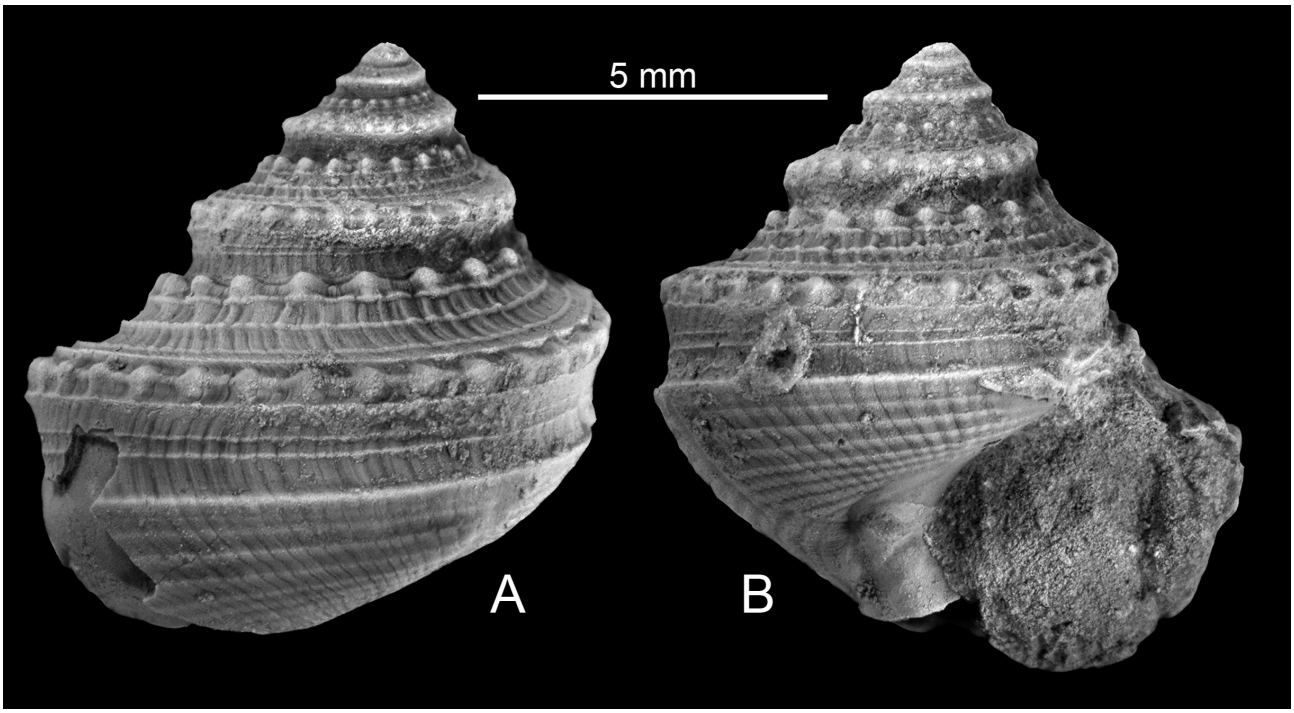

FIGURE 51. *Wortheniella*? *liebeneri* (Kittl, 1891); **A–B.** Lectotype, GBA 1894/005/0004, 4350, original of Kittl (1891, pl. 2, fig. 16), St. Cassian Formation.

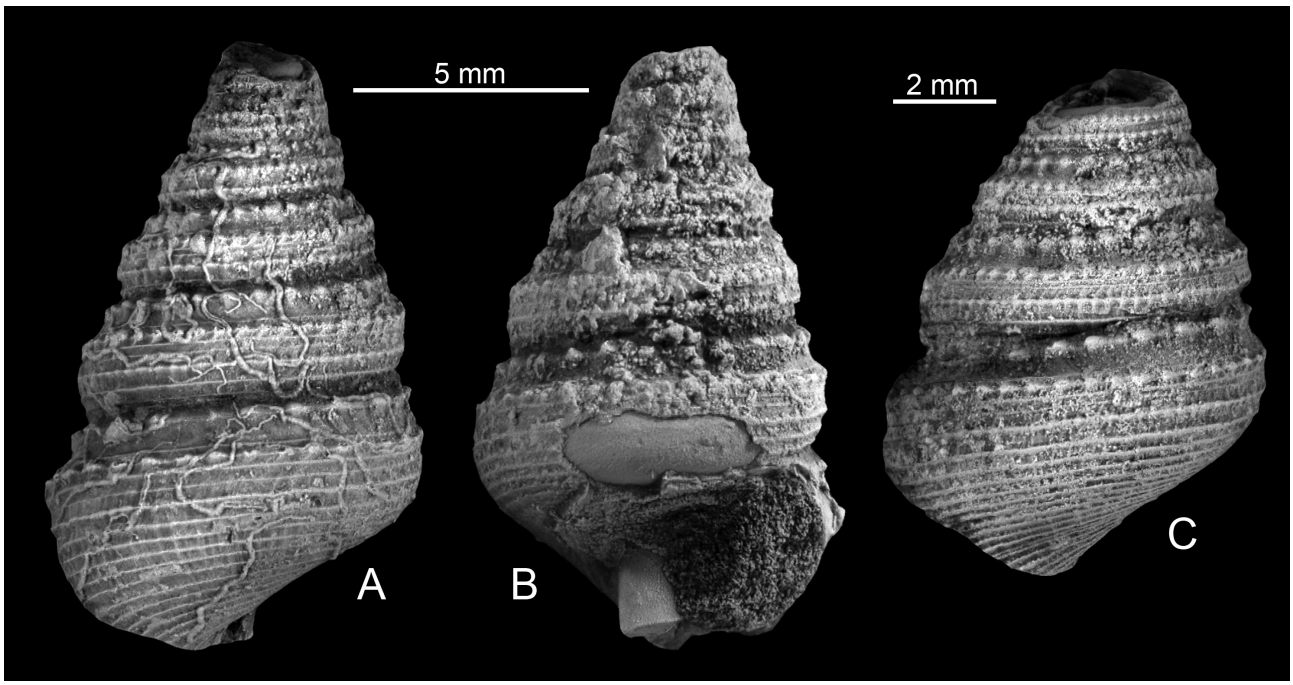

FIGURE 52. *Wortheniella*? *margaritacea* (Laube, 1868); **A–C.** NHMW 1899/0007/0003, original of Kittl (1891, pl. 2, fig. 30), St. Cassian Formation; **D.** NHMW 1865/0009/0040/1, St. Cassian Formation.

Discussion. Klipstein (1844) recognized this species and noted the name "*Pleurotomaria königii*" on a handwritten label (Fig. 1F). *Wortheniella klipsteini* **sp. nov.** differs from *W. canalifera* in having a narrower selenizone with numerous node-like lunulae, a narrower ramp and lateral whorl face and in having an outer basal edge representing the whorl periphery. *Wortheniella coralliophila* (Kittl, 1891) has a wider selenizone with strong and widely spaced lunulae, a narrow but strongly concave lateral whorl face, a rounded outer basal edge and a flatter base. The specimens figured by Zardini (1978, pl. 5, fig. 1, pl. 6, fig. 4) and Nützel & Kaim (2014, figs 4a–d, 4g–h, as *Wortheniella coralliophila* and *W.* cf. *canalifera*) also represent *Wortheniella klipsteini* **sp. nov.** The specimen assigned to *Wortheniella coralliophila* by Nützel & Kaim (2014) has a narrower selenizone than *W. coralliophila* and its selenizone is ornamented with smaller and more numerous lunulae, which are characteristic features of *Wortheniella klipsteini* **sp. nov.** The specimen assigned to *W.* cf. *canalifera* by Nützel & Kaim (2014) has numerous small lunulae; lunulae are absent in the lectotype of *W. canalifera*. *Wortheniella klipsteini* **sp. nov.** differs from *Wortheniella*? *liebeneri* (Kittl, 1891) **comb. nov.** (original of Kittl 1891, pl. 2, fig. 16, GBA 1894/005/0004, 4350, herein designated as lectotype of *Worthenia liebeneri*, figured here in Fig. 51) by having less prominent subsutural nodes and selenizone nodes and in having a basal carina representing the whorl periphery. *Wortheniella*? *margaritacea* (Laube, 1868) **comb. nov.** (original of Kittl, 1891, pl. 2, fig. 30, NHMW 1899/0007/0003, figured here in Fig. 52) is higher-spired, with convex lateral whorl face and additional spiral cords (one of which is nodular) on the lateral whorl face.

Two specimens with preserved early teleoconch from Zardini's collection are figured herein (Fig. 50D–K). These specimens show planispiral, but not nested (immersed), early whorls with spiral cords and therefore *Wortheniella klipsteini* **sp. nov.** has a similar ontogenetic development as other *Wortheniella* species.

Wortheniella paolofedelei sp. nov.

Fig. 53

LSID. urn:lsid:zoobank.org:act:F882F1F7-6C2D-434A-A5BE-C782D8A88D7F

1978	*Wortheniella subpunctata* Laube, 1868—Zardini, pl. 6, fig. 5.
1980	*Wortheniella* cfr. *subpunctata* Laube—Zardini, pl. 1, figs 10–11.
2009	*Wortheniella subpunctata* (Laube, 1868)—Bandel, pl. 5, fig. 74 (non figs 71–73).

Derivation of name. After Paolo Fedele, Cortina d'Ampezzo for his helps in the understanding of the St. Cassian fauna and flora.

Holotype. MPRZ 2021 1–052.

Type locality, age, formation. Campo, Cortina d'Ampezzo, Italy, Late Triassic, Early Carnian, St. Cassian Formation.

Material. MPRZ 2021 1–052 holotype from Campo near Cortina d'Ampezzo.

Description. Shell trochiform, with gradate whorl profile; holotype comprising 5 complete whorls and adapical portion of the 6th whorl; first teleoconch whorl with 7 spiral cords, second whorl with three spiral cords; uppermost two cords shift abapically within third whorl forming median and basal angulations (on outer basal edge) respectively; additional spiral cords, threads and selenizone appear; whorl ramp steeply inclining with narrow shoulder, lateral whorl face subparallel to shell axis with outer basal edge representing periphery; from fourth whorl onward, whorl ramp and lateral whorl face ornamented with broad spiral cords and intercalated spiral threads; spiral cords and threads closely spaced, separated by narrow spiral furrows; subsutural spiral cord forms spirally elongated nodes on last whorls; growth lines oblique prosocline on ramp, prosocline on lateral whorl face; selenizone rounded, onset within third whorl, situated on median angulation, without visible lunulae, bordered by simple shell edges; base anomphalous, convex, ornamented with regularly spaced, flat spiral cords and opisthocyrt growth lines; aperture subrounded, as wide as high.

Discussion. *Wortheniella paolofedelei* **sp. nov.** differs from other *Wortheniella* species by its strong spiral cords. *Wortheniella paolofedelei* **sp. nov.** is only known from the Cortina basin. The ornament pattern of *Wortheniella paolofedelei* **sp. nov.** resembles that of *Sisenna ampezzana* Leonardi-Fiscon, 1947 (Leonardi-Fiscon 1947 p. 44, pl. 1, figs 3a–b; Leonardi-Fiscon, 1959, p. 11, pl. 1, figs 10a–b; Zardini 1978, pl. 3, figs 4–6, 12). However, the general whorl profile and the early whorls of *Sisenna ampezzana* are distinctly different (Fig. 12).

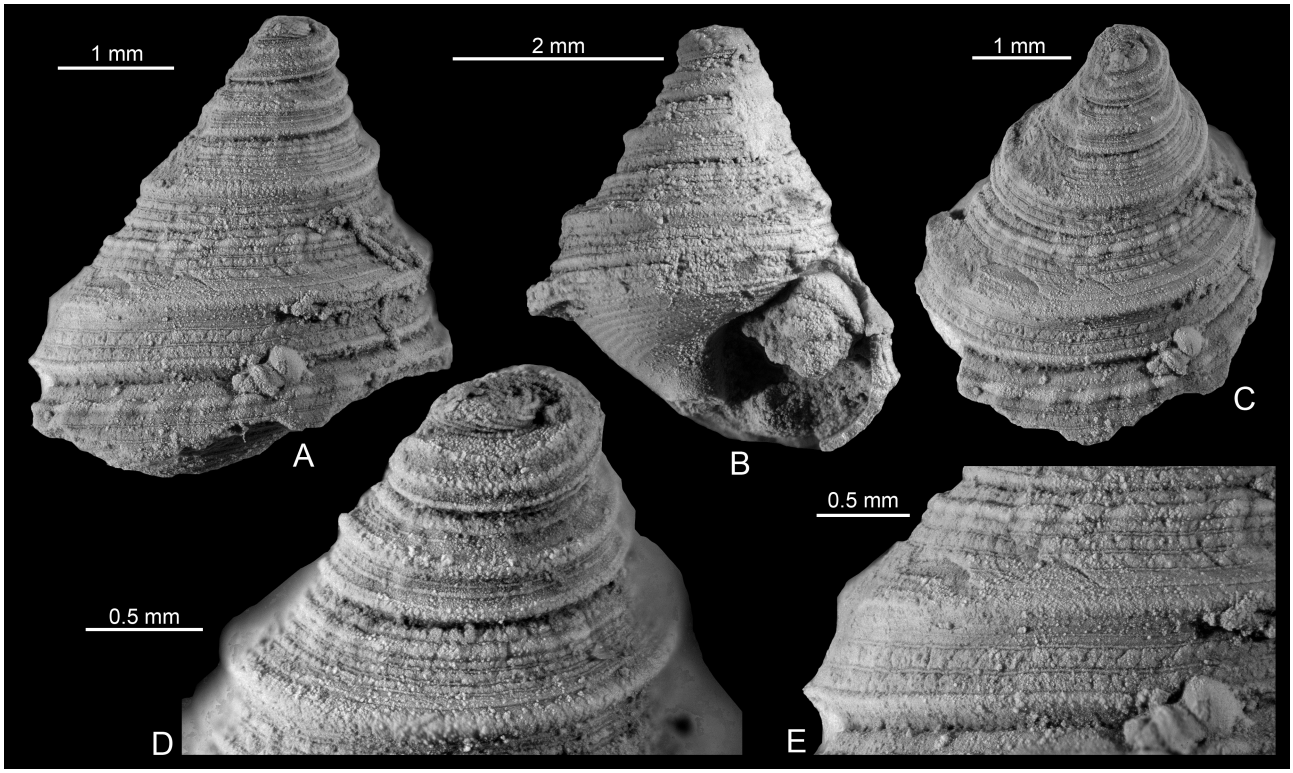

FIGURE 53. *Wortheniella paolofedelei* **sp. nov.**; **A–E.** Holotype, MPRZ 2021 1–052, Campo, St. Cassian Formation.

Genus *Bandelium* Schwardt, 1992

Type species: *Worthenia campensis* Zardini, 1980, St. Cassian Formation, Carnian, Campo, Cortina d'Ampezzo, South Tyrol, Italy; original designation.

Bandelium campense (Zardini, 1980)

Fig. 54

*1980	*Worthenia campensis* n. sp.—Zardini, p. 3, pl. 1, fig. 8.
1992	*Bandelium campense* (Zardini, 1980)—Schwardt, p. 54, pl. 9, fig. 3.
2009	*Bandelium campense* (Zardini, 1980)—Bandel, p. 19, pl. 7, figs 97–100.

Material. MPRZ 4340 C-Z (original of Zardini 1980, pl. 1, fig. 8) from Campo, St. Cassian Formation, reposited in Cortina Museum is herein designated as lectotype. MPRZ 2021 1–030 from Misurina, St. Cassian Formation.

Description. Shell minute, trochiform; largest shell with 4 whorls; first two whorls planispiral with immersed protoconch, later whorls dextral trochospiral; protoconch less than one whorl, 0.18 mm in width; first teleoconch whorl rounded, with strong prosocyrt ribs; second teleoconch whorl with two angulations, ribs form short spines or nodes at intersections with angulations; within 4th whorl (3rd teleoconch whorl) selenizone appears on subsutural angulation; selenizone convex, wide, covers 25 % of whorl face, ornamented with regularly spaced nodes; whorl face above selenizone narrow, concave; whorl face below selenizone with prosocyrt growth lines; whorl face between abapical edge of selenizone and suprasutural carina concave; suprasutural carina represents whorl periphery, ornamented with nodes which decrease in prominence throughout further ontogeny; whorl face between suprasutural carina and basal carina concave; whorl face and selenizone covered with tiny pustules on all teleoconch whorls; basal carina sharp; base convex, anomphalous.

Discussion. The strong axial ribs of the first two teleoconch whorls and the subsutural position of the early selenizone are characteristic features of *Bandelium.* The selenizone of *Bandelium campense* (Zardini, 1980) keeps

its original position high on the whorls throughout ontogeny. The selenizone of *Bandelium ruedigeri* (Schwardt, 1992) gradually shifts downwards during ontogeny and has a wider whorl face above the selenizone. Apart from that *Bandelium ruedigeri* (Schwardt, 1992) has a remarkable shell thickening at its basal lip and a short siphon-like furrow adjacent to it (Fig. 55F–H).

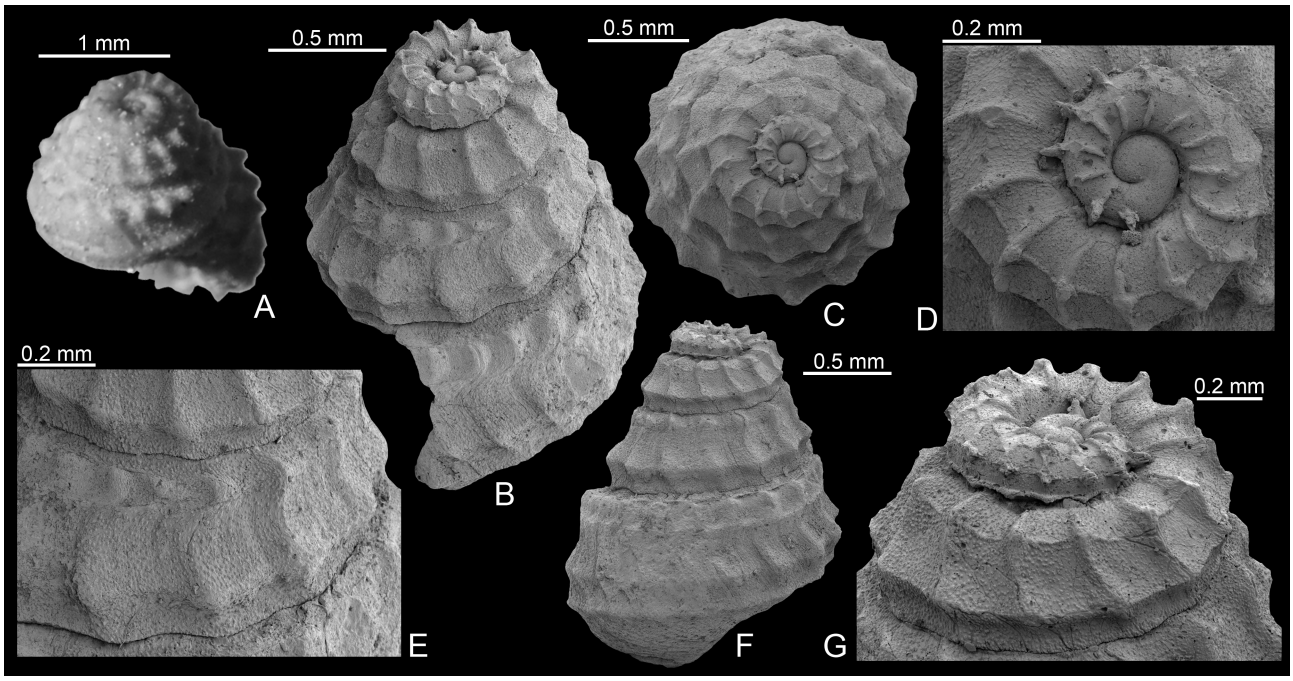

FIGURE 54. *Bandelium campense* (Zardini, 1980); **A.** Lectotype, MPRZ 4340 C-Z (original of Zardini 1980, pl. 1, fig. 8), Campo, St. Cassian Formation; **B–G.** MPRZ 2021 1–030, Misurina, St. Cassian Formation, SEM image.

Genus *Nodocingulum* gen. nov.
LSID. urn:lsid:zoobank.org:act:DFE09C43-AACB-4567-80D0-1D802AF1A85B

Type species. *Pleurotomaria coronata* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. From Latin *nodus*, meaning knot; Latin *cingulum*, meaning band, belt; referring nodular ornamentation on whorl face and selenizone; gender neuter.

Diagnosis. *Worthenia*-like gastropods with gradate spire and sloping ramp; first whorls planispiral with vetigastropod type protoconch of less than one whorl; early whorls with axial riblets and spiral cords forming a reticulate ornament; axial riblets and spiral cords may form nodes at intersections; after one or two teleoconch whorls v-shaped sinus develops at whorl angulation that later becomes selenizone; selenizone situated at angulation, ornamented with distinct lunulae and/or pronounced nodes or spines or with numerous small nodes; shell and aperture approximately as high as wide; teleoconch ornament consists of dominant spiral cords and weaker axial ribs, occasionally with axial folds (prominent axial ribs); intersections of spiral cords and axial ribs may be nodular.

Discussion. *Nodocingulum* **gen. nov.** differs from *Worthenia* by the gradual formation of a slit from a v-shaped sinus situated on the whorl angulation and its selenizone appears after the second teleoconch whorl. Moreover, the selenizone of *Nodocingulum* is ornamented with prominent knobs or notches or with one to two spiral carinae and lunulae. In the type species of *Worthenia*, *Worthenia tabulata* (Conrad, 1835), the early whorls are rounded, trochospirally coiled, the whorl face prior to the formation of the selenizone is rounded convex and the slit is developed from a u-shaped sinus on the convex whorl face within the second teleoconch whorl (at the end of second whorl) (Karapunar *et al*. in press). The early selenizone of *Worthenia* has crescent-shaped lunulae with a median thread. These characters are shared with other phymatopleurid genera such as *Phymatopleura*. On later whorls of *Worthenia*, the selenizone becomes angulated and is ornamented with strong knobs and spiral cords. Crescentic lunulae (characteristic among several phymatopleurid genera) are absent in the Triassic *Nodocingulum*, which have either straight or v-shaped lunulae. The differences in the ontogenetic development of the slit respectively the selenizone, the timing of the development of the whorl angulation and the ornamentation of the selenizone suggest

that several of the wortheniform taxa from the St. Cassian Formation differ considerably from the Palaeozoic genus *Worthenia* and are here united in *Nodocingulum* **gen. nov.**

The early whorls and selenizone development of the Triassic *Humiliworthenia* Yin & Yochelson, 1983a are unknown but its late whorls differ by having a smooth selenizone.

Wortheniella develops strong spiral cords and carinae before the onset of the selenizone, its whorl face is smooth or has a faint spiral ornament and selenizone lacks prominent knobs, notches or distinct lunulae. Axial ornamentation is absent or weak in *Wortheniella* in contrast to *Nodocingulum*, which is ornamented by both, axial and spiral ornamentation. Among the Triassic wortheniform genera, *Striacingulum* **gen. nov.** resembles *Nodocingulum* **gen. nov.** regarding the formation of the selenizone, but it differs by having a subsutural crest, a suprasutural crest on the lateral whorl face and dominant spiral cords before the onset of the selenizone.

Sisenna is much lower-spired genus, the angulation prior to the formation of the selenizone is formed much closer to the adapical suture. *Sisenna* has sinuous (subsutural opisthocline then prosocyrt) growth lines on its ramp, its lateral whorl face has strongly prosocyrt, asymmetric growth lines and it has an evenly rounded transition from the whorl face to the base (instead of an angular transition in *Nodocingulum*).

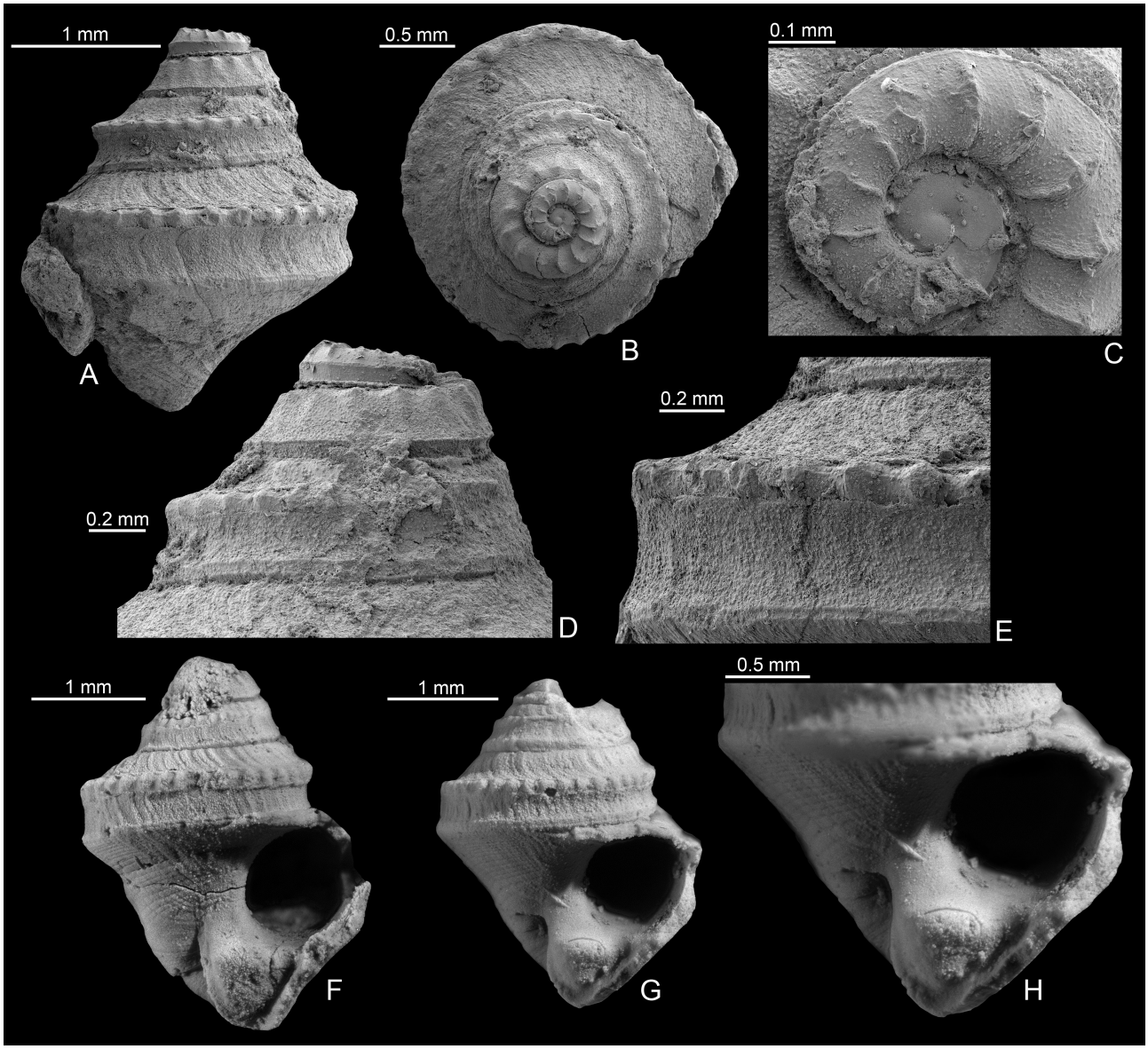

FIGURE 55. *Bandelium ruedigeri* (Schwardt, 1992); **A–E.** MPRZ 2021 1–012, Campo, St. Cassian Formation, SEM image; **F.** MPRZ 2021 1–058, St. Cassian Formation; **G–H.** MPRZ 2021 1–059, St. Cassian Formation.

Pseudoananias **gen. nov.** has a convex to slightly concave selenizone, which is formed at the end of the first teleoconch whorl and the selenizone is much wider when it is first formed than in *Nodocingulum*. *Pseudoananias* does not have distinct lunulae on its selenizone but faint crescentic growth lines. *Lineacingulum* **gen. nov.** has a narrow shoulder, circumumbilical carina, equally spaced axial threads both on its early and late whorl face, a wider selenizone with v-shaped thread-like lunulae and sinuous growth lines on its ramp. *Rinaldoella* differs from *Nodocingulum* by having a strong spiral ornament on the teleoconch before the onset of the selenizone. Moreover, *Rinaldoella* differs by having an abrupt onset of the slit from a u-shaped sinus and a concave, smooth selenizone. *Ananias* has a concave selenizone, smooth, convex teleoconch whorls before the onset of the selenizone and its selenizone appears from a narrow, u-shaped sinus.

Bandel misidentified *Nodocingulum coronatum* specimens as *Pseudoschizogonium elevatum* (Kittl, 1891) (Bandel 2009 pl. 3, figs 42–45; pl. 4, figs 46–47, non 48–49). *Pseudoschizogonium* Kutassy, 1937 resembles *N. coronatum* to some degree. This genus is based on the Late Triassic species *P. turriculatum* from Hungary. This species differs from *N. coronatum* in several respects: it is more low-spired, the ramp is horizontal, the shell lacks spiral cords and the upper angulation bears hollow spines rather than nodes. Judging from Kutassy's (1937) illustration, it does not have a real selenizone and its aperture is wider than high; therefore, *P. coronata* does probably not belong to *Pseudoschizogonium*. Bandel's (2009) diagnosis of the family Pseudoschizogoniidae Bandel, 2009 includes a fine spiral ornament and an aperture that is as high as wide. Both characters are not present in the type species of *Pseudoschizogonium* and hence the diagnosis of this family needs to be changed, preferably after a study of Kutassy's (1937) type material.

Included species. From the Carnian St. Cassian Formation: *Pleurotomaria subcoronata* Münster, 1841, *Pleurotomaria cirriformis* Laube, 1868, *Pleurotomaria granulosa* Klipstein, 1844, *Worthenia bieberi* Kittl, 1891, *Pleurotomaria johannisaustriae* Klipstein, 1844, *Pleurotomaria muensteri* Klipstein, 1844, *Pleurotomaria crenata* Münster, 1841, *Worthenia furcata* Kittl, 1891; the following species are assigned tentatively: *Pleurotomaria angulata* Münster, 1841, *Worthenia subtilis* Kittl, 1891. From the Norian of Italy: *Delphinula pygmaea* Stoppani, 1865 (see Pieroni 2019). From the Norian of Peru: *Worthenia rhombifera* Körner, 1937.

Nodocingulum coronatum (Münster, 1841) comb. nov.

Fig. 56

*1841	*Pleurotomaria coronata*—Münster, p. 109, pl. 11, figs 26a–b.
1850	*Pleurotomaria coronata* Münster, 1841—d'Orbigny, p. 195, no. 389.
1868	*Pleurotomaria coronata* Münster—Laube, p. 80, pl. 27, fig. 3.
1891	*Worthenia coronata* Münster sp.—Kittl, p. 184, pl. 2, figs 3–5.
1891	*Worthenia coronata* Münster sp. var. *depressa* m.—Kittl, p. 184, pl. 2, fig. 6.
1891	*Worthenia coronata* Münster sp. var. *bicoronata* Münster.—Kittl, p. 184, pl. 2, figs 9–10.
1895	*Worthenia coronata* Münster sp.—Böhm, p. 215, pl. 9, fig. 18.
1907	*Worthenia coronata* Mstr.—Broili, p. 77, pl. 6, fig. 25.
1907	*Worthenia subtilis* Klipstein Mscr. sp. (Kittl)—Broili, p. 80, pl. 6, fig. 34.
1907	*Worthenia münsteri* Klipstein—Broili, p. 78, pl. 6, fig. 30 (non fig. 31).
1959	*Worthenia coronata* Münster—Leonardi & Fiscon, p. 14, pl. 1, figs 17a–b.
1959	*Worthenia coronata* Münster var. *depressa* Kittl—Leonardi & Fiscon, p. 15, pl. 1, figs 18a–b.
1978	*Worthenia liebeneri* (Laube)—Zardini, p. 20, pl. 5, figs 9a–d.
non 1978	*Worthenia coronata* f. *bicoronata* (Münster)—Zardini, p. 19, pl. 4, fig. 11a–c.
?1978	*Worthenia coronata* f. typica (Münster)—Zardini, p. 19, pl. 4, figs 13a–d [the specimen figured in pl. 5, fig. 8a].
non 1978	*Worthenia coronata* f. *depressa* (Münster)—Zardini, p. 21, pl. 9, figs 19a–d.
non 1978	*Worthenia coronata* (Münster) n.f. *fasciata*—Zardini, p. 19, pl. 4, fig. 10a–c.
1978	*Worthenia joannisaustriae* (Klipstein)—Zardini, pl. 5, fig. 8a (non figs 8b–c).
non 1980	*Worthenia coronata* f. *bicoronata* Muenster—Zardini, p. 4, pl. 1, figs 13a–d.
1980	cfr. *Worthenia joannisaustriae* (Klipstein)—Zardini, pl. 1, figs 12a–b.
1992	*Wortheniella coronata* (Münster, 1841)—Schwardt, pl. 6, figs 1–2.
2009	*Zygites delphinula* (Laube, 1868)—Bandel, pl. 1, fig. 1.
2009	*Pseudoschizogonium elevatum* (Kittl, 1891)—Bandel, pl. 3, figs 42–45; pl. 4, figs 46–47 (non 48–49).
2014	*Temnotropis fallax* Kittl 1891—Nützel & Kaim, p. 412, figs 4m–p.

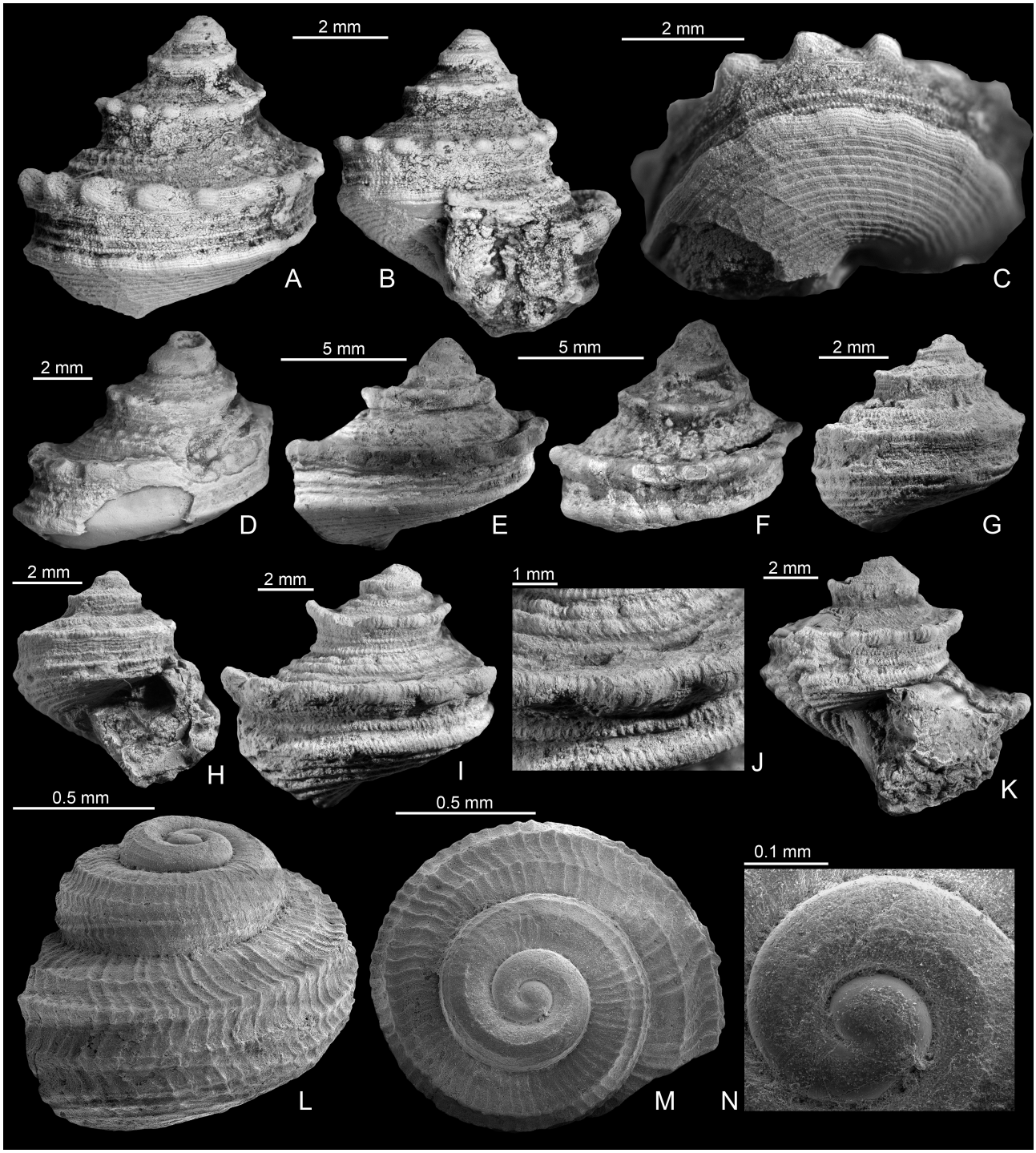

FIGURE 56. *Nodocingulum coronatum* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1217 original of Münster (1841, pl. 11, figs 26a–b), St. Cassian Formation; **D.** Paralectotype, SNSB-BSPG AS VII 2068, St. Cassian Formation; **E.** Lectotype of *Worthenia coronata* var. *depressa* Kittl, 1891, NHMW 1899/0005/0033 (original of Kittl 1891, pl. 2, fig. 6), St. Cassian Formation; **F.** Lectotype of *Worthenia coronata* var. *bicoronata* Kittl, 1891, NHMW 1899/0005/0035/1 (original of Kittl 1891, pl. 2, fig. 10), St. Cassian Formation; **G–H.** SNSB-BSPG 1903 IX 326 (original of Broili 1907, pl. 6, fig. 25), Pachycardientuffe, Upper Ladinian, Seiser Alm; **I–K.** SNSB-BSPG 1903 IX 335 (original of Broili 1907, pl. 6, fig. 34), Pachycardientuffe, Upper Ladinian, Seiser Alm; **L–N.** PZO 13689, juvenile specimen, Misurina, St. Cassian Formation, SEM image.

Material. SNSB-BSPG AS VII 1217 original of Münster (1841, pl. 11, figs 26a–b) herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG AS VII 2068, 2069, 2070 herein designated as paralectotypes from the St. Cassian Formation. SNSB-BSPG AS VII 2074 from the St. Cassian Formation. SNSB-BSPG 1903 IX 326 (original of Broili 1907, pl. 6, fig. 25), SNSB-BSPG 1903 IX 332 (original of Broili 1907, pl. 6, fig. 30), SNSB-BSPG 1903 IX 335 (original of Broili 1907, pl. 6, fig. 34), 1903 IX 1031 (additional material of Broili (1907); 6 specimens, one of which is not *Nodocingulum coronata*), 1903 IX 1047 (additional material of Broili (1907); 2 specimens) from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. SNSB-BSPG 1887 XI 75, specimen figured by Böhm (1895, pl. 9, fig. 18) from the Marmolada Limestone, Ladinian, Italy. NHMW 1899/0005/0035/1 (original of Kittl 1891, pl. 2, fig. 10) herein designated as lectotype of *Worthenia coronata* var. *bicoronata* Kittl; NHMW 1899/0005/0033 (original of Kittl 1891, pl. 2, fig. 6) herein designated as lectotype of *Worthenia coronata* var. *depressa* Kittl; both from the St. Cassian Formation. PZO 13689 from Misurina, St. Cassian Formation.

Description. Shell wortheniform; lectotype comprises about 6 whorls, 6.5 mm high, 6.2 mm wide; protoconch consisting of less than one whorl, smooth, diameter 0.17 mm; first whorl diameter 0.23 mm; first two whorls planispiral with protoconch shallowly immersed; early teleoconch whorls convex, rounded with wide almost horizontal ramp; v-shaped sinus appearing on third teleoconch whorl, giving rise to selenizone later; early teleoconch whorl ornamented with numerous thin axial riblets and few spiral cords of same strength; later teleoconch gradate with angulated whorl face; suture slightly incised; ramp flat, gently inclined; whorl face with angulation at median position; whorl face below median angulation straight, parallel to shell axis; selenizone prominent, elevated, situated on median angulation; selenizone ornamented with prominent, rounded knobs, ca. 15–17 per whorl; knobs especially pronounced on last whorl, pointing in an upward direction; knobs ornamented with spiral threads; ramp ornamented with straight prosocline axial riblets and spiral cords with fine granules at intersections; granules more prominent on subsutural spiral cords; whorl face below selenizone ornamented with spiral cords and slightly prosocyrt axial riblets; whorl face covered with granular micro-ornament; base flatly convex with angulated outer basal edge, opisthocyrt growth lines and ornamented with spiral cords; basal cords more prominent than cords on whorl face; outer basal edge ornamented occasionally with undulations; if present, undulations aligned with interspaces between knobs on selenizone; narrow umbilical chink formed by inner lip; aperture as high as wide, with angulated outer lip, flatly convex basal lip and almost straight inner lip.

Discussion. The lectotype designated herein is well-preserved and is probably the specimen illustrated by Münster (1841). Schwardt (1992) placed *P. coronata* in *Wortheniella*. The juvenile specimens illustrated by Schwardt (1992) do not yet show the typical strong nodes on the selenizone which develop only later during ontogeny. Schwardt (1992) noted that *P. coronata* had rib-like lunulae which is not the case in the lectotype but such rib-like lunulae are present in the specimen illustrated by Broili (1907, pl. 6, fig. 34; refigured in Fig. 56I–K). It is certain that the specimen assigned by Bandel (2009, pl. 1, fig. 1) to *Zygites delphinula* (Laube) is conspecific with the specimen assigned to *Wortheniella coronata* by Schwardt (1992, pl. 6, figs 1–2) and the juvenile specimen illustrated herein (Fig. 56L–N). Bandel also illustrated *N. coronatum* specimens under the name *Pseudoschizogonium* (Bandel 2009 pl. 3, figs 42–45; pl. 4, figs 46–47, non 48–49), which is a wrong generic attribution (see discussion of *Nodocingulum* above).

Bandel (2009) placed *Nodocingulum coronatum* in *Rinaldoella* Bandel, 2009 with the type species *Wortheniella rinaldoi* Schwardt, 1992 (Fig. 72). According to Bandel (2009, p. 18) the main diagnostic characters of *Rinaldoella* are an ornament of "fine spiral ribs crossed by collabral ribs that may form rows of granules or tubercles at crossing points" on the early teleoconch as well as a cancellate teleoconch ornament. However, in other respects, *Rinaldoella* in the composition proposed by Bandel (2009) is rather heterogeneous and obviously not monophyletic. Its type species has a concave selenizone lacking any nodes or spines and therefore it differs considerably from *N. coronatum* in this respect.

The specimen assigned to *Worthenia coronata* f. *fasciata* by Zardini (1978, pl. 4, fig. 10a–c) represents *Bandelastraea damon* (Laube, 1870), the type specimens of which are refigured herein (Fig. 79A–D).

***Nodocingulum subcoronatum* (Münster, 1841) comb. nov.**
Fig. 57

*1841	*Pleurotomaria subcoronata*—Münster, p. 109, pl. 11, figs 25a–b.
1850	*Pleurotomaria subcoronata* Münster, 1841—d'Orbigny, p. 195, no. 388.
1891	*Worthenia coronata* Münster sp. var. *ventricosa* m.—Kittl, p. 184, pl. 2, figs 7–8.
1907	*Worthenia coronata* var. *subcoronata* Mstr.—Broili, p. 77, pl. 6, fig. 27.

Material. SNSB-BSPG AS VII 1218 (original of Münster 1841, pl. 11, figs 25a–b) herein designated as lectotype; AS VII 1219 herein designated as paralectotype; both from the St. Cassian Formation. SNSB-BSPG 1903 IX 328 (original of Broili 1907, pl. 6, fig. 27) from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMW 1899/0005/0037/1 (original of Kittl 1891, pl. 2, fig. 7) herein designated as lectotype of *Worthenia coronata* var. *ventricosa* Kittl, NHMW 1899/0005/0037/2 (original of Kittl 1891, pl. 2, fig. 8) herein designated as paralectotype of *Worthenia coronata* var. *ventricosa* Kittl; both from the St. Cassian Formation.

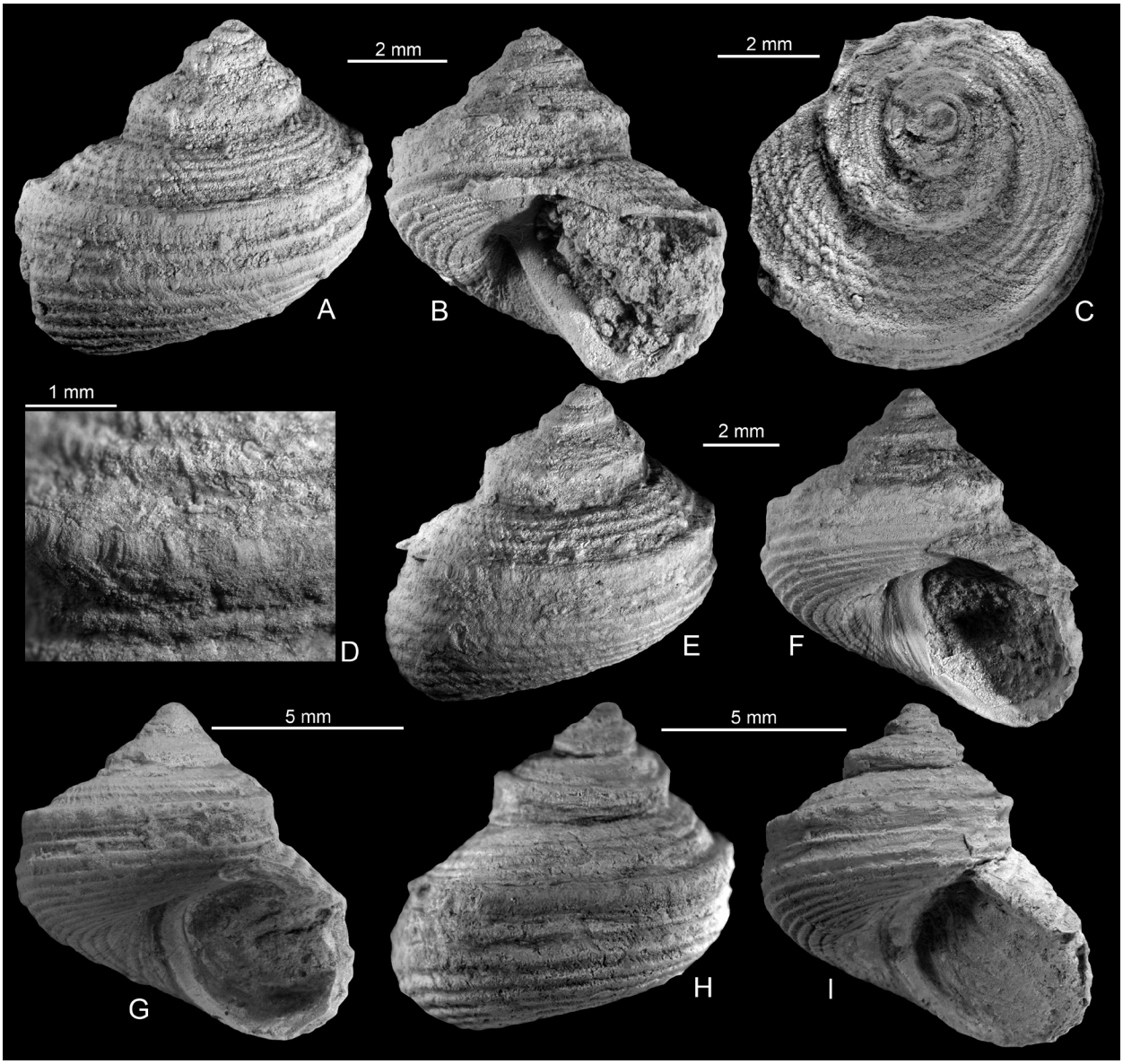

FIGURE 57. *Nodocingulum subcoronatum* (Münster, 1841); **A–D.** Lectotype, SNSB-BSPG AS VII 1218 (original of Münster 1841, pl. 11, figs 25a–b), St. Cassian Formation; **E–F.** Paralectotype, SNSB-BSPG AS VII 1219, St. Cassian Formation; **G.** Paralectotype of *Worthenia coronata* var. *ventricosa* Kittl, 1891, NHMW 1899/0005/0037/2 (original of Kittl 1891, pl. 2, fig. 8), St. Cassian Formation; **H–I.** Lectotype of *Worthenia coronata* var. *ventricosa* Kittl, 1891, NHMW 1899/0005/0037/1 (original of Kittl 1891, pl. 2, fig. 7), St. Cassian Formation.

Description. Shell trochiform; lectotype comprises about 4 preserved teleoconch whorls, 7.4 mm high, 7.0 mm wide; spire gradate with angulated whorl face; suture shallow; ramp convex, concave near selenizone; whorl face with angulation at median position; whorl face below median angulation straight, parallel to shell axis; selenizone elevated, situated at median angulation; selenizone with lunulae and widely spaced short hollow spines; ramp ornamented with straight prosocline strengthened growth lines and 3–5 spiral cords; whorl face below selenizone ornamented with 1–2 spiral cords; base convex with rounded outer basal edge, with opisthocyrt growth lines and ornamented with imbricated spiral cords, with narrow umbilicus; inner lip curved backwards, forming narrow umbilical chink; aperture as high as wide, slightly oblique, with angulated outer lip, convex basal lip and almost straight parietal lip.

Discussion. Münster (1841) noted that *Pleurotomaria coronata* might represent a variety of *P. subcoronata*. Subsequently, Laube (1864, 1868) and Kittl (1891) considered *P. subcoronata* to represent a synonym of *P. coronata* and this was followed by subsequent authors. However, *Nodocingulum subcoronatum* differs from *Nodocingulum coronatum* in having a more globular shape with a more rounded whorl face, a more rounded outer basal edge, stronger spiral cords on the whorl-face, much weaker spines on the selenizone which is also much narrower than in *N. coronatum*. These differences are well visible in Münster's (1841) type specimens of both species and it is unjustified to treat both taxa as synonyms at this point.

Nodocingulum cirriformis (Laube, 1868) comb. nov.

Fig. 58

*1868	*Pleurotomaria cirriformis* Laube—Laube, p. 56, pl. 27, fig. 10.
1891	*Worthenia cirriformis* Laube sp.—Kittl, p. 183, pl. 2, figs 1–2.
1991	*Temnotropis fallax*—Bandel, p. 40, pl. 14, fig. 5 (non 3–4, 6).

Material. NHMW 1899/0005/0028/1 (original of Kittl 1891, pl. 2, fig. 1), NHMW 1899/0005/0028/2 (original of Kittl 1891, pl. 2, fig. 2), NHMW 1899/0005/0027/2, NHMW 1899/0005/0027/1, NHMW 1899/0005/0027/2 from the St. Cassian Formation. MPRZ 2021 1–024 from Campo, St. Cassian Formation.

Description. Shell wortheniform with relatively high whorl expansion rate; spire low, gradate with angulated whorl face; protoconch with a diameter of 0.2 mm; first whorl slightly elevated, almost planispiral, with a diameter of 0.3 mm; suture incised; ramp convex, gently inclining, concave near selenizone, ornamented with spiral cords and densely spaced axial riblets formed by oblique prosocyrt growth lines; cords ornamented with nodes at intersections with riblets; selenizone situated at median angulation, which represents whorl periphery; selenizone ornamented with widely spaced, imbricated, short spines and crescentic growth lines in between; whorl face below selenizone concave, subparallel to shell axis, ornamented with oblique prosocyrt growth lines and nodular spiral cords; two spiral cords near abapical suture more prominent, lower one represents outer basal edge; base convex, with opisthocyrt growth lines and ornamented with nodular spiral cords, which are more prominent than those on whorl face; circumumbilical region smooth, narrowly phaneromphalous; aperture slightly wider than high, oblique; outer lip angulated, basal lip convex, inner lip straight, oblique.

Discussion. *Nodocingulum cirriformis* is characterized by its low spire, high expansion rate and widely spaced hollow spines on its selenizone.

Nodocingulum granulosum (Klipstein, 1844) comb. nov.

Fig. 59

*1844	*Pleurotomaria granulosa*—Klipstein, p. 169, pl. 10, fig. 33.
1850	*Turbo granulosus* d'Orb, 1847—d'Orbigny, p. 193, no. 343.
1891	*Worthenia beaumonti* Klipstein sp.—Kittl, p. 192, pl. 3, fig. 5.
1978	*Wortheniella beaumonti* (Klipstein)—Zardini, p. 18, pl. 4, figs 4–6.
1978	*Temnotropis carinata* (Münster)—Zardini, p. 17, pl. 2, figs 12a–d.
?1978	*Pleurotomaria costifer* (Koken)—Zardini, p. 18, pl. 3, fig. 13.
1992	*Wortheniella beaumonti* (Klipstein, 1843)—Schwardt, p. 43, pl. 6, figs 4–5.
2009	*Dictyotomaria subcancellata* (d´Orbigny, 1849)—Bandel, pl. 1, fig. 3 (non pl. 1, figs 2, 4–5).

2009 *Rinaldoella beaumonti* (Klipstein, 1843)—Bandel, pl. 7, figs 93–96 (non pl. 6, fig. 90; pl. 7, figs 91–92).
2014 *Rinaldoella beaumonti* (Klipstein, 1843)—Nützel & Kaim, p. 412, figs 4e–f, 4i.
2015 *Pseudoschizogonium elevatum*—Hausmann & Nützel, figs 5C1–2.

Material. NHMUK PI OR 35356(1), original of Klipstein (1844, pl. 10, fig. 33) herein designated as lectotype, from the St. Cassian Formation. NHMW 1899/0005/0070 (original of Kittl 1891, pl. 3, fig. 5), PZO 13697, PZO 13699 from the St. Cassian Formation. MPRZ 2021 1–005, MPRZ 2021 1–015 from Campo, St. Cassian Formation.

Description. Shell wortheniform; first whorl slightly elevated, almost planispiral, with a diameter of 0.3 mm; spire gradate with angulated whorl face; suture shallow; ramp flat, gently inclining, ornamented with oblique prosocline collabral threads and two to three spiral cords; collabral threads and spiral cords form nodes at intersections; whorl face with median angulation; selenizone appears within 3rd whorl, situated on median angulation, ornamented with thread-like lunulae and one median spiral cord; lunulae form nodes when intersecting with spiral cord; whorl face below median angulation concave, subparallel to shell axis, ornamented with oblique prosocyrt collabral threads and two to three spiral cords; lowermost spiral cord somewhat more prominent, representing outer basal edge and whorl periphery; base convex, ornamented with opisthocyrt collabral threads and spiral cords, phaneromphalous; aperture as high as wide, slightly oblique; outer lip angulated, basal lip convex, inner lip straight, slightly oblique.

Discussion. Kittl (1891) assigned his material representing *Nodocingulum granulosum* to *Worthenia beaumonti* (Klipstein, 1844). The specimen illustrated by Kittl (1891, pl. 3, fig. 5; figured here in Fig. 59D–F) is conspecific with *Pleurotomaria granulosa* Klipstein, 1844. Subsequent authors generally referred to Kittl's (1891) identification and called this species *W. beaumonti*.

The juvenile specimen assigned to *Rinaldoella beaumonti* by Bandel (2009 pl. 6, fig. 90; pl. 7, figs 91–92) represents *Rinaldoella rinaldoi* (Schwardt, 1992). The early teleoconch of *Rinaldoella rinaldoi* (Schwardt 1992, pl. 3, figs 1a-d) has an immersed protoconch, a higher whorl expansion rate, sharp axial ribs on the ramp and a concave selenizone (Fig. 72).

Nodocingulum granulosum differs from other *Nodocingulum* species in lacking spines or pronounced nodes on its selenizone, instead its lunulae form small nodes.

Nodocingulum bieberi (Kittl, 1891) comb. nov.

Fig. 60

*1891 *Worthenia bieberi* Kittl, n. f.—Kittl, p. 190, pl. 2, fig. 34.
1891 *Ptychomphalus*? *palaeopsis* Kittl, n. f.—Kittl, p. 205, pl. 3, fig. 16.

Material. NHMW 1899/0005/0049 (original of Kittl 1891, pl. 2, fig. 34), herein designated as lectotype, from the St. Cassian Formation. NHMW 1899/0005/0083 (original of Kittl 1891, pl. 3, fig. 16), herein designated as lectotype of *Ptychomphalus palaeopsis* Kittl. MPRZ 2021 1–057 from Campo, St. Cassian Formation.

Description. Shell wortheniform, with moderate spire height and angulated whorl profile; lectotype consisting of rapidly increasing four whorls; ramp flat to convex, gently inclining, forming groove near selenizone on last whorl, ornamented with spiral cords and prosocyrt axial threads; axial threads form nodes when passing over spiral cords; selenizone pronounced, slightly raised, angulated, representing median angulation of whorls, ornamented with closely spaced, thread-like lunulae, bordered by spiral cords; lateral whorl face concave, with a sharp outer basal edge, ornamented with spiral cords and slightly prosocyrt axial threads; base convex, ornamented with pronounced spiral cords and opisthocyrt axial threads, anomphalous.

Discussion. The lectotype of *Ptychomphalus*? *palaeopsis* Kittl, 1891 (60D–F) has a crushed last whorl. Its uncrushed early whorls have a single angulation where the selenizone is situated and have the same ornament as the lectotype of *Worthenia bieberi* (Fig. 60A–C). One specimen from Campo (Fig. 60G–K) has principally the same ornament pattern but the ornament is slightly more prominent and its early selenizone has short notches. This is regarded as intraspecific variation herein, but additional material might reveal that this specimen represents a distinct, yet undescribed species.

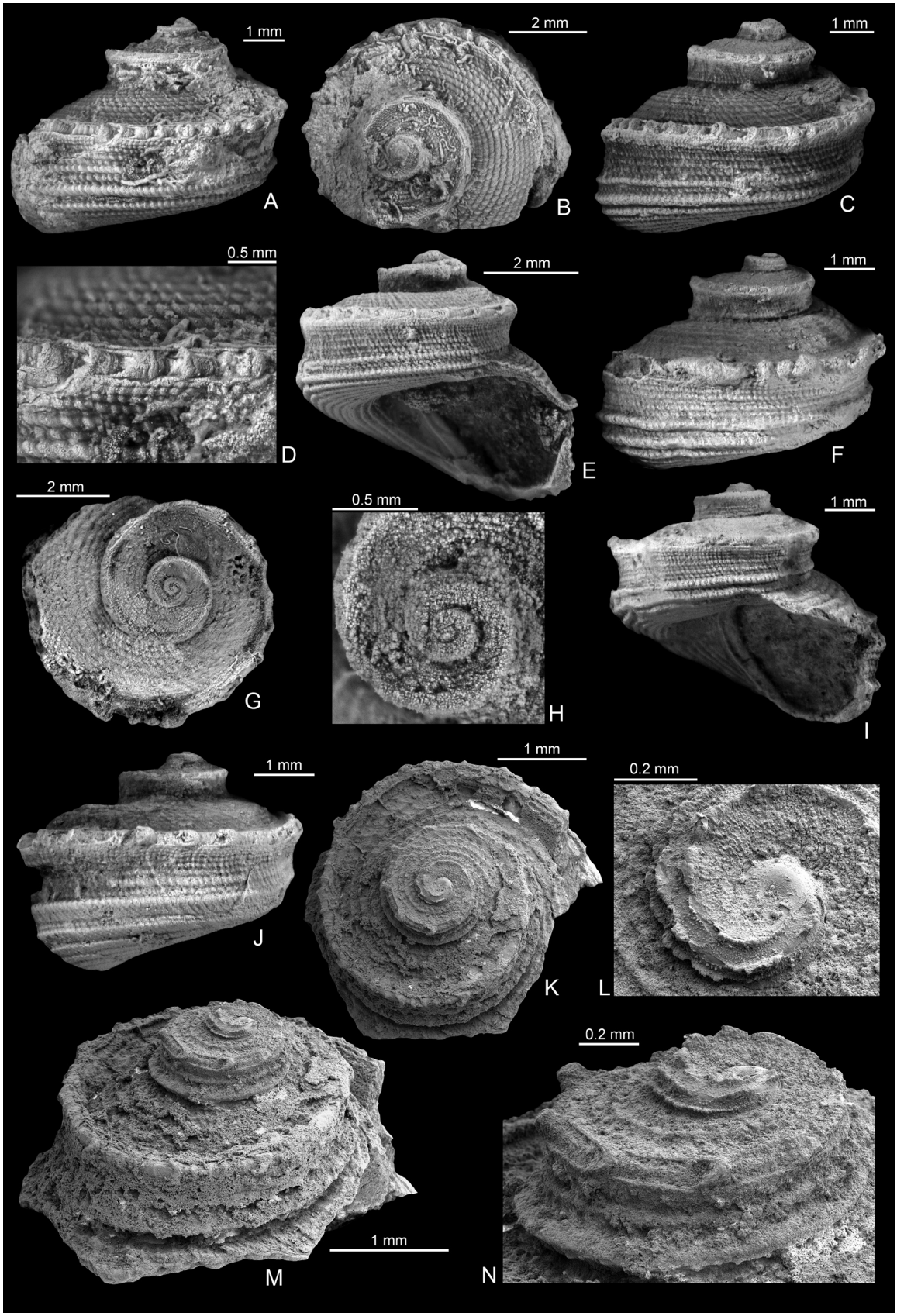

FIGURE 58. *Nodocingulum cirriformis* (Laube, 1868); **A–B.** NHMW 1899/0005/0027/1, St. Cassian Formation; **C–E.** NHMW 1899/0005/0027/2, St. Cassian Formation; **F–I.** NHMW 1899/0005/0028/1 (original of Kittl 1891, pl. 2, fig. 1), St. Cassian Formation; **J.** NHMW 1899/0005/0028/2 (original of Kittl 1891, pl. 2, fig. 2), St. Cassian Formation; **K–N.** MPRZ 2021 1–024, Campo, St. Cassian Formation, SEM image.

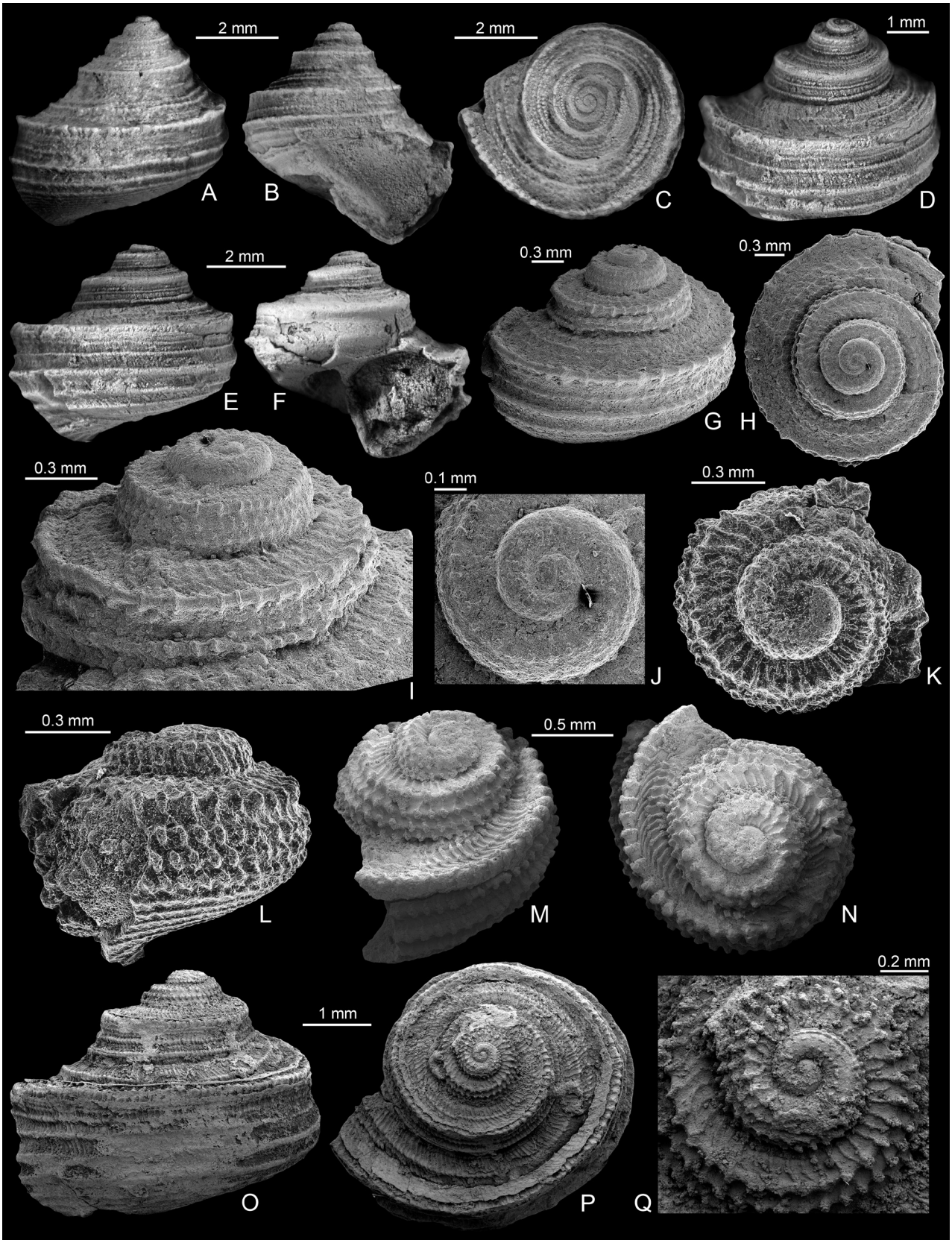

FIGURE 59. *Nodocingulum granulosum* (Klipstein, 1844); **A–C.** NHMUK PI OR 35356(1), original of Klipstein (1844, pl. 10, fig. 33), St. Cassian Formation; **D–F.** NHMW 1899/0005/0070 (original of Kittl 1891, pl. 3, fig. 5), St. Cassian Formation; **G–J.** PZO 13699, St. Cassian Formation, SEM image; **K–L.** PZO 13697, juvenile specimen, St. Cassian Formation, SEM image; **M–N.** MPRZ 2021 1–015, juvenile specimen, Campo, St. Cassian Formation, SEM image; **O–Q.** MPRZ 2021 1–005, Campo, St. Cassian Formation, SEM image.

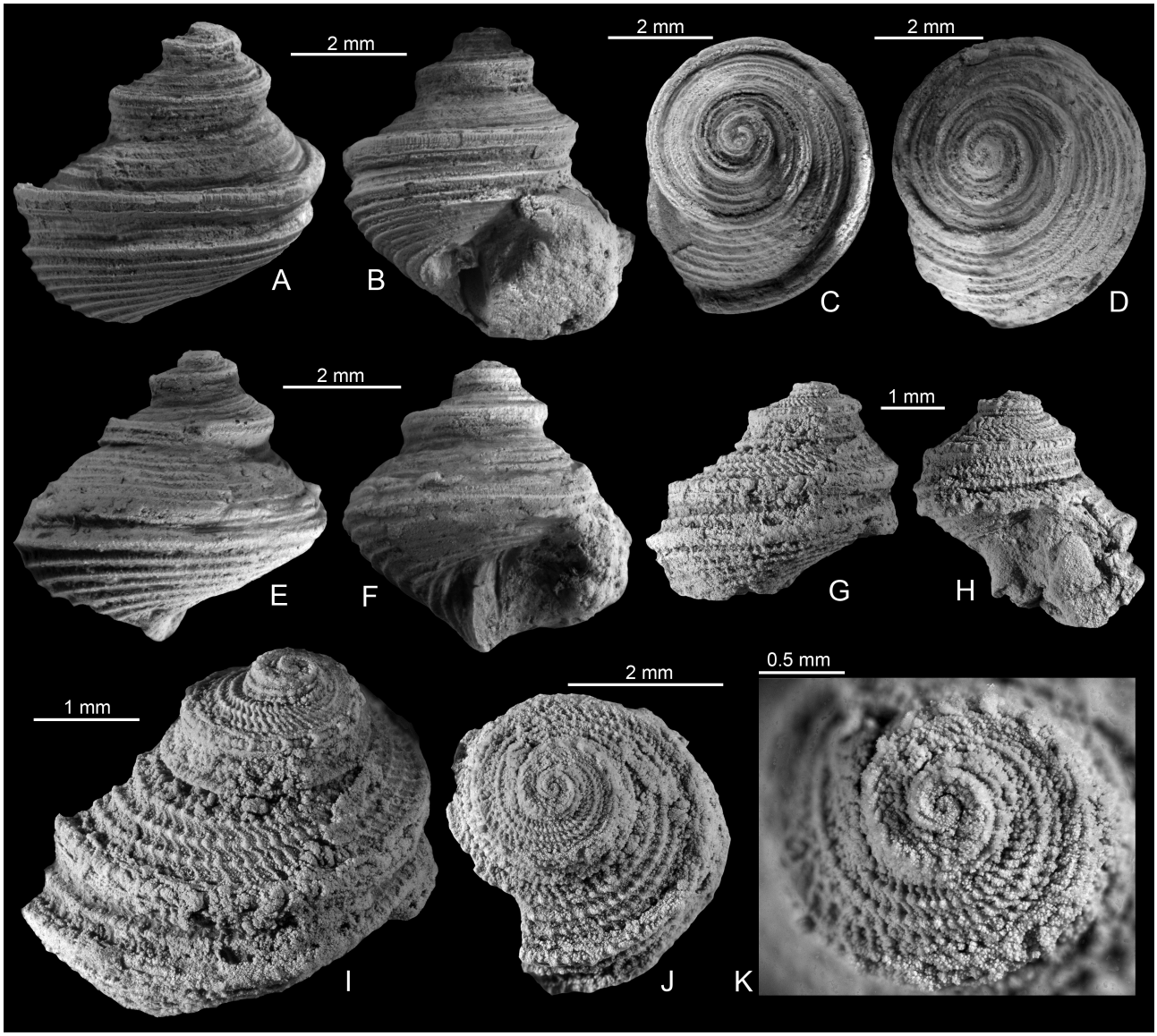

FIGURE 60. *Nodocingulum bieberi* (Kittl, 1891); **A–C.** NHMW 1899/0005/0049 (original of Kittl 1891, pl. 2, fig. 34), St. Cassian Formation; **D–F.** Lectotype of *Ptychomphalus palaeopsis* Kittl, 1891, NHMW 1899/0005/0083 (original of Kittl 1891, pl. 3, fig. 16), St. Cassian Formation; **G–K.** MPRZ 2021 1–057, Campo, St. Cassian Formation.

Nodocingulum johannisaustriae (Klipstein, 1844) comb. nov.

Fig. 61

*1844	*Pleurotomaria Johannis Austriae*—Klipstein, p. 161, pl. 10, figs 13a–c.
1844	*Pleurotomaria gracilis*—Klipstein, p. 170, pl. 11, figs 1a–b.
1850	*Turbo Johannis Austriae* d'Orb, 1847—d'Orbigny, p. 192, no. 333.
1868	*Pleurotomaria Johannis Austriae* Klipstein—Laube, p. 55, pl. 27, fig. 7.
1891	*Worthenia Joannis Austriae* Klipstein sp.—Kittl, p. 187, pl. 2, figs 17–19.
1891	*Worthenia dregeri* Kittl n. f.—Kittl 1891, p. 195, pl. 2 fig. 33.
?1959	*Worthenia* cfr. *joannis austriae* Klipstein vel *münsteri* Klipstein—Leonardi & Fiscon, p. 16, pl. 1, fig. 23.
1978	*Worthenia joannisaustriae* (Klipstein)—Zardini, pl. 5, figs 8b–c (non 8a).
non 1980	cfr. *Worthenia joannisaustriae* (Klipstein)—Zardini, pl. 1, figs 12a–b.
non 1983a	*Glabrocingulum* (*Ananias*) *joannis-austriae* (Klipstein)—Yin & Yochelson, p. 167, figs 4I–K.
non 1992	*Wortheniella joannisaustriae* (Klipstein, 1843)—Schwardt, p. 41, pl. 5, figs 1a–d.
non 2001	*Ananias johannisaustriae* (Klipstein, 1843)—Tong & Erwin, p. 10, pl. 1, figs 10–12.

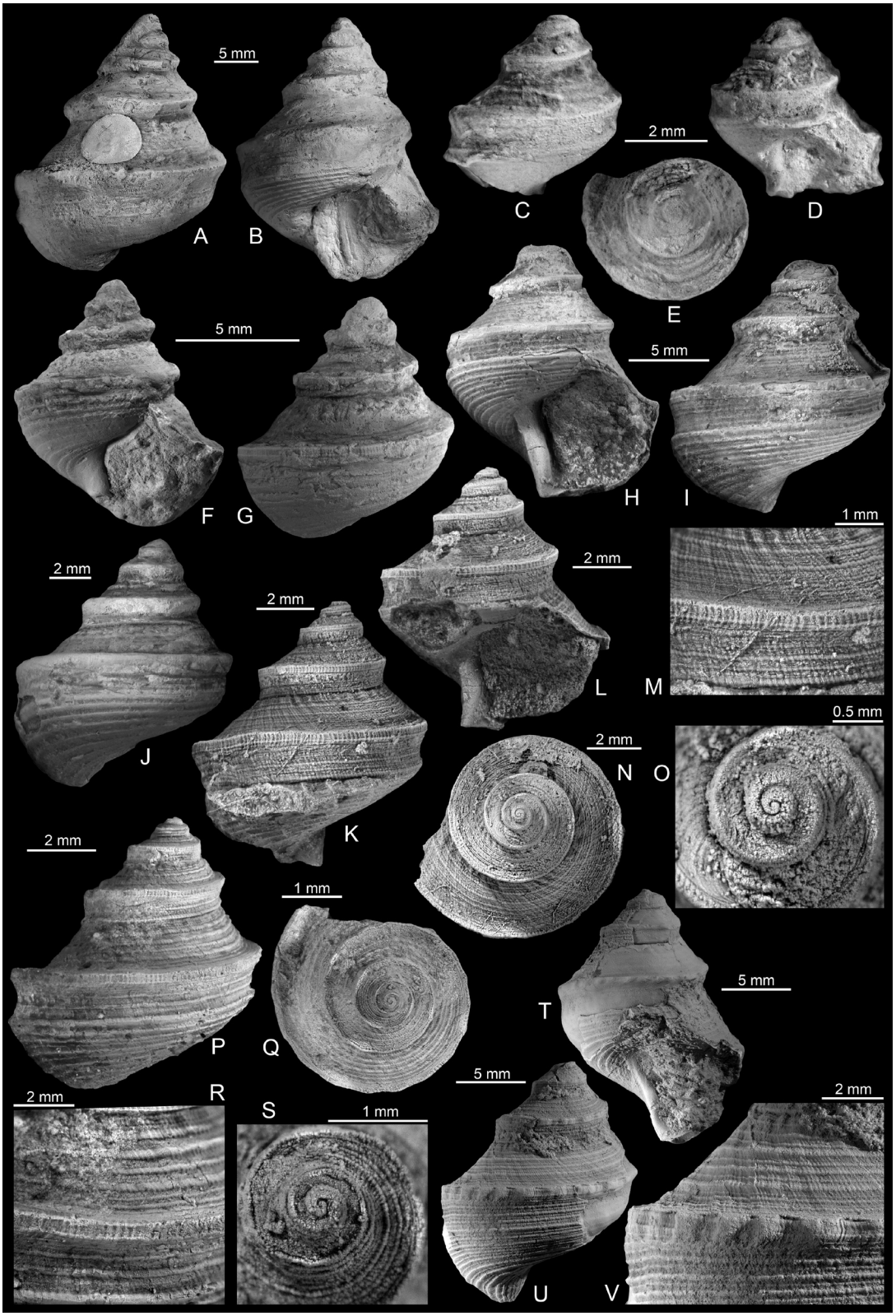

FIGURE 61. *Nodocingulum johannisaustriae* (Klipstein, 1844); **A–B.** Lectotype, NHMUK PI OR 35340(1), original of Klipstein (1844, pl. 10, fig. 13), St. Cassian Formation; **C–E.** Lectotype of *Pleurotomaria gracilis* Klipstein, 1844, NHMUK PI OR 35364 (original of Klipstein 1844, pl. 11, fig. 1), St. Cassian Formation; **F–G.** Lectotype of *Worthenia dregeri* Kittl, 1891, NHMW 1899/0005/0063 (original of Kittl 1891, pl. 2, fig. 33), St. Cassian Formation; **H–I.** NHMW 1865/0001/0058/2 (original of Kittl 1891, pl. 2, fig. 18), St. Cassian Formation; **J.** NHMW 1865/0001/0058/1 (original of Laube 1868, pl. 27, fig. 7), St. Cassian Formation; **K–O** NHMW 1899/0005/0043/1 (original of Kittl 1891, pl. 2, fig. 19), St. Cassian Formation; **P–S.** NHMW 2019/0175/0001/1, St. Cassian Formation; **T–V.** PZO 13683, Prato Piazzo, St. Cassian Formation.

Material. NHMUK PI OR 35340(1), original of Klipstein (1844, pl. 10, fig. 13), herein designated as lectotype from the St. Cassian Formation. NHMUK PI OR 35364 (original of Klipstein 1844, pl. 11, fig. 1), herein designated as lectotype of *Pleurotomaria gracilis* Klipstein from the St. Cassian Formation. NHMW 1899/0005/0063 (original of Kittl 1891, pl. 2, fig. 33) herein designated as lectotype of *Worthenia dregeri* Kittl from the St. Cassian Formation. NHMW 1865/0001/0058/1 (original of Laube 1868, pl. 27, fig. 7), NHMW 1865/0001/0058/2 (original of Kittl 1891, pl. 2, fig. 18), NHMW 1899/0005/0043/1 (original of Kittl 1891, pl. 2, fig. 19), NHMW 2019/0175/0001/1 from the St. Cassian Formation. PZO 13683 from Prato Piazzo, St. Cassian Formation.

Description. Shell wortheniform, with moderate spire height and angulated whorl profile; lectotype consisting of rapidly enlarging six whorls; ramp flat to slightly convex, gently inclining at an angle of 30°–40°, with almost straight prosocline axial growth lines and ornamented with faint spiral cords; selenizone bicarinate, slightly raised above rest of shell, representing median angulation, ornamented with closely spaced lunulae and two spiral lirae, bordered by simple shell edges; lateral whorl face concave, with or without outer basal edge, ornamented with spiral cords and with prosocline growth lines; base convex, ornamented with pronounced spiral cords and with opisthocyrt axial threads, anomphalous; outer lip angulated, basal lip convex, inner lip thickened, straight to slightly convex.

Discussion. The specimen figured by Zardini (1978, pl. 5, fig. 8a) is not the same specimen figured by him in pl. 5 fig. 8b–c but is the same specimen figured by Zardini (1978, pl. 4, fig. 13). This latter specimen is identified as *N. coronatum* herein. The specimen figured by Zardini (1980, pl. 1, figs 12a–b) differs in having a lower spire and in lacking two spiral cords on the selenizone (not bicarinate); therefore, it is not conspecific but might represent *N. granulosum*.

The specimen assigned to *Glabrocingulum* (*Ananias*) *joannisaustriae* by Yin & Yochelson (1983a) has a narrower ramp and not as rapidly enlarging whorls as the Cassian specimens and it lacks an angulated selenizone therefore it is not conspecific.

The specimen figured by Schwardt (1992, pl. 5, figs 1a–d) represents *Nodocingulum ernstkittli* **sp. nov.** (see the discussion on *N. ernstkittli*). *Worthenia dregeri* Kittl, 1891 is known only from its lectotype, which is a poorly preserved specimen (Fig. 61F–G) which seemingly lacks a distinct basal carina but shows the same surface and selenizone ornamentation. *Worthenia dregeri* is therefore regarded as junior synonym of *N. johannisaustriae*.

A single *Nodocingulum* specimen at hand (Fig. 61T–V) shows undulations respectively wide nodes on its selenizone but has the same shell shape and surface ornamentation as *N. johannisaustriae.* It is therefore placed in *N. johannisaustriae*. The presence of absence of nodes on selenizone is regarded as an intraspecific variation in *N. johannisaustriae*.

Nodocingulum muensteri (Klipstein, 1844) comb. nov.

Fig. 62

*1844	*Pleurotomaria münsteri*—Klipstein, p. 166, pl. 10, fig. 25 (non fig. 26).
1850	*Turbo münsteri* d'Orb, 1847—d'Orbigny, p. 193, no. 347.
non 1868	*Pleurotomaria münsteri* Klipstein—Laube, p. 55, pl. 27, fig. 8.
1891	*Worthenia coronata* Münster sp. var. *plicosa* m.—Kittl, p. 184, pl. 2, fig. 11.
non 1891	*Worthenia münsteri* Klipstein sp.—Kittl, p. 186, pl. 2, figs 20–21.
1907	*Worthenia münsteri* Klipstein—Broili, p. 78, pl. 6, fig. 31 (non fig. 30).
non 1975	*Worthenia münsteri* Klipstein—Chorowicz & Termier, p. 237, pl. 21, figs 3–4.
non 1978	*Worthenia münsteri* (Klipstein)—Zardini, pl. 5, figs 12–13.
non 1985	*Worthenia muensteri* (Klipstein)—Zardini, pl. 6, fig. 4.
non 1992	*Wortheniella joannisaustriae* (Klipstein, 1843)—Schwardt, p. 41, pl. 5, figs 1a–d.
non 1992	*Wortheniella muensteri* (Klipstein, 1845)—Schwardt, p. 39, pl. 5, figs 2a–d.
non 2009	*Rinaldoella muensteri* (Klipstein, 1843)—Bandel, pl. 5, fig. 75; pl. 6, 88–89.
non 1907	*Worthenia coronata* var. *plicosa* Kittl—Broili, p. 77, pl. 6, fig. 26.
non 1978	*Worthenia coronata* (Münster) f. *plicosa* (Münster)—Zardini, p. 19, pl. 4, figs 12a–d; pl. 31, figs 8a–c.
non 2009	*Pseudoschizogonium elevatum* (Kittl, 1891)—Bandel, pl. 4, figs 48–49.

Material. NHMUK PI OR 35366(1) original of Klipstein (1844, pl. 10, fig. 25), herein designated as lectotype from the St. Cassian Formation. SNSB-BSPG AS VII 1221, NHMW 1899/0005/0038/1, NHMW 1899/0005/0038/2 from the St. Cassian Formation. NHMW 1899/0005/0039 (original of Kittl 1891, pl. 2, fig. 11), herein designated as lectotype of *Worthenia coronata* var. *plicosa* Kittl, 1891 from the St. Cassian Formation. SNSB-BSPG 1903 IX 1033

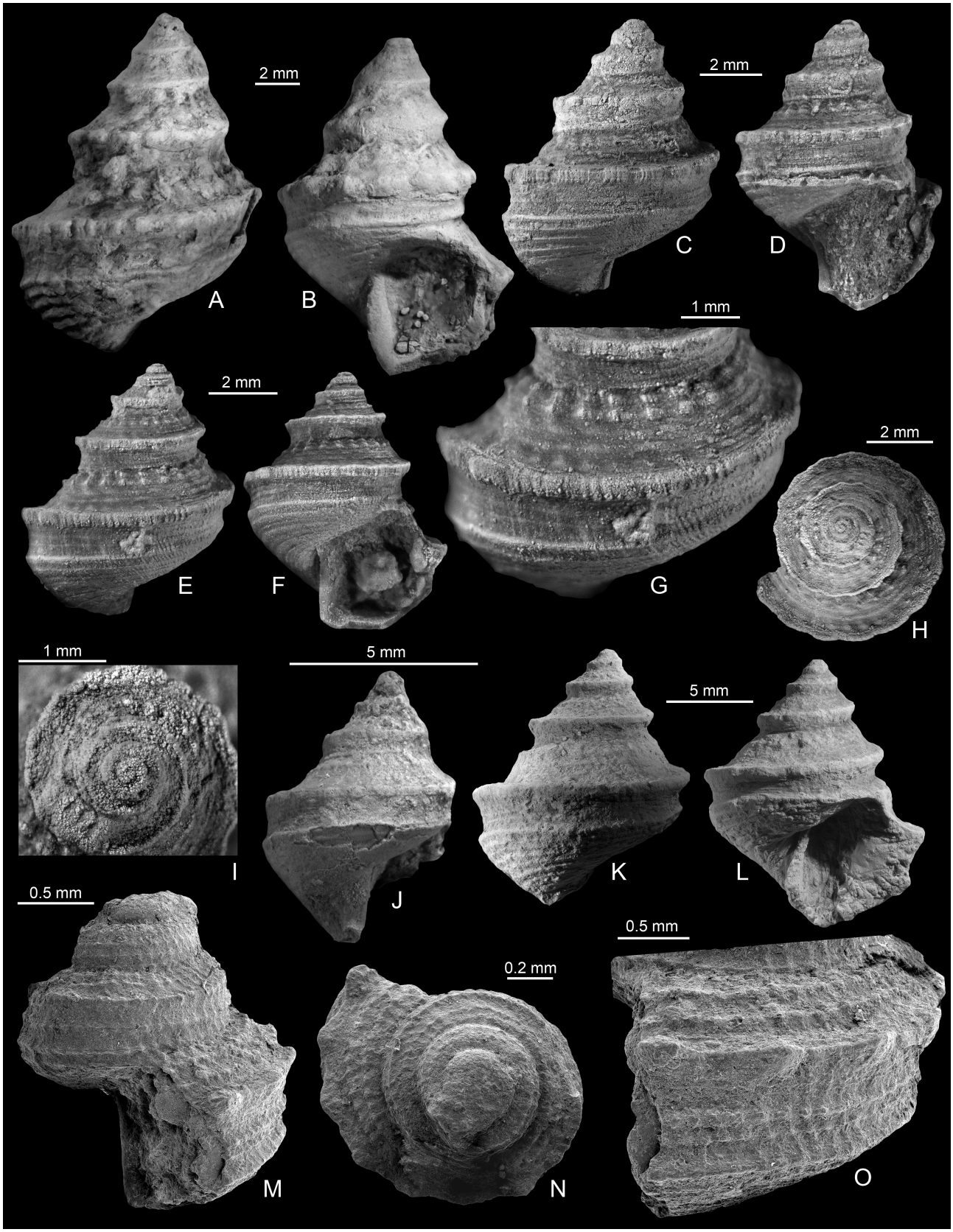

FIGURE 62. *Nodocingulum muensteri* (Klipstein, 1844); **A–B.** Lectotype, NHMUK PI OR 35366(1) original of Klipstein (1844, pl. 10, fig. 25), St. Cassian Formation; **C–D.** NHMW 1899/0005/0038/1, St. Cassian Formation; **E–I.** NHMW 1899/0005/0038/2, St. Cassian Formation; **J.** Lectotype of *Worthenia coronata* var. *plicosa* Kittl, 1891, NHMW 1899/0005/0039 (original of Kittl 1891, pl. 2, fig. 11), St. Cassian Formation; **K–L.** SNSB-BSPG 1903 IX 1033 (original of Broili 1907, pl. 6, fig. 31), Pachycardientuffe, Upper Ladinian, Seiser Alm; **M–O.** PZO 13694, Stuores, St. Cassian Formation.

(original of Broili 1907, pl. 6, fig. 31), SNSB-BSPG 1903 IX 1034 (additional material of Broili 1907; 2 specimens) from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. PZO 13694 from Stuores, St. Cassian Formation.

Description. Shell wortheniform, high-spired for the group; lectotype comprises about 6 whorls; spire gradate with angulated whorl face; suture shallow; early whorls slightly elevated; initial whorl 0.35 mm in diameter; ramp slightly convex near adapical suture, concave near selenizone, steeply inclined, ornamented with spiral cords and axial riblets with granules at intersections and bearing prosocline growth lines; granules more prominent, node-like near adapical suture; subsutural nodes connected by weak, short axial ribs; whorl face with median angulation at or above mid-whorl; selenizone prominent, bi-carinate, elevated, situated at median angulation, ornamented with prominent lunulae, two spiral lirae and weak knobs (or undulations), ca. 15–17 per whorl; whorl face below selenizone concave, parallel to shell axis, with slightly prosocyrt growth lines and ornamented with spiral cords; transition to base at angulated outer basal edge; base flatly convex, anomphalous, with opisthocyrt growth lines and ornamented with spiral cords; basal cords more prominent than spiral cords on whorl face; narrow umbilical chink formed by slightly reflexed inner lip; aperture as high as wide, with angulated outer lip, flatly convex basal lip and straight inner lip.

Discussion. Klipstein (1844) provided drawings of two specimens that he assigned to *Pleurotomaria muensteri*. These two specimens are not conspecific. The specimen illustrated by Klipstein (1844, pl. 10) in figure 25 is conspecific with *Worthenia coronata* var. *plicosa* Kittl, 1891 and the specimen in figure 26 represents *Pleurotomaria cancellatocingulata* Klipstein, 1844. We designate the specimen illustrated by Klipstein (1844, pl. 10, fig. 25) as lectotype of *P. muensteri*, which is also the specimen that previous authors have taken as reference for this species. In contrast to the figure provided by Klipstein (1844, pl. 10, fig. 25), the lectotype shows no distinct subsutural axial folds but the specimen is heavily encrusted. We found better-preserved specimens in the Kittl collection at the NHMW that are obviously conspecific with the lectotype of *Pleurotomaria muensteri* (Fig. 62C–I). The unrealistically pronounced axial folds on the specimen figured by Klipstein (1844, pl. 10, fig. 25) probably misguided Kittl (1891) in the identification of *Nodocingulum muensteri*. Subsequent authors referred to Kittl's (1891) identification of *Worthenia muensteri* for species identification; therefore, their assignments to *Nodocingulum muensteri* are incorrect as well. Kittl's (1891) specimens and most of specimens misidentified by the subsequent authors are assigned to *Nodocingulum ernstkittli* **sp. nov.**

The specimens figured as *Worthenia muensteri* by Broili (1907, pl. 6, figs 30–31) are slightly lower-spired but resemble *Nodocingulum muensteri* in ornamentation on whorl face and selenizone.

The specimen assigned to *Worthenia coronata* var. *plicosa* Kittl by Broili (1907, p. 77, pl. 6, fig. 26) is figured here (Fig. 62J) and represents *Wortheniella coralliophila* (Kittl, 1891).

The specimen figured by Zardini (1978, pl. 5, fig. 12) as *Worthenia muensteri* represents *Amplitomaria spuria* (Münster, 1841).

The juvenile specimen assigned to *Pseudoschizogonium elevatum* by Bandel (2009, pl. 4, figs 48–49) resembles *Nodocingulum muensteri*, but *N. muensteri* does not form spines on the selenizone, instead it forms weak knobs (or undulations). That juvenile specimen can be safely assigned to *Bandelastraea* and probably represents *Bandelastraea lancedelli* (Zardini, 1978) because it is higher-spired. Here, we illustrate a juvenile *Bandelastraea damon* (in Fig. 79H–J) to show the early ontogenetic development of *Bandelastraea*.

Nodocingulum ernstkittli sp. nov.

Fig. 63

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1891	*Worthenia münsteri* Klipstein sp.—Kittl, p. 186, pl. 2, fig. 20–21.
1978	*Worthenia münsteri* (Klipstein)—Zardini, pl. 5, fig. 13 (non fig. 12).
1985	*Worthenia muensteri* (Klipstein)—Zardini, pl. 6, fig. 4.
1992	*Wortheniella joannisaustriae* (Klipstein, 1843)—Schwardt, p. 41, pl. 5, figs 1a–d.
1992	*Wortheniella muensteri* (Klipstein, 1845)—Schwardt, p. 39, pl. 5, figs 2a–d.
2009	*Rinaldoella muensteri* (Klipstein, 1843)—Bandel, pl. 5, fig. 75; pl. 6, 88–89.

Derivation of name. After Ernst Kittl, who carefully studied all the specimens available to him and provided a comprehensive monograph on Cassian gastropods.

Holotype. NHMW 1899/0005/0045/2.

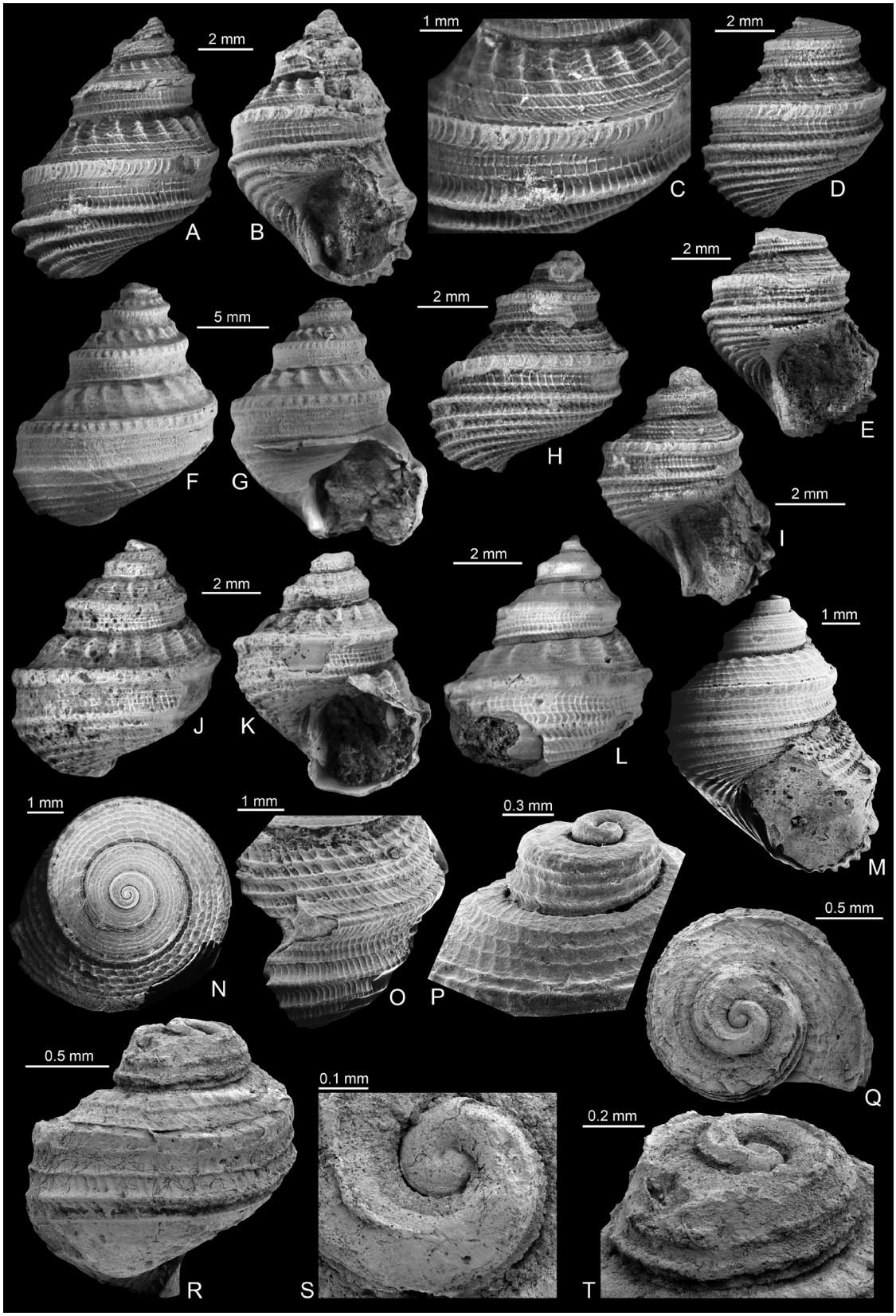

FIGURE 63. *Nodocingulum ernstkittli* **sp. nov.**; **A–C.** Holotype, NHMW 1899/0005/0045/2, St. Cassian Formation; **D–E.** Paratype, NHMW 1899/0005/0045/1, St. Cassian Formation; **F–G.** Paratype, NHMW 1899/0005/0046 (original of Kittl 1891, pl. 2, fig. 21), St. Cassian Formation; **H–I.** NHMW 1899/0005/0044/1, St. Cassian Formation; **J–K.** NHMW 1899/0006/0006/2, St. Cassian Formation; **L.** NHMW 1899/0006/0006/1, St. Cassian Formation; **M–P.** PZO 13696, St. Cassian Formation, SEM image; **Q–T.** MPRZ 2021 1–029, Misurina, St. Cassian Formation, SEM image.

Paratypes. NHMW 1899/0005/0045/1, NHMW 1899/0005/0046.

Type locality, age, formation. Italy, South Tyrol, Late Triassic, Early Carnian, St. Cassian Formation.

Material. NHMW 1899/0005/0045/2 (holotype), NHMW 1899/0005/0045/1 (paratype), NHMW 1899/0005/0046 (paratype, original of Kittl 1891, pl. 2, fig. 21), NHMW 1899/0005/0044/1, NHMW 1899/0006/0006/1, NHMW 1899/0006/0006/2, PZO 13696 from the St. Cassian Formation. MPRZ 2021 1–029 from Misurina, St. Cassian Formation.

Description. Shell wortheniform, moderately high-spired; spire gradate, whorl profile angulated at adapical edge of selenizone; first 1.5 whorls planispiral with slightly immersed protoconch; protoconch of about one whorl, without visible ornament, terminating abruptly at ledge with projection; protoconch diameter 0.22 mm; holotype consisting of four rapidly enlarging whorls (initial whorls missing); ramp convex, concave near selenizone, ornamented with axial folds and cancellate ornament formed by up to seven spiral cords and numerous prosocyrt, sharp axial threads; selenizone angulated, slightly raised above rest of shell, representing median angulation, ornamented with v-shaped lunulae which occasionally form nodes; lunulae asymmetric with zenith in adapical portion; selenizone bordered by simple, bent shell edges; lateral whorl face concave, ornamented with spiral cords and axial, prosocyrt threads; outer basal edge angulated at first basal spiral cord; suture slightly impressed, just below outer basal edge; base rounded, ornamented with pronounced spiral cords and opisthocyrt axial threads, anomphalous; outer lip angulated, basal lip convex, inner lip thickened, straight to slightly convex.

Discussion. *Nodocingulum ernstkittli* **sp. nov.** differs from *Nodocingulum muensteri* (Klipstein, 1844) in having distinct subsutural folds, a higher whorl expansion rate and only one carination on the selenizone. Moreover, the axial ribs of *N. ernstkittli* are sharper and more widely spaced. The specimens attributed to *Nodocingulum muensteri* by Zardini (1978, 1985), Schwardt (1992), and Bandel (1991, 2009) are not conspecific with the lectotype of *N. muensteri* and are assigned to *Nodocingulum ernstkittli* **sp. nov.** The specimen figured by Zardini (1978, pl. 5, fig. 12) as *Worthenia muensteri* represents *Amplitomaria spuria* (Münster, 1841).

The specimen assigned to *Wortheniella joannisaustriae* by Schwardt (1992, pl. 5, figs 1a–d) develops axial folds at the same ontogenetic stage (within 3rd whorl) as the specimen which was assigned to *Wortheniella muensteri* by Schwardt (1992, pl. 5, figs 2a–d). Both specimens are identical in all aspects and are thus conspecific and herein assigned to *N. ernstkittli*.

Nodocingulum furcatum (Kittl, 1891) comb. nov.

Fig. 64

1844	*Pleurotomaria beaumonti*—Klipstein, p. 163, pl. 10, fig. 18 [non *Pleurotomaria beaumonti* d'Archiac and Verneuil, 1842].
1868	*Pleurotomaria münsteri* Klipstein—Laube, p. 55, pl. 27, fig. 8.
*1891	*Worthenia furcata* Kittl, n. f.—Kittl, p. 187, pl. 2, fig. 22.
non 1891	*Worthenia beaumonti* Klipstein sp.—Kittl, p. 192, pl. 3, fig. 5.
non 1978	*Wortheniella beaumonti* (Klipstein)—Zardini, p. 18, pl. 4, figs 4–6.
non 1992	*Wortheniella beaumonti* (Klipstein, 1843)—Schwardt, p. 43, pl. 6, figs 4–5.
non 2009	*Rinaldoella beaumonti* (Klipstein, 1843)—Bandel, pl. 6, fig. 90; pl. 7, figs 91–96.
non 2014	*Rinaldoella beaumonti* (Klipstein, 1843)—Nützel & Kaim, p. 412, figs 4e–f, 4i.

Material. NHMW 1899/0005/0047 (original of Kittl 1891, pl. 2, fig. 22) herein designated as lectotype of *Worthenia furcata* Kittl from the St. Cassian Formation. NHMW 1865/0001/0063 from the St. Cassian Formation. NHMUK PI OR 35350(1) original of Klipstein (1844, pl. 10, fig. 18) herein designated as lectotype of *Pleurotomaria beaumonti* Klipstein from the St. Cassian Formation.

Discussion. Kittl (1891) recognized that the specimen assigned to *Nodocingulum muensteri* (*Pleurotomaria*) by Laube (1868) represents a distinct species and erected *Worthenia furcata* for it. *Pleurotomaria beaumonti* Klipstein, 1844 is in our opinion conspecific but Klipstein's (1844) *Pleurotomaria beaumonti* is preoccupied by *Pleurotomaria beaumonti* d'Archiac & Verneuil, 1842 from the Devonian of Germany. The lectotype of *Pleurotomaria beaumonti* Klipstein shows a similar whorl ornamentation as *Nodocingulum furcatum* (Kittl, 1891), but its whorls are not as high. The difference in whorl height is treated herein as intraspecific variability of *Nodocingulum furcatum*. The specimens attributed to *Pleurotomaria beaumonti* Klipstein by subsequent authors represent *Nodocingulum granulosum* (see discussion on *N. granulosum*).

Nodocingulum furcatum resembles *N. ernstkittli* **sp. nov.**, however, *N. furcatum* has a bicarinate selenizone and weak additional ribs intercalated between the main additional ribs near the selenizone so that the main subsutural ribs appear to be bifurcated.

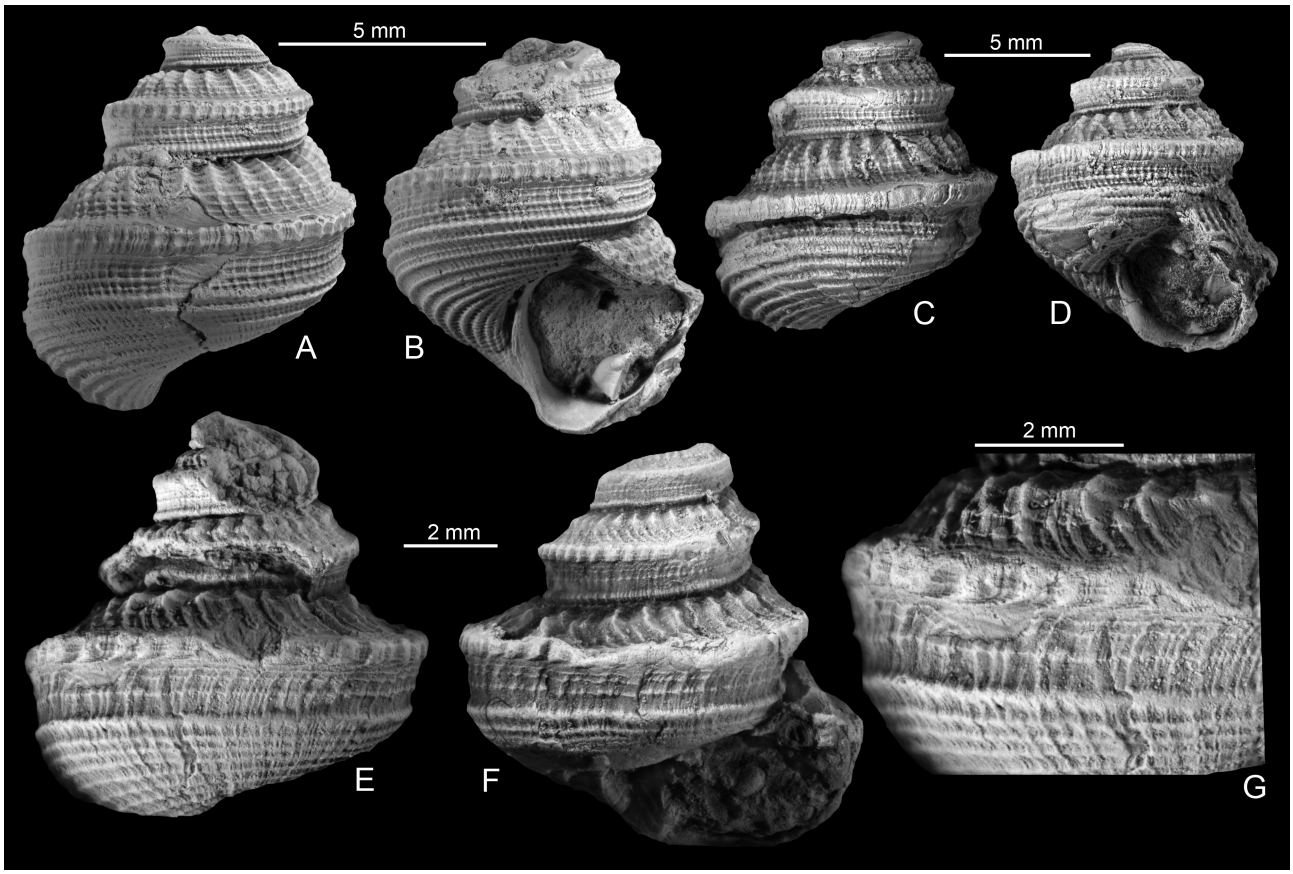

FIGURE 64. *Nodocingulum furcatum* (Kittl, 1891); **A–B.** Lectotype, NHMW 1899/0005/0047 (original of Kittl 1891, pl. 2, fig. 22), St. Cassian Formation; **C–D.** NHMW 1865/0001/0063, St. Cassian Formation; **E–G.** Lectotype of *Pleurotomaria beaumonti* Klipstein, 1844, NHMUK PI OR 35350(1) original of Klipstein (1844, pl. 10, fig. 18). St. Cassian Formation.

Nodocingulum crenatum (Münster, 1841) comb. nov.

Fig. 65

*1841	*Pleurotomaria crenata*—Münster, p. 113, pl. 12, fig. 15.
1850	*Turbo crenatus* d'Orb., 1847—d'Orbigny, p. 193, no. 352.
1891	*Worthenia crenata* Münster sp.—Kittl, p. 194, pl. 2, fig. 32.
1978	*Worthenia coronata* f. *bicoronata* (Münster)—Zardini, p. 19, pl. 4, fig. 11a–c.
1978	*Worthenia crenata* (Münster)—Zardini, p. 20, pl. 5, figs 5–6, 10; pl. 6, fig. 9.
1978	*Worthenia coronata* f. *depressa* (Münster)—Zardini, p. 21, pl. 9, figs 19a–d.
1980	*Worthenia coronata* f. *bicoronata* Muenster—Zardini, p. 4, pl. 1, figs 13a–d.
1985	*Worthenia crenata* f. juv. Kittl—Zardini, p. 13, pl. 5, figs 1a–b.
1992	*Wortheniella crenata* (Münster, 1841)—Schwardt, p. 37, pl. 4, figs 1–3.
1992	*Wortheniella subgranulata*—Schwardt, pl. 4, figs 4–5.
2009	*Rinaldoella crenata* (Münster, 1841)—Bandel, pl. 6, fig. 81, 83–84.
2009	*Rinaldoella subgranulata*—Bandel, pl. 6, fig. 78–80, 82.

Material. SNSB-BSPG AS VII 1519 (original of Münster 1841, pl. 12, fig. 15) herein designated as lectotype from the St. Cassian Formation. PZO 13693 from Misurina, St. Cassian Formation. MPRZ 2021 1–053, MPRZ 2021 1–054, MPRZ 2021 1–055, MPRZ 2021 1–009, MPRZ 2021 1–014, MPRZ 2021 1–021 from Campo, St. Cassian Formation.

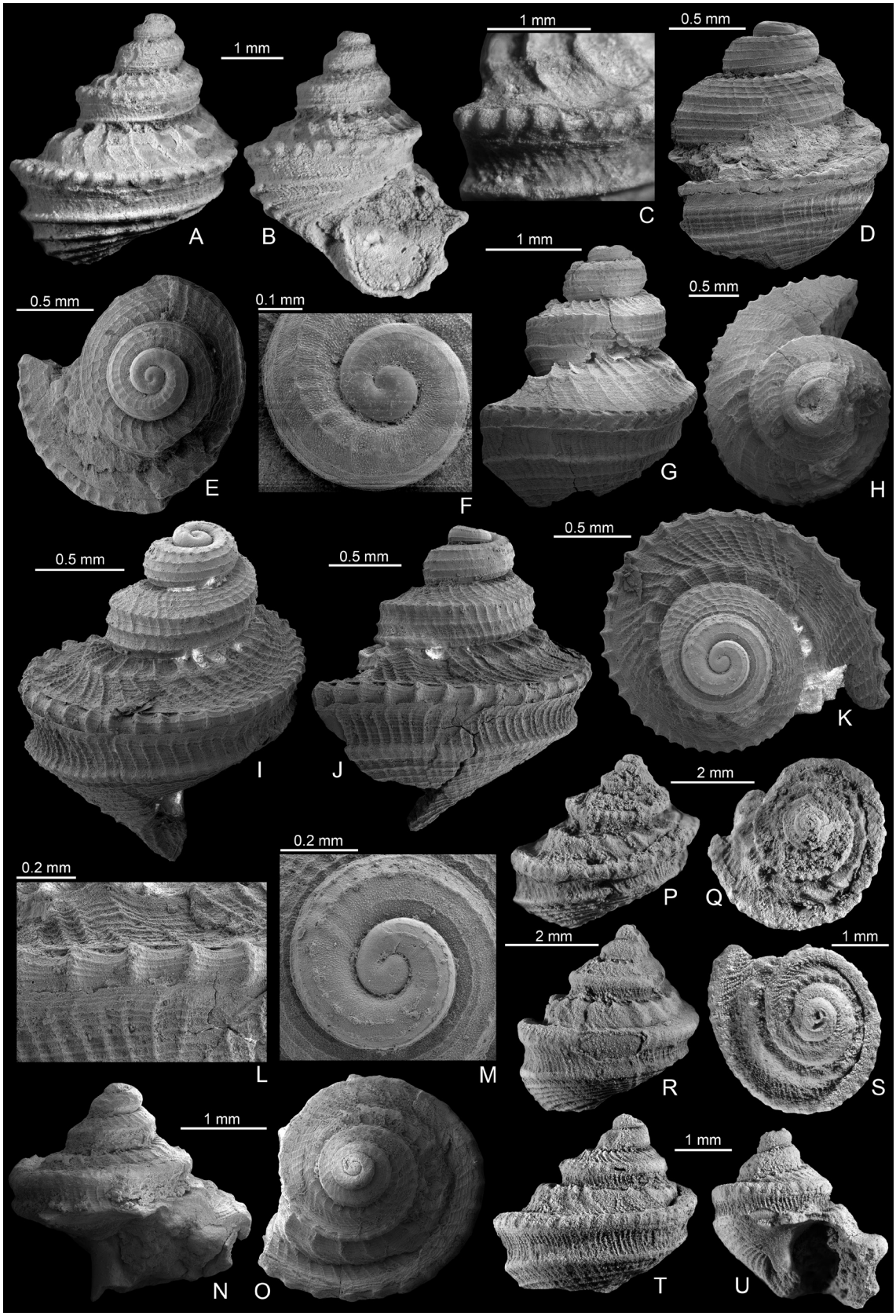

FIGURE 65. *Nodocingulum crenatum* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1519 (original of Münster 1841, pl. 12, fig. 15), St. Cassian Formation; **D–F.** PZO 13693, Misurina, St. Cassian Formation, SEM image; **G–H.** MPRZ 2021 1–021, Campo, St. Cassian Formation, SEM image; **I–M.** MPRZ 2021 1–009, Campo, St. Cassian Formation, SEM image; **N–O.** MPRZ 2021 1–014, Campo, St. Cassian Formation, SEM image; **P–Q.** MPRZ 2021 1–053, Campo, St. Cassian Formation; **R.** MPRZ 2021 1–054, Campo, St. Cassian Formation; **S–U.** MPRZ 2021 1–055, Campo, St. Cassian Formation.

Description. Shell wortheniform, very small; lectotype comprises about 5 whorls, 4.5 mm high, 3.5 mm wide; spire gradate with angulated whorl face; suture impressed; juvenile specimen with about two planispiral initial whorls; protoconch of less than one whorl, smooth, clearly demarcated from teleoconch, 0.18 mm in width; early teleoconch whorls evenly convex; first teleoconch whorl with spiral threads then with additional prosocline axial threads; whorl angulation starts to form on third whorl; selenizone appears on fourth whorl; at least early whorls ornamented with micro-ornament of pustules; mature whorls with prominent angulation in somewhat sub-median position; ramp convex, concave near selenizone, ornamented with regularly spaced, sharp prosocyrt/prosocline axial ribs and spiral threads; growth lines on ramp prosocyrt/prosocline; selenizone prominent, elevated, forming peripheral keel and angulation; selenizone with prominent, regularly spaced, crescent-shaped notches, bordered by shell edges; whorl face below selenizone concave, ornamented by spiral threads and bearing oblique prosocyrt growth lines, which have maximum convexity just below selenizone; base rounded convex, pseudo-umbilicate, ornamented with six regularly spaced spiral cords and opisthocyrt threads; outermost basal cord forms outer basal edge, not embraced by preceding whorls; aperture higher than wide, with angulated outer lip, rounded basal lip and almost straight inner lip.

Discussion. The specimens assigned to *Wortheniella subgranulata* by Schwardt (1992, pl. 4, figs 4–5) and Bandel (2009, pl. 6, fig. 78–80, 82) represent without doubt *Nodocingulum crenatum*. Previous observations on the early whorls of *Nodocingulum crenatum* (Bandel 2009, pl. 6 figs 78–84; Schwardt 1992, pl. 4, figs 1–5) and the juvenile specimen reported herein (Fig. 65I–M) show that the early whorls are planispiral, the early teleoconch before the onset of the selenizone is moderately high-spired and that the selenizone starts after the third whorl.

Pleurotomaria crenata Münster, 1841 is placed in the genus *Nodocingulum* due to the development of the selenizone from a v–shaped sinus on the median angulation and the presence of a reticulate ornament before the onset of the selenizone rather than strong spiral cords (as in *Rinaldoella*). Bandel (2009, pl. 6, fig. 78) documented the transition from a v-shaped sinus to the selenizone in *Nodocingulum crenatum* (misidentified as *Rinaldoella subgranulata*). The development of the selenizone and the ornamentation is similar to that of *Nodocingulum coronatum* (Fig. 56L–N; see also Schwardt 1992, pl. 6, figs 2–3).

Larger specimens of *Nodocingulum crenatum* have a wider last whorl and form prominent subsutural nodes (e.g., Zardini 1980, pl. 1, fig. 13; specimens in Fig. 65P–U) but their early whorls are identical with the type specimen and therefore, they are considered conspecific. Other intraspecific variations are seen in the strength of basal spiral cords and in the ornamentation on the selenizone, which consists either of short notches or small nodes.

Nodocingulum? *angulatum* (Münster, 1841) nomen dubium

Fig. 66

*1841	*Pleurotomaria*? *angulata*—Münster, p. 112, pl. 12, fig. 10.
1850	*Turbo pleurotomarioides* d'Orb., 1847—d'Orbigny, p. 193, no. 355.
1891	*Worthenia*? *angulata* Münster sp.—Kittl, p. 191.
?1978	*Worthenia coronata* (Münster) f. *plicosa* (Münster)—Zardini, p. 19, pl. 4, figs 12a–d; pl. 31, figs 8a–c.

Material. SNSB-BSPG AS VII 1517 (original of Münster 1841, pl. 12, fig. 10) herein designated as lectotype from the St. Cassian Formation.

Description. Shell wortheniform; lectotype comprises approximately 3 visible whorls (early whorls are encrusted); spire gradate with angulated whorl face; lectotype 10.0 mm high, 6.8 mm wide; suture impressed; ramp convex, concave near selenizone, ornamented with prosocyrt folds on convex portion of ramp; selenizone situated at whorl angulation, forming a keel, ornamented with prominent notches; whorl face below selenizone flatly concave; base rounded, anomphalous, ornamented with 6 spiral cords and collabral lirae; aperture higher than wide, with angulated outer lip, rounded basal lip and almost straight inner lip.

Discussion. The lectotype of *Nodocingulum*? *angulatum* is a strongly encrusted and poorly preserved specimen but the inner nacreous layer and the prosocyrt folds are visible on the ramp. It shares a similar shell size, whorl morphology and ornamentation with *Nodocingulum ernstkittli* **sp. nov.** However, the lectotype of *Nodocingulum*? *angulatum* has short notches on the selenizone, which are absent in *Nodocingulum ernstkittli* **sp. nov.** *Nodocingulum*? *angulatum* resembles *Nodocingulum crenatum* in ornamentation and whorl morphology but *Nodocingulum*? *angulatum* is much larger in size. Due to the heavy encrustation, *Nodocingulum*? *angulatum* is regarded as *nomen dubium*.

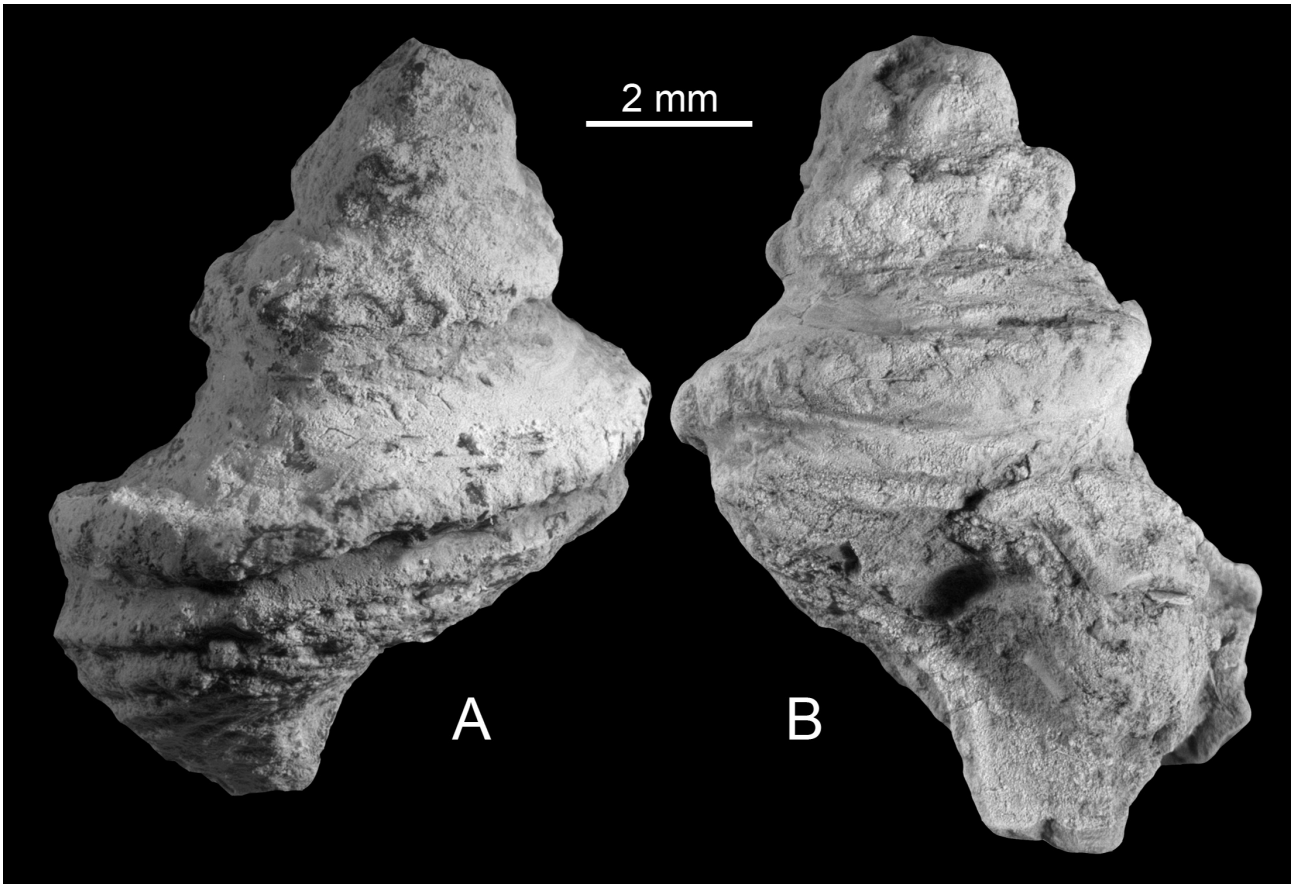

FIGURE 66. *Nodocingulum*? *angulatum* (Münster, 1841), **A–B.** Lectotype, SNSB-BSPG AS VII 1517 (original of Münster 1841, pl. 12, fig. 10), St. Cassian Formation.

***Nodocingulum*? *turris* sp. nov.**

Fig. 67

LSID. urn:lsid:zoobank.org:act:BEC29E25-EAF7-434F-8C0B-7C25D0D79F3B

1868	*Pleurotomaria subpunctata* Klipstein—Laube, p. 59, pl. 28, fig. 5. [non *Pleurotomaria subpunctata* Klipstein, 1844 = *Wortheniella canalifera* (Münster, 1841)].
1891	*Worthenia subpunctata* Laube sp.—Kittl, p. 189, pl. 2, fig. 28.
non 1978	*Wortheniella subpunctata* Laube, 1868—Zardini, p. 21, pl. 6, fig. 5.
non 1980	*Wortheniella* cfr. *subpunctata* Laube—Zardini, p. 3, pl. 1, figs 10–11.
non 1992	*Wortheniella subpunctata* (Laube, 1868)—Schwardt, p. 48, pl. 8, fig. 1.
non 2009	*Wortheniella subpunctata* (Laube, 1868)—Bandel, pl. 5, figs 71–74.

Derivation of name. From Latin *turris*, meaning tower.

Holotype. NHMW 1899/0005/0056.

Paratype. SNSB-BSPG 1964 XVII 195.

Type locality, age, formation. Italy, South Tyrol, Late Triassic, Early Carnian, St. Cassian Formation.

Material. NHMW 1899/0005/0056 (original of Kittl, pl. 2, fig. 28) holotype; SNSB-BSPG 1964 XVII 195 from the St. Cassian Formation.

Description. Shell wortheniform, high-spired for genus, holotype consisting of five whorls, 10 mm high, 6 mm wide; spire gradate; with angulation above mid-whorl; ramp straight, steeply inclined at an angle of 45°–55°; whorls ornamented with numerous fine, axial ribs and several spiral cords having the same strength as ribs; axial ribs and spiral cords forming cancellate pattern; axial ribs prosocline on ramp, orthocline prosocyrt below angulation; selenizone angulated, situated on whorl angulation, ornamented with a median spiral rib and prominent lunulae,

bordered by shell edges; lateral whorl face wider than ramp, flat, lying subparallel to shell axis; transition to base evenly rounded, marked by a spiral cord; base rounded convex, ornamented with spiral cords and with opisthocyrt growth lines, anomphalous; aperture higher than wide, with angulated outer lip, rounded basal lip and straight inner lip.

Discussion. *Nodocingulum*? *turris* **sp. nov.** is unusually high-spired for wortheniform Pleurotomariida. *Nodocingulum*? *turris* is only tentatively placed in *Nodocingulum* because its early whorls are unknown. It differs from all similar species by having a very high spire due to a wide lateral whorl face.

Nodocingulum? *turris* has been reported as *Pleurotomaria subpunctata* Klipstein by Laube (1868). However, Kittl (1891) considered Laube (1868) to be author of that taxon (*"Worthenia subpunctata* Laube sp." but not in the figure caption where he used *Worthenia subpunctata* (Klipstein)). Kittl (1891) noted that Laube's (1868 pl. 28, fig. 5) illustrated specimen does not represent *Pleurotomaria subpunctata* Klipstein (subjective synonym of *Wortheniella canalifera* (Münster, 1841) (see above). Kittl (1891) regarded Laube as the author of a new species and assigned it to *Worthenia.* He stated that he had examined Laube's specimen (housed in the K & K Reichsanstalt) and assigned it to *Worthenia subpunctata* as well as two additional specimens (housed in the Hofmuseum) one of which was illustrated by him (Kittl 1891, pl. 2, fig. 28). This specimen is well-preserved and is chosen as the holotype of *Nodocingulum*? *turris*.

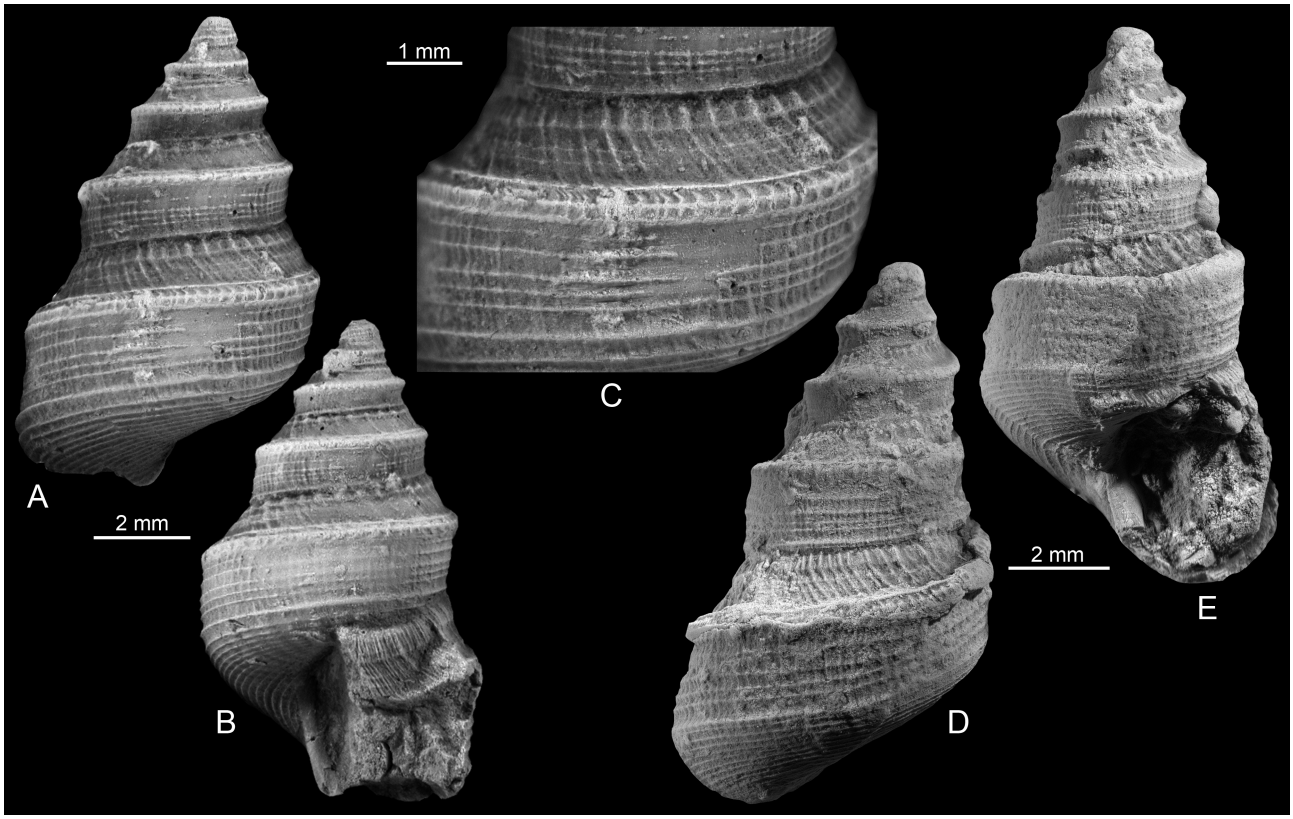

FIGURE 67. *Nodocingulum*? *turris* **sp. nov.**; **A–C.** Holotype, NHMW 1899/0005/0056, St. Cassian Formation; **D–E.** Paratype, SNSB-BSPG 1964 XVII 195, St. Cassian Formation.

The specimens assigned to *Wortheniella subpunctata* by Schwardt (1992, pl. 8, fig. 1) and Bandel (2009, pl. 5, figs 71–73) represent *Wortheniella coralliophila* (Kittl, 1891). The specimen illustrated by Bandel (2009, pl. 5, fig. 74) is assigned to *Wortheniella paolofedelei* **sp. nov.** The specimens assigned to *Wortheniella subpunctata* Laube, 1868 by Zardini (1978, pl. 6, fig. 5; 1980, pl. 1, figs 10–11) are not conspecific with *Nodocingulum*? *turris* (Kittl, 1891). Those specimens represent *Wortheniella paolofedelei* **sp. nov.**

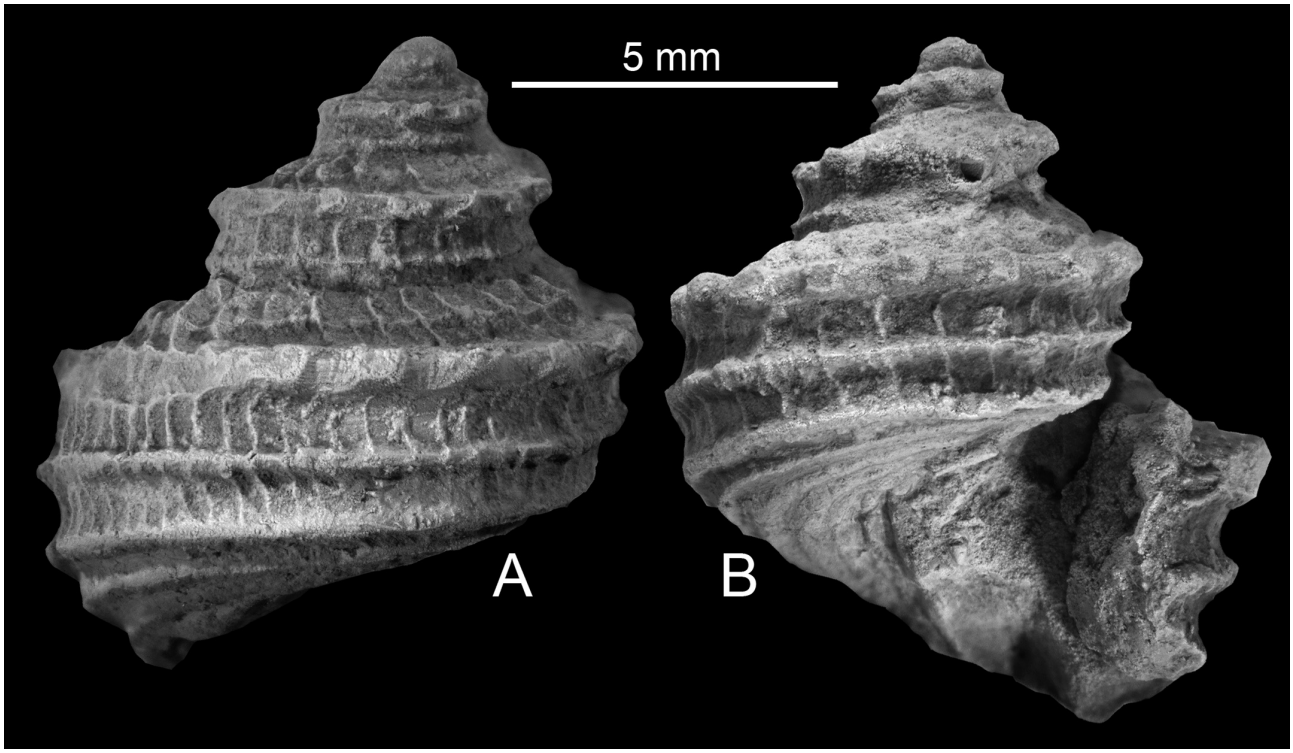

FIGURE 68. *Nodocingulum subtilis* (Kittl, 1891); **A–B.** Lectotype, NHMW 1899/0007/0005, original of Kittl (1891, pl. 3, fig. 14), St. Cassian Formation.

Genus *Striacingulum* gen. nov.
LSID. urn:lsid:zoobank.org:act:9A78873E-C19E-4F64-82EB-9BFA8196051F

Type species. *Pleurotomaria cancellatocingulata* Klipstein, 1844, St. Cassian Formation, Carnian, South Tyrol, Italy.

Derivation of name. From Latin *stria*, and *cingulum*, meaning 'striated girdle' because of the spiral carinae on whorl face; gender neuter.

Diagnosis. Shell gradate, with moderate spire height; early teleoconch ornamented with spiral cords; adult whorl face with three angulations with crests: subsutural angulation, median angulation (selenizone) and angulation on lateral whorl face; whorl face ornamented with nodes on subsutural angulation, with fine spiral threads and fine axial threads or strong axial ribs; selenizone ornamented with strong lunulae and one to three spiral cords; base with spiral cords and umbilical chink.

Discussion. *Striacingulum* **gen. nov.** differs from all other wortheniform taxa (i.e., *Worthenia, Worteniella, Humiliworthenia*, *Rinaldoella, Nodocingulum* **gen. nov.**, *Sisenna*, *Lineacingulum* **gen. nov.**, *Pseudoananias* **gen. nov.**, *Ananias*) by having a subsutural crest and crest on the lateral whorl face and by having a cancellate ornament on its selenizone. The ornamentation of the selenizone of *Nodocingulum* varies among its members, either consisting of nodes, notches, or thread-like lunulae with one spiral cord or carina (e.g., *Nodocingulum granulosum*). *Nodocingulum furcatum* has two carinations as is also the case in *Striacingulum toulai* but it does not develop a subsutural spiral crest and a spiral crest on the lateral whorl face.

Like *Striacingulum*, *Wortheniella* has spiral cords before the onset of the selenizone but they are much stronger in *Wortheniella* and *Wortheniella* has a different selenizone ornamentation (crest-like lunulae with one or two carinae) and lacks subsutural and suprasutural spiral carinations. In *Worthenia*, the teleoconch before the onset of selenizone is convex, without dominant spiral cords, its selenizone is formed from a u-shaped sinus on the convex whorl face (Karapunar *et al*. in press), not from a v-shaped sinus on a whorl angulation. The early shell of *Humiliworthenia* is unknown but it does not develop two spiral carinations on the ramp and lateral whorl face and its selenizone is smooth without lunulae. *Sisenna* is lower-spired, its early teleoconch before the onset of selenizone

has a single carination and the selenizone lacks spiral ornaments. *Lineacingulum* **gen. nov.** is lower-spired, has a circumumbilical carina, equally spaced axial threads on whorl face and v-shaped lunulae on the selenizone. Its early whorls are smooth or with distinct, regularly spaced collabral threads rather than spiral cords. *Pseudoananias* **gen. nov.** is lower spired and its selenizone is initially wide and convex, its late selenizone is convex to slightly concave without strong ornamentation. *Rinaldoella* and *Ananias* differ by having a concave selenizone apart from many other characters that separate them from *Striacingulum*.

Included species. *Pleurotomaria cancellatocingulata* Klipstein, 1844 and *Worthenia toulai* Kittl 1891.

Striacingulum cancellatocingulatum (Klipstein, 1844) comb. nov.

Fig. 69

*1844	*Pleurotomaria cancellato-cingulata*—Klipstein, p. 165, pl. 10, figs 23a–b.
1844	*Pleurotomaria münsteri*—Klipstein, p. 166, pl. 10, fig. 26 (non fig. 25).
1850	*Pleurotomaria cancellato-cingulata* Klipstein, 1844—d'Orbigny, p. 195, no. 395.
1891	*Worthenia turriculata* Kittl n. f.—Kittl, p. 197, pl. 2, fig. 31.
1905	*Worthenia arthaberi* n. sp.—Blaschke, p. 179, pl. 19, figs 11a–c.
1907	*Worthenia turriculata* Kittl—Broili, p. 79, pl. 6, fig. 33.
non 1909	*Worthenia turriculata* Kittl—Scalia, p. 301, pl. 9, fig. 27.
non 1914	*Worthenia turriculata* Kittl—Scalia, p. 10, pl. 1, figs 34a–b.
non 1959	*Worthenia turriculata* Kittl—Leonardi & Fiscon, p. 16, pl. 1, fig. 22.

Material. NHMUK PI OR 35345(1), original of Klipstein (1844, pl. 10, fig. 23), herein designated as lectotype, from the St. Cassian Formation. NHMUK PI OR 35367(1) original of Klipstein (1844, pl. 10, fig. 26) from the St. Cassian Formation. NHMW 1899/0006/0009 (original of Kittl 1891, pl. 2, fig. 31) herein designated as lectotype of *Worthenia turriculata* from the St. Cassian Formation. NHMW 1899/0005/0059/1 from the St. Cassian Formation. MPRZ 2021 1–004 from Milieres; MPRZ 2021 1–028 from Campo, St. Cassian Formation.

Description. Shell wortheniform, high-spired, comprising up to eight whorls, lectotype consisting of four whorls, early whorls are missing, 14.9 mm high, 12.2 mm wide; first two whorls seemingly planispiral (Fig. 69I–J); early teleoconch whorls convex; first whorl about 0.25 mm wide; whorl face of first two teleoconch whorls with equally strong spiral cords; median and basal spiral cords become more prominent within third teleoconch whorl and form angulations; selenizone develops on median angulation; selenizone with one spiral cord and distinct orthocline lunulae in early whorls; number of spiral cords on selenizone increases during ontogeny, with two spiral cords at 5th and 6th whorls and with three spiral cords at 7th and 8th whorls; ramp of early teleoconch with spiral cords and axial riblets; subsutural angulation forms from 5th whorl onward; subsutural angulation forms concave subsutural shoulder which is ornamented with axially elongated nodes; ramp concave between shoulder and selenizone; selenizone in late whorls strongly convex, rounded, forming peripheral crest at mid-whorl, ornamented with three spiral threads and orthocline lunulae forming cancellate pattern; pronounced rounded spiral carina low on lateral whorl face, occasionally with cancellate pattern; sharp spiral rib at outer basal edge and suture; lateral whorl face concave between selenizone, spiral carina and outer basal edge, ornamented with spiral threads; base rounded convex, ornamented with spiral cords, anomphalous; aperture subovate, outer and basal lips rounded, inner lip straight.

Discussion. Kittl (1891) placed *Pleurotomaria cancellatocingulata* tentatively in his newly erected species *Worthenia toulai* (NHMW 1899/0005/0077, original of Kittl 1891, pl. 3, figs 12–13, herein designated as lectotype of *Worthenia toulai* and figured in Fig. 70). *Striacingulum toulai* differs from *Striacingulum cancellatocingulatum* in having a lower spire with immersed first whorl, a sharp crest on the lateral whorl face (instead of a rounded one with cancellate ornament) and a bi-carinate selenizone instead of a selenizone with cancellate ornament. *Worthenia turriculata* Kittl, 1891 is similar to *Striacingulum cancellatocingulatum* in whorl and shell morphology and selenizone ornament; it is therefore regarded as a synonym. As also stated by Broili (1907), *Worthenia arthaberi* Blaschke, 1905 represents a junior synonym of this species as well.

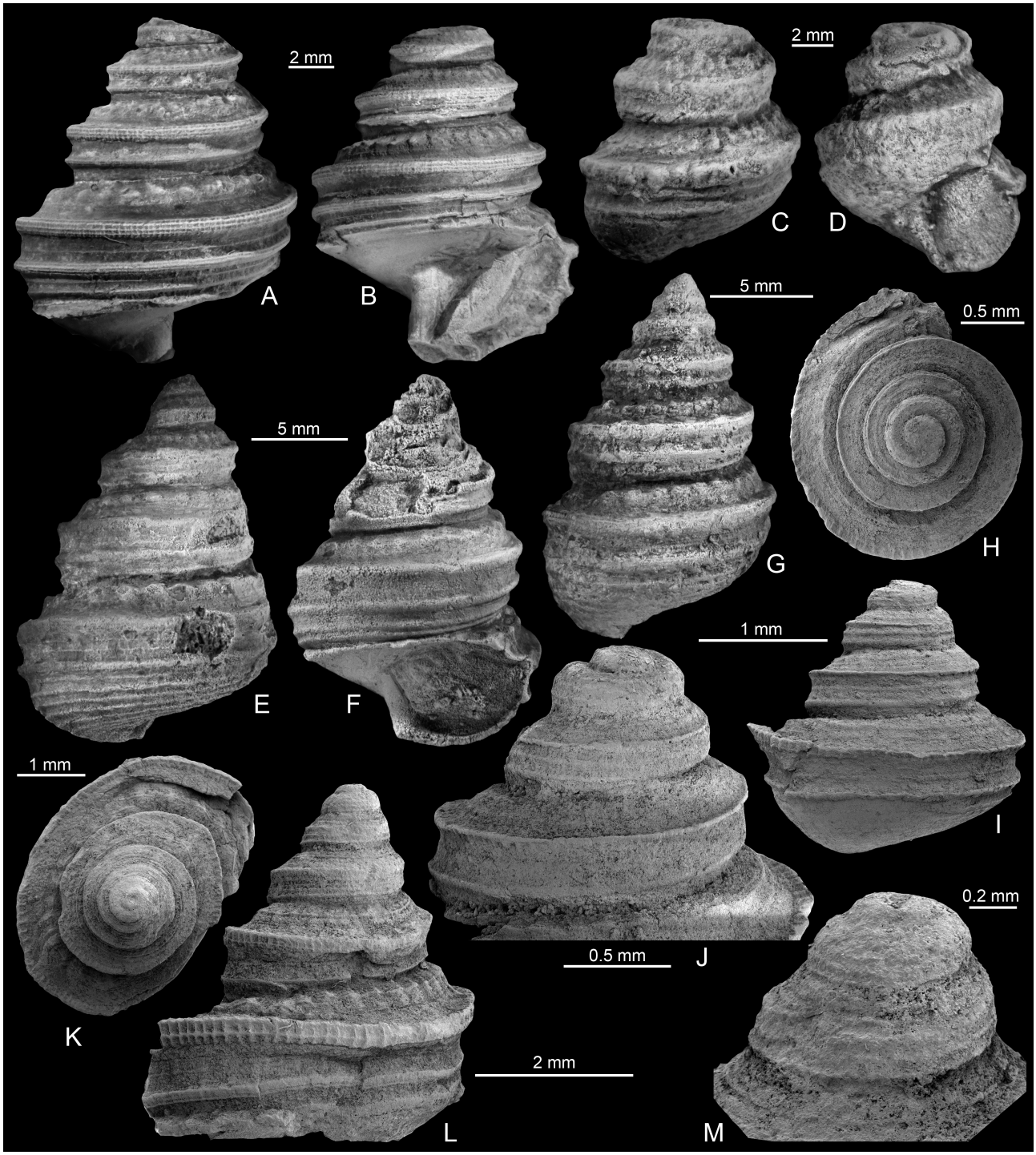

FIGURE 69. *Striacingulum cancellatocingulatum* (Klipstein, 1844); **A–B.** Lectotype, NHMUK PI OR 35345(1), original of Klipstein (1844, pl. 10, fig. 23), St. Cassian Formation; **C–D.** NHMUK PI OR 35367(1) original of Klipstein (1844, pl. 10, fig. 26), St. Cassian Formation; **E–F.** Lectotype of *Worthenia turriculata* Kittl, 1891, NHMW 1899/0006/0009 (original of Kittl 1891, pl. 2, fig. 31), St. Cassian Formation; **G.** NHMW 1899/0005/0059/1, St. Cassian Formation; **H–J.** MPRZ 2021 1–004, juvenile specimen, Milieres, St. Cassian Formation, SEM image; **K–M.** MPRZ 2021 1–028, Campo, St. Cassian Formation, SEM image.

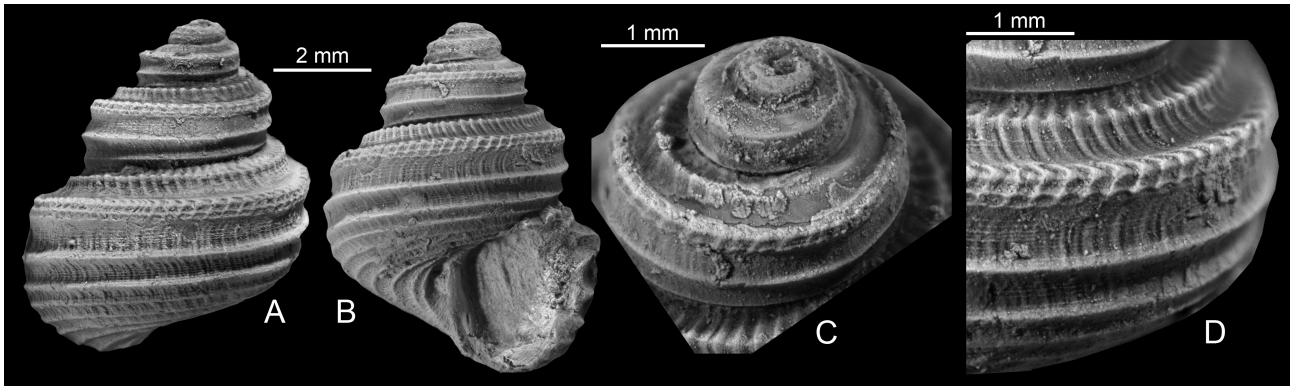

FIGURE 70. *Striacingulum toulai* (Kittl, 1891); **A–D.** Lectotype, NHMW 1899/0005/0077, original of Kittl (1891, pl. 3, figs 12–13), St. Cassian Formation.

Genus *Rinaldoella* Bandel, 2009

Type species. *Wortheniella rinaldoi* Schwardt, 1992, St. Cassian Formation, Carnian, South Tyrol, Italy; original designation.

Diagnosis (Bandel 2009, p. 18). Shell has a similar general shape as is found in *Wortheniella* but ornament of the first whorls of the teleoconch consists of fine spiral ribs crossed by collabral ribs that may form rows of granules or tubercles at crossing points. The ornament of the slit bearing teleoconch is dominated by spiral and axial ribs forming a cancellation. The type to the genus is *Wortheniella rinaldoi* Schwardt, 1992 from the St. Cassian Formation (Schwardt 1992, pl. 3, fig. 1a–d).

Emended diagnosis. Shell gradate; protoconch and early teleoconch immersed; teleoconch before onset of selenizone with spiral cords or spirally aligned prominent tubercles; onset of selenizone abrupt at end of second whorl, developing from u-shaped slit, concave, bordered by sharp crests or thick cords that angulate whorl profile; selenizone without lunulae; later teleoconch ornamented with strong spiral cords, tiny pustules and occasionally with sharp axial ribs and much finer spiral striae; base with spiral lirae, minutely phaneromphalous.

Discussion. Bandel (2009) introduced *Rinaldoella* and included besides the type species several other species for instance *Pleurotomaria muensteri* Klipstein, 1844 and *P. coronata* Münster, 1841. These species differ from the type species of *Rinaldoella* by having a convex or angulated, nodular selenizone and showing a gradual selenizone formation from a v-shaped sinus; thus, they represent *Nodocingulum* **gen. nov.** By contrast *Wortheniella rinaldoi*, the type species of *Rinaldoella*, has a concave, smooth selenizone. The fact that the morphology of the selenizone was not even mentioned in Bandel's (2009) diagnosis shows that too much emphasis was put on the morphology of the early whorl whereas other diagnostic characters were not considered. Therefore, we provide and emended diagnosis for *Rinaldoella*.

As discussed above (see *Lancedellia costata*), it is unknown whether *Lancedellia* and *Rinaldoella* represent synonyms. *Rinaldoella* resembles Scissurellidae with its overall small size, position of selenizone, planispirally coiled early whorls, sudden appearance of selenizone, and prominent selenizone borders. The shell microstructure of *Rinaldoella* needs to be examined in future studies to clarify its systematic placement: if it has nacre it would represent Pleurotomariida, if it lacks nacre it would probably belong to Scissurellidae.

Rinaldoella tornata sp. nov.

Fig. 71

LSID. urn:lsid:zoobank.org:act:58FE8B97-AA8A-430B-B3B7-536CD456BBB4

1992 *Wortheniella toulai* (Kittl, 1891)—Schwardt, p. 34, pl. 2, fig. 1.

Derivation of name. From Latin *tornata*, meaning rounded, turned on a lathe.

Holotype. MPRZ 2021 1–001.

Type locality, age, formation. Campo, Cortina d'Ampezzo, Italy, Early Carnian, St. Cassian Formation.

Material. MPRZ 2021 1–001 holotype, MPRZ 2021 1–022 and MPRZ 2021 1–032 from Campo, St. Cassian Formation.

Description. Shell minute, turbiniform; holotype comprising of 3.5 whorls, 2 mm high, 1.9 mm wide; protoconch of one whorl, 0.15 mm in width; first teleoconch whorl rounded, obliquely immersed, with tiny pustules; spiral cords appear within second teleoconch whorl; first spiral cord forms narrow shoulder; gently inclined ramp between first and second spiral cord; selenizone concave, onset at end of second whorl, bordered by second and third spiral cords, situated at median angulation, without visible lunulae or pustules; fourth and fifth spiral cords on lateral whorl face; whorl face further ornamented with spirally aligned small pustules on interspace between cords; base rounded, ornamented with less prominent and more closely spaced spiral cords, minutely phaneromphalous; aperture subrounded, as wide as high.

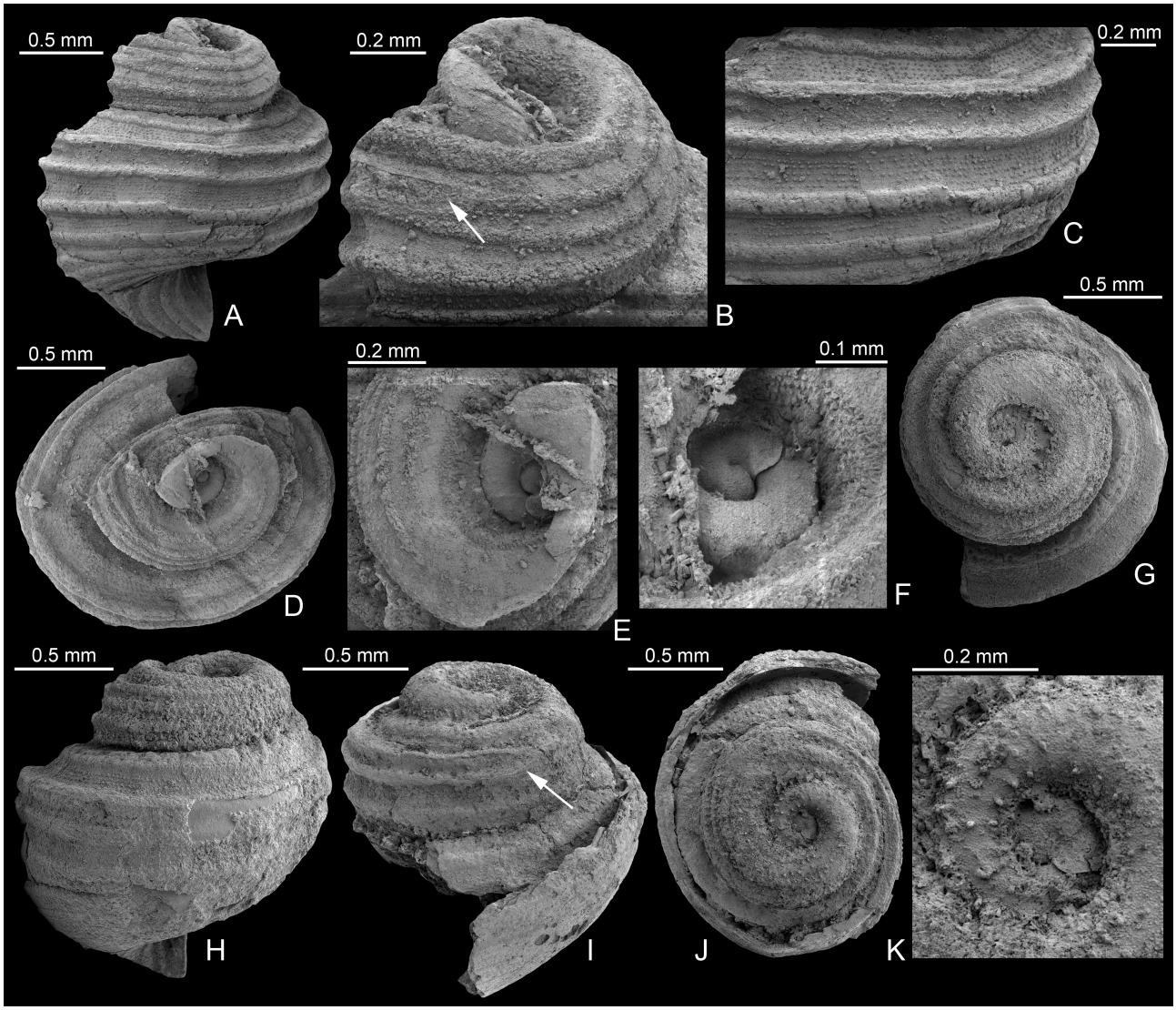

FIGURE 71. *Rinaldoella tornata* **sp. nov.**; **A–F.** Holotype, MPRZ 2021 1–001, Campo, St. Cassian Formation, SEM image, arrow indicates the onset of selenizone; **G–H.** MPRZ 2021 1–022, Campo, St. Cassian Formation, SEM image; **I–K.** MPRZ 2021 1–032, Campo, St. Cassian Formation, SEM image, arrow indicates the onset of selenizone.

Discussion. We studied *Rinaldoella rinaldoi* specimens in the Zardini collection in the Cortina Museum and found that all are very small suggesting that it is a minute species. This is also the case for *Rinaldoella tornata* **sp. nov.** Therefore, the studied specimens are regarded as adult. The same species was reported by Schwardt (1992) and assigned to *Worthenia toulai* Kittl, 1891. We place *Worthenia toulai* Kittl, 1891 in *Striacingulum* and figured the lectotype here (Fig. 70). *Rinaldoella tornata* **sp. nov.** differs distinctly from *Striacingulum toulai* (Kittl, 1891)

in having a concave selenizone, in whorl ornamentation and in being much smaller. *Rinaldoella rinaldoi* (Fig. 72) differs from *Rinaldoella tornata* **sp. nov.** in having prosocyrt axial ribs on the ramp and axial riblets on the lateral whorl face, the selenizone delimited by sharp edges rather than rounded spiral cords, and the whorl face before the onset of the selenizone ornamented with distinct nodes.

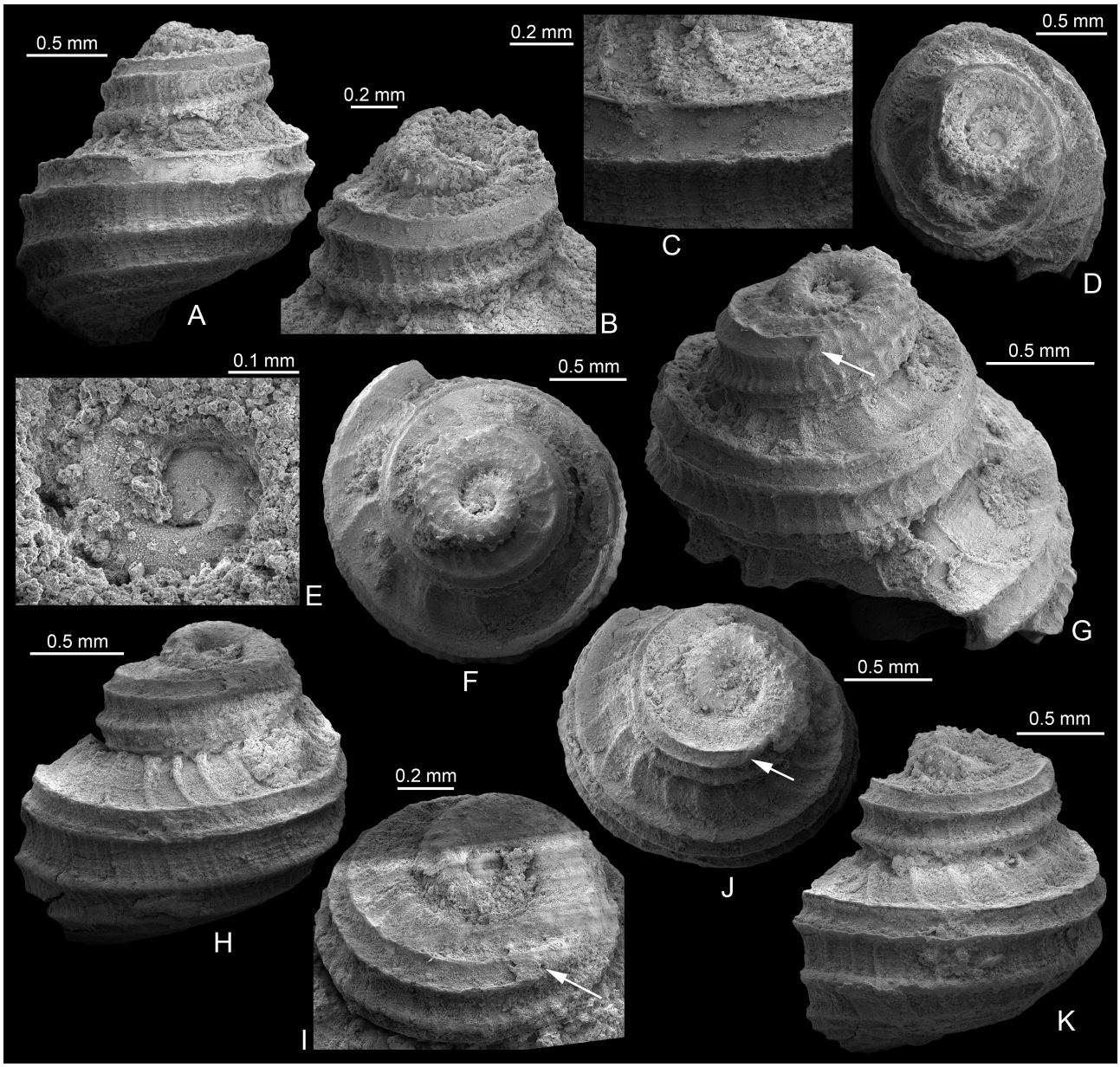

FIGURE 72. *Rinaldoella rinaldoi* (Schwardt, 1992); **A–E.** MPRZ 2021 1–010, Campo, St. Cassian Formation, SEM image; **F–G.** MPRZ 2021 1–011, Campo, St. Cassian Formation, arrow indicates the onset of selenizone, SEM image; **H–I.** MPRZ 2021 1–013, Campo, St. Cassian Formation, arrow indicates the onset of selenizone, SEM image; **J–K.** MPRZ 2021 1–019, Campo, St. Cassian Formation, SEM image, arrow indicates the onset of selenizone.

Non Pleurotomariida

Here, we treat species that were originally described as members of *Pleurotomaria* or Pleurotomariidae but do not represent Pleurotomariida. For the most part their placement was based on the erroneous conception of the presence of a selenizone. We also treat here species that have a selenizone but nevertheless do not belong in Pleurotomariida but to Seguenziida or *Murchisonia*-like Caenogastropoda.

Order Seguenziida

Superfamily Seguenzioidea Verrill, 1884

Family Laubellidae Cox, 1960 (in Knight et al.)

Genus *Laubella* Kittl, 1891

Type species. *Pleurotomaria delicata* Laube, 1868, St. Cassian Formation, Carnian, South Tyrol, Italy; subsequent designation by Woodward (1892). Kittl (1890) did not designate a type species but misidentified the subsequently designated *Pleurotomaria delicata* Laube, 1868.

Discussion. Bandel (2009) placed the family Laubellidae into Seguenzioidea due to the position of the slit high on the whorls, which is similar to the position of the slit or sinus in some recent sequenziid species. Indeed, some modern seguenziids are strikingly similar to *Laubella* for instance the genera *Seguenzia* and especially *Halystina* Marshall, 1991 (e.g., Salvador *et al*. 2014). Both, Laubellidae and Seguenziidae have a nacreous shell and Seguenziidae produce a selenizone-like shell deposition at the former shell slit or sinus high on the whorls. However, in contrast to Recent sequenziids, *Laubella* has a deep slit (up to one third of the last whorl in *Laubella delicata*) rather than a short sinus. It is rather unlikely that the slit or sinus of sequenziid is homologous with the slit of Pleurotomariida because of its almost subsutural position in *Laubella*. As already noted by Bandel (2009) "Laubellidae with the slit high up on the outer lip have four species that resemble modern *Seguenzia* but a relation to the Seguenziidae is doubtful". Nevertheless, Laubellidae is distinctly different from other known members of Pleurotomariida in terms of the position of selenizone, ontogenetic development etc. and is here kept in Seguenzioidea.

***Laubella delicata* (Laube, 1868)**
Fig. 73

*1868	*Pleurotomaria delicata* Laube—Laube, p. 57, pl. 27, fig. 5.
non 1890	*Laubella delicata* Laube sp.—Kittl, p. 207, figs 6–10.
1907	*Laubella* sp.—Broili, p. 81, pl. 7, fig. 4.
1978	*Worthenia texturata* (Münster)—Zardini, p. 21, pl. 6, figs 7–8.
1985	*Worthenia texturata* (Münster)—Zardini, pl. 6, fig. 7.
1991	*Laubella texturata* (Münster, 1841)—Bandel, p. 44, pl. 15, figs 6–7 (non pl. 15, figs 5).
1991	*Laubella bella* n. sp.—Bandel, p. 43, pl. 16, figs 1–2, 7; pl. 17, figs 1–2, 4.
non 1991	*Laubella delicata* (Laube, 1868)—Bandel, p. 41, pl. 15, figs 1–4.
non 2009	*Laubella delicata* (Laube, 1868)—Bandel, pl. 8, figs 108–110.

Material. GBA 1868/008/0003, 4356, original of Laube (1868, pl. 27, fig. 5), herein designated as lectotype; GBA 1868/008/0004, 4356, another specimen from Laube's collection herein selected as paralectotype; both from the St. Cassian Formation. SNSB-BSPG 1903 IX 344 (original of Broili 1907, pl. 7, fig. 4), from the Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMW 1990/0645/0000 (original of Bandel 1991, pl. 17, figs 1–2, 4) holotype of *Laubella bella*; NHMW 1990/0644/0000 (original of Bandel 1991, pl. 15, figs 6–7) from the St. Cassian Formation.

Description. Shell low turbiniform, globular, with gradate spire; lectotype consisting of 5 whorls, 5.2 mm high, 4.2 mm wide; first whorl planispiral with a carina facing towards apex; carina later turning into selenizone; whorl face has subsutural carina, median carina (with selenizone) and basal carina (edge); median carina situated high on whorl face; whorl face between carinae concave; whorls with cancellate ornament of equally strong and equally spaced prosocyrt axial and spiral threads; threads form minute nodes at intersections; selenizone rounded to convex in transverse section, representing median carina, ornamented with closely spaced orthocline lunulae and three spiral threads, forming cancellate pattern similar to that on whorl face; outer basal edge of spire whorls covered by succeeding whorls except on penultimate whorl because the last whorl is slightly deflected downwards so that basal carina becomes exposed; base rounded, ornamented as whorl face; inner lip arched, forming shallow fissure between parietal and columellar lip.

Discussion. In *Laubella delicata,* the selenizone, is lower on the whorl than in the specimens assigned to

Laubella delicata by Kittl (1890). Kittl's specimens are not conspecific with the lectotype and paralectotype of *Laubella delicata* (figured here in Fig. 73A–B). *Laubella bella* Bandel, 1991 (Fig. 73E–F) is identical with the lectotype of *Laubella delicata* (Laube, 1868) and therefore represents a younger synonym. The specimens identified as *Laubella delicata* by Kittl (1890) and Bandel (1991, 2009) represent *Laubella subsulcata* **sp. nov.** *Laubella delicata* differs from *Laubella subsulcata* **sp. nov.** by being broader and by having the selenizone lower on the whorl and thus more distant from the adapical suture. Moreover *L. delicata* has a s finer ornament. The specimen assigned to *Laubella texturata* (i.e., *Lineacingulum texturatum*) by Bandel (1991, pl. 15, figs 6–7) is figured herein (Fig. 73C) and represents *Laubella delicata*.

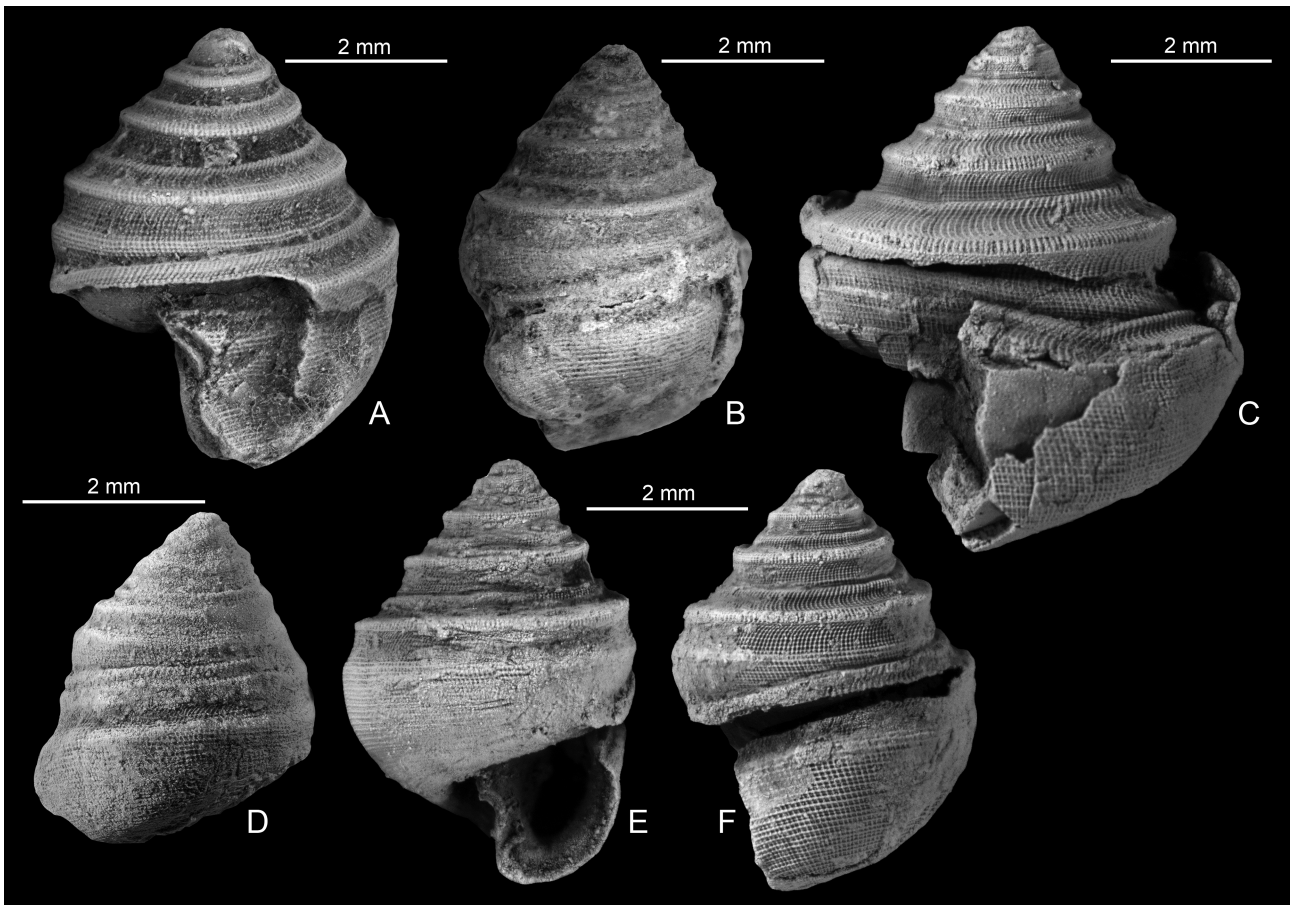

FIGURE 73. *Laubella delicata* (Laube, 1868); **A.** Lectotype, GBA 1868/008/0003, 4356, original of Laube (1868, pl. 27, fig. 5), St. Cassian Formation; **B.** Paralectotype, GBA 1868/008/0004, 4356, one specimen from Laube's collection herein selected as paralectotype St. Cassian Formation; **C.** NHMW 1990/0644/0000 (original of Bandel 1991, pl. 15, figs 6–7), St. Cassian Formation; **D.** SNSB-BSPG 1903 IX 344 (original of Broili 1907, pl. 7, fig. 4), Pachycardientuffe, Upper Ladinian, Seiser Alm; **E–F.** holotype of *Laubella bella* Bandel, 1991, NHMW 1990/0645/0000 (original of Bandel 1991, pl. 17, figs 1–2, 4), St. Cassian Formation.

***Laubella subsulcata* sp. nov.**
Fig. 74
LSID. urn:lsid:zoobank.org:act:360949BD-772C-4405-AC4B-84397B4949AB

1890 *Laubella delicata* Laube sp.—Kittl, p. 207, figs 6–10.
1978 *Laubella delicata* (Laube)—Zardini, p. 23, pl. 7, figs 7–8.
1991 *Laubella delicata* (Laube, 1868)—Bandel, p. 41, pl. 15, figs 1–4.
2009 *Laubella delicata* (Laube, 1868)—Bandel, pl. 8, figs 108–110.

Derivation of name. Latin, because of the concave depression (*sulcus*) below (*sub*-) the selenizone.

Holotype. NHMW 1884/D/186 [NHMW 1884/0001/0186].

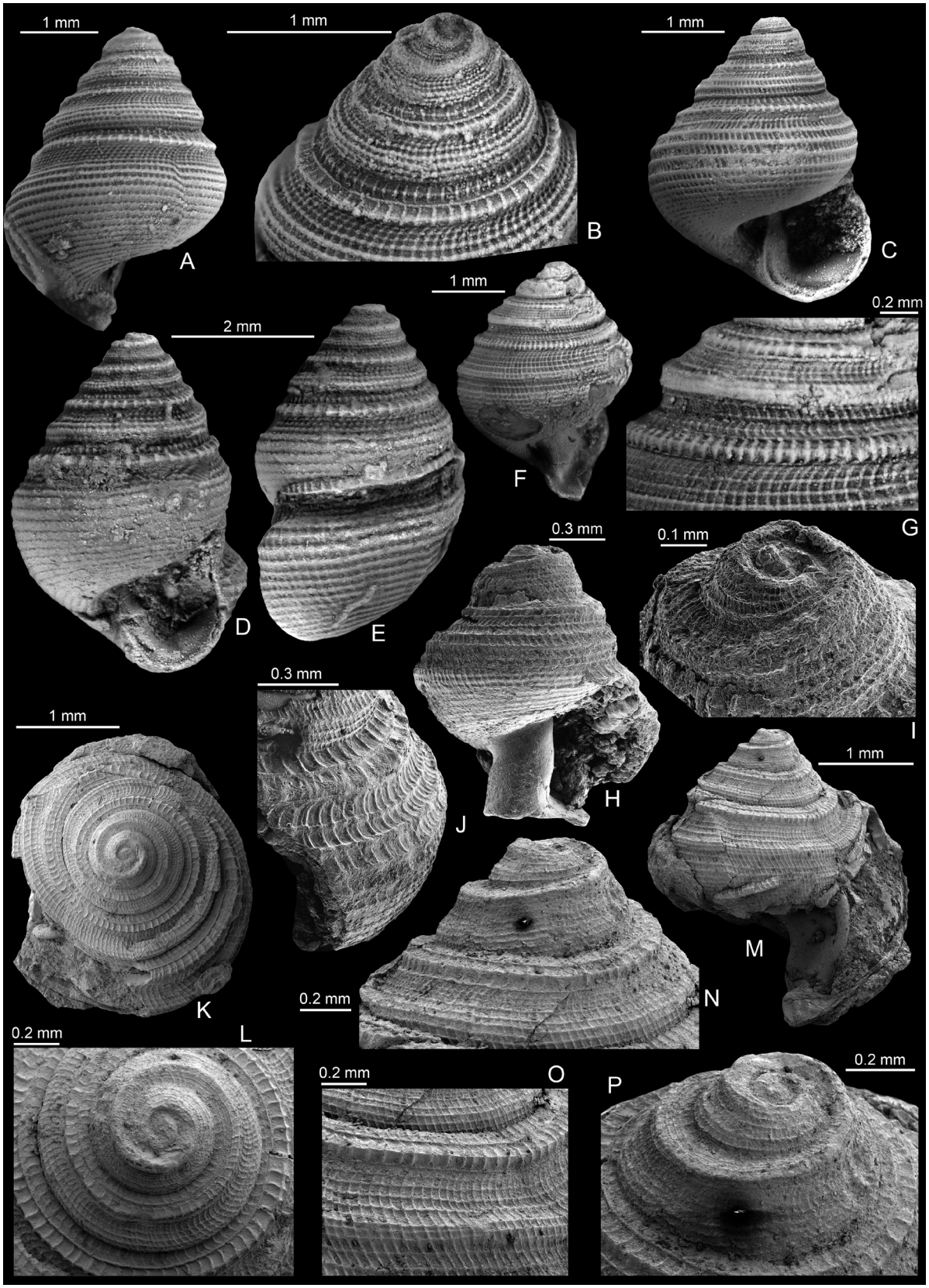

FIGURE 74. *Laubella subsulcata* **sp. nov.**; **A–B.** Holotype, NHMW 1884/0001/0186 (original of Bandel 1991, pl. 15, fig. 2), St. Cassian Formation; **C.** Paratype, NHMW 1884/0001/0159 (original of Bandel 1991, pl. 15, figs 1, 3), St. Cassian Formation; **D–E.** Paratype, NHMW 1899/0005/0105/1 (original of Kittl 1891, pl. 4, fig. 9), St. Cassian Formation; **F–G.** NHMW 1990/0647/0000/1, Misurina, St. Cassian Formation; **H–J.** PZO 13698, juvenile specimen, St. Cassian Formation, SEM image; **K–P.** MPRZ 2021 1–033, Misurina, St. Cassian Formation, SEM image.

Paratypes. NHMW 1899/0005/0105, 1884/D/159 [NHMW 1884/0001/0159].

Type locality, age, formation. Italy, South Tyrol, Late Triassic, Early Carnian, St. Cassian Formation.

Material. NHMW 1884/0001/0186 (original of Bandel 1991, pl. 15, fig. 2) holotype; NHMW 1884/0001/0159 (original of Bandel 1991, pl. 15, figs 1, 3) and NHMW 1899/0005/0105/1 (original of Kittl 1891, pl. 4, fig. 9), paratypes from the St. Cassian Formation. GBA 1868/008/0005, 4356, one specimen from Laube's collection labeled as *Pleurotomaria delicata*. NHMW 1990/0647/0000/1, MPRZ 2021 1–033 from Misurina, St. Cassian Formation. PZO 13698 from the St. Cassian Formation.

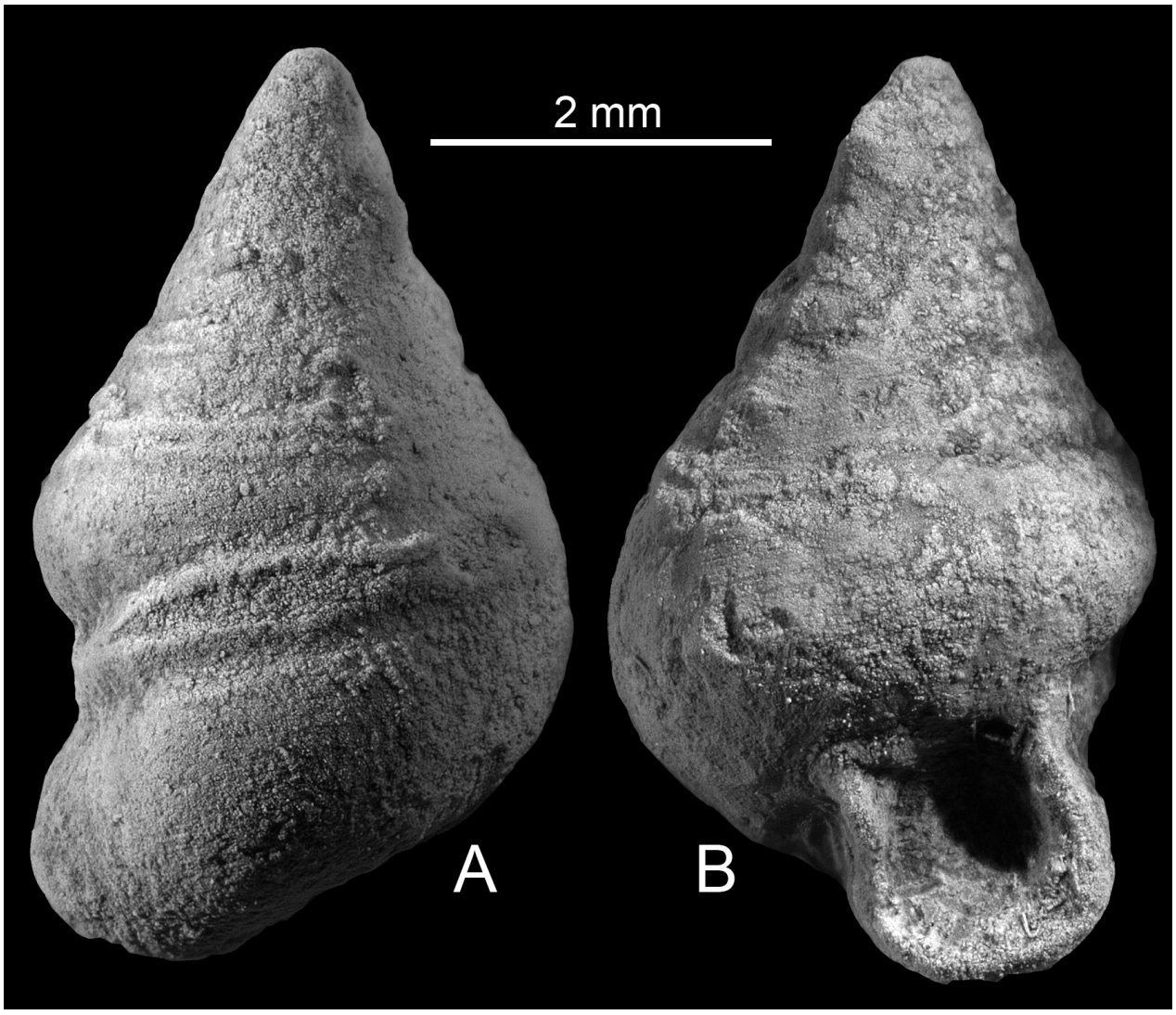

FIGURE 75. *Laubella triasica* (Zittel, 1882); **A–B.** Lectotype, SNSB-BSPG 1881 I 501 (the original of Zittel 1882, fig. 223), St. Cassian Formation.

Description. Shell turbiniform; holotype consisting of 5 whorls, 3.9 mm high, 2.8 mm wide; protoconch consisting of one planispiral whorl; first teleoconch whorl planispiral with a carina facing towards apex; carina with selenizone in later whorls; whorl face above selenizone concave, very narrow, as wide as selenizone, ornamented with orthocline or prosocyrt threads and one spiral thread; selenizone narrow, convex, rounded, situated high on the whorl, ornamented with widely spaced orthocline lunulae and one median spiral cord; whorl face below selenizone concave on upper half, convex on lower half forming periphery; whorl face below selenizone with cancellate ornament of prosocyrt threads and spiral cords forming nodes when intersecting; spiral cords increase in prominence towards abapical suture so that interspaces between axial threads and spiral cords become narrower; whorls embrace below mid whorl; base rounded ornamented with spiral cords and axial threads; aperture teardrop-shaped, with convex outer lip, rounded basal lip and convex inner lip; inner lip arched, forming shallow fissure between parietal and columellar lip.

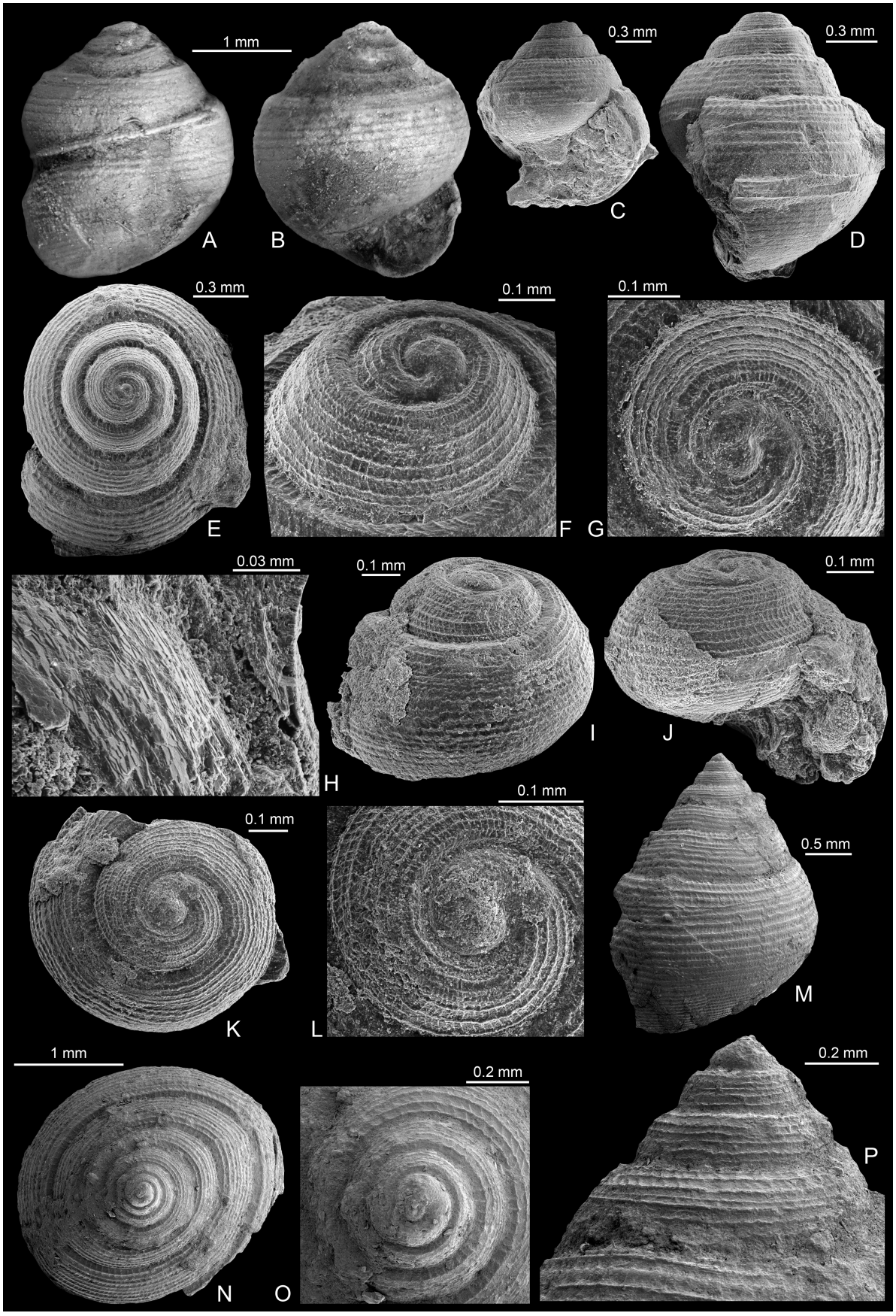

FIGURE 76. *Laubella minor* Kittl, 1891; **A–B.** Lectotype, NHMW 1899/0005/0106 (original of Kittl 1891 pl. 4, fig. 11), St. Cassian Formation; **C–H.** PZO 13702, St. Cassian Formation, SEM image; **I–L.** PZO 13703, juvenile specimen, St. Cassian Formation, SEM image; **M–P.** MPRZ 2021 1–039, St. Cassian Formation, SEM image.

Discussion. The new species *Laubella subsulcata* is based on the specimens previously regarded as *Laubella delicata* by Kittl (1890). *Cantantostoma triasica* Zittel, 1882 (Zittel 1882, p. 181, fig. 223) from the St. Cassian Formation was considered a synonym of *Laubella delicata* by Kittl (1890). Here we figure SNSB-BSPG 1881 I 501 (the original of Zittel 1882, fig. 223) and designate it as the lectotype of *Laubella triasica* (Zittel, 1882), which is an encrusted specimen (Fig. 75). *Laubella triasica* (Zittel, 1882) has similar whorl profile and position of selenizone as *Laubella subsulcata* **sp. nov.** However, it is much higher spired, coeloconoid, lacks the characteristic ornamentation of the selenizone and whorl face and has a constricted body whorl; therefore, it is not conspecific with *Laubella subsulcata* **sp. nov.** It is possible that *L. triasica* has an elongated trema at the end of the last whorl, but the shell is too encrusted to be sure. *Laubella minor* Kittl, 1891 (original of Kittl 1891 pl. 4, fig. 11, NHMW 1899/0005/0106 herein designated as lectotype and is figured in Fig. 76A–B) differs from *Laubella subsulcata* **sp. nov.** by the absence of a concave whorl face below the selenizone and by having a lower spire. The specimen assigned to *Laubella minor* by Bandel (1991, pl. 16, figs 3–6, 8; 2009, pl. 8, figs 111–112) is more high-spired than the lectotype of *Laubella minor* and has less prominent spiral ribs. *Laubella minor* seems to vary regarding the spire height of its early whorls. Specimens with more high-spired early whorls and less prominent spiral cords are found in the Zardini collection (Fig. 76M–P). The specimen assigned to *Colonia cincta* by Zardini (1978, pl. 10, fig. 6) represents *Laubella minor* with high-spired early whorls. The strength of the spiral cords of *Laubella subsulcata* **sp. nov.** seems also to be variable. Some of the studied specimens have weaker spiral cords and they develop a weak suprasutural carina (Fig. 74F–G, 74K–P).

Family Eucyclidae Koken, 1896

Discussion. The family Eucyclidae Koken, 1896 has been classified under the superfamily Eucycloidea (e.g., Bandel 2010; Szabó *et al*. 2019) or under Seguenzioidea Verrill, 1884 (e.g., Ferrari *et al*. 2014; Bouchet *et al*. 2017). Szabó *et al*. (2019) provisionally included the family Cirridae Cossmann, 1916 in the superfamily Eucycloidea following Conti & Monari (2001). The family Cirridae had been placed in Porcellioidea (formerly Cirroidea Cossmann, 1916; see Frýda *et al*. 2019) together with the family Porcelliidae Koken, 1895 (in Zittel). The families Cirridae and Porcelliidae share a change in coiling direction from dextral to sinistral or planispiral (e.g., Bandel 1993a; Frýda *et al*. 2008). Bandel (1993a) documented the change in coiling direction from dextral to sinistral in Jurassic cirrid species that he assigned to the genus *Hamusina* Gemmellaro, 1879. The Palaeozoic genus *Alaskacirrus* Frýda & Blodgett, 1998 and the members of Cassianocirrinae Bandel, 1993a from the Triassic were placed in the family Cirridae based on this character. It is possible that not all sinistrally coiled Jurassic Cirridae have a dextrally coiled early teleoconch as in *Alaskacirrus*, *Hamusina* and the members of Porcelliidae. However, this needs further study. If the change in coiling direction of the teleoconch whorls has the high systematic significance proposed by earlier workers, then Eucycloidea uniting Cirridae and Eucyclidae would probably be polyphyletic. Here, we continue to place Eucyclidae in the superfamily Seguenzioidea.

Genus *Paleunema* Kittl, 1891

Type species. *Pleurotomaria nodosa* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

Discussion. *Paleunema* Kittl, 1891, *Neoeunema* Bandel, 2010, *Ampezzalina* Bandel, 1993b and *Bandelastraea* Nützel & Kaim, 2014 (=*Cassianastraea* Bandel, 1993b) share some similarities such as the presence of axial lamellae which form spines or notches and the presence of spiral cords on the base. *Paleunema* and *Neoeunema* differ from *Ampezzalina* in having a convex base and straight growth lines rather than oblique prosocyrt growth lines on the whorl face. Previously, *Bandelastraea* and *Ampezzalina* Bandel, 1993b were placed in the family Turbinidae (Nützel & Kaim 2014), *Paleunema* in Amberleyidae (Knight *et al*. 1960) and *Neoeunema* in Eucyclidae (Bandel 2010). The phylogenetic relations between these four genera needs further study. At present, we place *Paleunema*, *Bandelastraea* and *Ampezzalina* within Eucyclidae Koken, 1896, which is considered as a senior synonym of Amberleyidae Wenz, 1938 (Ferrari *et al*. 2014; Bouchet *et al*. 2017).

***Paleunema nodosa* (Münster, 1841)**
Fig. 77

*1841	*Pleurotomaria nodosa*—Münster, p. 113, pl. 12, figs 14a–b.
1850	*Turbo nodosus* d'Orb., 1847—d'Orbigny, p. 192, no. 313.
1891	*Paleunema nodosa* Münster sp.—Kittl, p. 245, pl. 6, fig. 18.
non 1959	*Paleunema nodosum* Münster—Leonardi & Fiscon, p. 20, pl. 2, figs 5a–b.
1978	*Paleunema nodosa* (Münster)—Zardini, p. 29, pl. 13, figs 2–3.
1993b	*Cassianastrea haueri* (Kittl, 1891)—Bandel, p. 50, pl. 14, figs 4–5.

Material. SNSB-BSPG AS VII 1518 (original of Münster 1841, pl. 12, figs 14a–b) herein designated as lectotype from the St. Cassian Formation. NHMW 1899/0005/0017 (original of Kittl 1891, pl. 6, fig. 18) from the St. Cassian Formation.

Description. Shell trochiform; lectotype comprises about 3.5 preserved teleoconch whorls, 7.6 mm high, 6.1 mm wide; spire imbricated, steeply inclined with prominent suprasutural spiral bulge forming periphery and weaker one somewhat below adapical suture; whorl face convex above subsutural bulge, concave between bulges; whorl face and base ornamented with sharp, densely spaced, irregular collabral axial lamellae; axial lamellae unite to form nodes and short subsutural axial ribs on adapical bulge and above; lamellae forming prominent notches (crescentic hollow spines) at peripheral bulge; notches at peripheral bulge numbering ca. 20 on last whorl; whorl embrace just below abapical bulge; base convex, ornamented with 5 spiral cords intersecting with axial lamellae that are extensions from those on whorl face; axial lamellae between peripheral bulge and outermost spiral cord of base equal in strength with those on whorl face; basal spiral cords decrease in prominence towards shell axis; base anomphalous; aperture as wide as high with angulated outer lip, convex basal lip and convex inner lip.

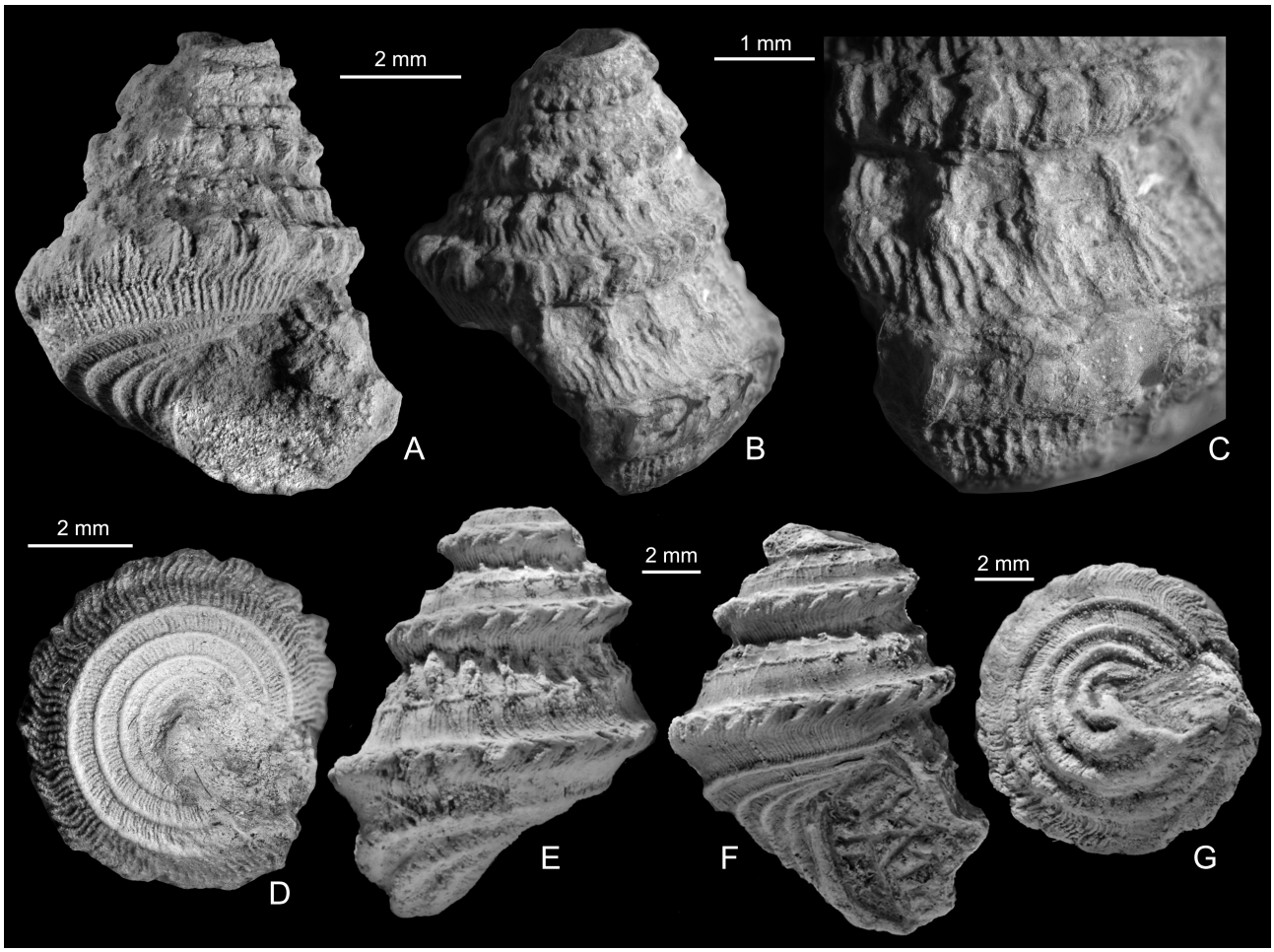

FIGURE 77. *Paleunema nodosa* (Münster, 1841); **A–D.** Lectotype, SNSB-BSPG AS VII 1518 (original of Münster 1841, pl. 12, figs 14a–b), St. Cassian Formation; **E–G.** NHMW 1899/0005/0017 (original of Kittl 1891, pl. 6, fig. 18), St. Cassian Formation.

Discussion. Bandel (1993b) questionably placed *Paleunema nodosa* (Münster, 1841) in synonymy with *Bandelastraea haueri* (Kittl, 1891); however, they are two distinct species.

The specimen assigned to *Paleunema nodosa* by Kittl (1891, pl. 6, fig. 18; figured here in Fig. 77E–G) differs slightly from the lectotype. In Kittl's specimen, the aperture is higher than wide and the suture is situated lower on the whorl (at the first basal cord) so that the peripheral carina is situated higher on the whorl face, and not directly above the suture as in the lectotype. Otherwise this specimen as well as the specimens illustrated by Zardini (1978, pl. 13, figs 2–3) closely resemble the lectotype and differences are interpreted as intraspecific variability.

Genus *Ampezzalina* Bandel, 1993b

Type species. *Pleurotomaria calcar* Münster, 1841, St. Cassian Formation, Carnian, South Tyrol, Italy; original designation, misidentified by Bandel (1993b); *Pleurotomaria calcar* Münster fixed as type species herein (ICZN Art. 70).

Remarks. Bandel (1993b) misidentified the type species, the juvenile specimens illustrated and described by him are much more slender than the lectotype designated herein and have three rows of hollow spines distributed over the entire whorl face which are not deflected downwards. By contrast, *Pleurotomaria calcar* Münster, which we fix as type species (ICZN Art. 70) of *Ampezzalina*, has very strong spines emerging just above the abapical suture; the spines are strongly deflected downward. Because of the Bandel's (1993b) misidentification of the type species, an emendation of the diagnosis of *Ampezzalina* is needed.

Emended diagnosis. Shell broadly trochiform; whorl face imbricated with pronounced suprasutural spiral carina forming periphery and transition to base, having two rows of prominent hollow spines that are strongly deflected downward, pointing in adapertural direction; base anomphalous, flat to slightly convex, jut out by crown of spines, with prominent spiral cords; aperture oblique with evenly arched columellar lip.

Discussion. Münster's (1841) type material of the type species is poorly preserved but the lectotype shows the prominent double row of spines at the outer basal edge of the whorls as does an additional specimen reposited in Palaeontological collections of the University of Tübingen (GPIT-PV-117918, Fig. 78C–F). This character and the lack of spines at mid-whorl separates it from the similar genus *Bandelastraea* Nützel & Kaim, 2014 (= *Cassianastraea* Bandel, 1993b non *Cassianastraea* Volz, 1896). It is possible that both genera are synonymous but better-preserved material of *A. calcar* is needed so that the ornament and ontogenetic change of the shell can be studied in more detail. The better knowledge of the type species of *Ampezzalina* and *Bandelastraea* shows that *Ampezzalina angulata* Nützel & Senowbari-Daryan, 1999 from the Late Triassic of Iran must be placed in *Bandelastraea* (*Bandelastraea angulata* **comb. nov.**).

Nützel & Kaim (2014) placed *Bandelastraea* in the family Turbinidae Rafinesque, 1815. As discussed previously *Paleunema*, *Ampezzalina* and *Bandelastraea* are probably closely related to each other and are preliminarily assigned to Eucyclidae Koken, 1896. The genus *Ampezzalina* is restricted to the Triassic apart from an uncertain report from the Permian of Thailand (Ketwetsuriya *et al*. 2020).

Ampezzalina calcar (Münster, 1841)

Fig. 78

*1841	*Pleurotomaria calcar*—Münster, p. 110, pl. 11, figs 28a–b.
1850	*Trochus subcalcar* d'Orb., 1847—d'Orbigny, p. 190, no. 268.
1891	*Pachypoma calcar* Münster sp.—Kittl, p. 243, pl. 6, figs 5–10.
non 1907	*Astralium* (*Pachypoma*) *calcar* Mstr.—Broili, p. 85, pl. 7, fig. 14.
non 1978	cfr. *Astraea* (*Pachypoma*) *calcar*—Zardini, p. 27, pl. 11, fig. 5.
non 1978	cfr. *Astraea* (*Pachypoma*) *calcar* n. f. juvenile—Zardini, p. 27, pl. 11, fig. 4.
non 1993b	*Ampezzalina calcar* (Münster, 1891)—Bandel, p. 51, pl. 14, fig. 6; pl. 15, figs 1–5.

Material. SNSB-BSPG AS VII 1514 (original of Münster 1841, pl. 11, figs 28a–b) herein designated as lectotype; SNSB-BSPG AS VII 1515 herein designated as paralectotype; both from the St. Cassian Formation. GPIT-PV-117918 reposited in Palaeontological collections of the University of Tübingen from the St. Cassian Formation.

Description. Shell trochiform, with imbricate whorls; lectotype comprises about 4 preserved teleoconch whorls, 18.9 mm high, 23.2 mm wide; suture incised; whorl face flatly convex, steeply inclined, with basal peripheral carina and basal ridge below carina; peripheral carina and basal ridge with prominent spines developed from notches; peripheral spines pointing downward, basal spines less prominent, also pointing downward; both rows of spines emerging at suture on spire whorls; whorl face with poorly preserved traces of sinuous (prosocline abapically, prosocyrt near peripheral carina), strengthened growth lines; base anomphalous, flat to slightly convex, jut out by crown of spines, with prominent spiral cords; aperture oblique with evenly arched columellar lip.

Discussion. The specimens assigned to *Pachypoma calcar* by Kittl (1891, pl. 6, figs 5, 7–8) might represent *Ampezzalina haueri* (Kittl, 1891). The specimens assigned to cfr. *Astraea* (*Pachypoma*) *calcar* by Zardini (1978, pl. 11, figs 4–5) and *Ampezzalina calcar* by Bandel (1993b, pl. 14, fig. 6; pl. 15, figs 1–5) can be placed in *Bandelastraea lancedelli* (Zardini, 1978) (Zardini 1978, pl. 13, fig. 7; = *Paleunema turricolata* Zardini, 1978, pl. 13, fig. 6).

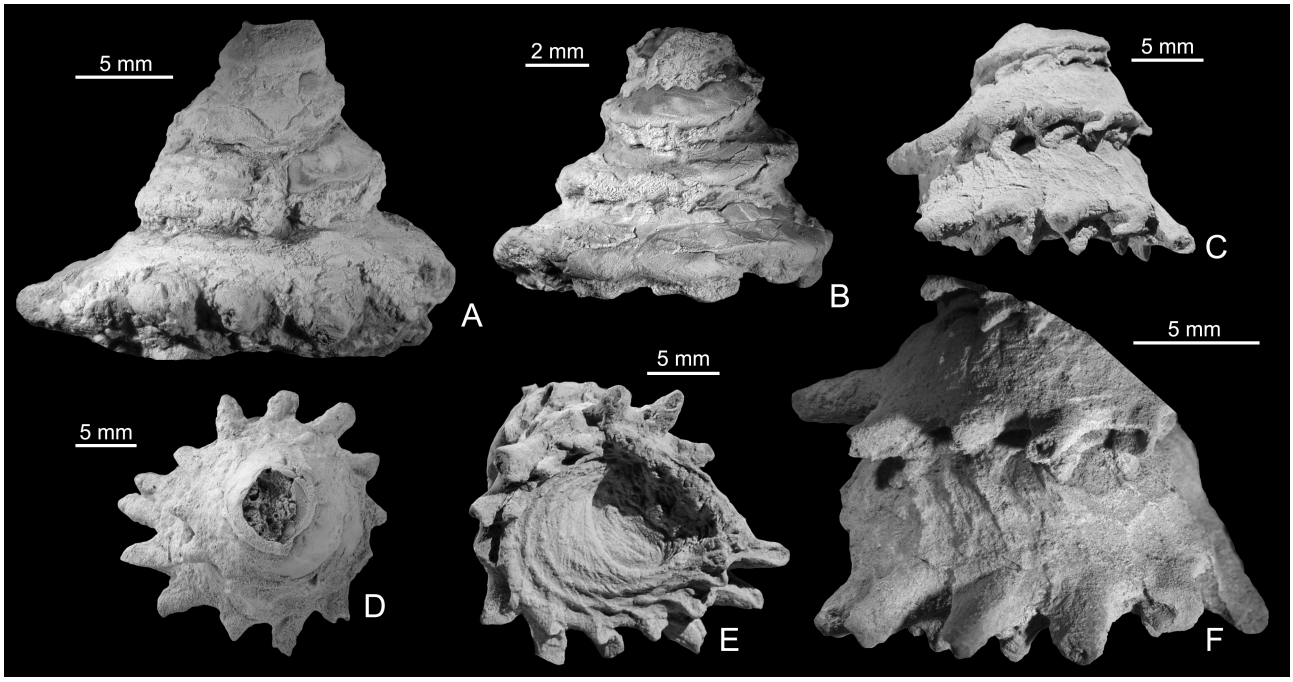

FIGURE 78. *Ampezzalina calcar* (Münster, 1841); **A.** Lectotype, SNSB-BSPG AS VII 1514 (original of Münster 1841, pl. 11, figs 28a–b), St. Cassian Formation; **B.** Paralectotype, SNSB-BSPG AS VII 1515, St. Cassian Formation; **C–F.** GPIT-PV-117918, St. Cassian Formation.

Pachypoma damon Laube, 1868, type species of *Bandelastraea*, has one spine bearing row on its ramp in addition to a peripheral spine bearing ridge and it has shorter spines. *Ampezzalina calcar* lacks a spine bearing rib on the ramp and it has a spine-bearing basal ridge below the peripheral carina, the rows of spines are lower on the whorls and deflected downward. Moreover, *Bandelastraea damon* has densely spaced collabral, prosocline axial lamellae on the whorl face. Here, we figure well-preserved specimens of the type lot of *Bandelastraea damon* (Laube, 1868) for comparison (Fig. 79) and designate the specimen that was illustrated by Laube (1868, pl. 34, fig. 10; GBA 1869/009/0001) as lectotype (Fig. 79A, B) and two other specimens as paralectotypes (GBA 1869/009/0002, Fig. 79C; GBA 1869/009/0003, Fig. 79D). We herein designate GBA 1869/009/0005 (original of Laube 1868, pl. 34, fig. 10) as lectotype of *Pachypoma endymion* Laube, 1868 (Fig. 79E–G).

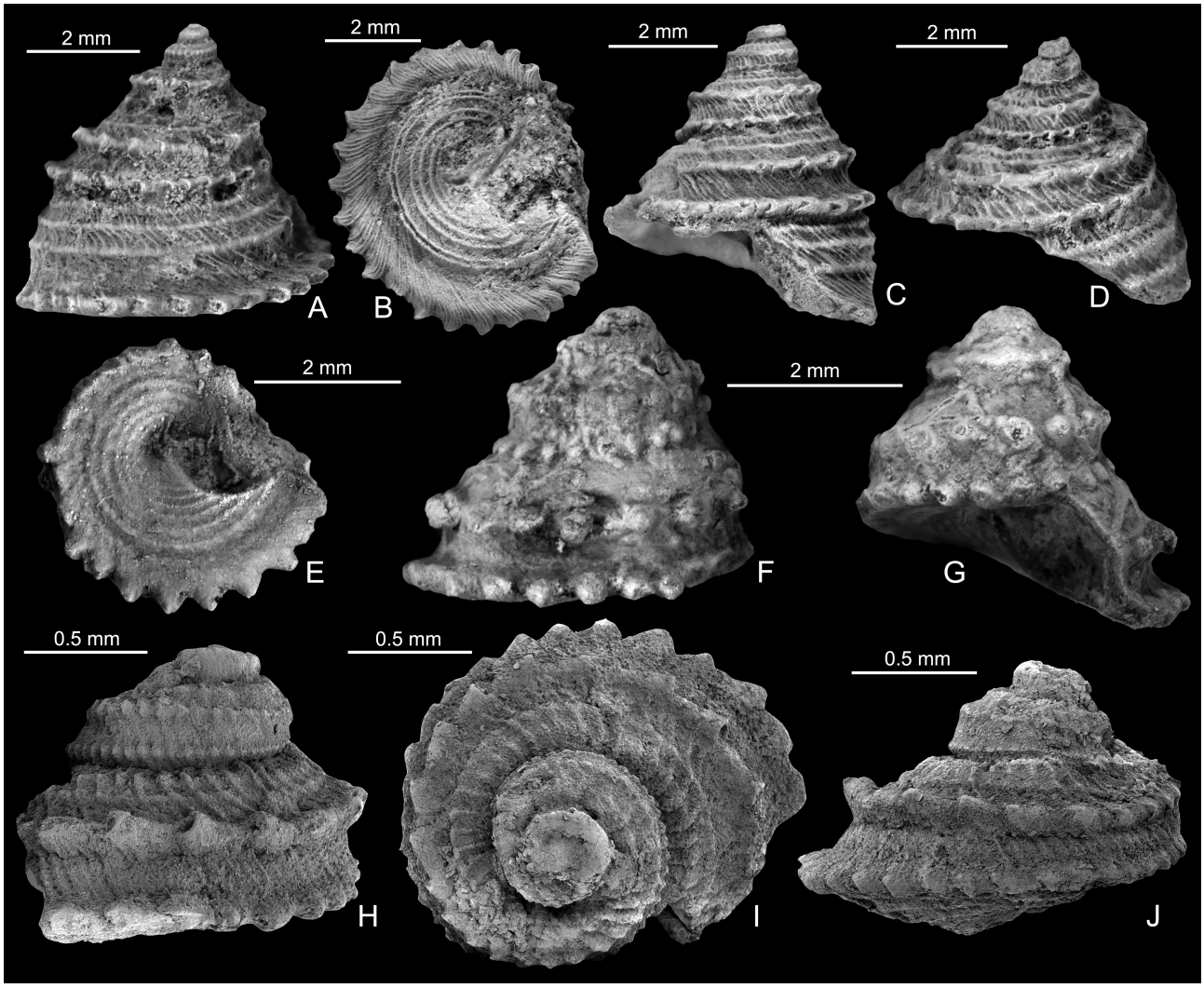

FIGURE 79. *Bandelastraea damon* (Laube, 1868); **A–B.** Lectotype (herein designated), GBA 1869/009/0001, original of Laube (1868, pl. 34, fig. 10); **C.** Paralectotype (herein designated), GBA 1869/009/0002; **D.** Paralectotype (herein designated), GBA 1869/009/0003; **E–G.** Lectotype (herein designated) of *Pachypoma endymion* Laube, 1868, GBA 1869/009/0005, original of Laube (1868, pl. 34, fig. 10); **H–J.** MPRZ 2021 1–003, juvenile specimen, Milieres, St. Cassian Formation, SEM image.

Genus *Triassocirrus* Yin & Yochelson, 1983b

Type species. *Triassocirrus guizhouensis* Yin & Yochelson, 1983b from the Anisian of Guizhou, China; original designation.

Discussion. Zittel (1882) erected the genus *Coelocentrus* Zittel, 1882 and included two species: *Cirrus goldfussi* d'Archiac and Verneuil, 1842 (from the Devonian) and *Cirrus polyphemus* Laube, 1870 (from the Triassic St. Cassian Formation) without designating either of them as a type species. Zittel (1882, p. 206) wrote "*Coelocentrus* Zitt. (*Cirrus* de Kon.)". The meaning of this statement is unclear, but Zittel probably meant that *Cirrus* in the sense of de Koninck belongs to *Coelocentrus*.

Lindström (1884, p. 200) designated *Cirrus goldfussi* d'Archiac and Verneuil, 1842 as type of *Coelocentrus*. Lindström stated: "*Coelocentrus* Zittel 1882, Handbuch d. Pal. 1 Bd., 206 = *Cirrus* De Kon. *Euomph*. *Goldfussi* D'Arch. & Vern is the type". This obviously not meant that *Coelocentrus* is seen as synonym of *Cirrus* but that *Cirrus* Sowerby, 1816 in the sense of de Koninck (1841) represents *Coelocentrus*. Lindström (1884, p. 200) was aware that *Cirrus* was erected by J. Sowerby (1816).

Later designations of *Cirrus polyphemus* as type species of *Coelocentrus* by Kittl (1891) and Koken (1896) are hence invalid. *Coelocentrus* Zittel, 1882 and *Omphalocirrus* Ryckholt, 1860 share the same type species *Cirrus*

goldfussi d'Archiac and Verneuil, 1842 and both genera are thus objective synonyms.

Yin & Yochelson (1983b) erected the genus *Triassocirrus* (type species *T. guizhouensis* Yin & Yochelson, 1983b, Anisian, China) for Triassic species previously included in *Coelocentrus*.

***Triassocirrus brandis* (Klipstein, 1844) comb. nov.**
Fig. 80

*1844 *Pleurotomaria brandis*—Klipstein, p. 164, pl. 10, figs 21a–c.
1850 *Turbo brandis* d'Orb., 1847—d'Orbigny, p. 193, no. 348.
1891 *Schizogonium* (?) *brandis* Klipst. sp.—Kittl, p. 245.

Material. NHMUK PI OR 35324(1), original of Klipstein (1844, pl. 10, fig. 21) herein designated as lectotype from the St. Cassian Formation.

Description. Shell much wider than high, with low, gradate spire; lectotype comprising four whorls; ramp slightly convex to almost flat, gently inclining or horizontal, ornamented with fine spiral striae and with prosocyrt growth lines; spine bearing carina between ramp and lower whorl face forming periphery; number of spines per whorl decreases and spines become more prominent during ontogeny; 12 spines on last whorl; lower whorl face concave, facing abapically, ornamented with fine spiral striae and with prosocyrt growth lines; base slightly convex, ornamented with fine spiral striae and with opisthocyrt growth lines, umbilicated, aperture subrectangular.

Discussion. *Triassocirrus brandis* (Klipstein, 1844) differs from *Triassocirrus tubifer* (Kittl, 1891) (original of Kittl 1891, text-fig. 7, NHMW 1899/0006/0016 designated as lectotype of *Coelocentrus tubifer* Kittl and refigured here in Fig. 81) by having an angular outer basal edge and from *Triassocirrus pichleri* (Laube, 1868) by having a less inclined more horizontal sutural ramp.

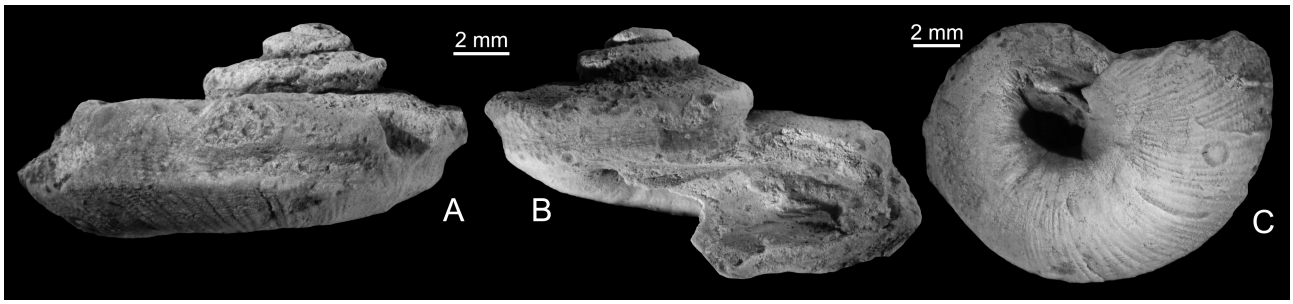

FIGURE 80. *Triassocirrus brandis* (Klipstein, 1844); **A–C.** Lectotype, NHMUK PI OR 35324(1), original of Klipstein (1844, pl. 10, fig. 21), St. Cassian Formation.

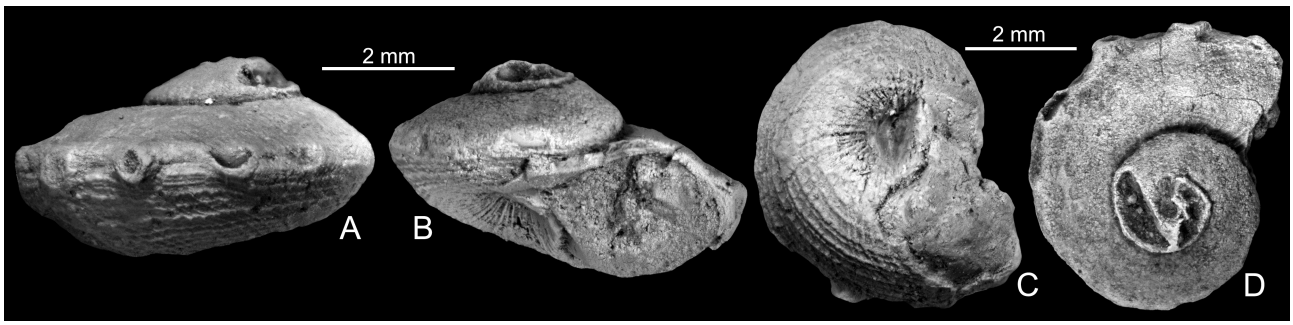

FIGURE 81. *Triassocirrus tubifer* (Kittl, 1891); **A–D.** Lectotype, NHMW 1899/0006/0016 (original of Kittl 1891, text-fig. 7), St. Cassian Formation.

Triassocirrus pentagonalis (Klipstein, 1844) nomen dubium

Fig. 82

*1844	*Pleurotomaria pentagonalis*—Klipstein, p. 164, pl. 10, figs 22a–b.
1850	*Turbo pentagonalis* d'Orb., 1847—d'Orbigny, p. 193, no. 349.
1891	*Coelocentrus pentagonalis* Klipstein sp.—Kittl, p. 231, pl. 4, fig. 27.
non 1978	*Coelocentrus pentagonalis* Klipstein—Zardini, p. 25, pl. 38, figs 16a–d.
?1993b	*Coelocentrus pentangularis* (Klipstein, 1843)—Bandel, p. 55, pl. 16, figs 1–3.

Material. NHMUK PI OR 35322, original of Klipstein (1844, pl. 10, fig. 22) herein designated as lectotype from the St. Cassian Formation.

Discussion. The lectotype designated herein is the specimen figured by Klipstein (1844, pl. 10, figs 22). The lectotype has artificially produced spines, which are result of very poor preparation. Klipstein's figure does not represent the true morphology of this species and therefore we declare that name to be a nomen dubium.

The specimen figured by Kittl (1891, pl. 4, fig. 27) as *Coelocentrus pentagonalis* (NHMW) is obviously well-preserved and could be used as holotype of a new species after study. The specimen figured by Zardini (1978, pl. 38, fig. 16) as *Coelocentrus pentagonalis* represents *Triassocirrus tubifer* Kittl, 1891 (lectotype figured here in Fig. 81).

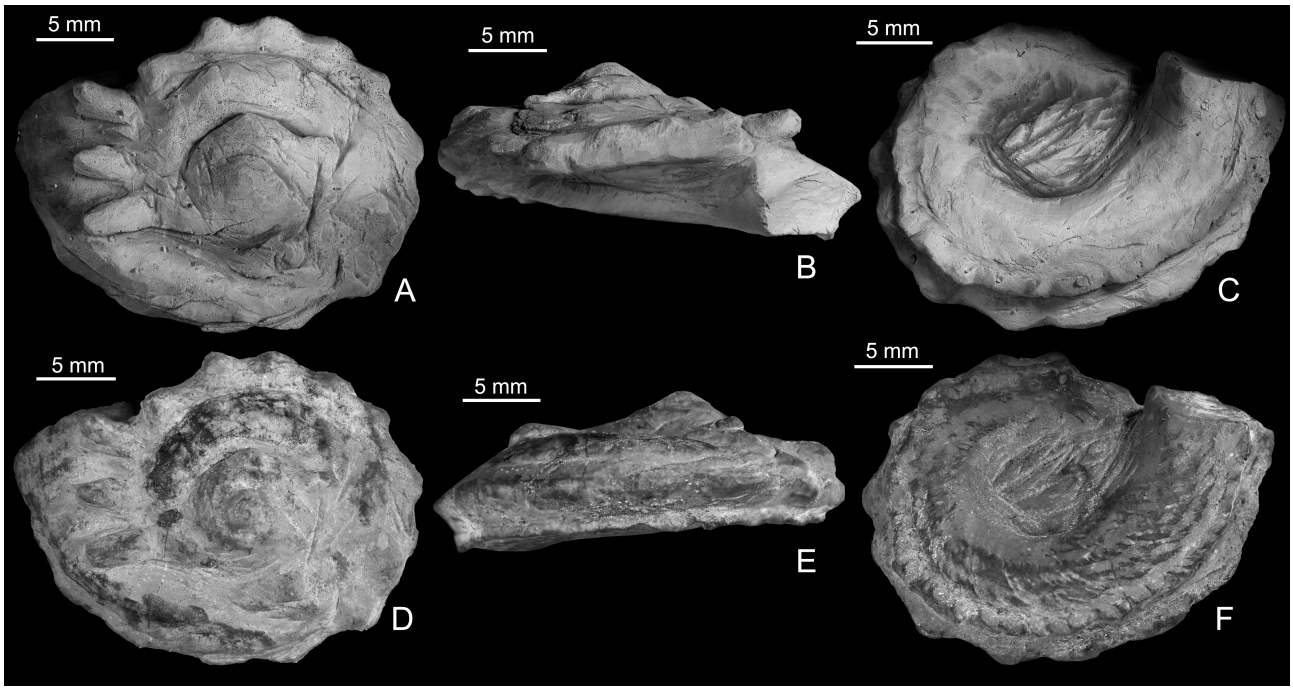

FIGURE 82. *Triassocirrus pentagonalis* (Klipstein, 1844); **A–F.** Lectotype, NHMUK PI OR 35322, original of Klipstein (1844, pl. 10, fig. 22), St. Cassian Formation; the specimen was not coated with ammonium chloride in Fig. 82D, E, F.

Subclass Caenogastropoda Cox, 1960

Superfamily Orthonematoidea Nützel & Bandel, 2000

Family Goniasmatidae Nützel & Bandel, 2000

Discussion. Bandel (2006) placed the Triassic *Murchisonia*-like gastropod genus *Cheilotomona* in Orthonematidae Nützel & Bandel, 2000 which is based on the slitless Late Palaeozoic genus *Orthonema*. He considered the slit-bearing Goniasmatidae to be synonymous with Orthonematidae. However, we do not follow this approach and place *Cheilotomona* in Goniasmatidae.

Genus *Cheilotomona* Strand, 1928
[nom. nov. pro *Cheilotoma* Koken, 1889 non *Cheilotoma* Chevrolat in Dejean, 1836 (Coleoptera)]

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

***Cheilotomona blumi* (Wissmann in Münster, 1841)**
Fig. 83, 84

*1841	*Pleurotoma blumi* Wissmann—Wissmann in Münster, p. 123, pl. 13, figs 47a–c.
1841	*Pleurotomaria nerei*—Münster, p. 113, pl. 12, fig. 17.
1841	*Cerithium acutum*—Münster, p. 122, pl. 12, fig. 37 (non pl. 13, fig. 37) [non Cerithium acutum Deshayes, 1833].
1841	*Fusus tripunctatus*—Münster, p. 123, pl. 13, fig. 49.
1844	*Pleurotomaria tricarinata*—Klipstein, p. 171, pl. 4, figs 31a–b.
1850	*Trochus nerei* d'Orb., 1847—d'Orbigny, p. 189, no. 259.
1850	*Pleurotomaria tricarinata* Klipstein, 1844—d'Orbigny, p. 194, no. 379.
1850	*Cerithium blumii* d'Orb., 1847—d'Orbigny, p. 196, no. 412.
1850	*Cerithium alceste* d'Orb., 1847—d'Orbigny, p. 196, no. 418 [nom. nov. pro *Cerithium acutum* Münster, 1841].
1868	*Murchisonia blumii* Münster sp.—Laube, p. 89, pl. 28, fig. 7.
1889	Cheilotoma Blumi Mü. sp.—Koken, p. 455, textfig. 21.
1889	Cheilotoma acutum Mü. sp.—Koken, p. 456, textfigs 22–23.
1891	*Murchisonia* (*Cheilotoma*) *acuta* Münster sp.—Kittl, p. 219, pl. 3, figs 24–25.
1891	*Murchisonia* (*Cheilotoma*) *tristriata* Münster sp.—Kittl, p. 222, text-fig. 4.
1891	*Murchisonia* (*Cheilotoma*) *blumi* Münster sp.—Kittl, p. 220, pl. 3, figs 26–31.
non 1926	*Murchisonia* (*Cheilotoma*) *acuta* (var.) Münster spec.—Reis, p. 95, pl. 1, figs 26–27.
1959	*Cheilotoma blumii* Münster—Leonardi & Fiscon, p. 20, pl. 1, figs 1a–b.
1978	*Cheilotoma blumi* (Münster)—Zardini, p. 22, pl. 6, fig. 11.
?1980	cfr. *Cheilotoma acuta* Muenster—Zardini, p. 4, pl. 1, fig. 15.
2006	*Cheilotomona acuta* (Münster, 1842)—Bandel, p. 93, pl. 6, figs 1–2.
2014	*Cheilotomona blumi* (Münster, 1841)—Nützel & Kaim, p. 415, figs 7a–b.

Material. SNSB-BSPG AS VII 1234 (original of Münster 1841, pl. 13, fig. 47b) herein designated as lectotype of *Pleurotomaria blumi*, AS VII 1233 (original of Münster 1841, pl. 13, fig. 47a) herein designated as paralectotype, AS VII 1235 (original of Münster 1841, pl. 13, fig. 47c) herein designated as paralectotype; AS VII 1491 (10 specimens from Münster's collection), AS VII 1492 (4 specimens from Münster's collection), AS VII 2066; all from the St. Cassian Formation. SNSB-BSPG AS VII 1232 (original of Münster 1841, pl. 12, fig. 17) herein designated as lectotype of *Pleurotomaria nerei* Münster from the St. Cassian Formation. SNSB-BSPG AS VII 1230 (original of Münster, pl. 12, fig. 37) herein designated as lectotype of *Cerithium acutum* Münster from the St. Cassian Formation. SNSB-BSPG AS VII 1229 (original of Münster, pl. 13, fig. 49) herein designated as lectotype of *Fusus tripunctatus* Münster from the St. Cassian Formation. NHMW 1899/0005/0120/1 (original of Kittl 1891, pl. 3 fig. 24), NHMW 1899/0005/0123 (original of Kittl 1891, text-fig. 4) from the St. Cassian Formation. NHMUK PI OR 35347(1) original of Klipstein (1844, pl. 4, fig. 31) herein designated as lectotype of *Pleurotomaria tricarinata* Klipstein from the St. Cassian Formation. PZO 13695 from the St. Cassian Formation. MB.Ga.4307.2, MB.Ga.4307.3, MB.Ga.4307.4, MB.Ga.4304.1 from the St. Cassian Formation.

Description. Shell medium sized, high spired; lectotype with 6 preserved whorls, 13.5 mm high, 8.0 mm wide; suture shallow, incised; first two whorls smooth, rounded; first whorl diameter 0.32–0.35 mm (3 measurements on SEM images); 3rd whorl convex with three spiral cords in subsutural, median and suprasutural position; on 4th whorl, straight to slightly prosocline axial ribs begin to appear, forming axially elongated nodes at intersections with spiral cords, especially pronounced on median spiral cord at which whorl face becomes increasingly angulated; on fifth to sixth whorls onset of an additional spiral cord above median cord, not nodular forming adapical border of selenizone in later whorls; median spiral cord most prominent, situated at mid-whorl, forming median angulation and whorl periphery; whorl face above median angulation steeply inclining, concave; whorl face below median angulation slightly concave to flat; median cord turns into lower margin of selenizone; selenizone starts on 7th whorl, ornamented with 1–2 spiral cords, bordered by spiral cords; lower edge of selenizone represents periphery; surface

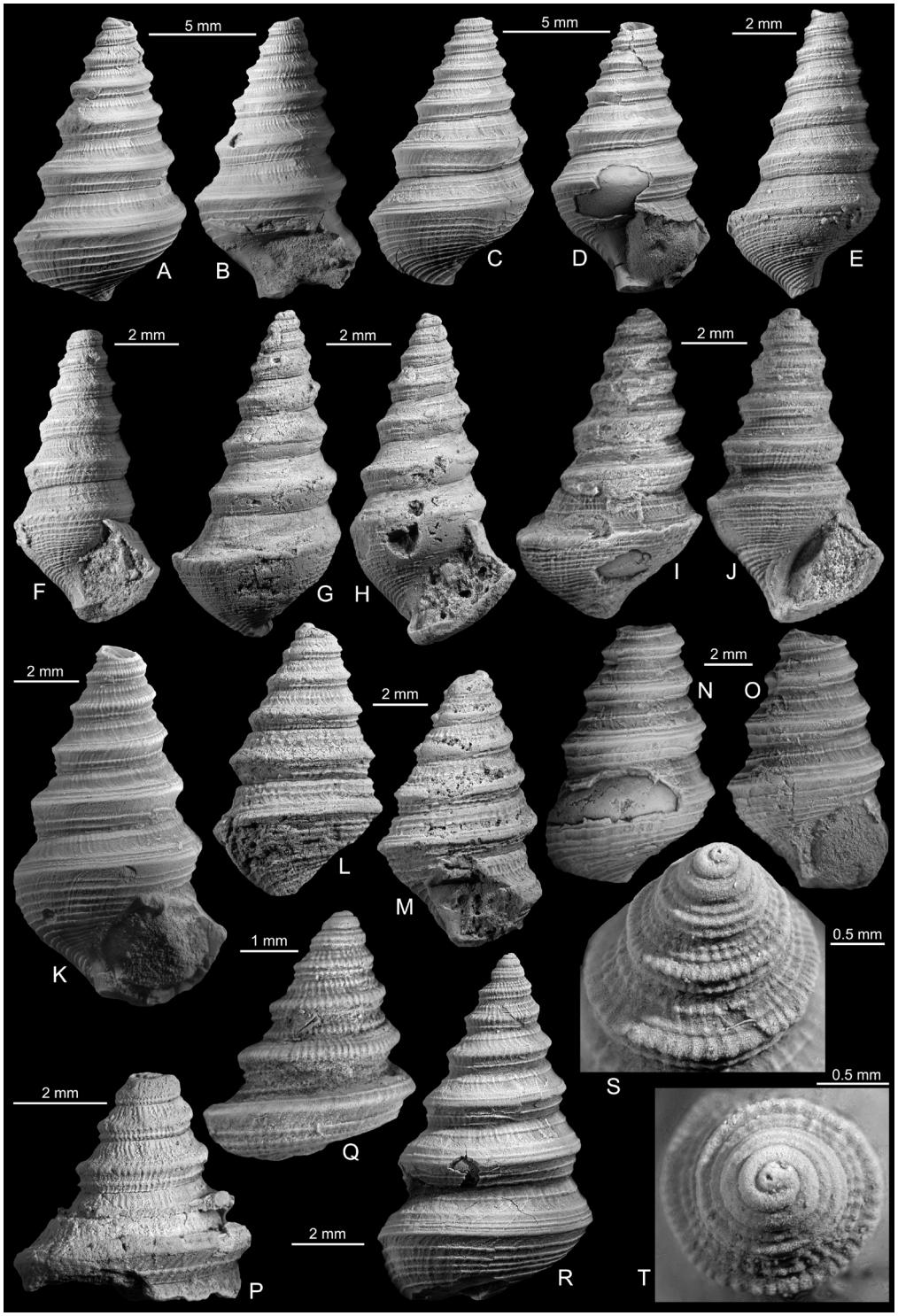

FIGURE 83. *Cheilotomona blumi* (Wissmann, 1841 in Münster); **A–B.** Lectotype, BSPG AS VII 1234 (original of Münster 1841, pl. 13, fig. 47b), St. Cassian Formation; **C–D.** Paralectotype, BSPG AS VII 1233 (original of Münster 1841, pl. 13, fig. 47a), St. Cassian Formation; **E–F.** Paralectotype, AS VII 1235 (original of Münster 1841, pl. 13, fig. 47c), St. Cassian Formation; **G–H.** Lectotype of *Cerithium acutum* Münster, 1841, SNSB-BSPG AS VII 1230 (original of Münster, pl. 12, fig. 37), St. Cassian Formation; **I–J.** NHMW 1899/0005/0120/1 (original of Kittl 1891, pl. 3 fig. 24), St. Cassian Formation; **K.** SNSB-BSPG AS VII 2066, St. Cassian Formation; **L–M.** Lectotype of *Fusus tripunctatus* Münster, 1841, SNSB-BSPG AS VII 1229 (original of Münster, pl. 13, fig. 49), St. Cassian Formation; **N–O.** Lectotype of *Pleurotomaria tricarinata* Klipstein, 1844, NHMUK PI OR 35347(1) original of Klipstein (1844, pl. 4, fig. 31), St. Cassian Formation; **P.** Lectotype of *Pleurotomaria nerei* Münster, 1844, SNSB-BSPG AS VII 1232 (original of Münster 1841, pl. 12, fig. 17), St. Cassian Formation; **Q.** NHMW 1899/0005/0123 (original of Kittl 1891, text-fig. 4), St. Cassian Formation; **R–T.** SNSB-BSPG AS VII 1491, St. Cassian Formation.

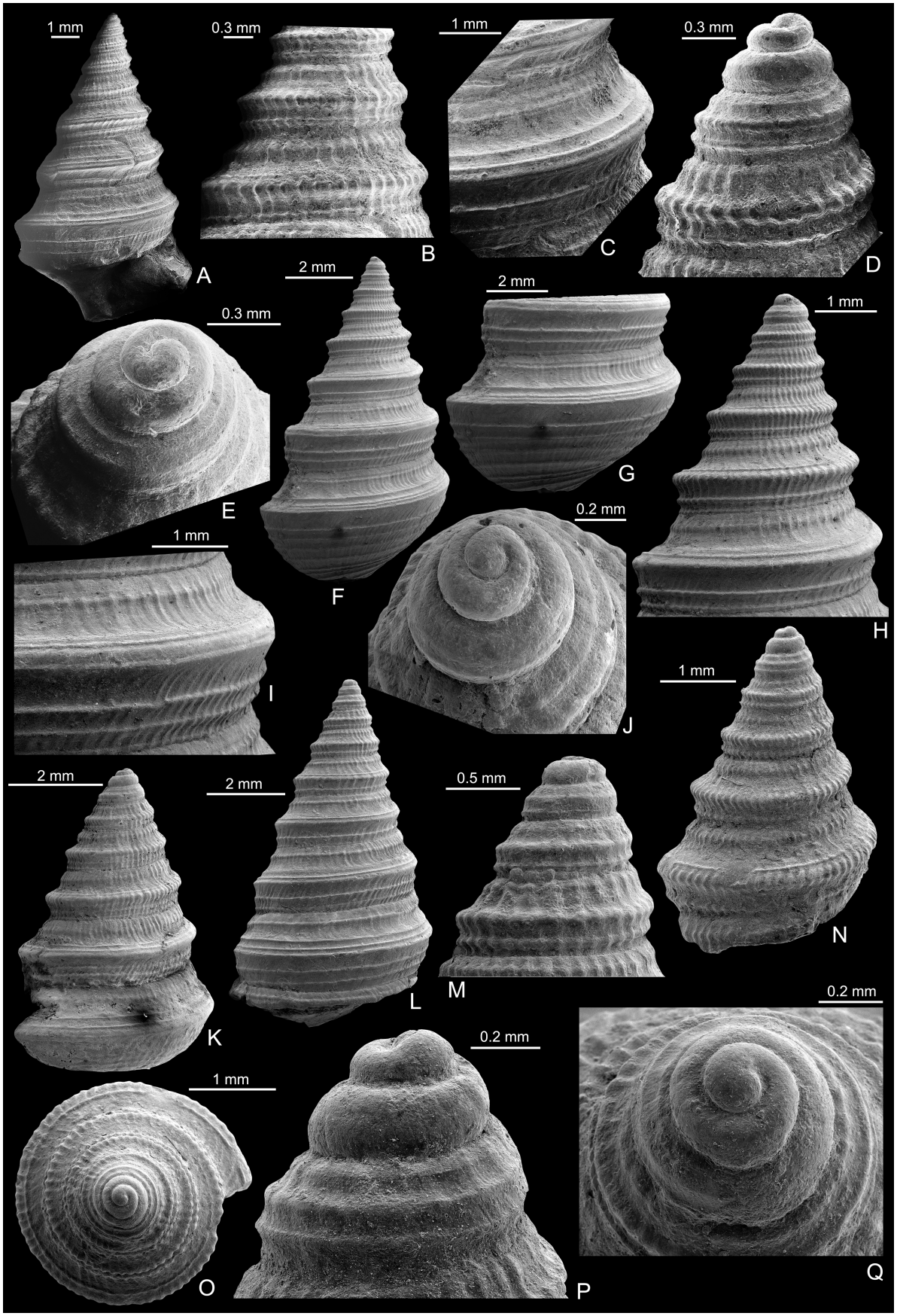

FIGURE 84. *Cheilotomona blumi* (Wissmann, 1841 in Münster); **A–E.** PZO 13695, St. Cassian Formation, SEM image; **F–J.** MB.Ga.4307.2, St. Cassian Formation, SEM image; **K.** MB.Ga.4307.3, St. Cassian Formation, SEM image; **L–M.** MB.Ga.4307.4, St. Cassian Formation, SEM image; **N–Q.** MB.Ga.4304.1, St. Cassian Formation, SEM image.

of selenizone inclined, directed adapically; axial ribs and nodes disappear during ontogeny, reduced to strengthened growth lines; whorl face above adapical border of selenizone flatly concave, with orthocline to opisthoclinegrowth lines; whorl face below selenizone concave to convex, with prosocyrt growth lines and ornamented with 2–3 suprasutural spiral cords; base convex, ornamented with spiral cords and with prosocyrt growth lines, anomphalous; aperture as high as wide, subcircular to rhomboid, with angulated outer lip, convex basal lip, almost straight inner lip, and short anterior siphonal outlet.

Discussion. *Cheilotomona blumi* as well as the genus *Cheilotomona* in general are characterized by a very late onset of the selenizone (on 7th whorl) and considerable ontogenetic change of shell ornamentation. The smooth protoconch (already correctly illustrated by Koken (1889, p. 455, fig. 21) has an initial whorl with a rather large diameter, which reflects non-planktotrophic larval development (see Nützel 2014). Bandel (2006) reported a smaller diameter (0.2 mm) for the protoconch of *C. acutum* which is a synonym of *C. blumi*. From the pictures provided by Bandel (2006, pl. 6, figs 1–2), the first whorl is also measured as 0.3 mm. Although the transition from protoconch to teleoconch is not demarcated by a sinusigera, the first two smooth whorls are interpreted as the protoconch herein.

Cheilotomona blumi displays considerable intraspecific variability and as a result several subjective synonyms have been introduced. As previously proposed by Laube (1868), *Pleurotomaria nerei* Münster, 1841 (lectotype refigured here in Fig. 83P), *Fusus tripunctatus* Münster, 1841 (lectotype refigured here in Fig. 83L–M) and *Pleurotomaria tricarinata* Klipstein, 1844 (lectotype refigured here in Fig. 83N–O) represent *Cheilotomona blumi*.

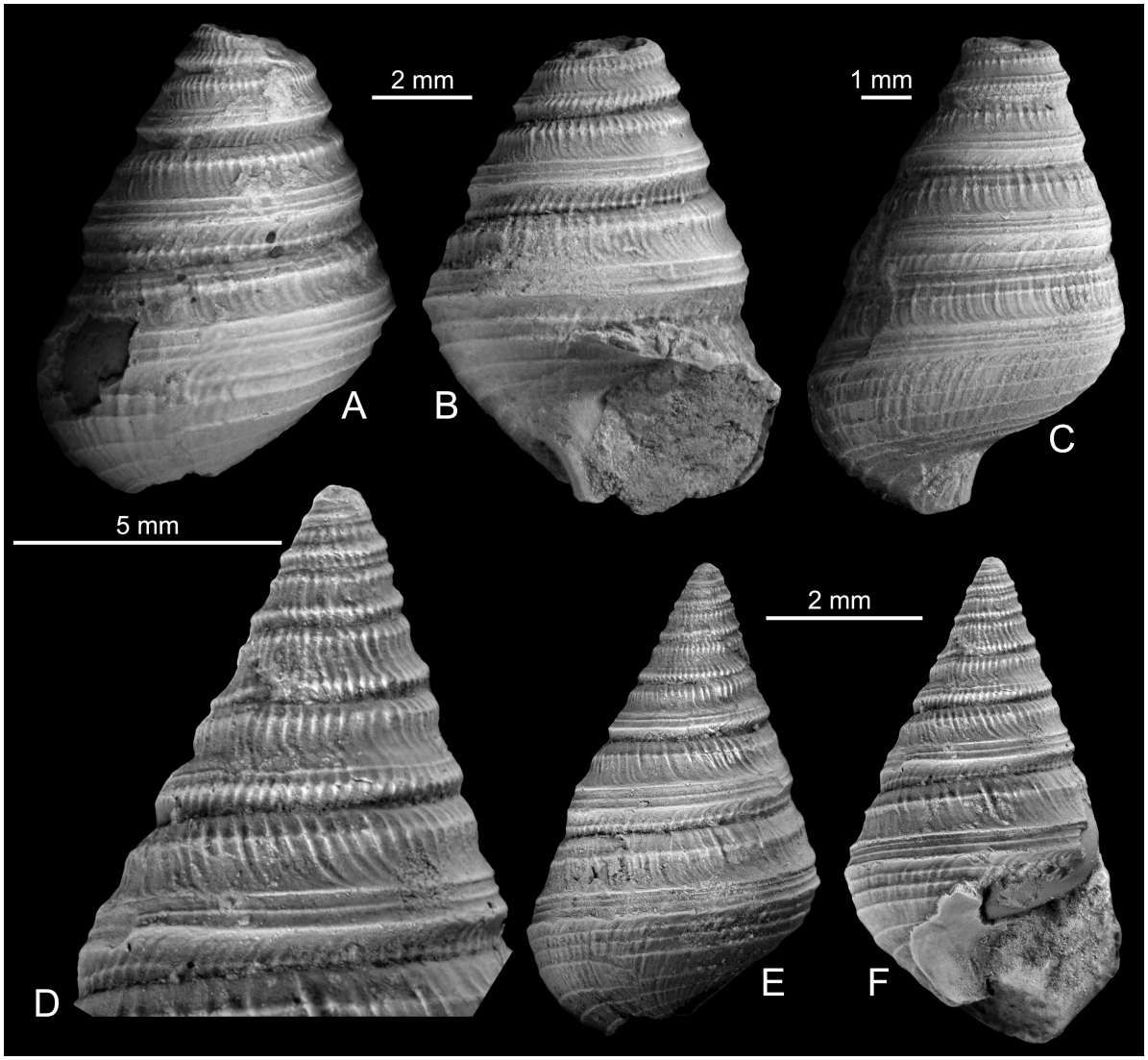

FIGURE 85. *Cheilotomona obtusa* (Klipstein, 1844); **A–B.** Lectotype, NHMUK PI OR 35342(1), original of Klipstein (1844, pl. 10, fig. 29), St. Cassian Formation; **C.** NHMW 1899/0005/0113 original of Kittl (1891, pl. 3, fig. 21), St. Cassian Formation; **D–F.** Lectotype of *Pleurotomaria calosoma* Laube, 1868, GBA 1894/005/0002, 4344, original of Laube (1868, pl. 28, fig. 1) and Kittl (1891, pl. 3, fig. 20), St. Cassian Formation.

Laube (1868) also synonymized *Cerithium acutum* Münster, 1841 (lectotype figured here in Fig. 83G–H) with *Cheilotomona blumi*. However, Kittl (1891) regarded *Cerithium acutum* Münster as a separate species. In the description of *Cerithium acutum*, Münster (1841) assigned the drawing in plate 12, figure 37 to it, but in the plate captions he omitted the caption for the that figure. Instead, Münster (1841) gave *Cerithium acutum* as caption of plate 13, figure 37. Münster (1841) gave no description for this specimen (pl. 13, fig. 37), which obviously represents another species. Here we regard the specimen figured by Münster (1841, in pl. 12, fig. 37) as *Cerithium acutum* as all subsequent authors did. *Cerithium acutum* Münster is identical with *Cheilotomona blumi* in all aspects except of having a somewhat lower spiral angle. We share the opinion of Laube (1868) and regard *Cerithium acutum* as a variant of *Cheilotomona blumi*. However, Bandel (2006, p. 93) maintained *Cheilotomona acuta* (Münster, 1841) but discussed an ontogentic change into *Cheilotomona blumi*. If *Cerithium acutum* represents a separate species, then *Cerithium alceste* d'Orbigny, 1850 should be used as the species name because *Cerithium acutum* is preoccupied by Deshayes (1833).

Tichy (1980) regarded *Cheilotomona calosoma* (Laube, 1868) (= *Cheilotomona obtusa* Klipstein, 1844) as a variant of *Cheilotomona blumi* (Münster, 1841), an opinion we do not follow. *Cheilotomona obtusa* (Klipstein, 1844) (= *Cheilotomona calosoma* (Laube, 1868)) differs in the position of the suture which is much closer to the selenizone and has a convex whorl profile instead of a gradate whorl profile. Herein, we designate the specimen figured by Klipstein (1844, pl. 10, fig. 29, NHMUK PI OR 35342(1)) as lectotype of *Pleurotomaria obtusa* Klipstein, 1844 and designate the specimen figured by Laube (1868, pl. 28, fig. 1; GBA 1894/005/0002, 4344) as lectotype of *Pleurotomaria calosoma* Laube, 1868 which was also illustrated by Kittl (1891, pl. 3, fig. 20). These lectotypes are illustrated here in Fig. 85.

Some *Cheilotomona blumi* type specimens have multiple repaired injuries and multiple drill holes (also see Klompmaker *et al*. 2016). One type specimen (SNSB-BSPG AS VII 2066, Fig. 83K) has two repaired injuries and one drill hole before the onset of the selenizone and five repaired injuries and five drill holes after the onset of the selenizone. The repaired injuries are interpreted as unsuccessful predatory attacks (Klompmaker *et al*. 2016). The studied specimens suggest that *Cheilotomona blumi* was exposed to durophagy and drilling predation during its lifetime irrespective of the presence of a selenizone and withstood predation.

Cheilotomona tristriata (Münster, 1841)

Fig. 86

*1841	*Trochus tristriatus*—Münster, p. 108, pl. 11, fig. 19.
1844	*Trochus acuticarinatus*—Klipstein, p. 152, pl. 9, figs 20a–c.
1850	*Trochus tristriatus* Münster, 1841—d'Orbigny, p. 190, no. 265.
1850	*Trochus asius* d'Orb., 1847—d'Orbigny, p. 189, no. 255.
non 1891	*Murchisonia* (*Cheilotoma*) *tristriata* Münster sp.—Kittl, p. 222, text-fig. 4.
1891	*Flemingia*? *acutecarinata* Klipstein sp.—Kittl, p. 254, pl. 12, fig. 21.

Material. SNSB-BSPG AS VII 1231 (original of Münster 1841, pl. 11, fig. 19) herein designated as lectotype from the St. Cassian Formation. NHMUK PI OR 35292(1) original of Klipstein (1844, pl. 9, fig. 20) herein designated as lectotype of *Trochus acuticarinatus* Klipstein from the St. Cassian Formation.

Description. Shell medium sized, trochiform; lectotype with 5 whorls, 4.6 mm high, 4.3 mm wide; initial whorls not preserved; earliest preserved whorl with three spiral cords; median cord turns into prominent carina situated at midwhorl, representing median angulation and whorl periphery, later turning into lower margin of selenizone; additional spiral cord appears above median carina in 4th whorl, which later represents upper border of selenizone; whorl face above selenizone gently inclining, slightly convex, with subsutual cord and faint prosocyrt growth lines; selenizone formed beginning from 5th preserved whorl of lectotype, concave, bordered adapically by spiral cord, and abapically by median carina; whorl face below selenizone concave, lying subparallel to shell axis, with faint prosocyrt growth lines; transition to base with angulated outer basal edge, where whorls embrace; base convex, ornamented with spiral cords and faint prosocyrt growth lines, anomphalous; aperture wider than high, subovate, with angulated outer lip, convex basal and inner lips.

Discussion. The lectotype of *Trochus tristriatus* Münster, 1841 is poorly preserved (Fig. 86A–B) but is conspecific with the lectotype of *Trochus acuticarinatus* Klipstein, 1844, which shows the growth lines better. The

specimen assigned to *Murchisonia* (*Cheilotoma*) *tristriata* by Kittl (1891, text-fig. 4) is slightly crushed (figured herein Fig. 83Q) and represents *Cheilotomona blumi*. One gastropod steinkern was reported by Toula (1896) as "*Trochus* (*Flemingia*?) aff. *acuticarinata* Klipst. spec." from the Anisian of Turkey. It is not sure whether this specimen belongs to *Cheilotomona* or not. It is well possible that it represents *Vistilia* Koken, 1896.

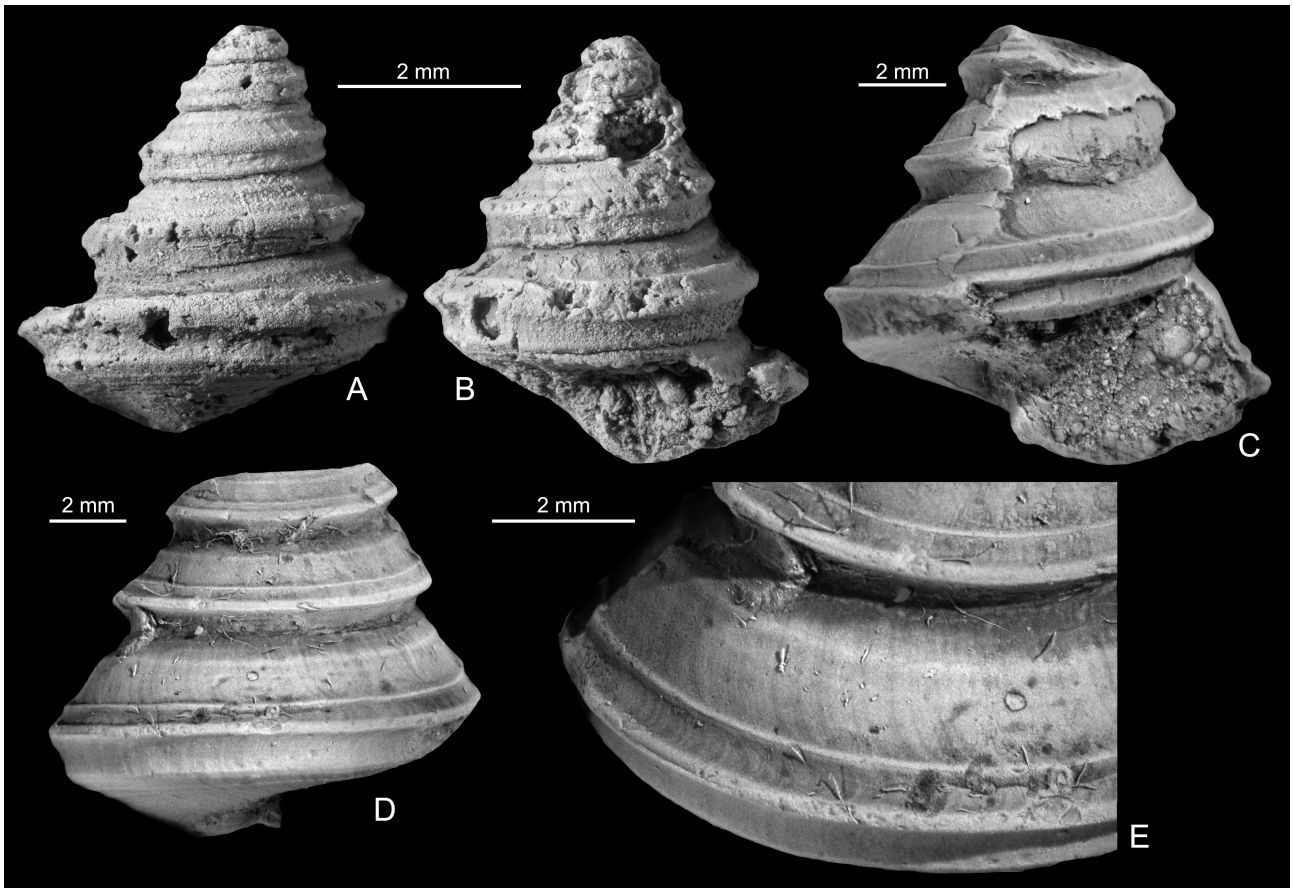

FIGURE 86. *Cheilotomona tristriata* (Münster, 1841); **A–B.** Lectotype, SNSB-BSPG AS VII 1231 (original of Münster 1841, pl. 11, fig. 19), St. Cassian Formation; **C–E.** Lectotype of *Trochus acuticarinatus* Klipstein, 1844, NHMUK PI OR 35292(1) original of Klipstein (1844, pl. 9, fig. 20), St. Cassian Formation.

Cheilotomona subgranulata (Klipstein, 1844)

Fig. 87

*1844	*Pleurotoma subgranulata*—Klipstein, p. 183, pl. 12, fig. 3.
1850	*Cerithium subgranulatum* d'Orb., 1847—d'Orbigny, p. 197, no. 412.
1868	*Murchisonia subgranulata* Klipstein sp.—Laube, p. 90, pl. 28, fig. 8.
1891	*Murchisonia* (*Cheilotoma*) *subgranulata* Klipstein sp.—Kittl, p. 221, pl. 3, figs 23, 32.
non 1962	*Cheilotoma subgranulata* Klipstein—Sachariewa-Kowatschewa, p. 101, pl. 7, figs 1, 3–7, 13–14.

Material. NHMUK PI OR 35709(1) original of Klipstein (1844, pl. 12, fig. 3) herein designated as lectotype from the St. Cassian Formation. NHMUK PI GG 1940, NHMW 1899/0005/0122 (original of Kittl, pl. 3, fig. 32) from the St. Cassian Formation.

Description. Shell medium-sized, high spired; lectotype with 6 whorls, 9.4 mm high, 4.2 mm wide; apex missing; earliest preserved whorls with median angulation, subsutural and suprasutural spiral cords and axial ribs, which form nodes when intersecting with median angulation and spiral cords; selenizone formed at the beginning of 5th preserved whorl, angulated, bordered by spiral cords, situated on median carina, representing periphery, ornamented with prominent lunulae and occasionally with spiral threads; whorl face above selenizone concave, with spiral cords and prosocyrt axial ribs; nodes at intersections of spiral cords and axial ribs; whorl face below selenizone concave, ornamented with spiral cords, threads and prosocyrt axial ribs, forming nodes at intersections; transition to base

evenly rounded; base convex, elongated, ornamented as in lower whorl face, anomphalous; aperture higher than wide, ear-shaped, with angulated outer lip, convex basal and inner lips; tend to form anterior short siphon where basal and inner lips meet.

Discussion. The lectotype is slightly encrusted but a better-preserved shell from the NHMUK London (Fig. 87C–D) is conspecific with the lectotype. *Cheilotomona subgranulata* Klipstein, 1844 resembles *Cheilotomona acuta* (= *Cheilotomona blumi*) regarding its slender shell shape, but it has a nodular axial ornament throughout its ontogeny, and it differs by its angulated selenizone with pronounced lunulae. *Cheilotomona subgranulata* differs from all other *Cheilotomona* species by having an angulated selenizone and in that the selenizone represents the whorl periphery. The selenizone in other *Cheilotomona* species is flat and its lower edge forms the whorl periphery.

The specimens assigned to *Cheilotoma subgranulata* by Sachariewa-Kowatschewa (1962) may belong to *Trochus bipunctatus* Münster, 1841 ("*Cheilotomona*" *subpunctata*). Kittl (1891) placed *Trochus bipunctatus* Münster, 1841 within *Cheilotoma* Koken, 1889 [= *Cheilotomona* Strand, 1928]. The assignment of *Trochus bipunctatus* (original of Münster 1841, pl. 11, fig. 14 SNSB-BSPG AS VII 1228 herein designated as lectotype of *Trochus bipunctatus* Münster and figured here in Fig. 88) to *Cheilotomona* is unlikely because the lectotype has a different ornamentation pattern, lacks a selenizone and has very low whorls.

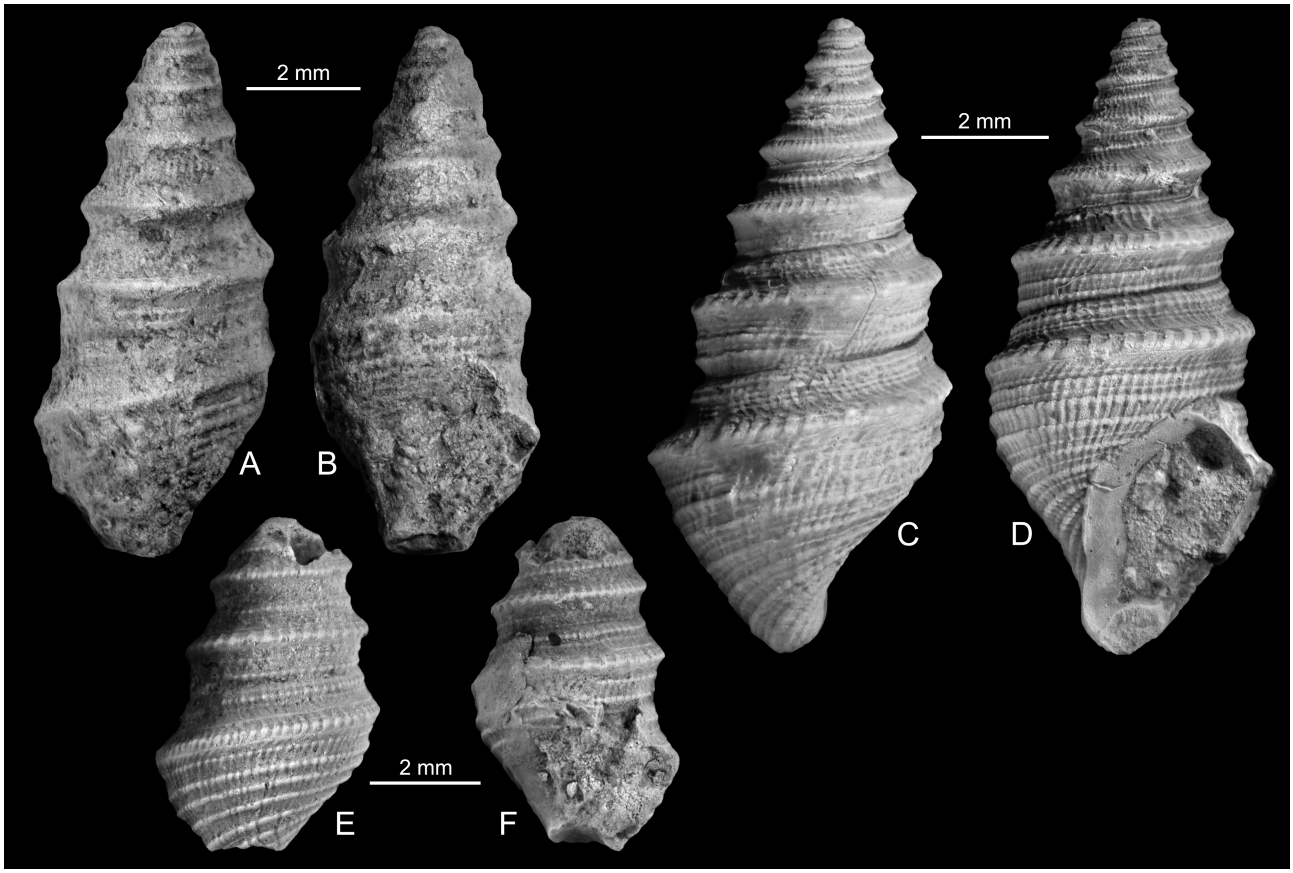

FIGURE 87. *Cheilotomona subgranulata* (Klipstein, 1844); **A–B.** Lectotype, NHMUK PI OR 35709(1) original of Klipstein (1844, pl. 12, fig. 3), St. Cassian Formation; **C–D.** NHMUK PI GG 1940, St. Cassian Formation; **E–F.** NHMW 1899/0005/0122 (original of Kittl, pl. 3, fig. 32), St. Cassian Formation.

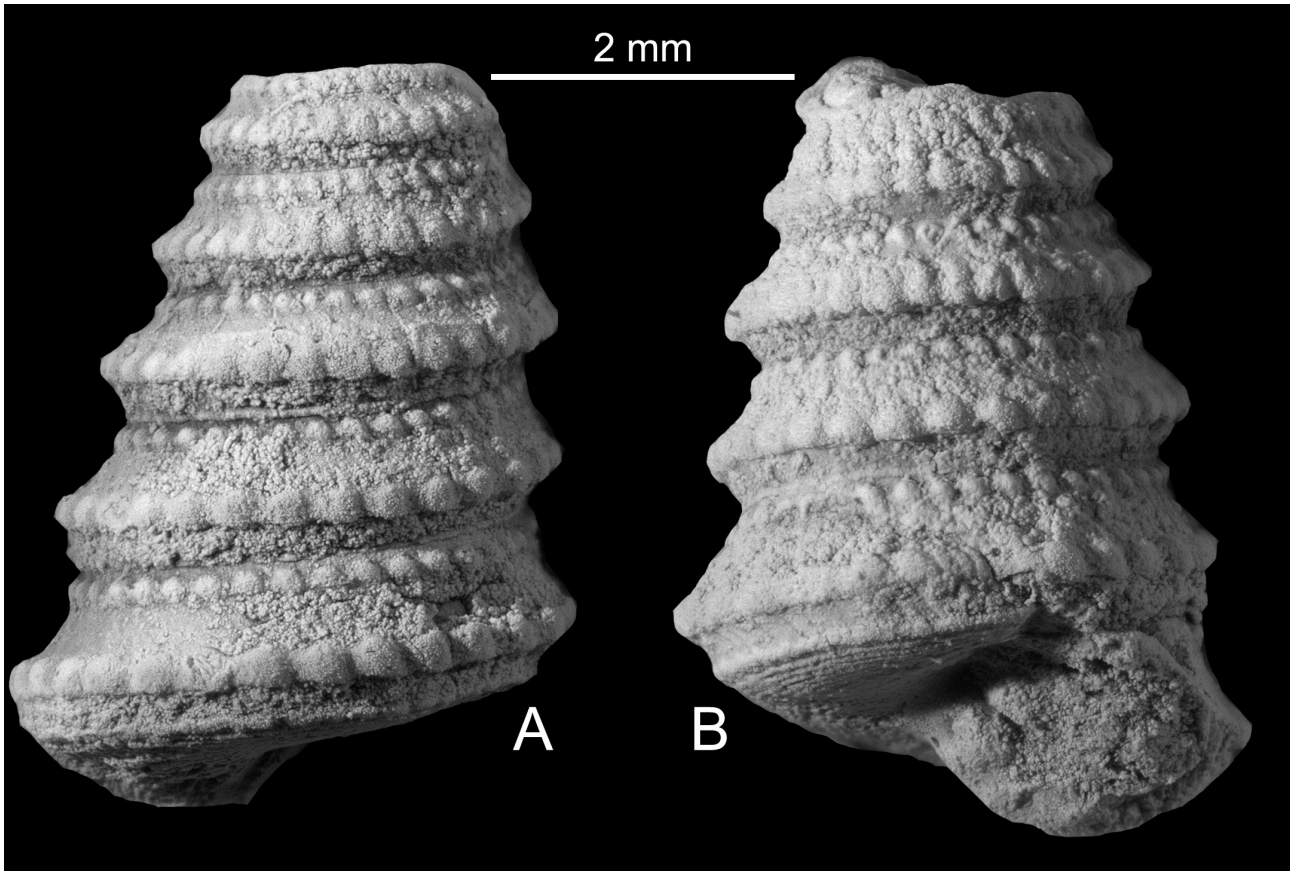

FIGURE 88. "*Trochus*" *bipunctatus* Münster, 1841; **A–B.** Lectotype, SNSB-BSPG AS VII 1228 original of Münster (1841, pl. 11, fig. 14), St. Cassian Formation.

Genus *Cochlearia* Braun, 1841 (in Münster)

Type species. *Cochlearia carinata* Braun, 1841 (in Münster), St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

Discussion. The name *Cochlearia* Braun, 1841 (in Münster) was replaced by *Chilocyclus* Bronn, 1851 (in Bronn & Roemer) because it was allegedly preoccupied by *Cochlearia* Linnaeus which is, however, a plant genus. As stated by Kittl (1892) the name is also preoccupied by *Cochlearia* Klein, 1753, a name that is not available because it is pre-Linnean.

The family assignment of *Cochlearia* is uncertain. Based on the high-spired shape and the trumpet-shaped, circular aperture, Wenz (1938) placed it tentatively in the cerithioid family Diastomatidae. Nützel (2013), based on the same characters, placed it in Sabrinellidae Bandel, 2010. Here, we report the presence of a selenizone in *Cochlearia* for the first time and hence, these previous family assignments are no longer valid. The family assignment remains doubtful; knowledge of protoconch morphology and shell microstructure are necessary for a better substantiated systematic placement of *Cochlearia*. Except for its characteristic aperture, it resembles the Triassic murchisonimorph genus *Trypanocochlea* Tomlin, 1931 (replacement name for *Verania* Koken, 1896) and the Late Palaeozoic *Goniasma* Tomlin, 1930 (replacement name for *Goniospira* Girty). At present we place *Cochlearia* tentatively in Goniasmatidae Nützel & Bandel, 2000. However, Kittl (1892, p. 53) stated that it has an inner nacreous layer. If so, it represents a vetigastropod.

***Cochlearia carinata* Braun, 1841 (in Münster)**
Fig. 89

*1841	*Cochlearia carinata* Braun—Münster, p. 104, pl. 10, fig. 27.
1850	*Rissoa subcarinata* d'Orb., 1847—d'Orbigny, p. 183, no. 96.
1851	*Chilocyclus carinatus*—Bronn (in Bronn & Roemer), p. 75, pl. 12.1, fig. 12a–b.
1868	*Cochlearia carinata* Braun—Laube, p. 20, pl. 23, figs 5a–b.
1892	*Chilocyclus carinata* Braun sp. (Münster)—Kittl, p. 52, pl. 5, figs 47–50 (see for extensive synonymy list).
?1980	*Genere e specie ind.*—Zardini, p. 13, pl. 6, fig. 11.
2013	*Chilocyclus carinatus* (Braun in Münster, 1841)—Nützel, fig. 2A.

Material. NHMUK PI OR 35824(1) from Klipstein collection. GBA 1868/008/0025, original of Laube (1868, pl. 23, fig. 5b) which is also figured by Kittl (1891, pl. 5, fig. 47) from the St. Cassian Formation.

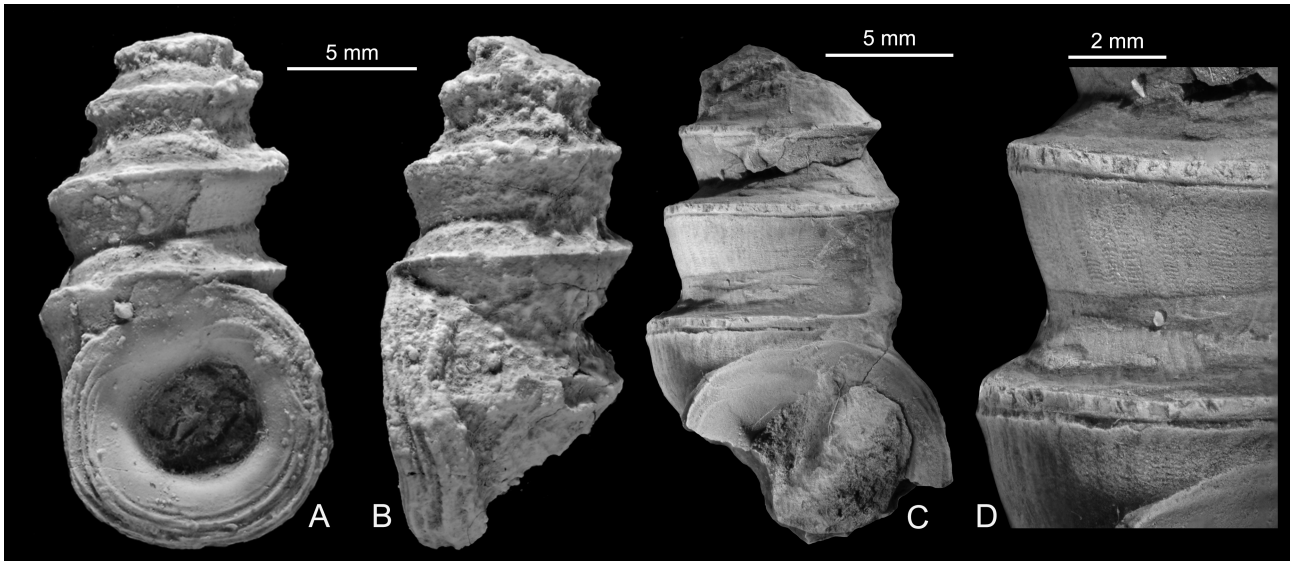

FIGURE 89. *Cochlearia carinata* Braun, 1841 (in Münster); **A–B.** GBA 1868/008/0025, original of Laube (1868, pl. 23, fig. 5b) and Kittl (1891, pl. 5, fig. 47), St. Cassian Formation; **C–D.** NHMUK PI OR 35824(1), St. Cassian Formation.

Description. Shell high-spired, with angulated whorls; ramp concave, gently inclining; lower whorl face straight to slightly convex, steeply inclining adaxially towards abapical suture; whorl face ornamented with undulating spiral striae; selenizone angulated, narrow smooth, situated at whorl angulation; aperture circular, lips expanding outwards, like a trumpet.

Discussion. The original material of Braun, 1841 (in Münster) was not found at the BSPG as was also stated by Kittl (1892). One specimen from the Klipstein's collection housed in the NHMUK London and one specimen from Laube's collection (GBA) are figured herein. The selenizone of *C. carinata* was well illustrated by Kittl (1892, pl. 5, fig. 49) but he called it a keel.

Order Neogastropoda Wenz, 1938

Family Purpurinidae Zittel, 1895

Genus *Pseudoscalites* Kittl, 1892

Type species. *Pseudoscalites elegantissimus* Kittl, 1892, St. Cassian Formation, Carnian, South Tyrol, Italy; by monotypy.

***Pseudoscalites cochlea* (Münster, 1841) comb. nov.**
Fig. 90A–C

*1841	*Pleurotomaria cochlea*—Münster, p. 112, pl. 12, fig. 9.
1850	*Pleurotomaria cochlea* Münster, 1841—d'Orbigny, p. 195, no. 382.

Material. SNSB-BSPG AS VII 1216 original of Münster (1841, pl. 12, fig. 9) herein designated as lectotype from the St. Cassian Formation.

Description. Shell fusiform with gradate spire; lectotype comprises about 3 preserved teleoconch whorls (apex missing), 10.0 mm high, 7.8 mm wide; spire low, gradate; ramp slightly inclined, with peripheral angulation and basal bulge; peripheral angulation ornamented with undulating crest; whorl face below peripheral angulation shallowly concave, forming a bulging outer basal edge at suture; base convex, extended, anomphalous, ornamented with spiral threads and with prosocyrt growth lines; aperture twice as high as wide, with angulated outer lip, convex basal lip and slightly convex columellar lip, short anterior siphonal outlet.

Discussion. Laube (1864) and Kittl (1892) considered *Pleurotomaria cochlea* to represent a synonym of *Pleurotomaria crenata*; however, these two species differ in both, size and morphology. Kittl (1892) stated that the type of *P. cochlea* is poorly preserved (which we can confirm) and that it could be conspecific with *Pseudoscalites elegantissimus*. We studied the type specimen of *P. elegantissimus* illustrated by Kittl (1892, pl. 6, fig. 12) and designated herein as lectotype (GBA 1894/005/0007; Fig. 90D–E). *Pseudoscalites elegantissimus* Kittl, 1892 resembles *Pseudoscalites cochlea* (Münster, 1841) (see also Bandel 1994 and Nützel & Erwin 2004). The specimens assigned to *Pseudoscalites elegantissimus* by Kittl (1892) are much better-preserved than the lectotype of *Pseudoscalites cochlea*; it is possible but not sure that both taxa are synonymous.

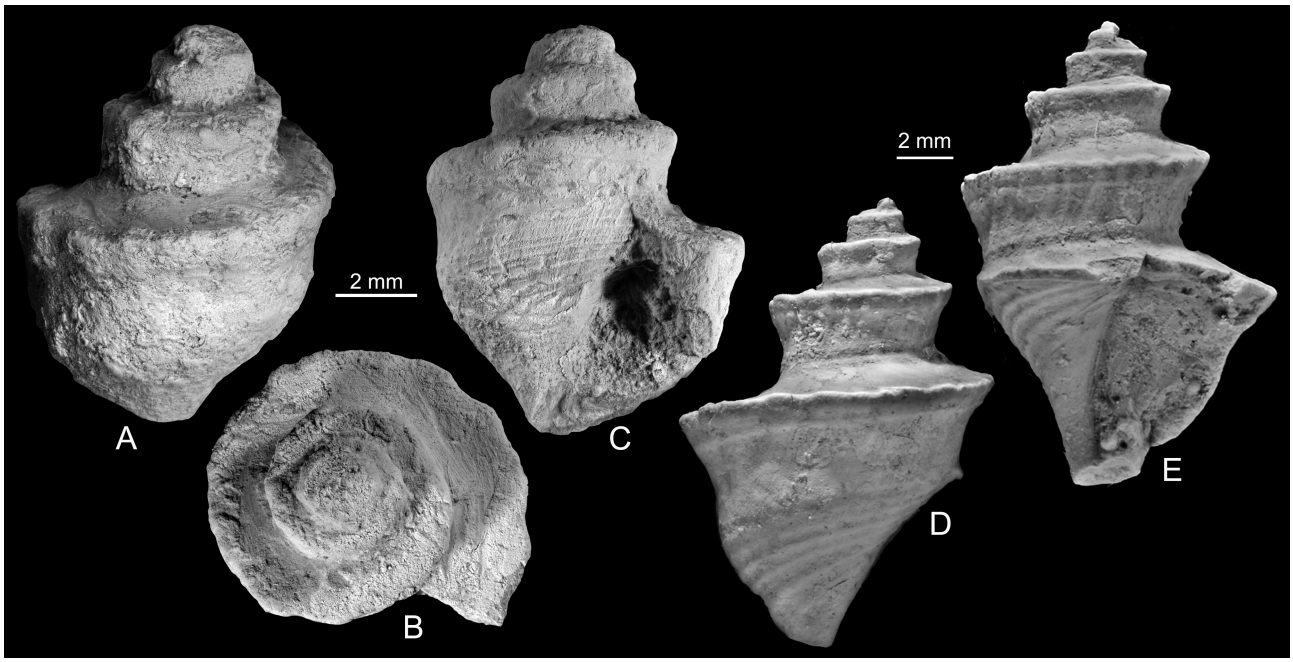

FIGURE 90. A–C. Lectotype of *Pseudoscalites cochlea* (Münster, 1841), SNSB-BSPG AS VII 1216 original of Münster (1841, pl. 12, fig. 9), St. Cassian Formation; **D–E.** Lectotype of *Pseudoscalites elegantissimus* Kittl, 1891, GBA 1894/005/0007, original of Kittl (1892, pl. 6, fig. 12), St. Cassian Formation.

Subclass Neritimorpha Koken, 1896

Order Cycloneritida Bandel & Frýda, 1999

Superfamily Neritopsoidea Gray, 1847

Family Delphinulopsidae Blodgett, Frýda & Stanley, 2001

Genus *Delphinulopsis* Laube, 1870
(= *Schwardtopsis* Bandel, 2007)

Type species. *Pleurotomaria binodosa* Münster, 1841 (= *Naticella muensteri* Klipstein, 1844), St. Cassian Formation, Carnian, South Tyrol, Italy; as *Delphinulopsis arietina* Laube, 1870 (= *Pleurotomaria binodosa* Münster, 1841) in Laube (1870, p. 30).

***Delphinulopsis binodosa* (Münster, 1841)**
Fig. 91

*1841	*Pleurotomaria binodosa*—Münster, p. 111, pl. 12, fig. 6.
1844	*Naticella münsteri*—Klipstein, p. 198, pl. 13, figs 18a–b.
1850	*Trochus helirius* d'Orb., 1847—d'Orbigny, p. 190, no. 272.
1850	*Stomatia münsteri* d'Orb., 1847—d'Orbigny, p. 194, no. 375.
1870	*Fossariopsis münsteri* Klipstein sp.—Laube, p. 18, pl. 33, fig. 1.
1870	*Delphinulopsis arietina* Laube—Laube, p. 32, pl. 33, fig. 5.
non 1870	*Delphinulopsis binodosa* Laube—Laube, p. 30, pl. 33, fig. 3.
1892	*Delphinulopsis binodosa* Münster sp.—Kittl, p. 61, pl. 8, figs 36–43.
1894b	*Delphinulopsis binodosa* Münster sp.—Kittl, p. 124, pl. 2, fig. 2.
1907	*Delphinulopsis binodosa* Münster—Broili, p. 90, pl. 7, figs 32–34.
1959	*Fossariopsis binodosa* Münster n. var. *carinata*—Leonardi & Fiscon, p. 28, pl. 2, figs 21–22.
1947	*Fossariopsis binodosa* Münster n. var. *carinata*—Leonardi & Fiscon, p. 8, pl. 1, figs 12a–b.
1959	*Fossariopsis binodosa* Münster—Leonardi & Fiscon, p. 28, pl. 9, figs 28a–b.
1978	*Delphinulopsis binodosa* (Münster)—Zardini, p. 39, pl. 24, figs 1a–b (non pl. 23, figs 8, 10).
?1978	*Delphinulopsis binodosa* (Münster) f. *carinata* (Leonardi-Fiscon)—Zardini, p. 39, pl. 23, fig. 9, 11.
2007	*Delphinulopsis binodosa* (Münster, 1841)—Bandel, p. 234, figs 5A–E.
non 2007	*Schwardtopsis münsteri* (Klipstein, 1843)—Bandel, p. 236, figs 5F–I.

Material. SNSB-BSPG AS VII 1663, original of Münster (1841, pl. 12, fig. 6) herein designated as lectotype (Fig. 91A–C) from the St. Cassian Formation. SNSB-BSPG 1903 IX 369 (original of Broili 1907, pl.7, fig. 32), 1903 IX 1107 (original of Broili 1907, pl.7, fig. 33), 1903 IX 1105 (two specimens, additional material of Broili 1907) from Pachycardientuffe, Upper Ladinian, Seiser Alm, Italy. NHMUK PI OR 35813(1), original of Klipstein (1844, pl. 13, fig. 18) herein designated as lectotype of *Naticella münsteri* Klipstein (Fig. 91D–F) from the St. Cassian Formation.

Description. Shell as high as wide, dextrally coiled; lectotype comprises at least 4 whorls (early whorls are encrusted), 7.5 mm high, 6.5 mm wide; whorls rapidly expanding, last whorl much larger than spire; spire acute, distinctly elevated; whorls angulated, ornamented with 4 carinae: subsutural, peripheral, subperipheral and basal carina; carina with coarse nodes ca. 7 on last half whorl of lectotype; whorl face between suture and subsutural carina concave almost horizontal; subsutural carina somewhat below suture, weakly angulating whorl face; whorl face between subsutural carina and peripheral carina concave, gently inclining at an angle of ca. 30°; peripheral carina strongly angulating whorl face; whorl face between peripheral and subperipheral carina straight to slightly concave, more or less parallel to shell axis; subperipheral carina in suprasutural position in spire whorls; whorl face strongly concave between subperipheral and basal carina; basal carina strongly angulating base, forming crest around pseudo-umbilicus; whorl face with rough of growth lines; growth lines prosocyrt and prosocline on subsutural bulge becoming opisthocline near peripheral carina, orthocline to straight opisthocyrt between peripheral and subperipheral carina; suture situated between subperipheral and basal carina; base narrow, pseudoumbilicate, with rough prosocyrt growth lines; aperture roughly D-shaped with a columellar septum and half covered with thick inductura, outer lip angulated, inner lip almost straight to slightly arched.

Discussion. Laube (1870) misidentified a specimen with two carinae as *Delphinulopsis binodosa* Münster and erected a new species *Delphinulopsis arietina* based on specimens which have four carinae on the whorls. *Delphinulopsis arietina* is a younger synonym of *Delphinulopsis binodosa* (Kittl 1892). Later, Kittl (1892) erected a new species *Delphinulopsis laubei* Kittl, 1892 based on the misidentified specimen of Laube with two carinae. *Delphinulopsis laubei* was erroneously synonymized with *Delphinulopsis binodosa* by Bandel (2007) but it represents a valid species.

Kittl (1892) regarded *Naticella muensteri* Klipstein, 1844 as a younger synonym of *Delphinulopis binodosa* and included the specimens that were assigned to *Fossariopsis muensteri* Klipstein by Laube (1870, pl. 33, fig. 1). Bandel (2007) regarded *Naticella muensteri* Klipstein as a separate species and included the specimens previously assigned to *Delphinulopsis binodosa* by Zardini (1978, pl. 23, figs 8, 10) to this species. Bandel (2007) erected a new genus *Schwardtopsis* Bandel, 2007 based on the Laube's description of *Fossariopsis muensteri* (Klipstein, 1844). The lectotype of *Naticella muensteri* Klipstein is refigured herein (Fig. 91D–F); it is clearly conspecific with the *Delphinulopsis binodosa* and hence *N. muensteri* represents a subjective junior synonym of *Delphinulopsis binodosa*; therefore, *Schwardtopsis* is a younger subjective synonym of *Delphinulopsis*. Even the specimens that were misidentified as *Naticella muensteri* by Bandel (2007) cannot be used to erect a new genus. According to Bandel (2007), *Delphinulopsis* is differentiated from *Schwardtopsis* by its more openly coiled shell and larger callus. However, the lectotype of *Delphinulopsis binodosa* (refigured herein in Fig. 91A–C) is not openly coiled. On the other hand, the more openly coiled specimens illustrated by Zardini (1978, pl. 23, figs 9, 11) and Bandel (2007, figs 5A–E) are herein regarded as conspecific with *D. binodosa* and open coiling seems to be subject of intraspecific variability.

The specimen figured by Broili (1907, pl. 7, fig. 33) has a lower whorl expansion rate, which is regarded as a variation.

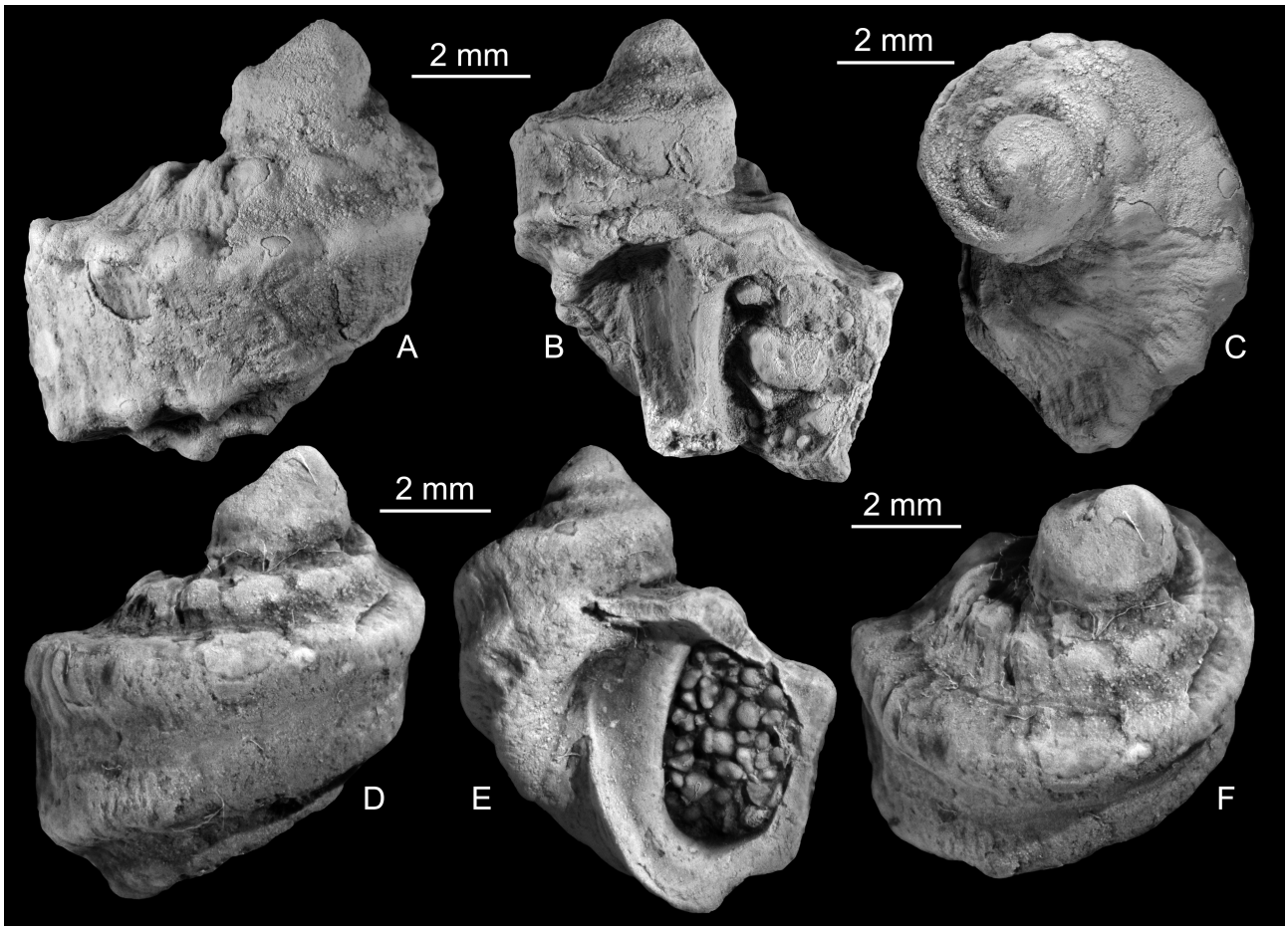

FIGURE 91. *Delphinulopsis binodosa* (Münster, 1841); **A–C.** Lectotype, SNSB-BSPG AS VII 1663, original of Münster (1841, pl. 12, fig. 6), St. Cassian Formation; **D–F.** Lectotype of *Naticella münsteri* Klipstein, 1844, NHMUK PI OR 35813(1), original of Klipstein (1844, pl. 13, fig. 18), St. Cassian Formation.

The diversity of the Pleurotomariida after the end-Permian mass extinction

The St. Cassian Formation has yielded the most diverse marine invertebrate fauna in the Triassic (Roden *et al*. 2020). With 546 species, gastropods represent by far the most diverse group of this fauna. This is a quarter of the total Triassic gastropod diversity (548 species out of 2177 nominate species). After the current revision, the

updated list of Cassian gastropods consists of 75 slit-bearing pleurotomariidan species which are dextrally coiled and 2 sinistrally coiled species belonging to the family Cirridae (Appendix S1). All together they correspond to 14 % of all gastropod species known from the St. Cassian Formation. The St. Cassian Formation yields members of approximately 44 % of pleurotomariidan genera reported from the Triassic (29 out of 66 genera), although it comprises only approximately 20 % of the Triassic pleurotomariidan species (a total of 386 nominate species including Cirridae).

As other gastropod clades, Pleurotomariida experienced a major extinction at the end Permian (Figure 97). Only 11 pleurotomariidan genera that occurred within the Permian (out of 77 genera) survived into the Triassic (Figure 96, Appendix S2 for the Permian and Triassic pleurotomariidan genera). The diversity of Pleurotomariida in the Early Triassic is very low but increased rapidly as did the diversity of the other gastropod groups until the end of the Anisian (Figures 92–93) (Erwin 1990; Nützel 2005). Pleurotomariida represented approximately 30 % of abundance and species diversity of Anisian gastropod faunas, similar to the proportion they had in Late Palaeozoic faunas (Figure 95, Appendix S3). In the Ladinian, species diversity of Pleurotomariida decreased slightly (Figure 92) and they constituted only a minor part of known gastropod faunas (e.g., Marmolada Limestone: Kittl 1894b; Esino Limestone: Kittl 1899). The low relative abundance of Pleurotomariida persisted during the Early Carnian. For instance, in the St. Cassian Formation the abundance of pleurotomariidans in surface samples are mostly low (e.g., 4 % in Hausmann & Nützel 2014) and they are very rare in bulk samples (e.g., 0.5 % in Hausmann & Nützel 2014 and personal observation) although they consist 14 % of the total gastropod species diversity of the St. Cassian Formation. Only the pleurotomariidan species *Rhaphistomella radians* forms 35 % of the specimens of the *Rhaphistomella radians*/*Palaeonucula strigilata* association and 8.5 % in the *Palaeonucula strigilata/Dentalium undulatum* association (Fürsich & Wendt 1977). Generally, the relative abundance of Pleurotomariida remains low worldwide in the Late Triassic (Figure 95).

Although many pleurotomariidan genera originated within the Early Carnian (mostly known from the St. Cassian Formation), the number of boundary crosser genera declined from the Ladinian-Carnian boundary onward, which is in contrast to all other gastropod groups (Figures 94). This reflects that many Carnian genera are singletons i.e., restricted to this stage and therefore not crossing boundaries. It could also mean that the recovery of Pleurotomariida was interrupted selectively by an extinction event within the Carnian, probably by the Carnian pluvial event (CPE) (Simms & Ruffell 1989; Dal Corso 2020). Intensification of extinction in marine environments during the CPE has been reported for various groups such as bryozoans (Simms & Ruffell 1989), conodonts (Rigo *et al*. 2007), crinoids (Hagdorn 2011), and fishes (Romano *et al*. 2016). It is estimated that 33 % of the marine animal genera became extinct during the CPE (Dal Corso 2020). All major gastropod groups decreased in species diversity after the Carnian (Figure 92), and all experienced high extinction on the genus level within the Carnian, but none of the major gastropod groups seems to be affected as much as Pleurotomariida in generic diversity (Figure 94). However, it must be taken into account that the exceptional high diversity of the St. Cassian Formation, a Liberation Fossil-Lagerstätte according Roden *et al*. (2020), potentially biases Triassic diversity curves (see also Nützel 2005).

It can be assumed that the geographic restriction of newly originated genera might be one reason for the loss of generic diversity after the CPE. Most of the newly originated Triassic pleurotomariidan genera were restricted to the tropical zone within the Tethys (e.g., Marmolada Limestone, Qingyan Formation, St. Cassian Formation, Pachycardientuffe, Hallstatt Limestone). This significant loss might suggest that the members of Pleurotomariida were more vulnerable to the environmental changes that occurred during the Carnian than other gastropod groups. During the CPE carbonate deposition was perturbated and clastic sediment influx increased in Tethyan shallow water environments (Simms & Ruffell 1989; Rigo *et al*. 2007; Dal Corso 2020). It is possible that the respiratory system of pleurotomariidans with two ctenidia (Yonge 1947; Yonge 1973; Hickman 1984) was insufficient to cope with high sediment load and prevented them to occupy the shallow shelf seas during the CPE. The high sediment load might also have narrowed their habitat area. The shift in major reef builders might also have affected Pleurotomariida, given the fact that the living members are spongivorous grazers (Hickmann 1984; Harasewych 2002) and fossil members have been found associated with sponge fossils (Batten 1958; Finks 1960). Before the CPE, the main reef builders were calcisponge/algal and *Tubiphytes*/algal crust reefs and these types of reefs were dominant from the Permian to the Early Carnian whereas scleractinian corals became dominant reef builders afterwards (e.g., Simms & Ruffell 1989; Flügel 2002). It is interesting that the diversity curve of reef building sphinctozoan (= thalamid) sponges in the Permian and Triassic (Senowbari-Daryan 1991; Riedel & Senowbari-Daryan 1991; Flügel 2002; Wu & Fan 2002) is very similar to that of Pleurotomariida (Figure 96).

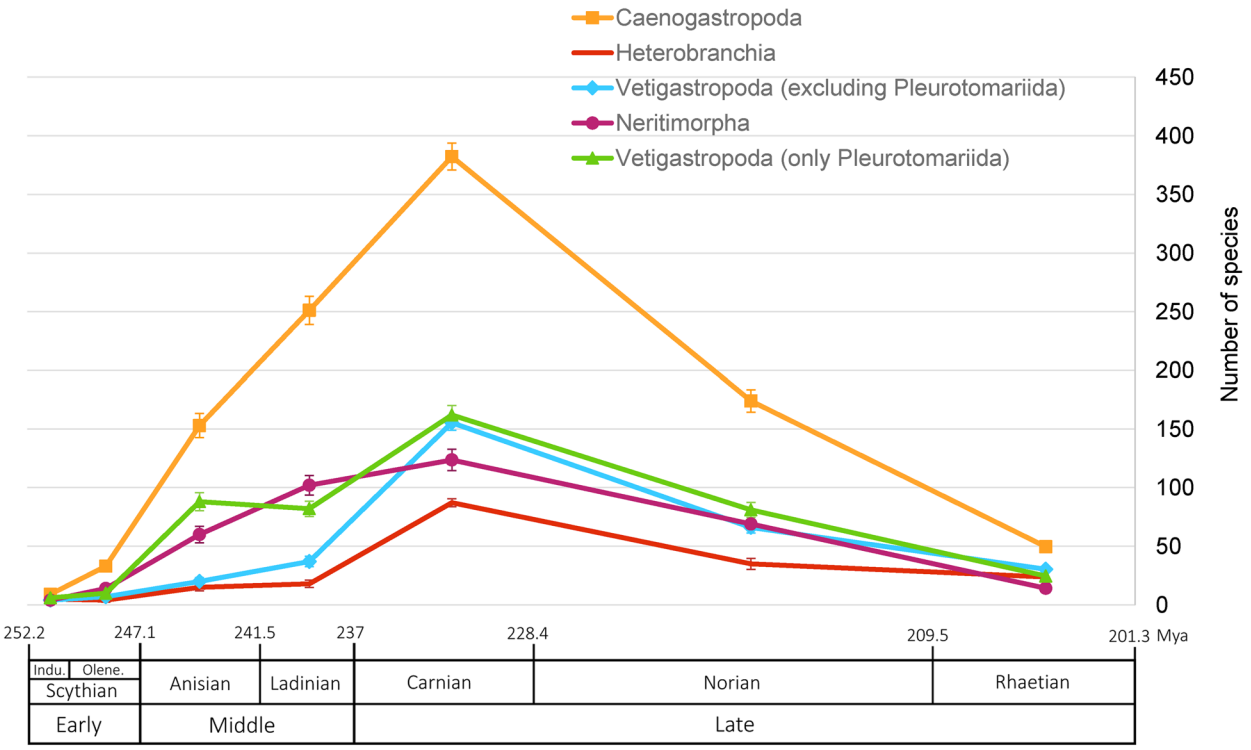

FIGURE 92. Species diversity curves of major gastropod groups during the Triassic (species in bin method). Error bars represent 95 % confidence intervals.

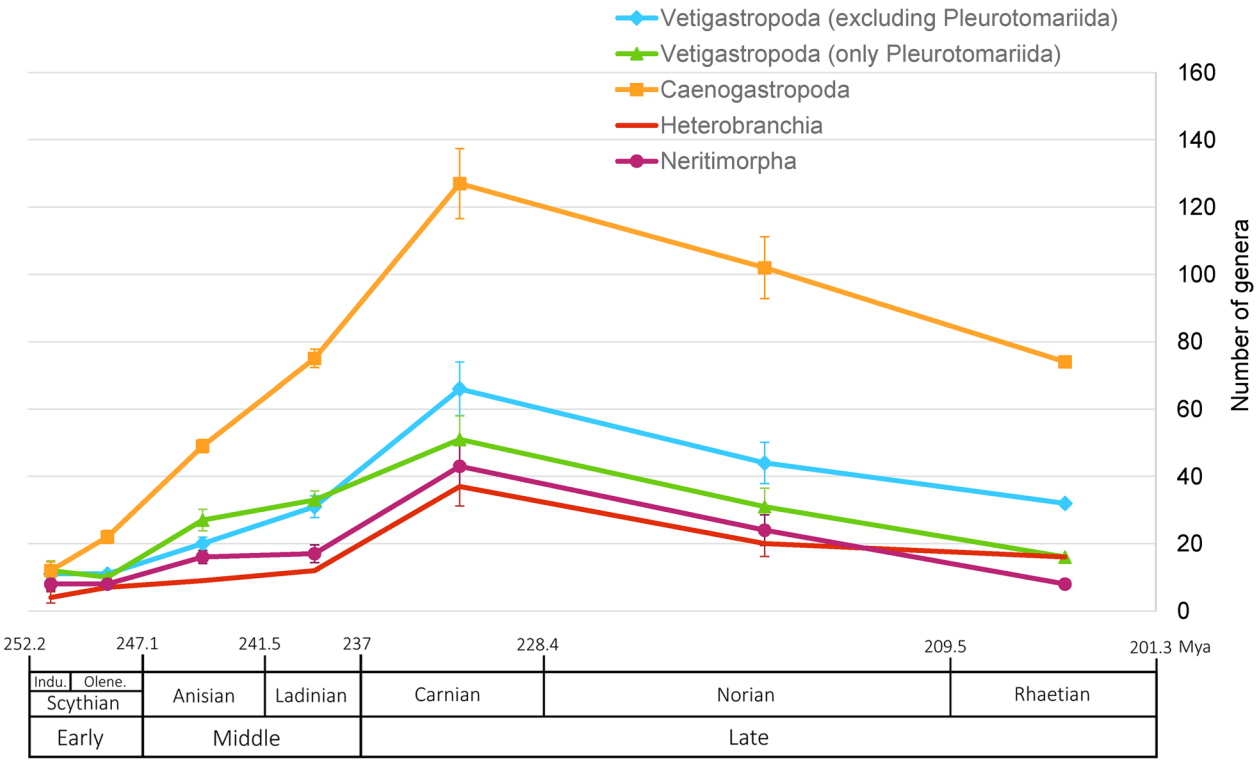

FIGURE 93. Generic diversity curves of major gastropod groups during the Triassic (range through method). Error bars represent 95 % confidence intervals.

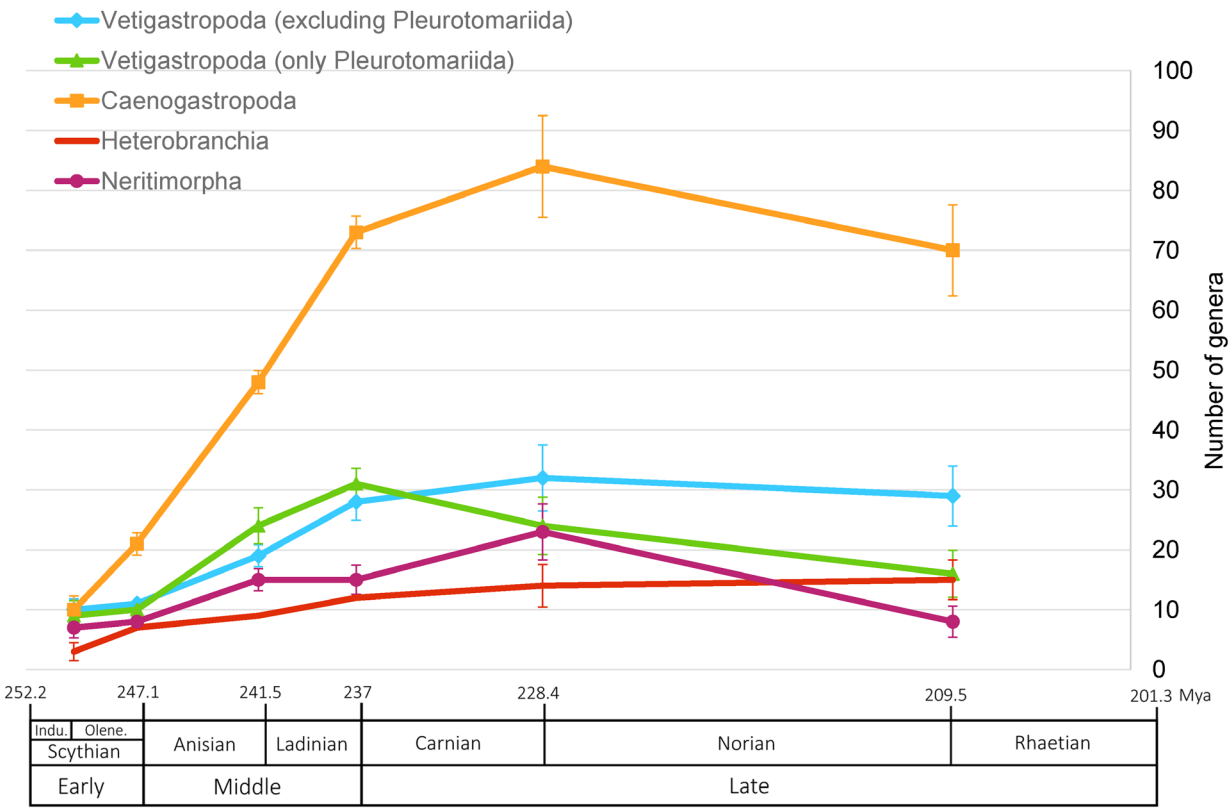

FIGURE 94. Diversity curves of boundary crosser genera belonging to the major gastropod groups during the Triassic (range through method). Error bars represent 95 % confidence intervals.

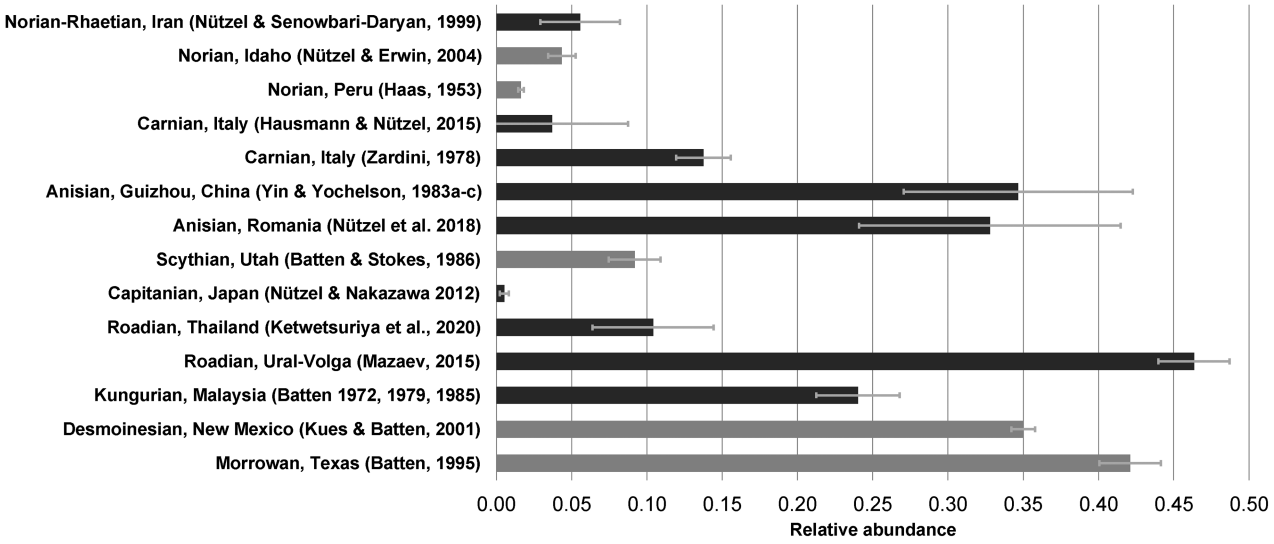

FIGURE 95. Relative abundance of Pleurotomariida in different gastropod assemblages ranging from the Pennsylvanian (Late Carboniferous) to the Norian. The samples from Tethys Ocean deposits are given in black bar, the samples from Panthalassa Ocean deposits are given in gray bar. See Appendix S3 for the species diversity and palaeoenvironment interpretation. Error bars represent 95 % confidence intervals.

The diversification of Pleurotomariida at the family level during the Triassic is remarkable. Many new families had their first occurrence within the Triassic: Kittlidiscidae, Zygitidae, Schizogoniidae, Wortheniellidae, Stuorellidae, Rhaphistomellidae, Temnotropidae, Trochotomidae, Lancedelliidae (all with a type genus from the St. Cassian

Formation except Trochotomidae). Here the good preservation of gastropods from the St. Cassian Formation plays a pivotal role because it allows to study shells preserved in great detail and thus improves taxonomy. The earliest members of the family Pleurotomariidae (e.g., *Tahua* Begg & Grant-Mackie, 2003 =?*Ramusatomaria* Szabó *et al*., 2019) and Ptychomphalidae were also reported from the Triassic (Begg & Grant-Mackie 2003; Ferrari 2015). Although it is uncertain whether this high origination rate of families is merely a preservational artefact by the good preservation present in the St. Cassian Formation, it is certain that the Pleurotomariida show a remarkably high morphological disparity within the Triassic, especially when compared to post-Triassic times. Despite the originations of new genera and families, the diversification of the Pleurotomariida at the species level did not become as high as that of Caenogastropoda (Figures 92–93).

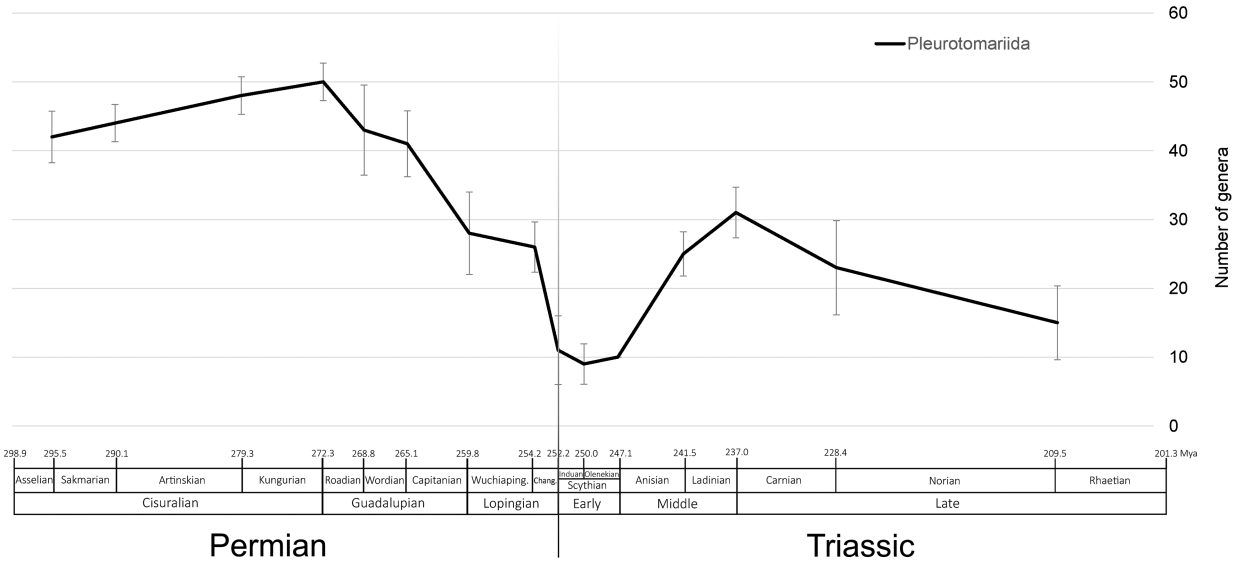

FIGURE 96. Diversity curve of the boundary crosser Pleurotomariida genera (range through method) from the Permian to the Triassic.

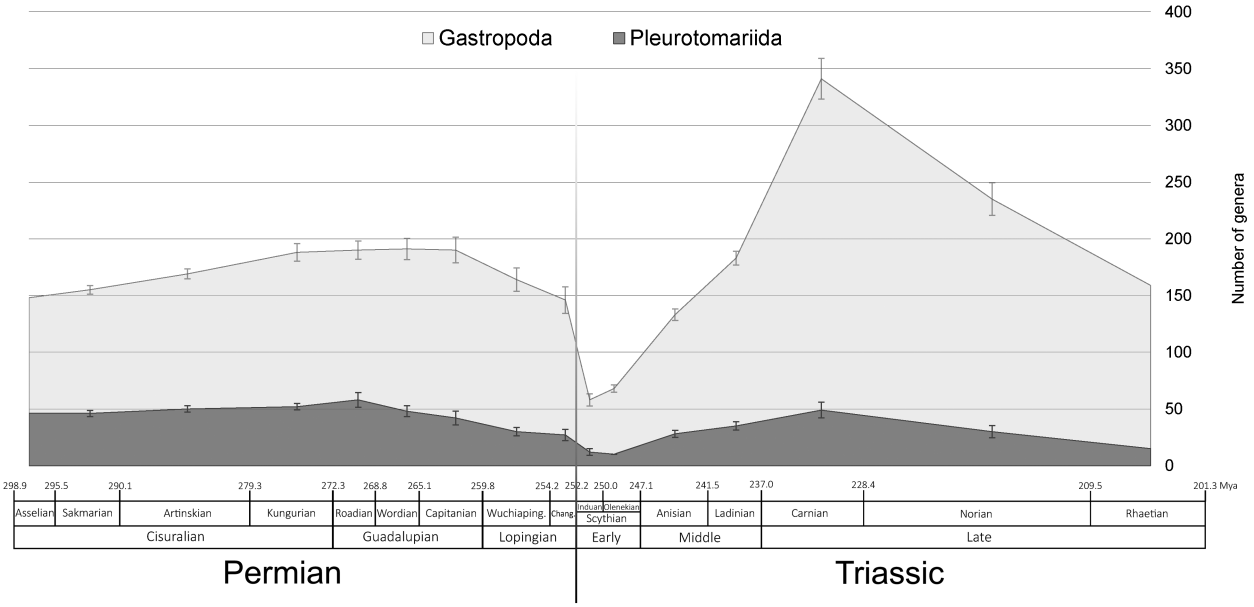

FIGURE 97. Generic diversity curves of Pleurotomariida (dark gray) and all gastropods (light gray) from the Permian to the Triassic (range through method). Permian data of all gastropods are taken from the PBDB.

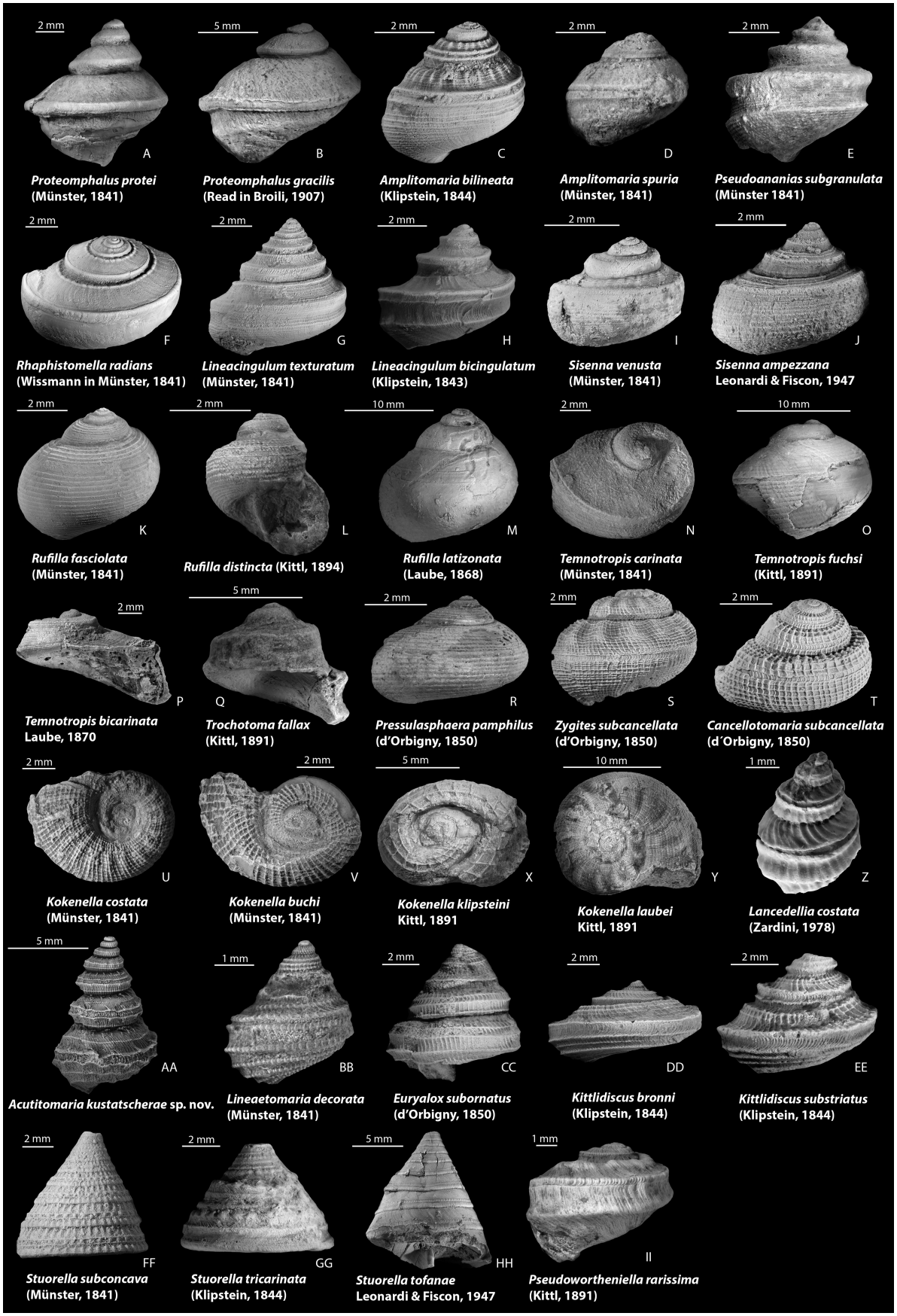
2 mm
A
Proteomphalus protei (Münster, 1841)
5 mm
B
Proteomphalus gracilis (Read in Broili, 1907)
2 mm
C
Amplitomaria bilineata (Klipstein, 1844)
2 mm
D
Amplitomaria spuria (Münster, 1841)
2 mm
E
Pseudoananias subgranulata (Münster 1841)
2 mm
F
Rhaphistomella radians (Wissmann in Münster, 1841)
2 mm
G
Lineacingulum texturatum (Münster, 1841)
2 mm
H
Lineacingulum bicingulatum (Klipstein, 1843)
2 mm
I
Sisenna venusta (Münster, 1841)
2 mm
J
Sisenna ampezzana Leonardi & Fiscon, 1947
2 mm
K
Rufilla fasciolata (Münster, 1841)
2 mm
L
Rufilla distincta (Kittl, 1894)
10 mm
M
Rufilla latizonata (Laube, 1868)
2 mm
N
Temnotropis carinata (Münster, 1841)
10 mm
O
Temnotropis fuchsi (Kittl, 1891)
2 mm
P
Temnotropis bicarinata Laube, 1870
5 mm
Q
Trochotoma fallax (Kittl, 1891)
2 mm
R
Pressulasphaera pamphilus (d'Orbigny, 1850)
2 mm
S
Zygites subcancellata (d'Orbigny, 1850)
2 mm
T
Cancellotomaria subcancellata (d´Orbigny, 1850)
2 mm
U
Kokenella costata (Münster, 1841)
2 mm
V
Kokenella buchi (Münster, 1841)
5 mm
X
Kokenella klipsteini Kittl, 1891
10 mm
Y
Kokenella laubei Kittl, 1891
1 mm
Z
Lancedellia costata (Zardini, 1978)
5 mm
AA
Acutitomaria kustatscherae sp. nov.
1 mm
BB
Lineaetomaria decorata (Münster, 1841)
2 mm
CC
Euryalox subornatus (d'Orbigny, 1850)
2 mm
DD
Kittlidiscus bronni (Klipstein, 1844)
2 mm
EE
Kittlidiscus substriatus (Klipstein, 1844)
2 mm
FF
Stuorella subconcava (Münster, 1841)
2 mm
GG
Stuorella tricarinata (Klipstein, 1844)
5 mm
HH
Stuorella tofanae Leonardi & Fiscon, 1947
1 mm
II
Pseudowortheniella rarissima (Kittl, 1891)

FIGURE 98.

FIGURE 98 (continued). Pleurotomariida from the St. Cassian Formation; **A.** *Proteomphalus protei* (Münster, 1841), NHMW 1899/0005/0082/1 (original of Kittl 1891, pl. 1, fig. 11), St. Cassian Formation; **B.** *Proteomphalus gracilis* (Read, 1907 in Broili), lectotype, SNSB-BSPG 1903 IX 325 (original of Broili 1907, pl. 6, fig. 24), Pachycardientuffe, Upper Ladinian, Seiser Alm; **C.** *Amplitomaria spuria* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1222, (original of Münster 1841, pl. 11, figs 29a–b), St. Cassian Formation; **D.** *Amplitomaria bilineata* (Klipstein, 1844), lectotype, NHMUK PI OR 35355(1) (original of Klipstein 1844, pl. 10, fig. 12), St. Cassian Formation; **E.** *Pseudoananias subgranulata* (Münster 1841), lectotype, SNSB-BSPG AS VII 2071, St. Cassian Formation; **F.** *Rhaphistomella radians* (Wissmann, 1841 in Münster), lectotype, SNSB-BSPG AS VII 1224 (original of Münster 1841, pl. 12, figs 8a–b), St. Cassian Formation; **G.** *Lineacingulum texturatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1220 (original of Münster 1841, pl. 12, figs 1a–b); **H.** *Lineacingulum bicingulatum* (Klipstein, 1844), lectotype, NHMUK PI OR 35331(1) (original of Klipstein 1844, pl. 10, fig. 10), St. Cassian Formation; **I.** *Sisenna venusta* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1215 (original of Münster 1841, pl. 12, figs 13a–b), St. Cassian Formation; **J.** *Sisenna ampezzana* Leonardi & Fiscon, 1947, PZO 13684, Rumerlo Misurina mix, St. Cassian Formation; **K.** *Rufilla fasciolata* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1593 (original of Münster 1841, pl. 12, figs 21a–b), St. Cassian Formation; **L.** *Rufilla distincta* (Kittl, 1894), lectotype, NHMW 1899/0005/0075 (original of Kittl 1894a, pl. 8, fig. 1), St. Cassian Formation; **M.** *Rufilla latizonata* (Laube, 1868), NHMW 1990/0638/0000 (original of Bandel 1991, pl. 12, figs 5–6), St. Cassian Formation; **N.** *Temnotropis carinata* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1803 (original of Münster 1841, pl. 9, figs 16a–b), St. Cassian Formation; **O.** *Temnotropis fuchsi* (Kittl, 1891), lectotype, NHMW 1899/0005/0100 (original of Kittl 1891, pl. 1, fig. 22), St. Cassian Formation; **P.** *Temnotropis bicarinata* Laube, 1870, NHMW 1899/0005/0024/2, St. Cassian Formation; **Q.** *Trochotoma fallax* (Kittl, 1891), lectotype, NHMW 1899/0005/0026 (original of Kittl 1891, pl. 5, figs 18–19), St. Cassian Formation; **R.** *Pressulasphaera pamphilus* (d'Orbigny, 1850), GBA 1868/008/0001, 4339, original of Laube (1868, pl. 28, fig. 2), St. Cassian Formation; **S.** *Zygites subcancellata* (d'Orbigny, 1850), NHMW 1899/0005/0087/1, original of Bandel (1991, pl. 1, fig. 7), St. Cassian Formation; **T.** *Cancellotomaria subcancellata* (d´Orbigny, 1850), lectotype, SNSB-BSPG AS VII 1213 (original of Münster 1841, pl. 12, figs 16a–b), St. Cassian Formation; **U.** *Kokenella costata* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1495 (original of Münster 1841, pl. 11, fig. 6), St. Cassian Formation; **V.** *Kokenella buchi* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1494 (original of Münster 1841, pl. 11, figs 5a–d), St. Cassian Formation **X.** *Kokenella klipsteini* Kittl, 1891, lectotype, NHMW 1899/0005/0021 (original of Kittl 1891, pl. 1, fig. 34), St. Cassian Formation; **Y.** *Kokenella laubei* Kittl, 1891, lectotype, NHMW 1899/0005/0018 (original of Kittl 1891, pl. 1, fig. 33), St. Cassian Formation; **Z.** *Lancedellia costata* (Zardini, 1978), lectotype, MPRZ 1263 M-Z (original of Zardini 1978, pl. 13, fig. 5), Misurina, St. Cassian Formation; **AA.** *Acutitomaria kustatscherae* **sp. nov.**, holotype, NHMW 1990/0642/0000 (original of Bandel 1991, pl.17, figs 5–8), Alpe di Specie (Seelandalpe), St. Cassian Formation; **BB.** *Lineaetomaria decorata* (Münster, 1841), NHMW 1884/0001/0143/1, St. Cassian Formation; **CC.** *Euryalox subornatus* (d'Orbigny, 1850), lectotype, NHMUK PI OR 35312(1), original of Klipstein (1844, pl. 9, fig. 9), St. Cassian Formation; **DD.** *Kittlidiscus bronni* (Klipstein, 1844), NHMW 1899/0005/0089, original of Kittl (1891, text-fig. 2), St. Cassian Formation; **EE.** *Kittlidiscus substriatus* (Klipstein, 1844); lectotype, NHMUK PI OR 35326(1), original of Klipstein (1844, pl. 10, fig. 15), St. Cassian Formation; **FF.** *Stuorella subconcava* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1226 (original of Münster 1841, pl. 11, figs 13a–b), St. Cassian Formation; **GG.** *Stuorella tricarinata* (Klipstein, 1844), lectotype, NHMUK PI OR 35291(1), original of Klipstein (1844, pl. 9, fig. 10), St. Cassian Formation; **HH.** *Stuorella tofanae* Leonardi & Fiscon, 1947, NHMW 1990/0634/0000 (original of Bandel 1991, pl. 11, fig. 4), Alpe di Specie (Seelandalpe), St. Cassian Formation; **II.** *Pseudowortheniella rarissima* (Kittl, 1891), NHMW 1899/0006/0010/1, St. Cassian Formation.

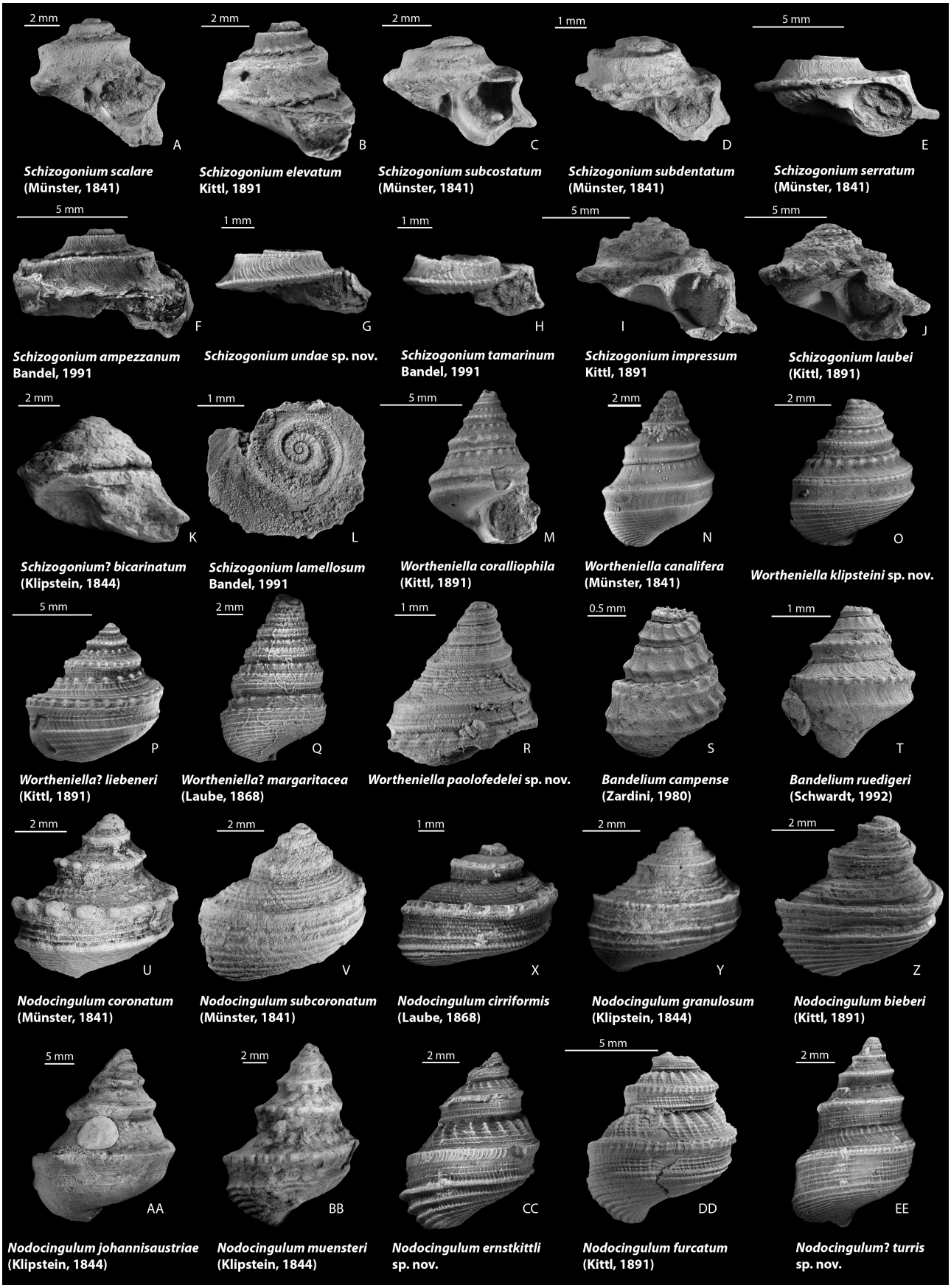
2 mm
A
Schizogonium scalare (Münster, 1841)
2 mm
B
Schizogonium elevatum Kittl, 1891
2 mm
C
Schizogonium subcostatum (Münster, 1841)
1 mm
D
Schizogonium subdentatum (Münster, 1841)
5 mm
E
Schizogonium serratum (Münster, 1841)
5 mm
F
Schizogonium ampezzanum Bandel, 1991
1 mm
G
Schizogonium undae sp. nov.
1 mm
H
Schizogonium tamarinum Bandel, 1991
5 mm
I
Schizogonium impressum Kittl, 1891
5 mm
J
Schizogonium laubei (Kittl, 1891)
2 mm
K
Schizogonium? bicarinatum (Klipstein, 1844)
1 mm
L
Schizogonium lamellosum Bandel, 1991
5 mm
M
Wortheniella coralliophila (Kittl, 1891)
2 mm
N
Wortheniella canalifera (Münster, 1841)
2 mm
O
Wortheniella klipsteini sp. nov.
5 mm
P
Wortheniella? liebeneri (Kittl, 1891)
2 mm
Q
Wortheniella? margaritacea (Laube, 1868)
1 mm
R
Wortheniella paolofedelei sp. nov.
0.5 mm
S
Bandelium campense (Zardini, 1980)
1 mm
T
Bandelium ruedigeri (Schwardt, 1992)
2 mm
U
Nodocingulum coronatum (Münster, 1841)
2 mm
V
Nodocingulum subcoronatum (Münster, 1841)
1 mm
X
Nodocingulum cirriformis (Laube, 1868)
2 mm
Y
Nodocingulum granulosum (Klipstein, 1844)
2 mm
Z
Nodocingulum bieberi (Kittl, 1891)
5 mm
AA
Nodocingulum johannisaustriae (Klipstein, 1844)
2 mm
BB
Nodocingulum muensteri (Klipstein, 1844)
2 mm
CC
Nodocingulum ernstkittli sp. nov.
5 mm
DD
Nodocingulum furcatum (Kittl, 1891)
2 mm
EE
Nodocingulum? turris sp. nov.

FIGURE 99.

FIGURE 99 (continued). Pleurotomariida from the St. Cassian Formation; **A.** *Schizogonium scalare* (Münster, 1841), paralectotype, SNSB-BSPG AS VII 1661, St. Cassian Formation; **B.** *Schizogonium elevatum* Kittl, 1891, lectotype, NHMW 1899/0005/0138/1 (original of Kittl 1891, pl. 5, fig. 17), St. Cassian Formation; **C.** *Schizogonium subcostatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1516 (original of Münster 1841, pl. 12, figs 3a–b), St. Cassian Formation; **D.** *Schizogonium subdentatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1662 (original of Münster 1841, pl. 12, figs 5a–c), St. Cassian Formation; **E.** *Schizogonium serratum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1225 (original of Münster 1841, pl. 11, figs 7a–b), St. Cassian Formation; **F.** *Schizogonium ampezzanum* Bandel, 1991, holotype, NHMW 1990/0626/0000 (original of Bandel 1991, pl. 7, figs 4, 7), St. Cassian Formation; **G.** *Schizogonium undae* **sp. nov.**, holotype, NHMW 1990/0624/0003/1, Alpe di Specie (Seeland Alpe), St. Cassian Formation; **H.** *Schizogonium tamarinum* Bandel, 1991, NHMW 1899/0005/0127 (original of Kittl 1891, pl. 5, fig. 1), St. Cassian Formation; **I.** *Schizogonium impressum* Kittl, 1891, lectotype, NHMW 1899/0005/0134 (original of Kittl 1891, pl. 5, fig. 8), St. Cassian Formation; **J.** *Schizogonium laubei* Kittl, 1891, lectotype, NHMW 1899/0005/0132 (the original of Kittl 1891, pl. 5, fig. 7), St. Cassian Formation; **K.** *Schizogonium? bicarinatum* (Klipstein, 1844), lectotype, NHMUK PI OR 35337(1), original of Klipstein (1844, pl. 14, fig. 32), St. Cassian Formation; **L.** *Schizogonium lamellosum* Bandel, 1991, MPRZ 2021 1–056, Campo, St. Cassian Formation; **M.** *Wortheniella coralliophila* (Kittl, 1891), lectotype, NHMW 1899/0006/0008 (original of Kittl, 1891, pl. 2, fig. 27), St. Cassian Formation; **N.** *Wortheniella canalifera* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1223 (original of Münster 1841, pl. 12, fig. 4), St. Cassian Formation; **O.** *Wortheniella klipsteini* **sp. nov.**, holotype, NHMUK PI OR 35351, St. Cassian Formation; **P.** *Wortheniella*? *liebeneri* (Kittl, 1891), lectotype, GBA 1894/005/0004, 4350, original of Kittl (1891, pl. 2, fig. 16), St. Cassian Formation; **Q.** *Wortheniella*? *margaritacea* (Laube, 1868), NHMW 1899/0007/0003, original of Kittl (1891, pl. 2, fig. 30), St. Cassian Formation; **R.** *Wortheniella paolofedelei* **sp. nov.**, holotype, MPRZ 2021 1–052, Campo, St. Cassian Formation; **S.** *Bandelium campense* (Zardini, 1980), MPRZ 2021 1–030, Misurina, St. Cassian Formation; **T.** *Bandelium ruedigeri* (Schwardt, 1992), MPRZ 2021 1–012, Campo, St. Cassian Formation; **U.** *Nodocingulum coronatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1217 original of Münster (1841, pl. 11, figs 26a–b), St. Cassian Formation; **V.** *Nodocingulum subcoronatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1218 (original of Münster 1841, pl. 11, figs 25a–b), St. Cassian Formation; **X.** *Nodocingulum cirriformis* (Laube, 1868), NHMW 1899/0005/0027/2, St. Cassian Formation; **Y.** *Nodocingulum granulosum* (Klipstein, 1844), NHMUK PI OR 35356(1), original of Klipstein (1844, pl. 10, fig. 33), St. Cassian Formation; **Z.** *Nodocingulum bieberi* (Kittl, 1891), NHMW 1899/0005/0049 (original of Kittl 1891, pl. 2, fig. 34), St. Cassian Formation; **AA.** *Nodocingulum johannisaustriae* (Klipstein, 1844), lectotype, NHMUK PI OR 35340(1), original of Klipstein (1844, pl. 10, fig. 13), St. Cassian Formation; **BB.** *Nodocingulum muensteri* (Klipstein, 1844), lectotype, NHMUK PI OR 35366(1) original of Klipstein (1844, pl. 10, fig. 25), St. Cassian Formation; **CC.** *Nodocingulum ernstkittli* **sp. nov.**, holotype, NHMW 1899/0005/0045/2, St. Cassian Formation; **DD.** *Nodocingulum furcatum* (Kittl, 1891), lectotype, NHMW 1899/0005/0047 (original of Kittl 1891, pl. 2, fig. 22), St. Cassian Formation; **EE.** *Nodocingulum*? *turris* **sp. nov.**, holotype, NHMW 1899/0005/0056, St. Cassian Formation.

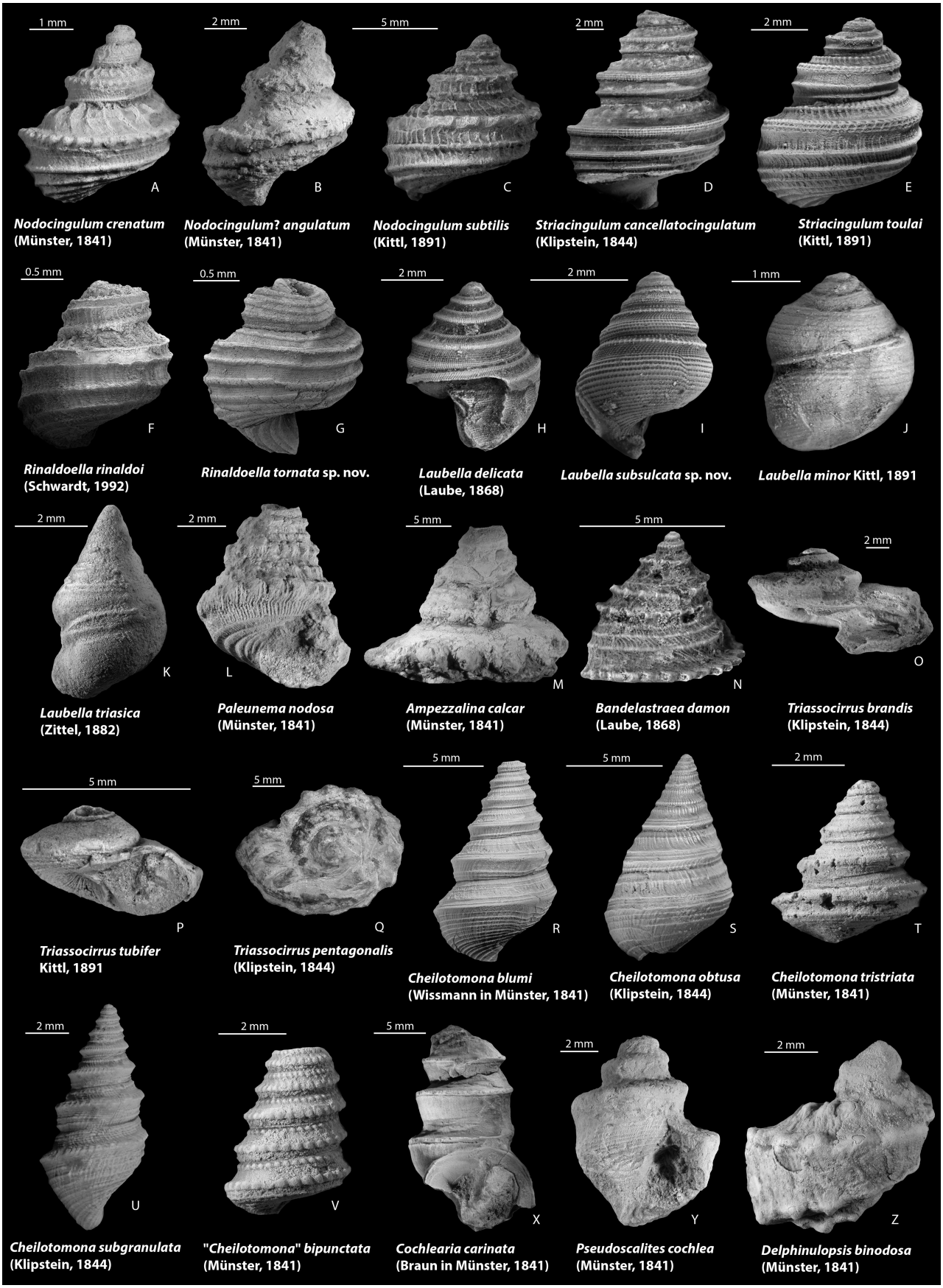
1 mm
A
Nodocingulum crenatum (Münster, 1841)
2 mm
B
Nodocingulum? angulatum (Münster, 1841)
5 mm
C
Nodocingulum subtilis (Kittl, 1891)
2 mm
D
Striacingulum cancellatocingulatum (Klipstein, 1844)
2 mm
E
Striacingulum toulai (Kittl, 1891)
0.5 mm
F
Rinaldoella rinaldoi (Schwardt, 1992)
0.5 mm
G
Rinaldoella tornata sp. nov.
2 mm
H
Laubella delicata (Laube, 1868)
2 mm
I
Laubella subsulcata sp. nov.
1 mm
J
Laubella minor Kittl, 1891
2 mm
K
Laubella triasica (Zittel, 1882)
2 mm
L
Paleunema nodosa (Münster, 1841)
5 mm
M
Ampezzalina calcar (Münster, 1841)
5 mm
N
Bandelastraea damon (Laube, 1868)
2 mm
O
Triassocirrus brandis (Klipstein, 1844)
5 mm
P
Triassocirrus tubifer Kittl, 1891
5 mm
Q
Triassocirrus pentagonalis (Klipstein, 1844)
5 mm
R
Cheilotomona blumi (Wissmann in Münster, 1841)
5 mm
S
Cheilotomona obtusa (Klipstein, 1844)
2 mm
T
Cheilotomona tristriata (Münster, 1841)
2 mm
U
Cheilotomona subgranulata (Klipstein, 1844)
2 mm
V
"Cheilotomona" bipunctata (Münster, 1841)
5 mm
X
Cochlearia carinata (Braun in Münster, 1841)
2 mm
Y
Pseudoscalites cochlea (Münster, 1841)
2 mm
Z
Delphinulopsis binodosa (Münster, 1841)

FIGURE 100.

FIGURE 100 (continued). Pleurotomariida (A–G) and non-pleurotomariidan gastropoda previously assigned to Pleurotomariida (H–Z) from the St. Cassian Formation; **A.** *Nodocingulum crenatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1519 (original of Münster 1841, pl. 12, fig. 15), St. Cassian Formation; **B.** *Nodocingulum*? *angulatum* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1517 (original of Münster 1841, pl. 12, fig. 10), St. Cassian Formation; **C.** *Nodocingulum subtilis* (Kittl, 1891), lectotype, NHMW 1899/0007/0005, original of Kittl (1891, pl. 3, fig. 14), St. Cassian Formation; **D.** *Striacingulum cancellatocingulatum* (Klipstein, 1844), NHMUK PI OR 35345(1), original of Klipstein (1844, pl. 10, fig. 23), St. Cassian Formation; **E.** *Striacingulum toulai* (Kittl, 1891), lectotype, NHMW 1899/0005/0077, original of Kittl (1891, pl. 3, figs 12–13), St. Cassian Formation; **F.** *Rinaldoella rinaldoi* (Schwardt, 1992), MPRZ 2021 1–010, Campo, St. Cassian Formation; **G.** *Rinaldoella tornata* **sp. nov.**, holotype, MPRZ 2021 1–001, Campo, St. Cassian Formation; **H.** *Laubella delicata* (Laube, 1868), lectotype, GBA 1868/008/0003, 4356, original of Laube (1868, pl. 27, fig. 5), St. Cassian Formation; **I.** *Laubella subsulcata* **sp. nov.**, holotype, NHMW 1884/0001/0186 (original of Bandel 1991, pl. 15, fig. 2), St. Cassian Formation; **J.** *Laubella minor* Kittl, 1891, lectotype, NHMW 1899/0005/0106 (original of Kittl 1891 pl. 4, fig. 11), St. Cassian Formation; **K.** *Laubella triasica* (Zittel, 1882), lectotype, SNSB-BSPG 1881 I 501 (the original of Zittel 1882, fig. 223), St. Cassian Formation; **L.** *Paleunema nodosa* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1518 (original of Münster 1841, pl. 12, figs 14a–b), St. Cassian Formation; **M.** *Ampezzalina calcar* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1514 (original of Münster 1841, pl. 11, figs 28a–b), St. Cassian Formation; **N.** *Bandelastraea damon* (Laube, 1868), lectotype, GBA 1869/009/0001, original of Laube (1868, pl. 34, fig. 10); **O.** *Triassocirrus brandis* (Klipstein, 1844), lectotype, NHMUK PI OR 35324(1), original of Klipstein (1844, pl. 10, fig. 21), St. Cassian Formation; **P.** *Triassocirrus tubifer* (Kittl, 1891), lectotype, NHMW 1899/0006/0016 (original of Kittl 1891, text-fig. 7), St. Cassian Formation; **Q.** *Triassocirrus pentagonalis* (Klipstein, 1844), lectotype, NHMUK PI OR 35322, original of Klipstein (1844, pl. 10, fig. 22), St. Cassian Formation; **R.** *Cheilotomona blumi* (Wissmann, 1841 in Münster), paralectotype, BSPG AS VII 1233 (original of Münster 1841, pl. 13, fig. 47a), St. Cassian Formation; **S.** *Cheilotomona obtusa* (Klipstein, 1844), lectotype of *Pleurotomaria calosoma* Laube, 1868, GBA 1894/005/0002, 4344, original of Laube (1868, pl. 28, fig. 1) and Kittl (1891, pl. 3, fig. 20), St. Cassian Formation; **T.** *Cheilotomona tristriata* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1231 (original of Münster 1841, pl. 11, fig. 19), St. Cassian Formation; **U.** *Cheilotomona subgranulata* (Klipstein, 1844), NHMUK PI GG 1940, St. Cassian Formation; **V.** "*Cheilotomona*" *bipunctata* Münster, 1841, lectotype, SNSB-BSPG AS VII 1228 original of Münster (1841, pl. 11, fig. 14), St. Cassian Formation; **X.** *Cochlearia carinata* (Braun in Münster, 1841), NHMUK PI OR 35824(1), St. Cassian Formation; **Y.** *Pseudoscalites cochlea* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1216 original of Münster (1841, pl. 12, fig. 9), St. Cassian Formation; **Z.** *Delphinulopsis binodosa* (Münster, 1841), lectotype, SNSB-BSPG AS VII 1663, original of Münster (1841, pl. 12, fig. 6), St. Cassian Formation.

Despite a considerable recovery, Pleurotomariida failed to reach their Permian generic diversity in the Triassic (Fig. 96). Pleurotomariida were outnumbered by Caenogastropoda which diversified much faster. The relatively low diversity of Pleurotomariida within the Triassic is in contrast to the proliferation of the class Gastropoda as a whole. Their low abundance in Late Triassic gastropod faunas played a major role in their ongoing post-Palaeozoic decline in diversity. The proportion of Pleurotomariida genera to the total gastropod generic diversity decreased from 26 % during the entire Permian (PBDB data, acquired 19 May 2020) to 18 % during the entire Triassic (Figure 97). At the end of the Triassic, Pleurotomariida went through another bottleneck and only a few genera survived into the Jurassic (e.g., *Pleurotomaria*, *Trochotoma*, *Sisenna*). No new family originated within the Jurassic and Pleurotomariida were only present with the families Rhaphistomellidae (*Sisenna*), Pleurotomariidae, Trochotomidae, Ptychomphalidae, and Cirridae (see the discussion of Eucyclidae in the Systematic Palaeontology section). Although Pleurotomariida were one of the characteristic elements of the Jurassic gastropod faunas (e.g., Monari *et al*. 2011, 2017), they formed only minor portions of Jurassic gastropod assemblages (e.g., Conti *et al*. 2004; Nützel & Gründel 2015; Szabó *et al*. 2019).

A striking character that appeared among Triassic Pleurotomariida is the delay in the timing of slit/selenizone formation during ontogeny. This character is seen in different lineages within Pleurotomariida (e.g., *Acutitomaria kustatscherae* **gen. et sp. nov.**, *Pseudomurchisonia insueta* Koken, 1896, *Stuorella tofanae* Leonardi & Fiscon, 1947, "*Pleurotomaria*" *leda* Kittl, 1894b) but also in slit bearing Caenogastropoda (e.g., *Cheilotomona*, *Trypanocochlea*). The extinction of slit bearing groups (Bellerophontida, Murchisonioidea) within the Triassic and the parallel evolution of the delay in the timing of the slit and selenizone could suggest a selective pressure against the presence of a slit within the Triassic (see Kaim & Nützel 2011 for the extinction of Bellerophontida). It seems plausible that these taxa with a late formation of the selenizone may have eventually given rise to new forms lacking a selenizone. One example of the loss of the selenizone within a lineage was proposed for Cirridae (Bandel 1993a).

Remarks on slit-band gastropods not belonging to Pleurotomariida

Several genera and species of slit-bearing gastropods not belonging to Pleurotomariida have been reported from the St. Cassian Formation (e.g., *Cheilotomona*, *Cochlearia*, *Laubella*). Some have a selenizone but lack a nacreous shell layer and belong to Scissurelloidea (the little slit shells) or Fissurelloidea (order Lepetellida). Seven species and four genera assigned to Scissurelloidea or Fissurelloidea have been described form the St. Cassian Formation: *Emarginula muensteri* Pictet, 1855 (=*Emarginula zardini* Garavello-Spaetti), *Emarginula seelandica* Zardini, 1978, *Emarginula ampezzana* Zardini, 1978, *Emarginula ladina* Zardini, 1985, *Ampezemarginula cristata* (Zardini, 1978), *Zardinitrochus suessi* (Kittl, 1891), *Triassurella carnica* Nützel & Geiger, 2006.

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References

Agassiz, L. (1837) *Großbritanniens Mineral-Conchologie oder ausgemahlte Abbildungen und Beschreibungen der Schaltier-Überreste, welche zu verschiedenen Zeiten und in verschiedenen Tiefen der Erde erhalten worden sind; von James Sowerby*. H. Nicolet, Neuchatel, 689 pp.

Archiac, V. de & Verneuil, M.E. de (1842) On the fossils of the older deposits in the Rhenish Provinces; preceded by a general-survey of the fauna of the Palaeozoic rocks, and followed by a tabular list of the organic remains of the Devonian system in Europe. *Transactions of the Geological Society of London*, Series 2, 6, 303–410. https://doi.org/10.1144/transgslb.6.2.303

Arthaber, G. von (1914) Die Trias von Bithynien (Anatolien). *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, 27, 85–206.

Bandel, K. (1991) Schlitzbandschnecken mit perlmutteriger Schale aus den triassischen St. Cassian Schichten der Dolomiten. *Annalen des Naturhistorischen Museums Wien*, Reihe A, 92, 1–53.

Bandel, K. (1992) Über Caenogastropoden der Cassianer Schichten (Obertrias) der Dolomiten (Italien) und ihre taxonomische Bewertung. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, 73, 37–97.

Bandel, K. (1993a) Evolutionary history of sinistral archaeogastropods with and without slit (Cirroidea, Vetigastropoda). *Freiberger Forschungshefte*, C 450, 41–81.

Bandel, K. (1993b) Trochomorpha (Archaeogastropoda) aus den St. Cassian-Schichten (Dolomiten, Mittlere Trias). *Annalen des Naturhistorischen Museums Wien*, Reihe A, 95, 1–99.

Bandel, K. (1994) Comparison of Upper Triassic and Lower Jurassic Gastropods from the Peruvian Andes (Pucará Group) and the Alps (Cassian Formation). *Palaeontographica*, Abteilung A, 233, 127–160.

Bandel, K. (2006) Families of the Cerithioidea and related superfamilies (Palaeo-Caenogastropoda; Mollusca) from the Triassic to the Recent characterized by protoconch morphology—including the description of new taxa. *Freiberger Forschungshefte*, *C*, 511, 59–138.

Bandel, K. (2007) Description and classification of Late Triassic Neritimorpha (Gastropoda, Mollusca) from the St Cassian Formation, Italian Alps. *Bulletin of Geosciences*, 83, 215–274.

https://doi.org/10.3140/bull.geosci.2007.03.215
Bandel, K. (2009) The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St. Cassian Formation with evaluation of the taxonomic value of the selenizone. *Berliner paläobiologische Abhandlungen*, 10, 5–47.
Bandel, K. (2010) Relationships of the Triassic Eucycloidea Koken, 1897 (Mollusca, Gastropoda) to modern genera such as *Pagodatrochus*, *Calliotropis* and *Euchelus*, based on morphology of the early shell. *Bulletin of Geosciences*, 85, 435–486. https://doi.org/10.3140/bull.geosci.1208
Bandel, K. & Frýda, J. (1999) Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. *Geologica et Palaeontologica*, 33, 219–235.
Batten, R.L. (1958) Permian Gastropoda of the southwestern United States. 2. Pleurotomariacea: Portlockiellidae, Phymatopleuridae, and Eotomariidae. *Bulletin of the American Museum of Natural History*, 114, 153–246.
Batten, R.L. (1964) Some Permian Gastropoda from Eastern Arizona. *American Museum Novitates*, 2165, 1–16.
Batten, R.L. (1966) The Lower Carboniferous gastropod fauna from the Hotwells Limestone of Compton Martin, Somerset, Part 1. *Palaeontographical Society Monographs*, 119, 1–52.
Batten, R.L. (1967) Thoughts on the genus *Ptychomphalina* Fischer 1887 and the family Eotomariidae Wenz, 1938. *Journal of Paleontology*, 41, 262–264.
Batten, R.L. (1972) Permian gastropods and chitons from Perak, Malaysia. Part 1. Chitons, bellerophontids, euomphalids and pleurotomarians. *Bulletin of the American Museum of Natural History*, 147, 1–44.
Batten, R.L. (1979) Permian gastropods from Perak, Malaysia. Part 2. The trochids, patellids, and neritids. *American Museum Novitates*, 2685, 1–26.
Batten, R.L. (1985) Permian gastropods from Perak, Malaysia. Part 3. The murchisoniids, cerithiids, loxonematids, and subulitids. *American Museum Novitates*, 2829, 1–40.
Batten, R.L. (1989) Permian Gastropoda of the southwestern United States. 7. Pleurotomariacea: Eotomariidae, Lophospiriidae, Gosseletinidae. *American Museum Novitates*, 2958, 1–64.
Batten, R.L. (1995) Pennsylvanian (Morrowan) gastropods from the Magdalena Formation of the Hueco Mountains, Texas. *American Museum Novitates*, 3122, 1–46.
Batten, R.L. & Stokes, W.L. (1986) Early Triassic gastropods from the Sinbad Member of the Moenkopi Formation, San Rafael Swell, Utah. *American Museum Novitates*, 2864, 1–33.
Begg, J.G. & Grant-Mackie, J.A. (2003) New Zealand and New Caledonian Triassic Pleurotomariidae (Gastropoda, Mollusca). *Journal of The Royal Society of New Zealand*, 33, 223–268. https://doi.org/10.1080/03014223.2003.9517729
Blaschke, F. (1905) Die Gastropodenfauna der Pachycardientuffe der Seiseralpe in Südtirol nebst einem Nachtrag zur Gastropodenfauna der roten Raibler Schichten vom Schlernplateau. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, 17, 161–221.
Blodgett, R.B., Frýda, J. & Stanley, G.D.J. (2001) Delphinulopsidae, a new neritopsoidean gastropod family from the Upper Triassic (upper Carnian or lower Norian) of the Wallowa terrane, northeastern Oregon. *Journal of the Czech Geological Society*, 46, 305–318.
Böhm, J. (1895) Die Gastropoden des Marmolatakalkes. *Palaeontographica*, 42, 211–308.
Bouchet, P., Lozouet, P., Maestrati, P. & Heros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, 75, 421–436. https://doi.org/10.1046/j.1095-8312.2002.00052.x
Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, 61, 1–526. https://doi.org/10.4002/040.061.0201
Broili, F. (1907) Die Fauna der Pachycardientuffe der Seiser Alp. Scaphopoden und Gastropoden. *Palaeontographica*, 54, 69–138.
Bronn, H.G. & Roemer, F. (1851–1856) *Lethaea Geognostica, oder Abbildungen und Beschreibungen der für die Gebirgs-formationen bezeichnendsten Versteinerungen*. Schweizerbart, Stuttgart, viii + 612 pp.
Chorowicz, J. & Termier, G. (1975) Une faunule silicifiée nouvell dans le Trias moyen de la Svilaja (Yougoslavie). *Annales de la Société Geologique du Nord*, 95, 231–242.
Chronic, H. (1952) Molluscan Fauna from the Permian Kaibab Formation, Walnut Canyon, Arizona. *Bulletin of the Geological Society of America*, 63, 95–166. https://doi.org/10.1130/0016-7606(1952)63[95:MFFTPK]2.0.CO;2
Cleevely, R.J. (1983) *World palaeontological collections*. British Museum (Natural History), 365 pp.
Conrad, T.A. (1835) Description of five new species of fossil shells in the collection presented by Mr. Edward Miller to the Geological Society. *Transactions of the Geological Society of Pennsylvania*, 1, 267–270.
Conti, M.A. & Fischer, J.C. (1981) Preliminary notes on the Aalenian Gastropods of Case Canepine (Umbria, Italy). *In:* Farinacci, A. & Elmi, S. (Ed.), *Rosso Ammonitico Symposium Proceedings*. Edizioni Tecnoscienza, Roma, pp. 137–145.
Conti, M.A & Monari, S. (2001) Middle Jurassic Gastropods from the Central High Atlas, Morocco. *Geobios*, 34, 183–214. https://doi.org/10.1016/S0016-6995(01)80060-7
Conti, M.A., Monari, S. & Szabó, J. (2004) An overview of the Jurassic gastropods from Rocca Busambra (north-western Sicily,

Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 110, 43–51.
Cossmann, M. (1897) Die Gastropoden der Trias um Hallstatt, von E. Koken (1). *Revue critique Paléozoologie*, 1, 139–143.
Cossmann, M. (1916) *Essais de Paléoconchologie comparée*. Chez l'auteur, Paris, 292 pp.
Cox, L.R. (1960) Thoughts on the classification of the Gastropoda. *Proceedings of the Malacological Society of London*, 33, 239–261.
Cox, L.R. & Knight, J.B. (1960) Suborders of Archaeogastropoda. *Proceeding of the Malcological Society*, 33, 262–264.
Cuvier, G. (1795) Second mémoire sur l'rorganisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordres, lu à la Société d'histoire naturelle de Paris, le 11 Prairial, an 3. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts*, 2, 433–449.
Dal Corso, J., Bernardi, M., Sun, Y., Song, H., Seyfullah, L.J., Preto, N., Gianolla, P., Ruffell, A., Kustatscher, E., Roghi, G., Merico, A., Hohn, S., Schmidt, A.R., Marzoli, A., Newton, R.J., Wignall, P.B. & Benton, M.J. (2020) Extinction and dawn of the modern world in the Carnian (Late Triassic). *Science Advances*, 6, eaba0099.
Dejean, P.F.M.A. (1836) *Catalogue des Coléoptères de la collection de M. le Comte Dejean. Livraison 5*. Méquignon-Marvis, Paris, pp. 443.
Deshayes, G.-P. (1824–1837) *Description des coquilles fossiles des environs de Paris, Tome 2*. l'Auteur, Baudouin, Be´chet, Treuttel, Paris, pp. pp. 1–80 (1824), pp. 81–162 (1825), pp. 163–290 (1832), pp. 291–429 (1833), pp. 430–494 (1834), pp. 495–780 (1835), pp. 781–814 (1837).
Diener, C. (1926) *Fossilium Catalogus, I Animalia, 34, Glossophora triadica*. W. Junk, Berlin, 242 pp.
Engeser, T.S. & Taylor, P.D. (1989) Supposed Triassic bryozoans in the Klipstein Collection from the Italian Dolomites redescribed as calcified demosponges. *Bulletin of the British Museum, Natural History*, Geology, 45, 39–55.
Erwin, D.H. (1990) Carboniferous-Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. *Paleobiology*, 16, 187–203.
https://doi.org/10.1017/S0094837300009878
Erwin, D.H. & Pan, H.-Z. (1996) Recoveries and radiations after the Permo-Triassic mass extinction. *In*: Hart, M.B. (Ed.), *Biotic recovery from mass extinction events. Geological Society Special Publication 102*. Geological Society of London, London, pp. 223–229.
https://doi.org/10.1144/GSL.SP.1996.001.01.15
Eudes-Deslongchamps, J.A. (1843) Mémoire sur les *Trochotoma*, nouveau genre de coquilles fossiles voisin des Pleurotomaires et appartenant, comme eux, aux terrains secondaires. *Mémoires de la Société linnéenne de Normandie*, 7, 99–110.
Eudes-Deslongchamps, M.E. (1863–1869) *Notes Paleontologiques*. Savy, Caen, Paris, 392 pp.
Ferrari, S.M. (2015) Systematic revision of Late Triassic marine gastropods from Central Peruì: considerations on the Late Triassic/Early Jurassic faunal turnover. *Andean Geology*, 42, 71–96.
Ferrari, S.M., Kaim, A. & Damborenea, S.E. (2014) The genera *Calliotropis Seguenza* and *Ambercyclus* n. gen. (Vetigastropoda, Eucyclidae) from the Early Jurassic of Argentina. *Journal of Paleontology*, 88, 1174–1188.
https://doi.org/10.1666/13-147
Ferrari, S.M., Damborenea, S.E., MancenÞido, M.O. & Griffin, M. (2015) Early Jurassic Trochotomidae (Vetigastropoda, Pleurotomarioidea) from the Neuqueìn Basin, Argentina. *Journal of Paleontology*, 89, 331–345.
https://doi.org/10.1017/jpa.2014.28
Finks, R.M. (1960) Late Paleozoic sponge faunas of the Texas region: the siliceous sponges. *Bulletin of the American Museum of Natural History*, 120, 1–160.
Fischer, J.-C. & Weber, C. (1997) *Révision Critique de la Paléontologie Francaise d'Alcide d'Orbigny (incluant la réédition de l'original). Vol. II. Gastropodes Jurassiques*. Muséum National d'Histoire Naturelle and Masson, Paris, 300 pp.
Fischer, P. (1880–1887) s.n. *In*: *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des molluscques vivants et fossiles*. *Vols. 1–10.* F. Savy, Paris, pp. 1–112, (1880), pp. 113–192 (1881), pp. 193–304 (1881), pp. 305–416 (1882), pp. 417–512 (1885), pp. 513–608 (1883), pp. 609–688 (1884), pp. 689–784 (1885), pp. 785–896 (1885), pp. 897–1008 (1886), pp. 1009–1369 (1887).
Flügel, E. (2002) Triassic Reef Patterns. *SEPM Special Publication*, 72, 391–463.
https://doi.org/10.2110/pec.02.72.0391
Foster, W.J., Danise, S. & Twitchett, R.J. (2017) A silicified Early Triassic marine assemblage from Svalbard. *Journal of Systematic Palaeontology*, 15, 851–877.
https://doi.org/10.1080/14772019.2016.1245680
Frýda, J. (1998) New Silurian and Devonian gastropod genera of Bohemia. *Earth Science (Chikyu Kagaku)*, 52, 229–234.
Frýda, J. & Blodgett, R.B. (1998) Two new cirroidean genera (Vetigastropoda, Archaeogastropoda) from the Emsian, (late Early Devonian) of Alaska with notes on the early phylogeny of Cirroidea. *Journal of Paleontology*, 72, 265–273.
https://doi.org/10.1017/S0022336000036271
Frýda, J., Blodgett, R.B., Lenz, A.C. & Manda, S. (2008) New Porcellioidean gastropods from Early Devonian of Royal Creek area, Yukon Territory, Canada, with notes on their early phylogeny. *Journal of Paleontology*, 82, 595–603.
https://doi.org/10.1666/07-024.1
Frýda, J., Ebbestad, J.O.R. & Frýdová, B. (2019) The oldest members of Porcellioidea (Gastropoda): a new link between Baltica and Perunica. *Papers in Palaeontology*, 5, 281–297.
https://doi.org/10.1002/spp2.1241

Fucini, A. (1913) Nuovo contributo alla conoscenza dei Gasteropodi Liassici della Montagna del Casale (Sicilia). *Palaeontographia Italica, Memorie di Paleontologia*, 19, 1–30.
Fürsich, F.T. & Wendt, J. (1977) Biostratinomy and Palaeoecology of the Cassian Formation (Triassic) of the Southern Alps. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 22, 257–323. https://doi.org/10.1016/0031-0182(77)90005-0
Gemmellaro, G.G. (1879) Sui fossili del calcare cristallino delle Montagne del Casale e di Bellampo nella provincia di Palermo. *Giornale di scienze naturali ed economiche*, 14, 157–223.
Gemmellaro, G.G. (1889) La Fauna dei calcari con Fusulina della valle del fiume Sosio nella Provincia di Palermo. *Giornale di Science Naturali ed Economiche*, 20, 97–182.
Giebel, C.G. (1852) *Deutschlands Petrefacten: Ein systematisches Verzeichniss aller in Deutschland und den angrenzenden Landern vorkommenden Petrefacten nebst Angabe der Synonymen und Fundorte*. Abel, Leipzig, 706 pp.
Goldfuss, G.A. (1841–1844) s.n. *In*: *Petrefacta Germaniae*. Arnz, Düsseldorf, pp. 1–20, pls. 166–171, (1841), pp. 21–28, pls. 172–195, (1844), pp. 29–128, pls. 196–200, (1844).
Golikov, A.N. & Starobogatov, Y.I. (1975) Systematics of prosobranch gastropods. *Malacologia*, 15, 185–232.
Gordon, M.J. & Yochelson, E.L. (1987) Late Mississippian Gastropods of the Chainman Shale, West-Central Utah. *U. S. Geological Survey Professional Paper*, 1368, 1–112. https://doi.org/10.3133/pp1368
Gray, J.E. (1828) *Spicilegia Zoologica; or original figures and short systematic descriptions of new and unfigured animals*. Treüttel, Würtz & Co., London, 12 pp.
Gray, J.E. (1847) A list of genera of Recent Mollusca, their synonyms and types. *Proceedings of the Zoological Society of London*, 15, 129–219.
Gründel, J. (2011) Die Ptychomphalidae WENZ, 1938, (Ptychomphaloidea, Gastropoda) im Jura. *Freiberger Forschungshefte*, C 539, 59–69.
Gründel, J., Keupp, H. & Lang, F. (2017) Die Arten der Patellogastropoda und Vetigastropoda (Gastropoda) aus den Korallenriffen des oberen Kimmeridgiums (oberer Jura) von Saal bei Kelheim und dem Gebiet Nattheim (Süddeutschland). *Zitteliana*, 89, 171–228.
Haas, O. (1953) Mesozoic invertebrate faunas of Peru. *Bulletin of the American Museum of Natural History*, 101, 1–328.
Häberle, D. (1908) Paläontologische Untersuchung triadischer Gastropoden aus dem Gebiet von Predazzo. *Verhandlungen des naturhistorisch-medizinischen Vereins zu Heidelberg*, 9, 247–631.
Hagdorn, H. (2011) Triassic: the crucial period of post-Palaeozoic crinoid diversification. *Swiss Journal of Palaeontology*, 130, 91–112. https://doi.org/10.1007/s13358-010-0009-9
Hall, J. & Clarke, J.M. (1888) *Palaeontology. Vol. VII. Text and plates. Containing descriptions of the trilobites and other Crustacea.* Benthuysen & Sons, Albany, 236 pp.
Hansen, T. (2019) Gastropods from the Cretaceous-Palaeogene boundary in Denmark. *Zootaxa*, 4654 (1), 1–196. https://doi.org/10.11646/zootaxa.4654.1.1
Harasewych, M.G. (2002) Pleurotomarioidean gastropods. *Advances in Marine Biology*, 42, 237–294. https://doi.org/10.1016/S0065-2881(02)42015-9
Hausmann, I.M. & Nützel, A. (2015) Diversity and palaeoecology of a highly diverse Late Triassic marine biota from the Cassian Formation of north Italy. *Lethaia*, 48, 235–255. https://doi.org/10.1111/let.12102
Hausmann, I.M., Nützel, A., Roden, V.J. & Reich, M. (2021) Palaeoecology of tropical marine invertebrate assemblages from the Late Triassic of Misurina, Dolomites, Italy. *Acta Palaeontologica Polonica*, 66, 143–192. https://doi.org/10.4202/app.00659.2019
Hickman, C.S. (1984) *Pleurotomaria*: Pedigreed perseverance? *In:* Eldredge, N. & Stanley, S.M. (Ed.), *Living Fossils*. Springer, New York, Berlin, Heidelberg and Tokyo, pp. 225–231.
Hörnes, M. (1855) Über die Gastropoden und Acephalen der Hallstätter Schichten. *Denkschriften der keiserlichen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Classe*, 9, 33–56.
Kaim, A. & Nützel, A. (2011) Dead bellerophontids walking—the short Mesozoic history of the Bellerophontoidea (Gastropoda). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 308, 190–199. https://doi.org/10.1016/j.palaeo.2010.04.008
Karapunar, B., Nützel, A., Seuss, B. & Mapes, R.H. (2021) Taxonomy and diversity of slit-band gastropods (order Pleurotomarida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA. *Papers in Palaeontology*. [in press]
Ketwetsuriya, C., Nützel, A. & Kanjanapayont, P. (2016) Permian gastropods from the Tak Fa Limestone, Nakhon Sawan, Northern Thailand. *Bulletin of Geosciences*, 91, 481–513. https://doi.org/10.3140/bull.geosci.1617
Ketwetsuriya, C., Karapunar, B., Charoentitirat, T. & Nützel, A. (2020) Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa*, 4766 (1), 1–47. https://doi.org/10.11646/zootaxa.4766.1.1
Kiel, S. & Bandel, K. (2000) New slit-bearing Archaeogastropoda from the Late Cretaceous of Spain. *Berliner geowissenschaftliche Abhandlungen*, Reihe E, 34, 269–277.

Kiener, L.C. (1834–50) *Spécies général et iconographie des coquilles vivantes, comprenant la collection du Muséum d'histoire naturelle de Paris, la collection Lamarck, celle du prince Masséna, (appartenant maintenant à m. le baron Benjamin Delessert), et les découvertes récentes des voyageurs: Genres Calcar, Trochus, Xenophora, Tectarius et Riscella*. Duménil and J. B. Baillière, Paris, 827 pls, 132 pp.
Kittl, E. (1891) Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. I. Theil. *Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums*, 6, 166–262.
Kittl, E. (1892) Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. II. Theil. *Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums*, 7, 35–97.
Kittl, E. (1894a) Die Gastropoden der Schichten von St. Cassian der südalpinen Trias. III. Theil. *Annalen des Kaiserlich-Königlichen Naturhistorischen Hofmuseums*, 9, 143–277.
Kittl, E. (1894b) Die triadischen Gastropoden der Marmolata und verwandter Fundstellen in den weißen Riffkalken Südtirols. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, 44, 99–182.
Kittl, E. (1899) Die Gastropoden der Esinokalke, nebst einer Revision der Gastropoden der Marmolatakalke. *Annalen des kaiserlich königlichen naturhistorischen Hofmuseums*, 14, 1–237.
Klein, J.T. (1753) *Tentamen methodi ostracologicae, sive Dispositio naturalis cochlidum et concharum in suas classes, genera et species, iconibus singolorum generum aeri incisis illustrata: Accedit lucubratiuncula de formatione, cremento et coloribus testarum quæ sunt cochlidum et concharum*. apud G.J. Wishoff, Lugduni Batavorum, 177 + 44 + 16 pp.
Klipstein, A. von (1843–1845) s.n. *In*: *Beitrag zur geologischen Kenntnis der östlichen Alpen*. G. F. Heyer's Verlag, Gießen, pp. 1–144, pls. 1–9 (1843), pp. 145–240, pls. 10–15 (1844), pp. 241–311, pls. 16–20 (1845).
Klompmaker, A.A., Nützel, A. & Kaim, A. (2016) Drill hole convergence and a quantitative analysis of drill holes in mollusks and brachiopods from the Triassic of Italy and Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 457, 342–359.
https://doi.org/10.1016/j.palaeo.2016.06.017
Knight, J.B. (1941) Palaeozoic Gastropod Genotypes. *Geological Society of America Special Papers*, 32, 1–510.
https://doi.org/10.1130/SPE32-p1
Knight, J.B. (1945) Some new genera of Paleozoic Gastropoda. *Journal of Paleontology*, 19, 573–587.
Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. (1960) Systematic descriptions. *In:* Moore, R.C. (Ed.) *Treatise on Invertebrate Paleontology. Part 1. Mollusca 1*. Geological Society of America and University of Kansas Press, Lawrence, Kansas, pp. I169–I310.
Koken, E. (1889) Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband*, 6, 440–463.
Koken, E. (1894) Die Gastropoden der Schichten mit Arcestes Studeri. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, 44, 441–458.
Koken, E. (1896) Die Gastropoden der Trias um Hallstatt. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt*, 46, 37–126.
Koken, E. (1897) Gastropoden der Trias um Hallstatt. *Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt*, 17, 1–111.
Kollarova-Andrusova, V. & Kochanova, M. (1973) *Die Molluskenfauna des Bleskovy pramen bei Drnava (Nor, Westkarpaten)*. Slovenskej Akademie vied, Bratislava, 1–215.
Koninck, L.G. de (1842–1844) *Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique*. H. Dessain, Liege, 636 pp.
Koninck, L.G. de (1883) Faune du calcaire carbonifère de la Belgique. Quatrième partie, Gastéropodes (suite et fin). *Annales du Musée Royal d´Histoire naturelle de Belgique*, 8, 1–240.
Körner, K. (1937) Marine (Cassianer-Raibler) Trias am Nevado de Acrotambo (Nord-Peru). *Paläontographica*, Abteilung A, 86, 145–237.
Kues, B.S. & Batten, R.L. (2001) Middle Pennsylvanian gastropods from the Flechado Formation, north-central New Mexico. *Journal of Paleontology*, 75 (Supplement to No 1), 1–95.
https://doi.org/10.1666/0022-3360(2001)75[1:MPGFTF]2.0.CO;2
Kutassy, E. (1937) Triadische Faunen aus dem Bihargebirge. 1. Gastropoden. *Geologica Hungarica Series Palaeontologica*, 13, 1–80.
Lamarck, J.B. (1804) *Mémoires sur les fossiles des environs de Paris*. Annales du Museum National d'Histoire Naturelle, Paris, 491 pp.
Laube, G.C. (1864) Bemerkungen über die Münster´schen Arten von St. Cassian in der Münchener paläontologischen Sammlung. *Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt*, 3, 1–11.
Laube, G.C. (1868) Die Fauna der Schichten von St. Cassian. III. Abtheilung. Gastropoden. I. Hälfte. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch- Naturwissenschaftliche Classe*, 28, 29–94.
Laube, G.C. (1870) Die Fauna der Schichten von St. Cassian. IV. Abtheilung. Gastropoden. II. Hälfte. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch- Naturwissenschaftliche Classe*, 30, 1–48.
Leonardi, P. & Fiscon, F. (1947) Nuove forme di gasteropodi della fauna Cassiana di Cortina d'Ampezzo. *Memorie del Museo di Storia Naturale della Venezia Tridentina*, 8 (3), 41–54.
Leonardi, P. & Fiscon, F. (1959) La fauna Cassiana di Cortina D'Ampezzo. *Memorie degli Istituti di Geologia e Mineralogia*

dell' Università di Padova, 11, 1–103.
Lindström, G. (1884) On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 19 (No. 6), 1–250.
Longstaff, J. (1912) Some new Lower Carboniferous Gasteropoda. *Quarterly Journal of the Geological Society*, 68, 295–309. https://doi.org/10.1144/GSL.JGS.1912.068.01-04.24
Marshall, B.A. (1991) Mollusca Gastropoda: Seguenziidae from New Caledonia and the Loyalty Islands. *Resultats des campagnes MUSORSTOM*, 7, 41–109.
Mazaev, A.V. (2006) Permian gastropods from Kulogory Formation of northern Moscow Syneclise. *Paleontological Journal*, 40, 42–53.
https://doi.org/10.1134/S0031030106040046
Mazaev, A.V. (2015) Upper Kazanian (Middle Permian) Gastropods of the Volga–Urals Region. *Paleontological Journal*, 49, 869–986.
https://doi.org/10.1134/S0031030115080018
Mazaev, A.V. (2019) Lower Permian Gastropods of Shakhtau (Asselian—Sakmarian Boundary Beds, Southern Cisuralia). *Paleontological Journal*, 53, 1237–1345.
https://doi.org/10.1134/S0031030119120025
Monari, S., Valentini, M. & Conti, M.A. (2011) Earliest Jurassic Patellogastropod, Vetigastropod, and Neritimorph Gastropods from Luxembourg with Considerations on the Triassic—Jurassic Faunal Turnover. *Acta Palaeontologica Polonica*, 56, 349–384.
https://doi.org/10.4202/app.2010.0098
Monari, S. & Gatto, R. (2013) *Pleurotomaria* Defrance, 1826 (Gastropoda, Mollusca) from the lower Bajocian (Middle Jurassic) sediments of Luxembourg, with considerations on its systematics, evolution and palaeobiogeographical history. *Palaentology*, 56, 751–781.
https://doi.org/10.1111/pala.12014
Monari, S., Gatto, R. & Valentini, M. (2017) Vetigastropoda and Neritimorpha from the Lower Bajocian of Luxembourg and palaeobiogeography of Aalenian–Bajocian (Middle Jurassic) gastropods of western Europe. *Journal of Systematic Palaeontology*, 16 (6), 449–492.
https://doi.org/10.1080/14772019.2017.1312578
Münster, G. zu (1834) Über das Kalkmergel-Lager von St. Cassian in Tyrol und die darin vorkommenden Ceratiten. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Peterfaktenkunde*, 1834, 1–15.
Münster, G. zu (1841) Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. *In*: Wissmann, H.L., Münster, G. zu & Braun, K.F. (Eds.), *Beiträge zur Geologie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian*. Buchner, Bayreuth, pp. 25–152.
Nützel, A. (1998) Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner geowissenschaftliche Abhandlungen Reihe E*, 26, 1–229.
Nützel, A. (2005) Recovery of gastropods in the Early Triassic. *Comptes Rendus Palevol*, 4, 501–515.
https://doi.org/10.1016/j.crpv.2005.02.007
Nützel, A. (2010) A review of the Triassic gastropod genus *Kittliconcha* Bonarelli, 1927–implications for the phylogeny of Caenogastropoda. *Zitteliana*, A50, 9–20.
Nützel, A. (2013) Revision of genus *Sabrinella* (Gastropoda) and a new minute vetigastropod from the Late Triassic Cassian Formation (N Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 269, 63–72.
https://doi.org/10.1127/0077-7749/2013/0335
Nützel, A. (2014) Larval ecology and morphology in fossil gastropods. *Palaeontology*, 57, 479–503.
https://doi.org/10.1111/pala.12104
Nützel, A. & Bandel, K. (2000) Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 9, 557–569.
https://doi.org/10.1127/njgpm/2000/2000/557
Nützel, A. & Erwin, D.H. (2004) Late Triassic (Late Norian) gastropods from the Wallowa Terrane (Idaho, USA). *Paläontologische Zeitschrift*, 78, 361–416.
https://doi.org/10.1007/BF03009231
Nützel, A. & Geiger, D.L. (2006) A new scissurelloid genus and species (Mollusca, Gastropoda) from the Late Triassic Cassian Formation. *Paläontologische Zeitschrift*, 80, 277–283.
https://doi.org/10.1007/BF02988441
Nützel, A. & Gründel, J. (2015) Early Jurassic (Pliensbachian) gastropods from Franconia, Southern Germany. *Palaeontographica*, Abteilung A, 1–89.
https://doi.org/10.1127/pala/305/2015/1
Nützel, A. & Kaim, A. (2014) Diversity, palaeoecology and systematics of a marine fossil assemblage from the Late Triassic Cassian Formation at Settsass Scharte, N Italy. *Paläontologische Zeitschrift*, 88, 405–431.
https://doi.org/10.1007/s12542-013-0205-1
Nützel, A., Kaim, A. & Grădinaru, E. (2018) Middle Triassic (Anisian, Bithynian) gastropods from North Dobrogea (Romania) and their significance for gastropod recovery from the end-Permian mass extinction event. *Papers in Palaeontology*, 4,

477–512.
https://doi.org/10.1002/spp2.1115
Nützel, A. & Mapes, R.H. (2001) Larval and juvenile gastropods from a Mississippian black shale: Paleoecology, and implications for the evolution of the Gastropoda. *Lethaia*, 34, 143–162.
https://doi.org/10.1080/00241160152418447
Nützel, A. & Nakazawa, K. (2012) Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology*, 10, 103–169.
https://doi.org/10.1080/14772019.2010.549659
Nützel, A. & Pan, H.-Z. (2005) Late Paleozoic evolution of the Caenogastropoda: larval shell morphology and implications for the Permian/Triassic mass extinction event. *Journal of Paleontology*, 79, 1175–1188.
https://doi.org/10.1666/0022-3360(2005)079[1175:LPEOTC]2.0.CO;2
Nützel, A. & Senowbari-Daryan, B. (1999) Gastropods from the Upper Triassic (Norian-Rhaetian) Nayband Formation of central Iran. *Beringeria*, 23, 93–132.
Orbigny, A.D. de (1850) *Prodrome de paléontologie stratigraphique universelle des animaux mollusques & rayonnés, faisant suite au Cours élémentaire de paléontologie et de géologie stratigraphiques*. *Tome 1*. V. Masson, Paris, 394 pp.
Perner, J. (1903) *Systême silurien du centre de la Bohême, par Joachim Barrande. 1ére partie: Recherches paléontologiques. Vol. 4. Gastéropodes. Tome 1*. Author, Prague, 164 pp.
Phillips, J. (1829) *Illustrations of the Geology of Yorkshire, or, A Description of the Strata and Organic Remains of the Yorkshire Coast: Accompanied by a Geological Map, Sections, and Plates of the Fossil Plants and Animals*. Wilson & Sons, York, 192 pp.
Phillips, J. (1841) *Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon and West Somerset*. Longman Brown, 231 pp.
Pieroni, V. (2019) The Norian *Worthenia*-like gastropods (Main Dolomite, Upper Triassic): reclassification of the specimens housed at the "Antonio Stoppani" Natural Museum, Italy. *Natural History Sciences*, 6, 37–40.
https://doi.org/10.4081/nhs.2019.398
Pieroni, V., Monari, S. & Todd, J.A. (2021) A new caenogastropod from the upper Rhaetian of Lombardy: Palaeobiogeographical history and implications for the Early Jurassic gastropod recovery. *Acta Palaeontologica Polonica*, 66, 193–206.
https://doi.org/10.4202/app.00792.2020
Quenstedt, F.A. (1856–1857) *Der Jura*. *1–4 Lfg*. Laupp & Siebeck, Tübingen, pp. 1–208, taf. 1–24 (July 1856), pp. 209–368, taf. 25–48, 1 Profiltafel [Lias] (December 1856), pp. 369–576, taf. 49–72, 1 Profiltafel [Brauner Jura] (April 1857), pp. I–VI + 57–842, taf. 73–100, 1 Profiltafel [Weißer Jura] (October 1857).
Quenstedt, F.A. (1881–1884) *Petrefaktenkunde Deutschlands, Erste Abteilung. Band 7. Gasteropoden*. Fues's, Leipzig, 867 pp.
Quenstedt, W. (1963) *Clavis bibliographica. Fossilium Catalogus I: Animalia. Pars 102*. W. Junk, s'Gravenhage, 118 pp.
Rafinesque, C.S. (1815) *Analyse de la nature, ou tableau de l'univers et des corps organisés*. Aux dépens de l'auteur, Palermo, 224 pp.
Reis, O.M. (1926) Die Fauna des Wettersteinkalks 3. Teil: Gastropoden, Bivalven, Brachiopoden, etc. *Geognostisches Jahresheft, Sonderabdruck*, 1926, 87–138.
Riedel, P. & Senowbari-Daryan, B. (1991) Pharetronids in Triassic Reefs. *In*: Reitner, J. & Keupp, H. (Eds.), *Fossil and Recent Sponges*. Springer-Verlag, Berlin, pp. 465–477.
https://doi.org/10.1007/978-3-642-75656-6_38
Rigo, M., Preto, N., Roghi, G., Tateo, F. & Mietto, P. (2007) A rise in the Carbonate Compensation Depth of western Tethys in the Carnian (Late Triassic): Deep-water evidence for the Carnian Pluvial Event. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 246, 188–205.
https://doi.org/10.1016/j.palaeo.2006.09.013
Roden, V.J., Hausmann, I.M., Nützel, A., Seuss, B., Reich, M., Urlichs, M., Hagdorn, H. & Kiessling, W. (2020) Fossil liberation: a model to explain high biodiversity in the Triassic Cassian Formation. *Palaeontology*, 63, 85–102.
https://doi.org/10.1111/pala.12441
Romano, C., Koot, M.B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., Bucher, H. & Kriwet, J. (2016) Permian-Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biological Reviews*, 91, 106–147.
https://doi.org/10.1111/brv.12161
Ryckholt, P.d. (1860) Revue des genres qui composent la famille des Haliotidae, d'Orbigny. *Journal de Conchyliologie*, 2e Série, 4, 183–188.
Sachariewa-Kowatschewa, K. (1962) Die Trias von Kotel (Ost-Balkan). II. Teil. Scaphopoden und Gastropoden. *Annuaire de l'Université de Sofia, Faculté de Biologie, Géologie et Géographie*, Livre 2, Géologie, 55, 91–140.
Salvador, R.B., Cavallari, D.C. & Simone, L.R. (2014) Seguenziidae (Gastropoda: Vetigastropoda) from SE Brazil collected by the Marion Dufresne (MD55) expedition. *Zootaxa*, 3878 (6), 536–550.
https://doi.org/10.11646/zootaxa.3878.6.2
Salvini-Plawen, L.v. (1980) A reconsideration of systematics in the Mollusca. *Malacologia*, 19, 249–278.
Scalia, S. (1909) Il gruppo del Monte Judica. *Bollettino della Societaì geologica italiana*, 28, 269–340.
Scalia, S. (1914) La fauna del Trias superiore del gruppo di Monte Judica, Parte III. *Atti della Accademia gioenia di scienze*

naturali in Catania, Serie V, 7, Memoria XXIV, 1–25.
Schindel, D.E. (1982) Punctuations in the Pennsylvanian evolutionary history of *Glabrocingulum* (Mollusca: Archaeogastropoda). *Geological Society of America Bulletin*, 93, 400–408.
https://doi.org/10.1130/0016-7606(1982)93%3C400:PITPEH%3E2.0.CO;2
Schnetzer, R. (1934) Die Muschelkalkfauna des Öfenbachgrabens bei Saalfelden. *Palaeontographica*, Abteilung A, 81, 1–159.
Schwardt, A. (1992) Revision der *Wortheniella*-Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten). *Annalen des Naturhistorischen Museums Wien*, Serie A, 94, 23–57.
Senowbari-Daryan, B. (1991) „Sphinctozoa": An Overview. *In:* Reitner, J. & Keupp, H. (Eds.), *Fossil and Recent Sponges*. Springer-Verlag, Berlin, pp. 224–242.
Simms, M.J. & Ruffell, A.H. (1989) Synchroneity of climatic change and extinctions in the Late Triassic. *Geology*, 17, 265–268.
https://doi.org/10.1130/0091-7613(1989)017%3C0265:SOCCAE%3E2.3.CO;2
Skwarko, S.K. (1967) First Upper Triassic and ?Lower Jurassic marine Mollusca of New Guinea. *Bulletin Bureau of Mineral Resources, Geology and Geophysics, Ministry of National Development, Commonwealth of Australia*, 75, 38–83.
Sowerby, J. (1812–1821) *The Mineral Conchology of Great Britain*. *I–IV*. B. Meredith, London, pp. i–vii + 9–236, pls. 1–102 (1812–1814), pp. 1–239, pls. 103–203 (1815–1818), pp. 1–186, pls. 204–306 (1818–1821), pp. 1–104, pls. 307–327 (1821–1822).
Stiller, F. (2001) Fossilvergesellschaftungen, Paläoökologie und paläosynökologische Entwicklung im Oberen Anisium (Mittlere Trias) von Qingyan, insbesondere Bangtoupo, Provinz Guizhou, Südwestchina. *Münstersche Forschungen zur Geologie und Paläontologie*, 92, 1–523.
Stoppani, A. (1858–60) Les pétrifications d'Ésino, ou Description des fossiles appartenant au dépôt triasique supérieur des environs d'Ésino en Lombardie. Joseph Bernardoni, Milan, 151 pp.
Stoppani, A. (1860–1865) Géologie et paléontologie des couches à *Avicula contorta* en Lombardie, comprenant des aperçus sur l'étage infraliasien en Lombardie et en Europe en général, et deux monographies des fossiles appartenant à la zone supérieure et à la zone inférieure des couches à *Avicula contorta* en Lombardie, une note supplémentaire. Joseph Bernardoni, Milan, 267 pp.
Strand, E. (1928) Miscellanea nomenclatorica zoologica et palaeontologica: I–II. *Archiv für Naturgeschichte*, 92A, 30–75.
Sturgeon, M.T. (1964) New Descriptions of Hitherto Inadequality known Pennsylvanian Gastropods. *Journal of Paleontology, reprint*, 38, No. 4, 739–748.
Swainson, W. (1840) *A treatise on malacology; or the natural classification of shells and shell-fish*. Printed for Longman, Orme, Brown, Green & Longmans, London, 419 pp.
Szabó, J. (1980) Lower and Middle Jurassic Gastropods from the Bakony Mountains (Hungary) Part 2. Pleurotomariacea and Fissurellacea (Archaeogastropoda). *Annales Historico-Naturales Musei Nationalis Hungarici*, 72, 49–71.
Szabó, J., Conti, M.A., Monari, S. & Wendt, J. (2019) Gastropods from the Jurassic neptunian sills of Rocca Busambra (north□ western Sicily, Italy): Patellogastropoda, Pleurotomarioidea, Scissurelloidea, Fissurelloidea and Eucycloidea. *Papers in Palaeontology*, 7 (Part 1), 27–110.
https://doi.org/10.1002/spp2.1258
Thomas, E.G. (1940) Revision of the Scottish Carboniferous Pleurotomariidae. *Geological Society of Glasgow Transactions*, 20, 30–72.
https://doi.org/10.1144/transglas.20.1.30
Tichy, G. (1980) Gastropoden als Leitfossilien? *Geologisch Paläontäontologische Mitteilungen Innsbruck*, 9, 239–261.
Tomlin, J.R.L.B. (1930) *Some preoccupied generic names.—II*. Journal of Molluscan Studies, 19, 22–24.
https://doi.org/10.1093/oxfordjournals.mollus.a064001
Tomlin, J.R.L.B. (1931) *Some preoccupied generic names.—III*. Journal of Molluscan Studies, 19, 174–175.
Tong, J. & Erwin, D.H. (2001) Triassic Gastropods of the Southern Quinling Mountains, China. *Smithsonian Contribution to Paleobiology*, 92, 1–47.
https://doi.org/10.5479/si.00810266.92.1
Toula, F. (1896) Eine Muschelkalkfauna am Golfe von Ismîd in Kleinasien. *Beiträge zur Paläontologie Oesterreich-Ungarns und des Orients*, 10, 153–190.
Ulrich, E.O. & Scofield, W.H. (1897) The lower Silurian Gastropoda of Minnesota. *The Geology of Minnesota: Paleontology*, 3, 813–1081
Urlichs, M. (2012) Stunting in some invertebrates from the Cassian Formation (Late Triassic, Carnian) of the Dolomites (Italy). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 265, 1–25.
https://doi.org/10.1127/0077-7749/2012/0241
Urlichs, M. (2017) Revision of some stratigraphically relevant ammonoids from the Cassian Formation (latest Ladinian-Early Carnian, Triassic) of St. Cassian (Dolomites, Italy). *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 283, 173–204.
https://doi.org/10.1127/njgpa/2017/0635
Verrill, A.E. (1884) Second catalogue of Mollusca recently added to the fauna of the New England coast and the adjacent part of the Atlantic, consisting mostly of deep-sea species, with notes on others previously recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 6, 139–194.

https://doi.org/10.5962/bhl.part.7412
Volz, W. (1896) Die Korallenfauna der Trias. II. Die Korallen der Schichten von St. Cassian in Süd-Tirol. *Palaeontographica*, 43, 1–123.
Walker, F. (1855) *List of the Specimens of Lepidopterous Insects in the Collection of the British Museum, Part IV.–Lepidoptera Heterocera*. Order of the Trustees, London, 777–1507 pp.
Wang, H. & Xi, Y. (1980) Late Permian and Early Triassic gastropods of western Guizhou. *In:* Nanking Institute of Geology and Palaeontology, Academia Sinica (Ed.), *Stratigraphy and palaeontology of Upper Permian coal bearing Formation in Western Guizhou and Eastern Yunan, China*. Science Press, Beijing, pp. 195–232.
Wanner, C. (1942) Neue Beiträge zur Gastropoden-Fauna des Perm von Timor. *In: Geological Expedition of the University of Amsterdam to the Sund Islands*. N.V. Noord-Hollandsche Uitgevers Maatschappij, Amsterdam, pp. 137–203.
Wenz, W. (1938–1944) Gastropoda. Teil I: Allgemeiner Teil und Prosobranchia. *In: Handbuch der Palaozoologie*. Gebrüder Borntraeger, Berlin, xii + 1639 pp.
Woodward, B.B. (1892) Mollusca. *Zoological Record*, 28, 1–114.
Wu, Y.-S. & Fan, J.-S. (2002) Permian-Triassic history of reefal thalamid sponges: evolution and extinction. *Acta Palaeontologica Sinica*, 41, 163–177.
Yin, H.-F. & Yochelson, E.L. (1983a) Middle Triassic Gastropoda from Qingyan, Guizhou Province, China: 1—Pleurotomariacea and Murchisoniacea. *Journal of Paleontology*, 57, 162–187.
Yin, H.-F. & Yochelson, E.L. (1983b) Middle Triassic Gastropoda from Qingyan, Guizhou Province, China: 3—Euomphalacea and Loxonematacea. *Journal of Paleontology*, 57, 1098–1127.
Yonge, C.M. (1947) The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 232, 443–518.
Yonge, C.M. (1973) Observation of the pleurotomarid *Entemnotrochus adansoniana* in its natural habitat. *Nature*, 241, 66–68. https://doi.org/10.1038/241066a0
Yoo, E.K. (1994) Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. *Records of the Australian Museum*, 46, 63–110. https://doi.org/10.3853/j.0067-1975.46.1994.18
Yu, W., Pan, H.-Z. & Wang, H. (1974) s.n. *In*: *A Handbook of the Stratigraphy and Palaeontology in Southwest China. Triassic—Gastropods*. Publishing House of Science, Beijing, pp. 320–326.
Zardini, R. (1978) *Fossili Cassiani (Trias Medio-Superiore) Atlante dei Gastropodi della formazione di S. Cassiano raccolti nella regione Dolomitica attorno a Cortina D'Ampezzo.* Edizioni Ghedina Cortina, Cortina D'Ampezzo, 58 pp.
Zardini, R. (1980) *Fossili Cassiani (Trias Medio-Superiore) primo aggiornamento all'Atlante dei Gasteropodi della formazione di S. Cassiano raccolti nella regione Dolomitica attorno a Cortina D'Ampezzo.* Edizioni Ghedina Cortina, Cortina D'Ampezzo, 16 pp.
Zardini, R. (1985) *Fossili Cassiani (Trias Medio-Superiore): primo aggiornamento all'Atlante dei bivalvi, e secondo aggiornamento all'Atlante dei gasteropodi, con illustrazioni dei gusci che hanno conservato la pigmentazione originaria: fossili raccolti nella formazione di S. Cassiano della regione dolomitica attorno a Cortina d'Ampezzo*. Edizioni Ghedina Cortina, Cortina D'Ampezzo, 17 pp.
Zieten, C.H. von (1830) s.n. *In*: *Die Versteinerungen Württembergs, oder naturgetreue Abbildungen der in den vollständigsten Sammlungen, namentlich der in dem Kabinet des Oberamts-Arzt Dr. Hartmann befindlichen Petrefacten, mit Angabe der Gebirgs-Formationen, in welchen dieselben vorkommen und der Fundorte.* Verlag & Lithograohie der Expedition des Werkes unserer Zeit, Stuttgart, pp. i–viii + 1–16, taf. 1–12 (1830), pp. 17–32, taf. 13–24 (1831), pp. 33–64, taf. 25–48 (1832), pp. 65–102, taf. 49–72 (1833).
Zittel, K.A. von (1881–1885) *Handbuch der Palaeontologie 1. Abtheilung Palaeozoologie, 2. Band Mollusca und Arthropoda*. von R. Oldenbourg, München and Leipzig, 893 pp.
Zittel, K.A. von (1895) *Grundzüge der Paläontologie (Paläozoologie), I Abteilung, Invertebrata*. Oldenbourg, München and Leipzig, 971 pp.

APPENDIX

S1. Pleurotomariida species from the St. Cassian Formation.

Taxon name	Synonyms
Acutitomaria kustatshcherae **gen. et sp. nov.**	
Amplitomaria spuria (Münster, 1841)	*Pleurotomaria concinna* Klipstein, 1844
Amplitomaria bilineata (Klipstein, 1844)	*Ptychomphalus neumayri* Kittl, 1891
Bandelium campense (Zardini, 1980)	
Bandelium ruedigeri (Schwardt, 1992)	
Cancellotomaria subcancellata (d'Orbigny, 1850)	*Pleurotomaria bittneri* Kittl, 1891
Cassianocirrus contrarius (Braun in Münster, 1841)	
Codinella zardini Bandel, 1991	
Euryalox subornatus (d'Orbigny, 1850)	*Trochus ornatus* Klipstein, 1844; *Trochus splendidus* Giebel, 1852
Kittlidiscus bronni (Klipstein, 1844)	*Pleurotomaria plana* Klipstein, 1844; *Solarium planum* Laube, 1868
Kittlidiscus substriatus (Klipstein, 1844)	*Schizodiscus planus* var. *elevata* Kittl, 1891
Kokenella buchi (Münster, 1841)	
Kokenella costata (Münster, 1841)	
Kokenella klipsteini Kittl, 1891	
Kokenella laubei Kittl, 1891	
Lancedellia costata (Zardini, 1978)	
Lineacingulum cassianum (Kittl, 1891)	
Lineacingulum texturatum (Münster, 1841)	*Pleurotomaria amalthea* Klipstein, 1844
Lineaetomaria decorata (Münster, 1841)	*Pleurotomaria triton* d'Orbigny, 1850; *Worthenia duplicata* Kittl, 1891
Nodocingulum bieberi (Kittl, 1891)	*Ptychomphalus*? *palaeopsis* Kittl, 1891
Nodocingulum cirriformis (Laube, 1870)	
Nodocingulum coronatum (Münster, 1841)	
Nodocingulum crenatum (Münster, 1841)	
Nodocingulum ernstkittli **sp. nov.**	
Nodocingulum furcatum (Kittl, 1891)	*Pleurotomaria beaumonti* Klipstein, 1844
Nodocingulum granulosum (Klipstein, 1844)	
Nodocingulum johannisaustriae (Klipstein, 1844)	*Pleurotomaria gracilis* Klipstein, 1844; *Worthenia dregeri* Kittl, 1891
Nodocingulum muensteri (Klipstein, 1844)	*Worthenia coronata* var. *plicosa* Kittl, 1891
Nodocingulum subcoronatum (Münster, 1841)	*Worthenia coronata* var. *ventricosa* Kittl, 1891
Nodocingulum? *angulatum* (Münster, 1841)	*Turbo pleurotomarioides* d'Orbigny, 1850
Nodocingulum? *subtilis* (Kittl 1891)	
Nodocingulum? *turris* **sp. nov.**	
Pressulasphaera pamphilus (d'Orbigny, 1850)	*Pleurotomaria calypso* Laube, 1868
Proteomphalus gracilis (Read in Broili, 1907)	
Proteomphalus protei (Münster, 1841)	
Pseudoananias subgranulata (Münster, 1841)	*Pleurotomaria meyeri* Klipstein, 1844; *Turbo salinarius* d'Orbigny, 1850
Pseudowortheniella rarissima (Kittl, 1891)	*Worthenia misurinensis* Zardini, 1985
Rhaphistomella radians (Wissmann, 1841)	*Solarium subpunctatum* Klipstein, 1844; *Euomphalus studeri* Klipstein, 1844

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S1. (Continued)

Taxon name	Synonyms
Rinaldoella rinaldoi (Schwardt, 1992)	
Rinaldoella tornata **sp. nov.**	
Rufilla fasciolata (Münster, 1841)	
Rufilla latizonata (Laube, 1868)	
Rufilla? *distincta* (Kittl, 1894)	
Schizogonium ampezzanum Bandel, 1991	
Schizogonium elevatum Kittl, 1891	*Schizogonium tetraptychum* Kittl, 1891
Schizogonium impressum Kittl, 1891	
Schizogonium laubei Kittl, 1891	
Schizogonium scalare (Münster, 1841)	*Trochus subscalaris* d'Orbigny, 1850
Schizogonium serratum (Münster, 1841)	
Schizogonium staolinensis Zardini, 1978	
Schizogonium subcostatum (Münster, 1841)	*Trochus timeus* d'Orbigny, 1850
Schizogonium subdentatum (Münster, 1841)	
Schizogonium subnodosum Zardini, 1978	*Schizogonium lamellosum* Bandel, 1991
Schizogonium tamarinum Bandel, 1991	
Schizogonium undae sp nov.	
Schizogonium? *bicarinata* (Klipstein, 1844)	
Sisenna ampezzana Leonardi & Fiscon, 1959	
Sisenna venusta (Münster, 1841)	*Pleurotomaria credneri* Klipstein, 1844; *Trochus salus* d'Orbigny, 1850
Striacingulum cancellatocingulata (Klipstein, 1844)	*Worthenia turriculata* Kittl, 1891; *Worthenia arthaberi* Blaeschke, 1905
Striacingulum toulai (Kittl, 1891)	
Stuorella costalaricensis Leonardi & Fiscon, 1959	
Stuorella subconcava (Münster, 1841)	*Trochus maximiliani leuchtenbergensis* Klipstein, 1844
Stuorella tofanae Leonardi & Fiscon, 1959	
Stuorella tricarinata (Klipstein, 1844)	*Sigaretus tenuicinctus* Klipstein, 1844
Temnotropis bicarinata Laube, 1870	
Temnotropis carinata (Münster, 1841)	
Temnotropis fuchsi Kittl, 1891	
Trochotoma fallax (Kittl, 1891)	
Wortheniella canalifera (Münster, 1841)	*Pleurotomaria subplicata* Klipstein, 1844; *Pleurotomaria subpunctata* Klipstein, 1844; *Trochus mineus* d'Orbigny, 1850
Wortheniella coralliophila (Kittl, 1891)	
Wortheniella klipsteini **sp. nov.**	
Wortheniella paolofedelei **sp. nov.**	
Wortheniella tenera Schwardt, 1992	
Wortheniella? *liebeneri* (Laube, 1869)	
Wortheniella? *margaritacea* (Laube, 1869)	
Zardinicirrus sinistralis Bandel, 1993	
Zygites subcancellata (d'Orbigny, 1850)	*Delphinula*? *cancellata* Klipstein, 1844; *Pleurotomaria delphinula* Laube, 1868

S2. Pleurotomariida genera occurred in the Permian and the Triassic.

Permian pleurotomariidan genera	Triassic pleurotomariidan genera
Aclisina de Koninck, 1881	*Acutitomaria* **gen. nov.**
Agnesia de Koninck, 1883	*Amplitomaria* **gen. nov.**
Altotomaria Ketwetsuriya *et al*., 2020	*Ananias* Knight, 1954
Ambozone Batten, 1972	*Bandelium* Schwardt, 1992
Ananias Knight, 1945	*Cancellotomaria* **gen. nov.**
Apachella Winters, 1956	*Cassianocirrus* Bandel, 1993
Arribazona Kues, 1990	*Cirrus* Sowerby, 1815
Austroscalata Waterhouse, 1987	*Codinella* Kittl, 1899
Baylea de Koninck, 1883	*Dictyotomaria* Knight, 1945
Bellazona Gordon & Yochelson, 1987	*Discocirrus* Ammon, 1892
Biarmeaspira Mazaev, 2006	*Discotoma* Haber, 1934
Bicarinella Waterhouse, 1966	*Enantiostoma* Koken, 1896
Borestus Thomas, 1940	*Euryalox* Cossmann, 1897
Bradyospira Batten, 1964	*Euzone* Koken, 1896
Callistadia Knight, 1845	*Eymarella* Cossmann, 1897
Callitomaria Batten, 1956	*Glabrocingulum* Thomas, 1940
Collabrina Waterhouse, 1978	*Gosseletina* Bayle, 1885
Dictyomaria Knight, 1945	*Guizhouspira* Wang, 1980 in Wang & Xi
Discotomaria Batten, 1956	*Hamusina* Gemmellaro, 1878
Eirlysia Batten, 1956	*Hesperocirrus* Haas, 1953
Euconospira Ulrich in Ulrich and Scofield, 1897	*Humiliworthenia* Yin & Yochelson, 1983
Fetaspira Mazaev, 2015	*Kamupena* Speden in Gair *et al*., 1962
Glabrocingulum Thomas, 1940	*Kittlidiscus* Haas, 1953
Globodoma Mazaev, 2006	*Kokenella* Kittl, 1891
Glyphodeta Donald, 1895	*Lancedellia* Bandel, 1991
Glyptomaria Knight, 1945	*Lineacingulum* **gen. nov.**
Gosseletina Fischer, 1885	*Lineatomaria* **gen. nov.**
Guizhouspira Wang, 1980	*Luciella* de Koninck, 1883
Helicospira Girty, 1915	*Luciellina* Kittl, 1900
Hesperiella Holzapfel, 1889	*Mamoeatomaria* Begg & Grant-Mackie, 2006
Juvenispira Mazaev, 2015	*Mellarium* Waterhouse, 1960
Lacunospira Batten, 1956	*Mourlonia* de Koninck, 1883
Lamellospira Batten, 1958	*Murchisonia* d'Archiac & Verneuil, 1841
Luciella de Koninck, 1883	*Murihikua* Begg & Grant-Mackie, 2003
Luciellina Kittl, 1900	*Nodocingulum* **gen. nov.**
Manzanospira Batten, 1989	*Ornatospira* Pan, 1982
Micheliopsis Termier & Termier, 1977	*Pareuryalox* Haas, 1953
Montospira Maxwell, 1964	*Pleurotomaria* Defrance, 1826
Mourlonia de Koninck, 1883	*Pressulasphaera* **gen. nov.**
Mourlonopsis Fletcher, 1958	*Proteomphalus* Gründel, 2011
Murchisonia d'Archiac & de Verneuil, 1841	*Pseudoananias* **gen. nov.**
Neilsonia Thomas, 1940	*Pseudomurchisonia* Koken, 1896
Nipponomaria Asato and Kase, 2016	*Pseudoschizogonium* Kutassy, 1937
Pandospira Waterhouse, 1963	*Pseudowortheniella* Bandel, 2009

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S2. (Continued)

Permian pleurotomariidan genera	Triassic pleurotomariidan genera
Paragoniozona Nelson, 1947	*Ptychomphalus* Agassiz, 1839
Perakella Mazaev, 2019	*Rasatomaria* Pieroni & Nützel, 2014
Permoconcha Likharev, 1967	*Rhaphistomella* Kittl, 1891
Pernotrochus Chronic, 1952	*Rinaldoella* Bandel, 2009
Peruvispira J. Chronic, 1949	*Rufilla* Koken, 1896
Phymatopleura Girty, 1939	*Schizogonium* Koken, 1889
Platyteichum Campbell, 1953	*Sisenna* Koken, 1896
Platyworthenia Chronic, 1952	*Sororcula* Haas, 1953
Plocostoma Gemmellaro, 1889	*Striacingulum* **gen. nov.**
Porcellia Leveille, 1835	*Stuorella* Kittl, 1891
Pseudobaylea Dickins, 1963	*Tahua* Begg & Grant-Mackie, 2003
Pseudophorus Meek, 1873	*Talantodiscus* Fischer, 1885
Ptychomphalina Fischer, 1885	*Temnotropis* Laube, 1870
Sallya Yochelson, 1956	*Trachybembix* Böhm, 1895
Schwedagonia Batten, 1956	*Transylvanella* Kutassy, 1937
Shansiella Yin, 1932	*Trochotoma* Eudes-Deslongchamps, 1843
Shedhornia Kulas & Batten, 1997	*Wannerispira* Kaim & Nützel, 2010
Shwedagonia Batten, 1956	*Worthenia* de Koninck, 1883
Sokella Mazaev, 2017	*Wortheniella* Schwardt, 1992
Spiraculinella Waterhouse, 1987	*Wortheniopsis* Böhm, 1895
Spiroscala Knight, 1945	*Zardinicirrus* Bandel, 1993
Spirovallum Waterhouse, 1963	*Zygites* Kittl, 1891
Stenozone Batten, 1972	
Takfaia Nützel & Ketwetsuriya, 2016	
Tapinotomaria Batten, 1956	
Termihabena Mazaev, 2019	
Trepospira Ulrich & Scofield, 1897	
Triredimiculum Waterhouse, 1983	
Walnichollsia Fletcher, 1958	
Wannerispira Kaim & Nützel, 2010	
Woolnoughia Dickins, 1963	
Worthenia de Koninck, 1883	

S3. Species diversity and relative abundance of Pleurotomariida in different assemblages from the Pennsylvanian to the Norian. Samples from the Tethys Ocean are given in white background, samples from the Panthalassa Ocean are given in gray background.

	Taxonomic composition	Relative Abundance	Sample size	Palaeoenvironment
Norian-Rhaetian, Iran (Nützel & Senowbari-Daryan 1999)	0.07	0.06	288	reefal limestone
Norian, Idaho (Nützel & Erwin 2001)	0.08	0.04	1954	reefal limestone
Norian, Peru (Haas 1953)	0.14	0.02	16456	gray bituminous limestone
Carnian, Italy (Hausmann & Nützel 2015)	0.08	0.04	54	basin marl and reefal limestone
Carnian, Italy (Zardini 1978)	0.15	0.14	1396	shallow subtidal, poorly lithified marl
Anisian, Guizhou, China (Yin & Yochelson 1983a-c)	0.32	0.35	150	pre-biohermal facies, shale and marl
Anisian, Romania (Nützel *et al*. 2018)	0.38	0.33	112	shallow marine, reefal limestone
Scythian, Utah (Batten & Stokes 1986)	0.08	0.09	1089	shallow subtidal, lagoon, packstone
Capitanian, Japan (Nützel & Nakazawa 2012)	0.08	0.01	2256	shallow subtidal, packstone
Roadian, Thailand (Ketwetsuriya *et al*. 2020)	0.23	0.10	221	shallow marine, carbonate platform
Roadian, Ural-Volga (Mazaev 2015)	0.38	0.46	1713	shallow subtidal, grainstone
Kungurian, Malaysia (Batten 1972, 1979, 1985)	0.25	0.24	916	shallow subtidal, limestone
Desmoinesian, New Mexico (Kues & Batten 2001)	0.29	0.35	14157	shallow marine, poorly lithified shale
Morrowan, Texas (Batten 1995)	0.44	0.42	2223	basin margin, offshore, cherty limestone

CHAPTER 6

Karapunar, B., & Nützel, A. (in prep.) Estimation of phylogeny of Pleurotomariida (Gastropoda) by using Parsimony and Bayesian methods.

Estimation of phylogeny of Pleurotomariida (Gastropoda) by using Parsimony and Bayesian methods

Baran Karapunar & Alexander Nützel

Abstract

To date, inference of evolutionary relationships of fossil gastropods are largely based on traditional systematic and taxonomic works. Quantitative phylogenetic analyses of fossil gastropods are lacking except of few studies and the phylogenetic relationships between the extinct and extant groups are commonly unresolved. Here we reconstruct phylogeny of Pleurotomariida (slit shells). Pleurotomariida is a gastropod group with the longest fossil record among living gastropods and one of the most diverse groups among Palaeozoic gastropods. Parsimony and Bayesian (Fossilized Birth Death (FBD) model) analyses are performed by using 93 morphological shell characters comprising 109 pleurotomariidan species representing 80 genera ranging from the Ordovician to the Recent. Parsimony analysis failed to reconstruct stratigraphically congruent trees and many nodes have a poor support. The FBD method incorporates the stratigraphic ranges of taxa for tree reconstruction. According to the Bayesian (FBD) phylogeny, Pleurotomariida split into three distinct lineages during the Devonian: Porcelliides, Pleurotomariini and Wortheniellini. Among them, Pleurotomariini and Wortheniellini survived the mass extinction at the end Permian. Although Wortheniellini showed a higher proliferation during the recovery in the Triassic, only Pleurotomariini could survive until today, suggesting that the resilience to extinctions did not depend on diversification dynamics of this clade. FBD tree further indicates that groups that are restricted to the Triassic originated during the Permian although fossil evidence form the Permian is lacking.

Introduction

Gastropoda is the largest molluscan class (86,717 species, MolluscaBase December 2021) representing one of the most diverse animal clades both, in Recent marine environments (e.g., Bouchet et al. 2002) and during the Phanerozoic (e.g., Sepkoski 1981). The early evolutionary history of Gastropoda is dominated by extinct gastropod groups (e.g., Koken 1889; Frýda et al.

2008), which were eventually replaced by groups that persisted today (e.g., Tracey et al. 1993). Reconstructing the phylogenetic relationships between extinct gastropod groups and between extinct and extant groups are major challenges. The phylogenetic relationships between the Palaeozoic and the Mesozoic gastropod lineages and their relationship to the modern lineages have not yet been resolved (Frýda et al. 2008). Most of the putative fossil record of the living gastropod groups (e.g., the basal gastropod clade Patellogastropoda) extends back to the Triassic (Frýda 2012), and most Palaeozoic groups got extinct either at the end-Permian mass extinction or shortly afterwards (Tracey et al. 1993). Pleurotomariida is the only living gastropod clade with a fossil record extending back to the Ordovician and Cambrian Periods (e.g., Knight et al. 1960; Wagner 2002). Pleurotomariida reached its peak generic diversity during middle to late Palaeozoic (Hickmann 1984) and represented one of the most diverse and abundant gastropod groups in the Late Palaeozoic and Early Mesozoic (Erwin 1990; Karapunar & Nützel 2021; Karapunar et al. 2022). In molecular phylogenies, Pleurotomariida are recovered as sister group to all other Vetigastropoda and as basal offshoot of living Gastropoda (Harasewych et al. 1997; Geiger & Thacker 2005; Williams & Ozawa 2006; Zapata et al. 2014; Cunha et al. 2021). A phylogenetic analysis of early Palaeozoic gastropods suggests, however, that Pleurotomariida is a derived clade (Wagner 2002). No comprehensive quantitative phylogenetic analysis involving a wide range of gastropods throughout the Phanerozoic has been conducted so far. The present contribution is the first phylogenetic analysis combining Palaeozoic and Mesozoic gastropods and the first attempt to reconstruct the phylogeny of Pleurotomariida with quantitative phylogenetic methods.

The knowledge of evolutionary relationships between the pleurotomariid genera is largely based on systematic and taxonomic studies. The last comprehensive compilations of pleurotomariidan genera were published by Wenz (1938–1944) and Knight et al. (1960) in the *Treatise*. Wagner's (2002) phylogenetic analysis was based on teleoconch characters of early Palaeozoic anisostrophically coiled gastropods (i.e., excluding bellerophontoids), which includes the oldest pleurotomariidan taxa. Wagner's (2002) resulting classification strongly deviates from the scheme proposed by Knight et al. (1960) and others. Since the publication of the *Treatise*, numerous new genera were described and the family level classifications were modified (e.g., Gordon & Yochelson 1987; Bandel 2009; Karapunar & Nützel 2021). Bouchet et al. (2017) published the family level classification reflecting the last consensus view on phylogenetic relationships between pleurotomariidan families. Apart from expert opinions on

the relationship between pleurotomariidan genera and families, the phylogeny of the entire group has never been reconstructed with quantitative phylogenetic methods.

The pleurotomariidan shell is characterized by a shell slit in the outer labrum, the presence of inner nacreous layer, and a larval shell of one whorl matching the so-called trochoid condition and reflecting non-planktotrophic larval development (Bandel 1982; Kaim 2004; Geiger et al. 2008; Nützel 2014). The slit reflects the soft body organization. It serves for the ventilation of the mantle cavity and can be regarded as a synapomorphy of the clade Pleurotomariida. Sinus and slit in the early Palaeozoic archaeogastropods are regarded homologous (Knight 1941; Yochelson 1984; Wagner 2002). Accordingly, the slit was derived gradually from a sinus during the course of gastropod evolution (Knight 1941; Yochelson 1984). The shell slit is also regarded a derived character in Gastropoda by neontologists (e.g., Lindberg & Ponder 2001) and plesiomorphic in living Vetigastropoda (Haszprunar 1988). The phylogenetic analysis by Wagner (2002) suggests that the slit evolved multiple times in early gastropod evolution (in Pleurotomariida, Bellerophontida and Euomphaloidea). Whether the slit reflects a similar soft body organization in these extinct slit-bearing groups is under debate. However, the slit and trema/tremata (that is a ‘single hole’/‘a row of holes’ formed by modification of a slit) can be homologous among the slit- and tremata-bearing vetigastropods with paired organs (i.e., Pleurotomariida, Haliotidae, Scissurellidae, Fissurellidae), considering that the condition of having paired organs and a slit are regarded ancestral in Vetigastropoda (Haszprunar 1988; Ponder & Lindberg 1997; Lindberg & Ponder 2001). With the presence of slit, the animal could control the water flow in the mantle cavity (Yonge 1947; Lindberg & Ponder 2001). Thus, the acquisition of slit in vetigastropods can be regarded as an evolutionary novelty. The evolution of slit also implies the deepening of mantle cavity during the course of gastropod evolution (Lindberg & Ponder 2001).

The gastropod shell has two primary functions: protection from the predators and providing a space that is isolated from the external environment, in which the animal can regulate its metabolism. Shell morphology can inform about underlying soft body anatomy (for instance an elongated aperture may indicate a single gill; Linsley 1977; McNair et al. 1981), direction of inhalant and exhalant currents (slits, tremata and siphons), physiology (high expansion rate may indicate higher metabolism; Vermeij 2002), life habit (sedentary lifestyle can be inferred from radial aperture, open coiling or shell form: Linsley 1977, Signor 1982; ratchet sculpture indicates burrowing habit either within sediment: Signor 1982, 1994, or intrusion in soft sponges for feeding: Nützel 2021). The shell is formed by different regions of mantle

epithelium and controlled by genes and proteins (Kocot et al. 2016; McDougall & Degnan 2018). Gastropod shells are diverse in morphology. This and the easy availability of shell characters are the reasons why the gastropod systematics on specific and generic levels is based mostly on shell characters. The gastropod shell is composed of two parts: the protoconch (including an embryonic shell only or both an embryonic and a larval shell if a bi-phasic life cycle is present) and the teleoconch (post metamorphic shell) (Nützel 2014). Protoconch characters and characters associated with soft anatomy are considered to be more informative than teleoconch characters in inferring phylogeny above generic level (Frýda et al. 2008). All vetigastropods including Pleurotomariida have a non-planktotrophic larval shell of one whorl (e.g., Bandel 1982; Nützel 2014), so presence/absence of potential larval planktotrophy is not informative within Vetigastropoda. However, it is diagnostic on the subclass level. The slit and its by-product selenizone reflect the soft anatomy in pleurotomariidan shell. Pleurotomariida possess paired organs including ctenidia, auricles and kidneys (e.g., Yonge 1947; Harasewych 2002). The paired organs are positioned bilaterally symmetrical on either side of the shell slit and the anus is situated at the proximal end of the slit (Hickman 1984, Harasewych 2002). The shell slit has a vital function: it facilitates the ventilation of the deep mantle cavity for respiration and dispose the excretory products (Yonge 1947; Voltzow et al. 2004). Slit and selenizone characters (e.g., position, shape, width, depth) have been widely used in the traditional classification of Pleurotomariida (e.g., Knight et al. 1960, Bayer 1965) and these characters are more conservative compared to other shell characters (Batten 1967; Karapunar & Nützel 2021; Karapunar et al. 2022). Phylogenetic analyses with slit-bearing early Palaeozoic gastropods also show that the characters associated with the presence of a sinus or slit show a low rate of change compared to other characters (Wagner 2001).

Material & Methods

Taxon sampling

Pleurotomariida is composed of more than 300 genera (unpublished data). However, not all of the genera are included in the present phylogenetic analyses. This is largely because many of them are based on insufficiently known type species or including only poorly documented species. In these cases, too many character states are unknown to include them in a meaningful way in a meaningful way. As a preparation for our analyses, we revised the Pleurotomariida from the Triassic St. Cassian Formation (Karapunar & Nützel 2021) and studied exceptionally

well-preserved specimens form the Pennsylvanian of the USA (Karapunar et al. 2022). This study helped to clarify the state of characters for many genera that had previously been unknown or poorly known especially for the characters concerning the early ontogenetic shells. Moreover, we included data from our taxonomic studies about gastropods from the Permian of Thailand (Ketwetsuriya et al. 2020), the Lower Jurassic of Germany (Gründel & Nützel 1998; Nützel & Gründel 2015) and the Triassic Marmolada Limestone, Italy (Nützel 2017). We also studied specimens which are housed in the Bayerische Staatssammlung für Paläontologie und Geologie (BSPG), Naturhistorisches Museum Wien (NHMW), Geologische Bundesanstalt (GBA) and the Natural History Museum, London (NHMUK). Among 110 species included in the analyses, only five species were not directly examined by the authors and their information were gathered from the literature (Knight 1941; Bayer 1965; Mazaev 2015, 2019). The inventory numbers of the studied specimens and the literature used in character scoring can be found in the Appendix 1.

The specimens from the museum collections were carefully assigned by the authors to previously described genera and species. If a specimen does not represent a previously described species, it is left in open nomenclature. Such specimens will be described in a separate future publication. A total of 109 species representing 81 genera were included in the analysis.

Information regarding the geological ages of the specimens (Appendix 4) were retrieved from the specimen labels and publications, where they were described. Out-of-date or regional stratigraphical ages were assigned to the most recent international geological ages according to the Geological time scale 2018 (Walker et al. 2018). The specimens were assigned to geochronological time units, at the highest resolution representing a geological age (e.g., Carnian) and the lowest resolution representing a geological period (e.g., Triassic). The minimum and maximum ages of the specimens (FAD, LAD) basically represent the upper or lower boundary of these time units, during which the species occurred.

Shell characters

The shell characters that have been used in the traditional classification of the family Pleurotomariidae (e.g., Bayer 1965; Harasewych & Kiel 2007) and the characters that were previously used in morphological phylogenetics of Early Palaeozoic gastropods (Wagner 2002) were taken into consideration when constructing the character list and many new (not used hitherto) characters were added. The character list comprises 93 characters (Appendix 2). All

characters are discrete, 22 of them have binary states and 71 of them are multistate. Eighty characters are unordered, 13 are ordered.

The whorl of the gastropod shell can be divided into shell sectors (Vermeij 2002). These sectors can be inferred from the growth lines and the change in ornamentation pattern. The pleurotomariidan whorl can be divided into two main sectors: whorl face and base, as is also the case in other gastropods. In descriptive terminology, whorl face is defined as the region between the adapical and abapical sutures and thus, in a strict sense, is only applicable to spire whorls. However, this definition may not correspond to homologous regions, because the boundary between the whorl regions do not always corresponds to the position of suture line. In most taxa, the abapical (lower) suture represent the boundary between the whorl face and base. However, in some taxa, the suture line is situated above the boundary between whorl face and base (e.g., *Glabrocingulum*). Hence, the position of the suture might be misleading to infer the boundary between the two sectors. If present, a basal angulation indicates the boundary which is commonly the case. The base can be defined as the region between the suture (or basal angulation) and the umbilicus. The base is a bonding surface of the succeeding whorl; hence, it affects the shape of the succeeding whorl where it is bonded. For that reason, the ornament type or the strength of ornament differ between the base and the whorl face in many gastropods. All nacreous gastropods (most vetigastropods, including Pleurotomariida) restrict prominent ornaments within whorl face and do not form prominent ornaments on their base (e.g., *Schizogonium*, *Bolma*). However, there are many exceptions in other gastropod groups. For example, the caenogastropod family Muricidae have the capability of remodeling the shell and can remove prominent ornaments such as long spines on their base (Carriker 1972). Formation of a thick inner lip or reduction of whorl overlap (e.g., *Epitonium*) are other strategies shown by gastropods with prominent basal ornament (Vermeij 1977). The whorl face sector can be further divided into three subsectors in Pleurotomariida, as was also previously recognized by P.J. Wagner (see Vermeij 2002): the slit, and the subsectors above and below the slit. The slit reflects the soft part anatomy and the characters related to the slit are regarded to be more conservative and hence more phylogenetically informative (see the introduction). Approximately 31% of the characters used in the analysis are related to the slit (29 out of 93; characters 0–24, 32–34, 37), 32 characters are related to the upper whorl face (chrs 27–37, 54–55, 60–71, 72–78), 21 characters are related to the lower whorl face (chrs 38–42, 55–56, 59–70, 77–78), 8 characters are used to code base (chrs 46–49, 57–58, 79–80).

Gastropod shell records the whole ontogeny during growth because it forms the shell by accretionary growth. This feature allows to study early ontogenetic characters and ontogenetic change of the different characters in gastropods. Previously, early ontogenetic characters (e.g., ornamentation, formation of selenizone) were used in classification because they are shared by the members of the same genus (Karapunar & Nützel 2021; Karapunar et al. 2022). Ontogeny related characters were previously also used in the phylogenetic analysis of gastropods (Wagner 2002). In the present character list, 63 characters are related to late ontogeny (chrs 4–8, 10–14, 16, 18–22, 24–26, 28, 30, 32–33, 35, 37–40, 42–58, 64–71, 73, 75, 77–80, 85, 87, 89, 92), 21 characters are related to early ontogeny (chrs 0, 1, 2, 15, 17, 23, 31, 34, 36, 59–63, 72, 74, 76, 83–84, 90–91) and 9 characters code ontogenetic change (characters 3, 9, 27, 29, 41, 81–82, 86, 88). Among the characters, 45 are related to axial sculpture (chrs 0, 1, 5, 6, 15–22, 26–29, 31, 34, 36, 37, 39–41, 46, 48–49, 51–58, 60–62, 69–76) and 31 are coding spiral elements (2, 3, 4, 7–14, 23–24, 30, 32–33, 35, 38, 42–45, 47, 63, 66–68, 77–80).

The character matrix (Appendix 3) was composed in Morphobank (https://morphobank.org/) and later modified in Mesquite (Maddison & Maddison 2021).

Parsimony analysis

Parsimony analysis was implemented in TNT (Goloboff & Catalano 2016), by using different algorithms. *Sinuopea sweeti* was selected as an outgroup taxon because it was recovered as a sister taxon of other early Palaeozoic gastropod taxa in the phylogenetic analysis conducted by Wagner (2002). The initial trees were produced by using the following values for the algorithms Sectorial search: RSS (minimum sector size 5, maximum sector size 54, that is the 50% of the number of ingroup taxa), CSS (100 rounds, minimum sector size 5); XSS (100 rounds); Ratchet (100 iterations); Drift (100 cycles); Tree fusing (100 rounds) with 1000 random additional sequences. After getting the initial trees, suboptimality criteria were set to retain trees with less than 10 steps with relative fit difference 0.1. Additional trees were searched with the traditional search algorithm by using the initial trees (with the command "bbreak"). Bremer supports were calculated with all trees (optimal trees, that is the most parsimonious trees [MPTs], and suboptimal trees, that is the trees having maximum of 10 more steps than MPTs). The strict consensus tree is calculated with the MPTs of all trees. The character matrix was resampled by using 1000 iterations for bootstrap supports.

Bayesian analysis

Fossilized Birth Death (FBD) process (tip dating Bayesian Inference method) is used herein, which incorporates stratigraphical range data (occurrence dates) into the analysis. The FBD process includes three models: morphological evolution model (=substitution model, that is the rate of evolution of character states; and site rate model, that is the rate of evolution of characters or among-character rate variation), evolutionary clock model (=branch rate model, that is the rate of evolution along the tree) and tree model (speciation, extinction, fossilization and sampling rates) (Warnock & Wright 2020; Wright et al. 2021). The FBD process is a continuous-time Markov process, that starts with a single lineage, which then splits or terminates and as a new lineage arises, a new FBD process starts (Gavryushkina & Zhang 2020). During this process, lineages can be sampled (according to the fossilization and sampling rates) and the sampled lineages form a sampled tree. Posterior probability distribution of tree topologies is generated through Markov Chain Monte Carlo (MCMC) sampling (Warnock & Wright 2020). Previously, FBD model was used to infer phylogenies based solely on morphological datasets (e.g., fossil echinoderms, Wright 2017; Wright et al. 2021) but it has never been used to infer phylogeny of gastropods.

The FBD method was implemented in RevBayes (Höhna et al. 2016). Mk Model (Lewis 2001) was used for a substitution model, which assumes that the change from one state to another is equally probable for all character states. Gamma distribution with four rate categories was used to model among-character rate variation (the site rate model). Uncorrelated lognormal relaxed evolutionary clock was used to model the character rate variation along the tree. Speciation, extinction and fossilization rates were drawn from exponential distributions. The origination time was set between 460–490 Mya, which was estimated according to the current knowledge on the oldest fossil record of Pleurotomariida (see introduction) and Gastropoda (e.g., Frýda et al. 2008). The sampling rate of extant taxa (rho) was set to 0.023 because only one extant species (out of 44, MolluscaBase) was included in the analysis. The analysis was run for 500,000 generations, 25% of which were discarded as burn-in. Convergence of the probabilities was confirmed in Tracer (Rambaut et al. 2018). Posterior trees were used to calculate posterior clade probabilities, that is the proportion of the appearance of a clade in sampled posterior trees. The summary of the trees is given as maximum sampled-ancestor clade credibility tree (MSACC tree), that is a tree with the maximum score of posterior clade probabilities

(Gavryushkina et al. 2017). The node ages were estimated by using the 95% highest posterior density (HPD) interval, which covers the 95% of the posterior distribution of node ages.

The RevBayes code was compiled by modifying the previously published codes (Heath et al. 2019; Wright 2020). The code is provided in the Appendix 5. Icytree is used for visualization of the Bayesian tree (Vaughan 2017).

The apomorphy list of the Bayesian tree (Appendix 8) is produced in the TNT. For this, the sampled ancestors (taxa recovered within branches) were reconstructed as terminal taxa (i.e., as sister taxon of the branch they were recovered).

Stratigraphical congruence analysis

There are several metrics to measure if a phylogeny is congruent with the stratigraphical information or not. The Stratigraphic Consistency Index (SCI, Huelsenbeck 1994) is the ratio of the number of stratigraphically consistent nodes (i.e., the oldest descendent of that node is the same age or younger than the oldest descendent of the sister taxon) to the number of all nodes (excluding the root node). The Relative Completeness Index (RCI, Benton & Storrs 1994) is the ratio between the observed ranges of taxa to the sum of the total ghost ranges (minimum implied gap, MIG). The corrected Manhattan Stratigraphic Measure (MSM*, Pol & Norell 2001) is the ratio between the minimum possible sum of ghost ranges (G_{min}) to the minimum implied gap (the sum of the total ghost ranges) [G_{min}/ MIG]. The Gap Excess Ratio (GER, Wills 1999) is the ratio of the difference between the maximum possible sum of ghost ranges (G_{max}) and minimum implied gap to the difference between maximum and minimum possible sums of ghost ranges [(G_{max}–MIG)/(G_{max}– G_{min})].

The metrics were calculated with the R package “strap” (Bell & Lloyd 2015). These metrics are designed for trees, in which all taxa are reconstructed at tips. In Parsimony analysis, all taxa are reconstructed at the tips of branches. However, in FBD analysis, some taxa are recovered within the branches. Therefore, the stratigraphical congruence analysis of the FBD tree (MSACC tree) was conducted by using two methods. In the first method, the taxa at branches were excluded and the analysis was conducted only with 95 taxa that were recovered at the tips (i.e., terminal taxa). In the second method, the taxa in the branches (i.e., sampled ancestors)

were reconstructed as sister taxon of the branch they were recovered, and the analysis was conducted with all 109 taxa. The R code used in the analysis is provided in the Appendix 5.

Results

Parsimony analysis

In the initial search, 286 trees of different scores were obtained, 5 of them representing most parsimonious trees (MPTs) with tree lengths of 1590 steps, consistency index (CI) of 0.131 and Retention index (RI) of 0.521. In the second search, which is done based on the initial trees, 99999 trees were obtained, 24 of them representing MPTs with tree lengths of 1590 steps, CI of 0.131 and RI of 0.521. A strict consensus tree of 24 MPTs is given in Fig. 1. The apomorphies is given in the Appendix 7.

Eleven groups are defined in the parsimonious tree. The groups reflect the taxonomic systematics of Pleurotomariida to some extent. However, overall group compositions indicate that compositions of pleurotomariidan families suggested by taxonomists are largely para- or polyphyletic. The clades (indicated with *), paraphyletic groups and their family compositions (in parentheses) are as following:

Euryzonines* (subfamily Euryzoniinae)
Kittlidiscides* (family Kittlidiscidae)
Zygitides* (family Zygitidae, family Phymatopleuridae in part)
Porcelliides* (family Porcelliidae)
Mourloniides (family Eotomariidae in part, family Phymatopleuridae in part), paraphyletic
Ptychomphalides (family Ptychomphalidae, subfamily Liospirinae), paraphyletic
Gosseletinides (family Gosseletinidae in part, family Rhaphistomellidae in part, family Luciellidae, family Trochotomidae, family Temnotropidae), paraphyletic
Wortheniellides (family Wortheniellidae, family Stuorellidae, family Schizogoniidae, family Eotomariidae in part, Family Rhaphistomellidae in part), paraphyletic
Clathrospirides* (family Eotomariidae in part, family Phymatopleuridae in part)
Phymatopleurides (family Phymatopleuridae in part, family Portlockiellidae, family Eotomariidae in part) paraphyletic
Pleurotomariides* (family Pleurotomariidae)

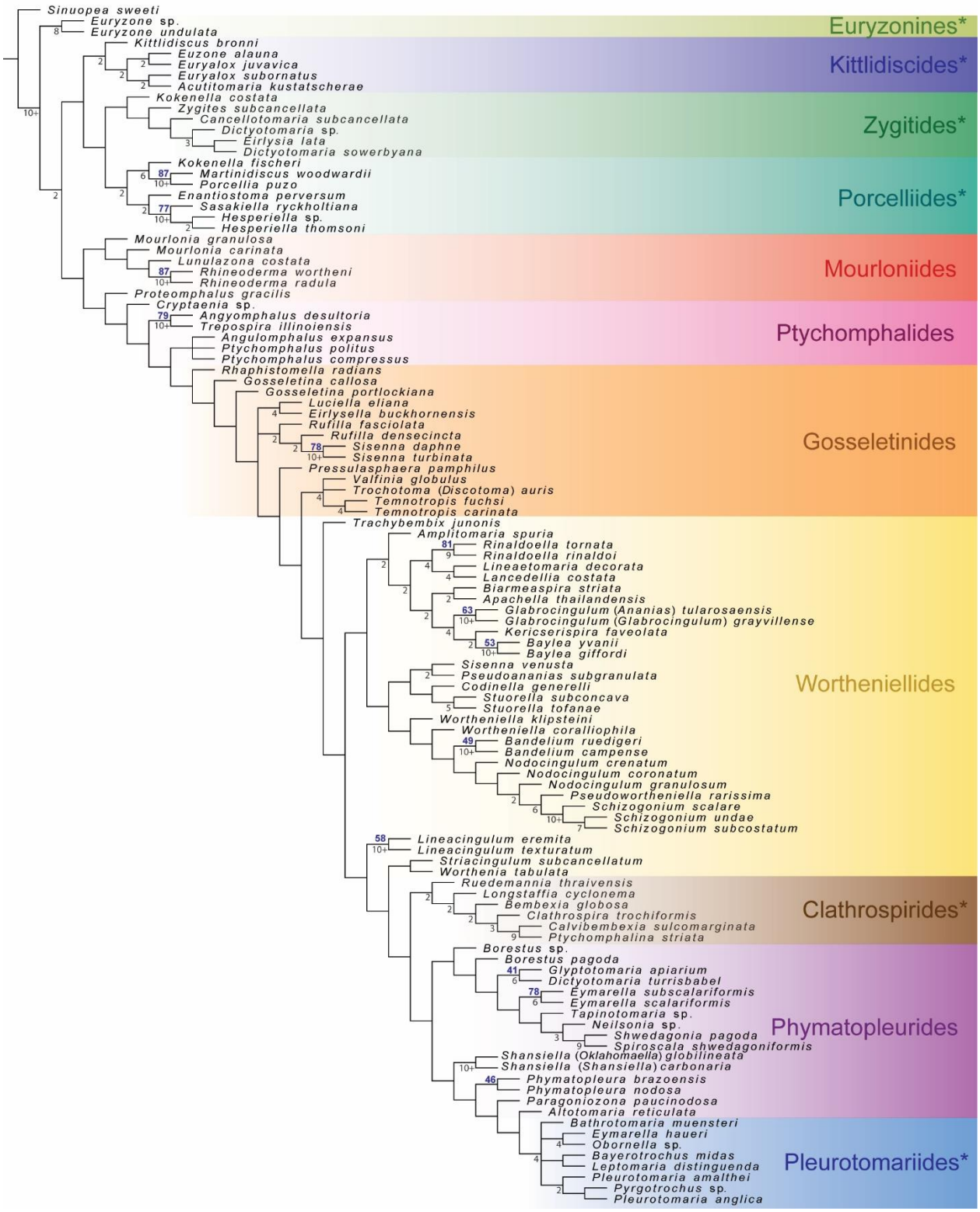

Figure 1: The strict consensus tree of 24 MPTs (1590 steps, CI: 0.131, RI: 0.521), reconstructed with Parsimony method. Bootstrap values >40% are indicated in blue above the nodes. Bremer support values >1 are indicated in black below the nodes. Clades are denoted by an asterisk (*), all other groups are paraphyletic.

Bayesian analysis

Eleven groups are recovered in the Maximum sampled-ancestor clade credibility tree (MSACC tree, Fig. 2). A total of 95 taxa were reconstructed at the tips, 14 taxa reconstructed within branches as sampled ancestors. Except Euryzonines, all monophyletic and paraphyletic groups recovered in the Parsimony analysis are present in the Bayesian phylogeny. However, their compositions are different than the composition of the groups in the parsimonious tree. Moreover, Glabrocingulini is the only group defined in the Bayesian analysis. The group compositions (monophyletic groups are indicated with *) partly reflect the current taxonomic systematics of Pleurotomariida:

Clathrospirides (family Eotomariidae in part), paraphyletic
Glabrocingulini (family Eotomariidae in part), paraphyletic
Porcelliides* (family Porcelliidae)
Phymatopleurides (family Phymatopleuridae, family Portlockiellidae, family Eotomariidae in part), paraphyletic
Zygitides (family Zygitidae), paraphyletic
Kittlidiscides* (family Kittlidiscidae)
Pleurotomariides* (family Pleurotomariidae)
Mourloniides (family Eotomariidae in part, family Phymatopleuridae in part), paraphyletic
Gosseletinides (family Gosseletinidae in part, subfamily Liospirinae, subfamily Euryzoniinae, family Luciellidae), paraphyletic
Wortheniellides* (family Wortheniellidae, family Stuorellidae, family Schizogoniidae, family Eotomariidae in part)
Ptychomphalides* (family Ptychomphalidae, family Temnotropidae, family Rhaphistomellidae in part, family Trochotomidae)

Additionally, Glabrocingulini, Phymatopleurides, Zygitides, Kittlidiscides and Pleurotomariides are collectively representing the clade Pleurotomariini. Mourloniides, Gosseletinides, Wortheniellides, Ptychomphalides are together representing the clade Wortheniellini. The apomorphies are given in the Appendix 8.

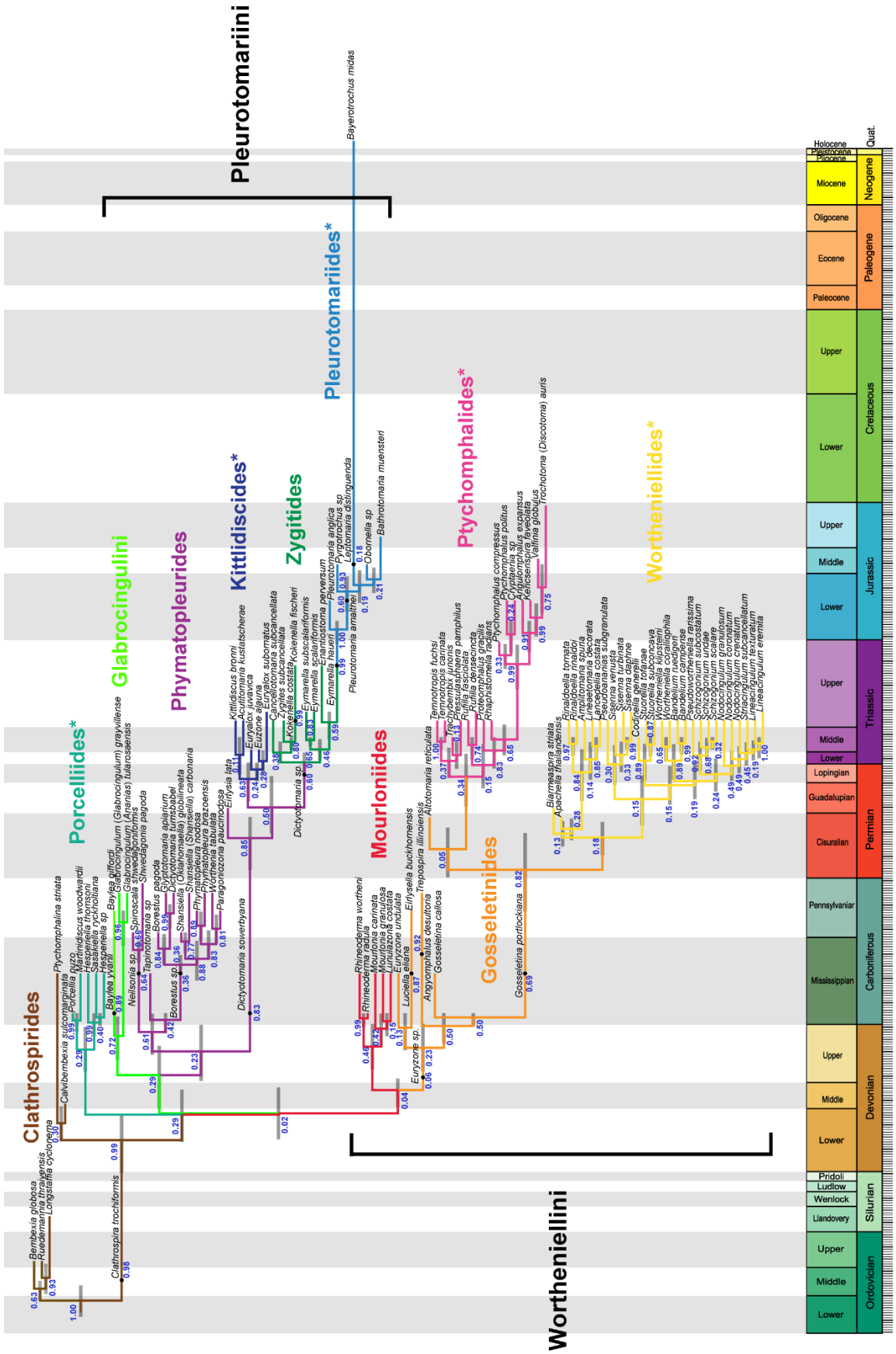

Figure 2: The maximum sampled-ancestor clade credibility tree, reconstructed with Bayesian method (Fossilized Birth Death). The numbers at nodes indicate posterior probability of clades. The error bars at the indicate 95% highest posterior density (HPD) interval for divergence times. Clades are denoted by an asterisk (*), all other groups are paraphyletic.

Stratigraphical congruence analysis

The stratigraphical congruence indices indicate that the most parsimonious trees are stratigraphically more inconsistent (i.e., the number of daughter lineages with older occurrences is higher) and have more ghost ranges (measured with different metrics; Appendix 6) than the bayesian tree. The phylogenies plotted against geological ages can be found in the Appendix 6.

Discussion

There are more than 300 valid pleurotomariidan genera and only 81 of them were included in the present analyses. The clade and group compositions reconstructed in this study are not in agreement with the current taxonomic systematics of Pleurotomariida. This suggests a reconsideration of the current systematics of Pleurotomariida. However, the tree topologies strongly vary with inclusion of more taxa or more characters and depend on the methodology used in tree reconstruction (Bayesian and Parsimony). Therefore, the systematics of the group should not be re-organized based solely on these results at this point because it would destabilize the systematics of the group. Re-arrangements should be made where both, phylogenetic and taxonomic methods suggest they are necessary.

Parsimony analysis

Parsimony analysis indicates that the generic composition of the families Porcelliidae, Luciellidae, Stuorellidae, Schizogoniidae and Pleurotomariidae are monophyletic. The composition of the families Ptychomphalidae, Trochotomidae and Wortheniellidae are paraphyletic. Tree topology suggests the generic composition of the families Eotomariidae, Phymatopleuridae, Zygitidae, Rhaphistomellidae, Lancedellidae are polyphyletic.

The family Eotomariidae is a large group composing of more than 90 genera and the evolutionary relationships between the genera is not clear (see Karapunar et al. 2022). In the current analysis, members of Eotomariidae are recovered as members of five distinct groups: Mourloniides, Ptychomphalides, Wortheniellides, Clathrospirides, Phymatopleurides. It is noteworthy that *Mourlonia* and *Ptychomphalina* are distantly placed in the tree (Mourloniides and Clathrospirides) considering the fact that they were once regarded synonyms due to morphological similarity (Knight et al. 1960). The current phylogeny supports the view of Gordon & Yochelson (1987), who considered the two genera separate and placed them in

separate tribes (Mourloniini and Ptychomphalinini). However, *Mourlonia* was recovered as sister group of *Lunulazona*, which is in contrast to the view of Gordon & Yochelson (1987). *Baylea*, *Glabrocingulum* (*Ananias*) and *Glabrocingulum* (*Glabrocingulum*) are the most diverse and globally distributed Upper Palaeozoic eotomariid genera and can be united under the tribe Glabrocingulini Gordon & Yochelson, 1987. The recovery of Glabrocingulini within the group Wortheniellides suggests a close relationship between the upper Palaeozoic Glabrocingulini and the Triassic Wortheniellidae, hence the latter might represent the surviving lineage of the former after the end-Permian mass extinction. The upper Palaeozoic eotomariid genera *Neilsonia*, *Shwedagonia* and *Spiroscala* are recovered within Phymatopleurides suggesting an affinity of the tribe Neilsoniini Gordon & Yochelson to Phymatopleuridae.

The members of Phymatopleuridae are recovered in Zygitides, Mourloniides, Wortheniellides in addition to Phymatopleurides. *Rhinoederma* and *Eirlysia* were previously considered as eotomariid genera but are now placed in Phymatopleuridae (Karapunar et al. 2022). However, *Rhinoederma* was recovered within the Mourlonides, in agreement with the older classification by Knight et al. (1960), and *Eirlysia* was recovered in Zygitides. Apart from *Eirlysia*, two members of *Dictyotomaria* (a phymatopleurid genus) were also reconstructed within Zygitides, although one *Dictyotomaria* was reconstructed in Phymatopleurides. The phylogeny suggests a possible relationsip between Zygitidae and some members of Phymatopleuridae but also reconstruct them as two distant groups. *Worthenia* was previously placed in Ruedemanninae (Knight et al. 1960), which was doubted by Karapunar et al. (2022) in the light of new information on the early ontogeny and was placed in Phymatopleuridae. However, in the analysis *Worthenia tabulata* was recovered between *Ruedemannia* (Clathrospirides) and Wortheniellides, somehow supporting the earlier opinions. *Tapinotomaria* was removed from Portlockiellidae and assigned to Phymatopleuridae previously (Karapunar et al. 2022). The analysis supports this placement and further suggests a close relationship between Portlockiellidae and Phymatopleuridae (both placed in Phymatopleurides) as previously suggested by Karapunar et al. (2022).

The composition of the family Rhaphistomellidae was enlarged by Karapunar & Nützel (2021) after an extensive study of the types of *Rhaphistomella, Sisenna* and *Rufilla*. Although the phylogeny supports the close relationship between *Sisenna* and *Rufilla*, it suggests that their classification together with *Rhaphistomella* and *Lineacingulum* under Rhaphistomellidae forms a polyphyly. The tree suggests a close affinity of *Rhaphistomella, Sisenna* and *Rufilla* to *Gosseletina*.

Kittlidiscidae and Temnotropidae are composed of a single genus each, so the analysis cannot argue for polyphyly within these families (unless the members of the same genus are reconstructed distantly, but this would further bring the reliability of this result into question). The tree reveals relationship of these families to other genera and families. *Euzone*, *Euryalox* and *Acutitomaria* seem to be closely related to *Kittlidiscus*, and hence Kittlidiscidae. These three genera were previously also considered closely related and were placed tentatively in Lancedellidae (Karapunar & Nützel 2021). *Lancedellia* is recovered within Wortheniellides, however its early ontogeny is not known (Karapunar & Nützel 2021) and could not be analyzed. If the early ontogeny of *Lancedellia* is found to be distinct, *Euzone*, *Euryalox* and *Acutitomaria* can be placed within Kittlidiscidae. Previously Temnotropidae was placed in Haliotioidea, which was refuted by Karapunar & Nützel (2021), and who argued possible derivation of Haliotidae from Trochotomidae. The parsimonious analysis reconstructed Temnotropidae as sister group of Trochotomidae. Although Haliotidae was not analyzed in the present study, it is likely that it was derived from these closely related groups.

Rinaldoella was recovered as a sister taxon of the two members of the family Lancedellidae (*Lancedellia* and *Lineaetomaria*). As previously discussed by Karapunar & Nützel (2021), *Lancedellia* and *Rinaldoella* might represent synonyms and *Rinaldoella* might belong to Scissurellidae. If so, Scissurellidae might be the living representative of Worhteniellides.

Although the Triassic families Stuorellidae, Schizogoniidae are recognized as distinct families, their relationship to other families were not known (Karapunar & Nützel 2021). The present phylogeny suggest that these two families are very closely related to the Triassic family Wortheniellidae. Moreover, the phylogeny indicates that Wortheniellides was the most diversified group within the Triassic.

One member of the Triassic genus *Kokenella* (Zygitidae) was recovered as sister taxon of the Palaeozoic genus *Porcellia* (Porcellidae) while the other was recovered as sister to all other Zygitides. These two genera are quite similar to each other in general whorl morphology but differ in selenizone characters and in the direction of coiling of first whorls. They were placed in the same family by Knight et al. (1960) but have no longer been considered as closely related due to differences in coiling in early ontogeny (see Karapunar & Nützel 2021). The phylogeny indicates that the change in coiling direction in early ontogeny might not be as highly informative to infer phylogeny as previously suggested (e.g., by Schwardt 1992; Frýda et al. 2008; Bandel 2009).

Trepospira and *Angyomphalus* were recovered within Ptyhcomphalides, indicating a close relationship between the Palaeozoic subfamily Liospirinae and Mesozoic family Ptyhcomphalidae, as also previously suggested by Karapunar & Nützel (2021) based on a taxonomic analysis.

Phymatopleurides and Pleurotomariides are recovered as sister groups. Seemingly the latter represents a linage that survived the end-Permian mass extinction from the Palaeozoic Phymatopleurides stock and persists until today. The Triassic genus *Eymarella* was recovered both, within Phymatopleurides and Pleurotomariides.

The tree suggests that the basal shift of the position of the selenizone occurred independently three times in the families Porcellidae (Porcelliides), Luciellidae (Gosseletinides) and Portlockiellidae (Phymatopleurides).

The members of the same genus are in some instances are distantly reconstructed in the tree (e.g., *Dictyotomaria*, *Eymarella*, *Sisenna*, *Kokenella*). This reflects in part the high variation of the morphology within the same genus, but also put the reliability of the results in question because genera like *Kokenella* are morphologically quite compact and a split seems unwarranted.

It can be expected that the taxa from older geological ages (e.g., early Palaeozoic) are more basally situated within the tree and the younger taxa (e.g., Mesozoic) are reconstructed more distant from the root. However, the stratigraphic order of the taxa is not congruent with their position along the tree (e.g., the Early Palaeozoic group Clathrospirides is placed in a more derived position than the Mesozoic groups Zygitides, Ptychomphalides and Wortheniellides). The parsimony analysis does not consider the ages when constructing the phylogenies although it is an important information which helps to decipher relationships between the taxa. On the other hand, the Fossilized Birth Death method incorporates the age information in the analysis. The stratigraphic congruence metrics indicate that maximum parsimonious trees are stratigraphically less consistent and have more ghost ranges than the Bayesian tree.

Bayesian analysis

Maximum sampled-ancestor clade credibility (MSACC) tree suggests that the taxonomic composition of family Eotomariidae is polyphyletic as is also suggested by Parsimony analysis and was previously discussed based on taxonomic analyses (Karapunar et al. 2022). Since the Fossilized Birth Death (FBD) method incorporates the age in the analysis, the FBD trees

estimate the diversification times (node ages). In the early Palaeozoic, Pleurotomariida was represented by the group Clathrospirides. They proliferated in the Devonian in three distinct lineages, one is Porcelliides, a lineage restricted to the Palaeozoic, and the other two are Pleurotomariini and Wortheniellini, who survived the end-Permian mass extinction.

The Bayesian analysis indicates that the generic composition of the families Zygitidae, Luciellidae, Trochotomidae, Stuorellidae, Schizogoniidae and Pleurotomariidae are monophyletic. The composition of Ptychomphalidae is found to be paraphyletic. The tree topology suggests that the generic composition of the families Eotomariidae, Phymatopleuridae, Porcelliidae, Wortheniellidae, Rhaphistomellidae, Lancedellidae are polyphyletic.

The eotomariid group Glabrocingulini (*Glabrocingulum* and *Baylea*) is recovered as sister group of Phymatopleurides, which has the genera *Shwedagonia*, *Neilsonia* and *Spiroscala* as the early offshoots. These three taxa have long been considered to be the members of Eotomariidae (Knight et al. 1960). However, the recovery of these three genera within Phymatopleurides also in the Parsimony analysis suggests a close affinity of these genera to the family Phymatopleuridae. Family Portlockiellidae and *Tapinotomaria* is recovered again in the Phymatopleurides corroborating the views of Karapunar et al. (2022) (see above). Unlike in the parsimonious tree, this time *Worthenia* is recovered within Phymatopleurides and support the placement of *Worthenia* in the family Phymatopleuridae (Karapunar et al. 2022). The members of Phymatopleurides (*Dictyotomaria* and *Eirylsia*) gave rise to the groups Kittlidiscides and Zygitides. As in the parsimony analysis, Kittlidiscides and Zygitides are recovered as sister groups. The members of these groups are known only from the Triassic, but the tree suggests that Kittlidiscides originated in the Permian and that a more detailed study of Permian deposits might reveal the early members of this clade. Again, the lancedellid genera *Acutitomaria*, *Euryalox* and *Euzone* were recovered within Kittlidiscides and hence strongly suggest placing these genera in the family Kittlidiscidae. In the parsimonious phylogeny, Zygitides and Pleurotomariides were reconstructed distant from each other, with the members of *Eymarella* reconstructed in both groups. In the Bayesian phylogeny, Zygitides represents the sister group of Pleurotomariides and the Triassic genus *Eymarella* is recovered as the ancestral lineage of Pleurotomariides (family Pleurotomaiidae). *Enantiostoma*, a taxon previously considered as member of Porcelliidae, is recovered within Zygitides. *Enantiostoma* is indeed very similar to *Kokenella* in whorl and selenizone morphology and differs in change in coiling direction in early ontogeny. The phylogeny indicates that the change in coiling

direction has happened at least once independent from Porcelliidae. As discussed above, the change in coiling direction of the teleoconch during early ontogeny might not be as important as previously suggested. The composition of Pleurotomariides support the monophyly of the family Pleurotomariidae. Pleurotomariides is the only group within Pleurotomariini who survived the end-Triassic extinction and persists until today.

The large clade Wortheniellini corresponds largely to Eotomariidae in the sense of Knight et al. (1960). The earliest offshoot of Wortheniellini is the group Mourloniides, which has the same group composition as in the parsimonious tree. The composition of Mourloniides argues against the proposal of Karapunar et al. (2022), who placed the genus *Rhineoderma* in the family Phymatopleuridae. Mourloniides is recovered as the sister group of Gosseletinides, which is composed of the families Euryzoniinae, Luciellidae and Eotomariidae in part and the subfamily Liospirinae. Unlike in the Parsimony analysis, Liospirinae (Gosseletinides) is reconstructed distant from Ptychomhalidae (Ptychomphalides). Gosseletinides gave rise to Ptychomphalides and Wortheniellides in the Palaeozoic. Although the members of these two groups are restricted to the Mesozoic, they seem to have originated during the Permian and if so, both survived the end-Permian extinction.

In Ptychomphalides, the families Temnotropidae and Ptychomphalidae represent sister groups. Ptychomphalides further comprises the members of Rhaphistomellidae (*Rhaphistomella* and *Rufilla*), which supports the opinion of Gründel (2011), who considered *Rhaphistomella* to be closely related to the family Ptychomphalidae. Ptychomphalidae is recovered as the sister group of Trochotomidae in the Bayesian tree, although Temnotropidae was recovered as sister group of Trochotomidae in the parsimonious tree. The phylogeny reconstructs *Kericserispira* as a member of Trochotomidae. *Kericserispira* is indeed shares a similar whorl and selenizone morphology with in *Trochotoma* and might belong to Trochotomidae. If the family Haliotidae was derived from Trochotomidae as previously proposed by Karapunar & Nützel (2021), then this lineage can be the second ancestral lineage (in addition to the Pleurotomariides) that persists until today.

Wortheniellides is the last group recovered within Wortheniellini. The Bayesian phylogeny suggests that the families Schizogoniidae, Stuorellidae and Lancedellidae are most closely related to Wortheniellidae. These families all together compose the clade Wortheniellides. Wortheniellides is the the clade that exhibited the most successful proliferation of Pleurotomariida during the Triassic but could not survive the extinction at the end-Triassic

despite its remarkable Triassic diversification. The tree indicates monophyletic composition of the family Worthenielliidae if the genus *Rinaldoella* is excluded. Similar to the Parsimony analysis, the Bayesian analysis suggests a close relationship of *Rinaldoella*, *Amplitomaria*, *Lancedellia* and *Lineaetomaria*. This indicates that the composition of Lancedellidae as proposed by Karapunar & Nützel (2021) is polyphyletic. As discussed above, if *Rinaldoella* is found to be a member of Scissurellidae, this family might be the living descendant of the clade Worthenielliini.

There are some points making the Bayesian tree controversial. *Biarmeaspira* was considered to be derived from *Baylea* (Mazaev 2015; Ketwetsuriya et al. 2020). However, in the analysis, *Biarmeaspira* (Glabrocingulides) was recovered in a group distant from *Baylea* (Phymatopleurides). Similarly, *Sisenna* and *Rufilla* are considered to be sister taxa (Karapunar & Nützel 2021), however they were recovered in closely related but distinct clades (Ptychomphalides and Worthenielliides) in the Bayesian tree.

Implications on classification

Both trees suggest that the large amount of the current taxa are not monophyletic. The Parsimony method produced a tree that is not congruent with stratigraphic data (App. 6-Fig. 1). CI and RI of the MPTs are relatively low and indicating that the characters show high rate of transformation. The relatively high number of character states per character might be a reason for high number of character states changes (or low CI and RI values). However, high transformation rates can also indicate that the characters used in the analysis are highly variable and hence less phylogenetically informative. Both in the Bayesian tree and in the parsimonious tree, clade supports are very low apart from few small clades. Therefore, a major revision of classification based solely on the phylogenies is not justified.

Conclusion

Although the group compositions and sister group relationship between the genera are similar in the trees reconstructed with parsimonious and Bayesian methods, the relationships between the groups to each other are considerably different in two phylogenies. In the tree reconstructed with parsimony analysis, the members of the same genus are recovered in different groups in three instances. Additionally, the position of genera and groups in the parsimonious tree do not fit their stratigraphical record. Generally, the support values of the Parsimony tree are low and

many traditional taxa appear to be paraphyletic. The phylogeny reproduced with Bayesian analysis is more plausible because the members of the same genus are not recovered distant from each other along the tree, and the position of lineages is congruent with their appearance in the fossil record. Both methods produce sister-group relationship between genera that are not congruent with the current systematics and suggest reconsideration of the taxonomic systematics of Pleurotomariida. The Bayesian phylogeny suggests that the groups consisting only of Triassic taxa probably were already present in the Permian although direct evidence is lacking. The extinction of Wortheniellides, the most diversified group in the Triassic, suggests that diversification dynamics did not play an important role in the survival of Pleurotomariida.

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References

Bandel, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies*, **7**: 1–198.

Bandel, K. 2009. The slit bearing nacreous Archaeogastropoda of the Triassic tropical reefs in the St. Cassian Formation with evaluation of the taxonomic value of the selenizone. *Berliner paläobiologische Abhandlungen*, **10**: 5–47.

Batten, R.L. 1967. Thoughts on the genus *Ptychomphalina* Fischer 1887 and the family Eotomariidae Wenz, 1938. *Journal of Paleontology*, **41**(1): 262–264.

Bayer, F.M. 1965. New pleurotomariid gastropods from the western Atlantic, with a summary of the recent species. *Bulletin of marine science*, **15**(4): 737–796.

Bell, M.A., & Lloyd, G.T. 2015. strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology*, **58**: 379–389.

Benton, M.J. & Storrs, G.W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology*, **22**(2): 111–114.

Bouchet, P., Lozouet, P., Maestrati, P. & Heros, V. 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, **75**: 421–436.

Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. & Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia*, **61**(1–2): 1–526.

Carriker, M.R. 1972. Observations on removal of spines by muricid gastropods during shell growth. *Veliger*, **15**(2): 69–74.

Erwin, D.H. 1990. Carboniferous-Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. *Paleobiology*, **16**: 187–203.

Frýda, J. 2012. Phylogeny of Palaeozoic gastropods inferred from their ontogeny. Pp. 395–435 in J.A. Talent (ed) *Earth and Life – Global Biodiversity, Extinction Intervals and Biogeographic Perturbations Through Time. Series: International Year of Planet Earth*. Springer, New York.

Frýda, J., Nützel, A. & Wagner, P.J. 2008. Paleozoic Gastropoda. Pp. 239–270 in W.F. Ponder and D.R. Lindberg (eds) *Phylogeny and Evolution of the Mollusca*. University of California Press, California.

Gavryushkina, A., Heath, T.A., Ksepka, D.T., Stadler, T., Welch, D. & Drummond, A.J. 2017. Bayesian total-evidence dating reveals the recent crown radiation of penguins. *Systematic Biology*, **66**(1): 57–73.

Gavryushkina, A. & Zhang, C. 2020. Total-Evidence Dating and the Fossilized Birth–Death Model. Pp. 175–193 in S.Y.W. Ho (ed) *The Molecular Evolutionary Clock: Theory and Practice*. Springer International Publishing, Cham.

Geiger, D.L. & Thacker, C.E. 2005. Molecular phylogeny of Vetigastropoda reveals non-monophyletic Scissurellidae, Trochoidea, and Fissurelloidea. *Molluscan Research*, **25**(1): 47–55.

Geiger, D.L., Nützel, A. & Sasaki, T. 2008. Vetigastropoda. Pp. 297–330 in W.F. Ponder and D.R. Lindberg (eds) *Phylogeny and Evolution of the Mollusca*. University of California Press, California.

Goloboff, P.A. & Catalano, S.A. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*, **32**(3): 221–238.

Gordon, M.J. & Yochelson, E.L. 1987. Late Mississippian Gastropods of the Chainman Shale, West-Central Utah. *U. S. Geological Survey Professional Paper*, **1368**: 1–112.

Gründel, J. 2011. Die Ptychomphalidae Wenz, 1938, (Ptychomphaloidea, Gastropoda) im Jura. *Freiberger Forschungshefte*, **C 539**: 59–69.

Gründel, J. & Nützel, A. 1998. Gastropoden aus dem oberen Pliensbachium (Lias delta 2, Zone des *Pleuroceras spinatum*) von Kalchreuth östlich Erlangen (Mittelfranken). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, **38**: 63–96.

Harasewych, M., Adamkewicz, S.L., Blake, J.A., Saudek, D., Spriggs, T. & Bult, C.J. 1997. Phylogeny and relationships of pleurotomariid gastropods (Mollusca: Gastropoda): an assessment based on partial 18S rDNA and cytochrome c oxidase I sequences. *Molecular Marine Biology and Biotechnology*, **6**: 1–20.

Harasewych, M.G. 2002. Pleurotomarioidean gastropods. *Advances in Marine Biology*, **42**: 237–294.

Harasewych, M.G. & Kiel, S. 2007. Upper Jurassic Pleurotomariidae (Gastropoda) from southwestern Madagascar. *The Nautilus*, **121**: 76–89.

Haszprunar, G. 1988. On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies*, **54**: 367–441.

Heath, T.A., Wright, A.M. & Pett, W. 2019. Combined-Evidence Analysis and the Fossilized Birth-Death Process for Stratigraphic Range Data, Joint inference of divergence times and phylogenetic relationships of fossil and extant taxa. (https://revbayes.github.io/tutorials/fbd/).

Hickman, C.S. 1984. *Pleurotomaria*: Pedigreed perseverance? Pp. 225–231 in N. Eldredge, Stanley, S. M. (ed) *Living Fossils*. Springer, New York, Berlin, Heidelberg, Tokyo.

Höhna, S., Landis, M.J., Heath, T.A., Boussau, B., Lartillot, N., Moore, B.R., Huelsenbeck, J.P. & Ronquist, F. 2016. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology*, **65**(4): 726–736.

Huelsenbeck, J.P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology*, **20**(4): 470–483.

Kaim, A. 2004. The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaeontologia Polonica*, **62**: 1–182.

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

Karapunar, B., Nützel, A., Seuss, B. & Mapes, R.H. 2022. Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA. *Papers in Palaeontology*.

Ketwetsuriya, C., Karapunar, B., Charoentitirat, T. & Nützel, A. 2020. Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. *Zootaxa*, **4766**(1): 1–47.

Knight, J.B. 1941. Palaeozoic Gastropod Genotypes. *Geological Society of America Special Papers*, **32**: 1–510.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. 1960. Systematic descriptions. Pp. I169–I310 in R.C. Moore (ed) *Treatise on Invertebrate Paleontology, Part 1, Mollusca 1*. Geological Society of America and University of Kansas Press, Kansas.

Kocot, K.M., Aguilera, F., McDougall, C., Jackson, D.J. & Degnan, B.M. 2016. Sea shell diversity and rapidly evolving secretomes: insights into the evolution of biomineralization. *Frontiers in Zoology*, **13**(1): 1–10.

Koken, E. 1889. Ueber die Entwicklung der Gastropoden vom Cambrium bis zur Trias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilageband*, **6**: 440–463.

Lewis, P.O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, **50**(6): 913–925.

Lindberg, D.R. & Ponder, W.F. 2001. The influence of classification on the evolutionary interpretation of structure - a re-evaluation of the evolution of the pallial cavity. *Organisms, Diversity & Evolution*, **1**: 273–299.

Linsley, R.M. 1977. Some "laws" of gastropod shell form. *Paleobiology*, **3**: 196–206.

Maddison, W.P. & Maddison, D.R. 2021. Mesquite: a modular system for evolutionary analysis. Version 3.70 http://www.mesquiteproject.org.

Mazaev, A.V. 2015. Upper Kazanian (Middle Permian) Gastropods of the Volga–Urals Region. *Paleontological Journal*, **49**: 869–986.

McDougall, C. & Degnan, B.M. 2018. The evolution of mollusc shells. *Wiley Interdisciplinary Reviews: Developmental Biology*, **7**(3): e313.

McNair, C.G., Kier, W.M., Lacroix, P.D. & Linsley, R.M. 1981. The functional significance of aperture form in gastropods. *Lethaia*, **14**(1): 63–70.

Nützel, A. 2017. On the pleurotomariid gastropod genus *Trachybembix* from the Middle Triassic Marmolada Limestone, South Alps, Italy. *Zitteliana*, **89**: 229–234.

Nützel, A. 2021. Gastropods as Parasites and Carnivorous Grazers: A Major Guild in Marine Ecosystems. Pp. 209–229 in K. De Baets and J.W. Huntley (eds) *The Evolution and Fossil Record of Parasitism: Identification and Macroevolution of Parasites*. Springer, Cham.

Nützel, A. & Gründel, J. 2015. Early Jurassic (Pliensbachian) gastropods from Franconia, Southern Germany. *Palaeontographica Abteilung A*, **305**: 1–89.

Pol, D. & Norell, M.A. 2001. Comments on the Manhattan stratigraphic measure. *Cladistics*, **17**(3): 285–289.

Ponder, W.F. & Lindberg, D.R. 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. *Zoological Journal of the Linnean Society*, **119**: 83–265.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, **67**(5): 901.

Schwardt, A. 1992. Revision der *Wortheniella*-Gruppe (Archaeogastropoda) der Cassianer Schichten (Trias, Dolomiten). *Annalen des Naturhistorischen Museums Wien, Serie A*, 94: 23–57

Sepkoski, J.J. 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleozoic*, **7**: 36–53.

Signor, P.W. 1982. Resolution of life habits using multiple morphologic criteria: Shell form and life-mode in turritelliform gastropods. *Paleobiology*, **8**: 378–388.

Signor, P.W. 1994. Ratchet riposte: more on gastropod burrowing sculpture. *Lethaia*, **26**: 379–383.

Tracey, S., Todd, J.A. & Erwin, D.H. 1993. Mollusca: Gastropoda. Pp. 131–167 in M.J. Benton (ed) *The Fossil Record 2*. Chapman & Hall, Cambridge.

Vaughan, T.G. 2017. IcyTree: rapid browser-based visualization for phylogenetic trees and networks. *Bioinformatics*, **33**(15), 2392–2394.

Vermeij, G.J. 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, **3**: 245–258.

Vermeij, G.J. 2002. Characters in context: molluscan shells and the forces that mold them. *Paleobiology*, **28(1)**: 41–54.

Voltzow, J., Morris, P.J. & Linsley, R.M. 2004. Anatomy of and patterns of water currents through the mantle cavities of pleurotomariid gastropods. *Journal of Morphology*, **262**(2): 659–666.

Wagner, P.J. 2001. Rate heterogeneity in shell character evolution among lophospiroid gastropods. *Paleobiology*, **27**: 290–310.

Wagner, P.J. 2002. Phylogenetic relationships of the earliest anisotrophically coiled gastropods. *Smithsonian Contributions to Paleobiology*, **88**: 1–152.

Walker, J.D., Geissman, J.W., Bowring, S.A., Babcock, L.E., 2018. Geologic Time Scale v. 5.0: Geological Society of America. https://doi.org/10.1130/2018.CTS005R3C.

Warnock, R.C. & Wright, A.M. 2020. *Understanding the tripartite approach to Bayesian divergence time estimation*. Cambridge University Press.

Wenz, W. 1938–1944. Gastropoda. Teil I: Allgemeiner Teil und Prosobranchia. P. xii + 1639 *Handbuch der Paläozoologie*. Gebrüder Borntraeger, Berlin.

Williams, S. & Ozawa, T. 2006. Molecular phylogeny suggests polyphyly of both the turban shells (family Turbinidae) and the superfamily Trochoidea (Mollusca: Vetigastropoda). *Molecular Phylogenetics and Evolution*, **39**(1): 33–51.

Wills, M.A. 1999. Congruence between phylogeny and stratigraphy: randomization tests and the gap excess ratio. *Systematic Biology*, **48**(3): 559–580.

Wright, A.M. 2020. Discrete morphology - Multistate Characters, Phylogenetic inference with discrete morphological data. (https://revbayes.github.io/tutorials/morph_tree/V2.html).

Wright, A.M., Wagner, P.J. & Wright, D.F. 2021. *Testing character evolution models in phylogenetic paleobiology: A case study with Cambrian echinoderms.* Cambridge University Press, 1–42 pp.

Wright, D.F. 2017. Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata). *Journal of Paleontology*, **91**(4): 799–814.

Yochelson, E.L. 1984. Historic and current considerations for revision of Paleozoic gastropod classification. *Journal of Paleontology*, **58, No. 1**: 259–269.

Yonge, C.M. 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **232**(591): 443–518.

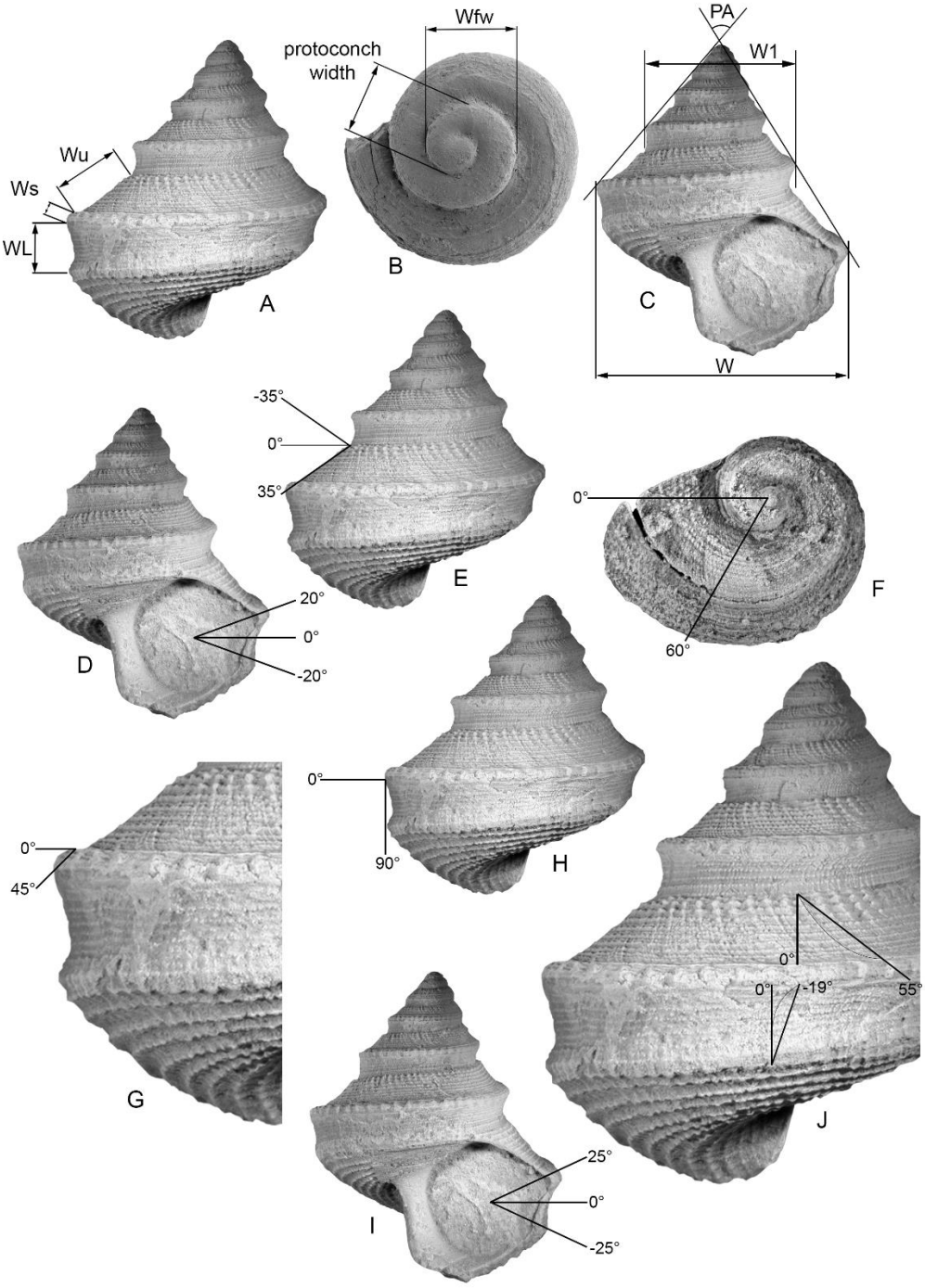
Zapata, F., Wilson, N.G., Howison, M., Andrade, S.C., Jörger, K.M., Schrödl, M., Goetz, F.E., Giribet, G. & Dunn, C.W. 2014. Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. *Proceedings of the Royal Society B: Biological Sciences*, **281**(1794): 20141739.

Appendix 1. Specimens used in the analyses

Name	Specimens	References
Acutitomaria kustatscherae Karapunar & Nützel, 2021		Karapunar & Nützel 2021
Altotomaria reticulata Ketwetsuriya et al., 2020		Ketwetsuriya et al. 2020
Amplitomaria spuria (Münster, 1841)		Karapunar & Nützel 2021
Angulomphalus expansus (J. Sowerby, 1821)		Gründel & Nützel 1998; Nützel & Gründel 2015
Angyomphalus desultoria Jeffery et al., 1994	Specimens housed in the BSPG	Jeffery et al. 1994
Apachella thailandensis Ketwetsuriya et al., 2020		Ketwetsuriya et al. 2020
Bandelium campense (Zardini, 1980)		Karapunar & Nützel 2021
Bandelium ruedigeri (Schwardt, 1992)		Karapunar & Nützel 2021
Bathrotomaria muensteri (Römer, 1839)	NHMUK PI G 12172	
Bayerotrochus midas (Bayer, 1965)		Bayer 1965
Baylea giffordi (Worthen, 1884)		Karapunar et al. 2022
Baylea yvanii (Lévéille, 1835)	NHMUK PI G 4435(1), NHMUK PI G 18607, NHMUK PI PG 1525	
Bembexia globosa Longstaff, 1924	NHMUK PI G 25355, NHMUK PI G 25356	
Biarmeaspira striata Mazaev, 2015		Mazaev 2015
Borestus pagoda Newell, 1935		Karapunar et al. 2022
Borestus sp.	NHMUK PI PG 412	
Calvibembexia sulcomarginata (Conrad, 1842)	NHMUK PI G 15325, NHMUK PI PG 3101	
Cancellotomaria subcancellata (d'Orbigny, 1850)		Karapunar & Nützel 2021
Clathrospira trochiformis (Portlock, 1843)	NHMUK PI G 25383, NHMUK PI G 25385	
Codinella generelli (Stoppani, 1860)	NHMW 1969/1104/0000, NHMW 1969/1105/0001, NHMW 1969/1105/0002, NHMW 1969/1106/0000	
Cryptaenia sp.	NHMUK PI G 28545, NHMUK PI G 28546, NHMUK PI G 45690, NHMUK PI 66678	
Dictyotomaria sowerbyana (de Koninck, 1843)	NHMUK PI PG 1739	
Dictyotomaria sp.	NHMUK PI G 51286	
Dictyotomaria turrisbabel Karapunar & Nützel, 2022		Karapunar et al. 2022
Eirlysella buckhornensis Karapunar & Nützel, 2022		Karapunar et al. 2022
Eirlysia lata Mazaev, 2015		Mazaev 2015
Enantiostoma perversum (Hörnes, 1856)	NHMW 1856/0047/0032/1, GBA [ZTYP 251, 2677]	
Euryalox juvavica (Koken, 1894)	NHMW 1926/0002/0455/2, GBA [ZTYP 251, 4230]	
Euryalox subornatus (d'Orbigny, 1850)		Karapunar & Nützel 2021
Euryzone sp.	NHMUK PI G 4507(1), NHMUK PI G 4507(2)	
Euryzone undulata (Phillips, 1836)	NHMUK PI G 128(1), NHMUK PI G 128(2)	
Euzone alauna (Koken, 1894)	NHMW 1926/0002/0457, BSPG 1877 X 296, a juvenile specimen housed in the BSPG	
Eymarella haueri (Hörnes, 1855)	NHMW 1856/0047/0034/1, NHMW 1856/0050/0051/2, NHMW 2019/0172/0002/1	
Eymarella scalariformis (Koken, 1896)	NHMW 2019/0172/0001/1, NHMW 2019/0172/0001/3, NHMW 2019/0172/0001/4, NHMW 2019/0172/0008/1	
Eymarella subscalariformis (Hörnes, 1855)	NHMW 1859/0005/0031, NHMW 1860/0005/0361	
Glabrocingulum (*Ananias*) *tularosaensis* (Kues, 2004)		Karapunar et al. 2022
Glabrocingulum (*Glabrocingulum*) *grayvillense* (Norwood & Pratten, 1855)		Karapunar et al. 2022
Glyptotomaria apiarium Knight, 1945		Karapunar et al. 2022
Gosseletina callosa (de Koninck, 1843)	NHMUK PI G 40915(1)	
Gosseletina portlockiana (de Koninck, 1843)	NHMUK PI G 139(1), NHMUK PI G 139(2)	
Hesperiella sp.	NHMUK PI G 5073(2)	
Hesperiella thomsoni (de Koninck, 1883)	NHMUK PI G 5067(1)	
Kericserispira faveolata (Eudes-Deslongcahamps, 1849)	NHMUK PI G 16009, NHMUK PI G 16025(1)	
Kittlidiscus bronni (Klipstein, 1844)		Karapunar & Nützel 2021
Kokenella costata (Münster, 1841)		Karapunar & Nützel 2021
Kokenella fischeri (Hörnes, 1856)	NHMW 1856/0046/0014, NHMW 2019/0177/0029/1, NHMW 2019/0177/0029/2	
Lancedellia costata (Zardini, 1978)		Karapunar & Nützel 2021
Leptomaria distinguenda (Tawney, 1873)	NHMUK PI 66422	
Lineacingulum eremita (Koken, 1896)	NHMW 2019/0177/0006	
Lineacingulum texturatum (Münster, 1841)		Karapunar & Nützel 2021
Lineaetomaria decorata (Münster, 1841)		Karapunar & Nützel 2021
Longstaffia cyclonema (Salter, 1873)	NHMUK PI G 8701(2), NHMUK PI G 13494(1), NHMUK PI G 13494(2)	
Luciella eliana (de Koninck, 1843)	NHMUK PI 48597	
Lunulazona costata Sadlick & Nielsen, 1963	NHMUK PI PG 3608, NHMUK PI PG 3609	
Martinidiscus woodwardii (Martin, 1809)	NHMUK PI PG 1854	
Mourlonia carinata (J. Sowerby, 1813)	NHMUK PI PG 26, NHMUK PI PG 138	

Mourlonia granulosa de Koninck, 1883	NHMUK PI G 5071(1)	
Neilsonia sp.	NHMUK PI PG 412	
Nodocingulum coronatum (Münster, 1841)		Karapunar & Nützel 2021
Nodocingulum crenatum (Münster, 1841)		Karapunar & Nützel 2021
Nodocingulum granulosum (Klipstein, 1844)		Karapunar & Nützel 2021
Obornella sp.	NHMUK PI MG 1558	
Paragoniozona paucinodosa Nelson, 1947		Karapunar et al. 2022
Phymatopleura brazoensis (Shumard, 1860)		Karapunar et al. 2022
Phymatopleura nodosa (Girty, 1912)		Karapunar et al. 2022
Pleurotomaria amalthei Quenstedt, 1858		Nützel & Gründel 2015
Pleurotomaria anglica (J. Sowerby, 1818)	NHMUK PI G 71505	
Porcellia puzo Lévéille, 1835	NHMUK PI G 18663	
Pressulasphaera pamphilus (d'Orbigny, 1850)		Karapunar & Nützel 2021
Proteomphalus gracilis (Read, 1907)		Karapunar & Nützel 2021
Pseudoananias subgranulata (Münster, 1841)		Karapunar & Nützel 2021
Pseudowortheniella rarissima (Kittl, 1891)		Karapunar & Nützel 2021
Ptychomphalina striata (J. Sowerby, 1817)	NHMUK PI 65069, NHMUK PI PG 141	
Ptychomphalus compressus (J. Sowerby, 1813)	NHMUK PI 43632	
Ptychomphalus politus (J. Sowerby, 1821)	NHMUK PI 60207	
Pyrgotrochus sp.	NHMUK PI G 11256	
Rhaphistomella radians (Wissmann, 1841)		Karapunar & Nützel 2021
Rhineoderma radula (de Koninck, 1843)	NHMUK PI 48590	
Rhineoderma wortheni (Hall, 1858)	NHMUK PI G 36646, NHMUK PI G 36653	
Rinaldoella rinaldoi (Schwardt, 1992)		Karapunar & Nützel 2021
Rinaldoella tornata Karapunar & Nützel, 2021		Karapunar & Nützel 2021
Ruedemannia thraivensis (Longstaff, 1924)	NHMUK PI G 46232, NHMUK PI GG 25407	
Rufilla densecincta (Koken, 1896)	NHMW 2019/0177/0012/1, GBA [ZTYP 251, 2554], a specimen housed in the BSPG	
Rufilla fasciolata (Münster, 1841)		Karapunar & Nützel 2021
Sasakiella ryckholtiana (de Koninck, 1843)	NHMUK PI G 5073(1)	
Schizogonium scalare (Münster, 1841)		Karapunar & Nützel 2021
Schizogonium subcostatum (Münster, 1841)		Karapunar & Nützel 2021
Schizogonium undae Karapunar & Nützel, 2021		Karapunar & Nützel 2021
Shansiella (*Oklahomaella*) *globilineata* Karapunar & Nützel, 2022		Karapunar et al. 2022
Shansiella (*Shansiella*) *carbonaria* (Norwood & Pratten, 1855)		Karapunar et al. 2022
Shwedagonia pagoda Mazaev, 2019		Mazaev 2019
Sinuopea sweeti (Whitfield, 1882)		Knight 1941
Sisenna daphne (Dittmar, 1866)	NHMW 2019/0172/0003/1, NHMW 2019/0172/0003/2, NHMW 2019/0172/0003/3	
Sisenna turbinata (Hörnes, 1855)	NHMW 2019/0177/0018/1, GBA [ZTYP 251, 2543], GBA [ZTYP 251, 2555], GBA [ZTYP 251, 2599]	
Sisenna venusta (Münster, 1841)		Karapunar & Nützel 2021
Spiroscala shwedagoniformis Karapunar & Nützel, 2022		Karapunar et al. 2022
Striacingulum subcancellatum (Klipstein, 1844)		Karapunar & Nützel 2021
Stuorella subconcava (Münster, 1841)		Karapunar & Nützel 2021
Stuorella tofanae Leonardi & Fiscon, 1959		Karapunar & Nützel 2021
Tapinotomaria sp.	NHMUK PI PG 411	
Temnotropis carinata (Münster, 1841)		Karapunar & Nützel 2021
Temnotropis fuchsi (Kittl, 1891)		Karapunar & Nützel 2021
Trachybembix junonis (Kittl, 1894)	NHMW 2019/0177/0001/1	Nützel 2017
Trepospira illinoiensis (Worthen, 1884)		Karapunar et al. 2022
Trochotoma (*Discotoma*) *auris* (Zittel, 1873)	NHMUK PI GG 18724, NHMUK PI GG 18725	
Valfinia globulus (Eudes-Deslongchamps, 1843)	NHMUK PI GG 10219	
Worthenia tabulata Conrad, 1835		Karapunar et al. 2022
Wortheniella coralliophila (Kittl, 1891)		Karapunar & Nützel 2021
Wortheniella klipsteini Karapunar & Nützel, 2021		Karapunar & Nützel 2021
Zygites subcancellata (d'Orbigny, 1850)		Karapunar & Nützel 2021

Appendix 2. The characters used in the analyses



App. 1-Figure 1: A. Wu: width of upper whorl face, **Ws:** width of selenizone, **WL:** width of lateral (lower) whorl face; width of whorl face equals to addition of the width of these three sectors (**Wwf**=Wu+Ws+WL). **B. Wfw:** width of first whorl. **C. PA:** pleural angle (chr. 26); whorl expansion rate=**W1/W**. **D.** Position of slit or selenizone (chr. 5). **E.** inclination of ramp (chr. 27)**. F.** Depth of adapical (upper) edge of slit (chr. 6). **G.** inclination of selenizone (chr. 38). **H.** inclination of lateral whorl face (chr. 40). **I.** Position of basal edge (chr. 45). **J.** Inclination of growth line on upper whorl face (upper measurement, chr. 55) and inclination of growth line on lower whorl face (lower measurement, chr. 57).

Slit (character of aperture) and selenizone

Chr. 0. Onset of slit/selenizone (ordered character)
0. Within 1st whorl (immediately after protoconch)
1. Within 2nd whorl
2. Within 3rd whorl
3. Within 4th whorl
4. Within 5th or 6th whorl

Chr. 1. Initial shape of slit/selenizone
0. U-shaped notch (crescentic)
1. V-shaped notch

Chr. 2. Shape of whorl region where slit/selenizone onsets
0. Angulated whorl face
1. Convex whorl face

Chr. 3. Ontogenetic change in position of slit/selenizone
0. Selenizone position same throughout ontogeny
1. Selenizone shifts abapically (downwards) during ontogeny

Chr. 4. Position of slit/selenizone (on last whorl) with respect to whorl center (App. 1-Fig. 1D; ordered character)
0. -31° – -60°
1. -6° – -30° (below mid- whorl)
2. -5° – 5° (at mid-whorl)
3. 6° – 30°
4. 31° – 60°
5. 61° – 90°

Chr. 5. Depth of adapical (upper) edge of slit (unknown for most taxa) (App. 1-Fig. 1F; ordered character)
0. < 5° (slit not developed, only a sinus present)
1. 6°– 30°
2. 31°– 60°
3. 61°– 90°
4. > 90°

Chr. 6. Depth of abapical (lower) edge of slit (ordered character)
0. More adaperturally (forward) positioned than adapical edge
1. Same as depth of adapical edge
2. More abaperturally (backward) positioned than adapical edge

Chr. 7. Trema
0. Absent
1. Trema present
2. Tremata (multiple trema) present

Chr. 8. Width of selenizone (Ws) compared to width of whorl face (Wwf) within last whorl (=Ws/Wwf, App. 1-Fig. 1A, ordered character)
0. < 0.0625 of whorl face (narrow)
1. 0.0625 – 0.125 (moderate)
2. 0.126 – 0.25 (wide)
3. > 0.25 (very wide)

Chr. 9. Ontogenetic change in proportional width of selenizone (relative to whorl face)
0. Selenizone becomes wider
1. Selenizone width remains constant
2. Selenizone becomes narrower

Chr. 10. Selenizone bordered by
0. indistinct edges of former slit (*Trepospira*)
1. spiral threads or lirae (*Worthenia*, *Baylea*, *Lineacingulum*, *Sisenna*, *Rufilla*, *Schizogonium*, *Wortheniella*)
2. sharp projecting edges of former slit (*Dictyotomaria*, *Glyptotomaria*, *Borestus*)
3. prominent spiral cords, that are thick edges of former slit (*Glabrocingulum*, *Amplitomaria*, *Lineatomaria*, *Euryalox*, *Kittlidiscus*)

Chr. 11. Vertical plates between spiral cords on selenizone borders
0. Absent
1. Present (e.g., *Oehlertia*)

Chr. 12. Frill on selenizone border
0. Absent
1. Present (e.g., *Luciella*)

Chr. 13. Elevation of selenizone borders with respect to rest of whorl face
0. As rest of whorl face
1. Selenizone borders slightly projecting (e.g., *Glabrocingulum*, *Worthenia*, *Temnotropis*)
2. Borders are distinctly elevated (e.g., *Lunulazona*, *Proteomphalus*, *Euzone*)

Chr. 14. Elevation of edges of selenizone with respect to selenizone borders
0. Distinctly sunken (e.g., *Dictyotomaria*, *Kokenella*, *Acutitomaria*)
1. Selenizone slightly depressed near selenizone borders (selenizone border well-defined, e.g., *Mourlonia*)
2. Flush to whorl face (e.g., *Trepospira*, *Rufilla*)

Chr. 15. Shape of selenizone in transverse section in early whorl

0. Angulated
1. Convex
2. Flat
3. Concave

Chr. 16. Shape of selenizone in transverse section in adult whorl
0. Angulated
1. Convex
2. Flat
3. Concave

Chr. 17. Strength of lunulae in early ontogeny
0. Faint or invisible (might be equal to growth lines)
1. Sharp, distinct (stronger than or equal to growth lines)
2. Thick (might be equal in axial ornaments' strength)
3. Node-forming
4. Forming hollow spines or short notches

Chr. 18. Strength of lunulae in late ontogeny
0. Faint or invisible (might be equal to growth lines)
1. Sharp, distinct (stronger than or equal to growth lines)
2. Thick (might be equal in axial ornaments' strength)
3. Node-forming
4. Forming hollow spines or short notches

Chr. 19. Change in thickness of lunula from one end to other
0. Thickness is same throughout
1. Thicker at its median position

Chr. 20. Space between lunulae
0. Closely spaced (width of interspace is less than or equal to width of lunula)
1. Widely spaced (width of interspace is more than width of lunula)
2. Very widely spaced (width of interspace is more than three times width of lunula)

Chr. 21. Shape of lunulae (shape of growth lines in taxa with smooth selenizone)
0. Crescentic
1. V-shaped

Chr. 22. Symmetry of lunulae (symmetry of growth lines in taxa with smooth selenizone)
0. Maximum convexity near adapical (upper) edge
1. Symmetrical
2. Maximum convexity near abapical (lower) edge

Chr. 23. Spiral ornament on selenizone in early ontogeny

0. Absent
1. One median cord
2. Multiple cords
3. Fine striation (weak grooves)

Chr. 24.Spiral ornament on selenizone in late ontogeny
0. Absent
1. One median cord
2. Multiple cords (e.g., *Worthenia*)
3. Fine striations (weak grooves) or threads

Whorl morphology in transverse section

Chr. 25.Pleural angle (App. 1-Fig. 1C; ordered character)
0. 5° – 30° (high spired)
1. 31° – 60° (moderately to high spired)
2. 61° – 90° (moderately to low spired)
3. 91° – 120° (low spired)
4. > 120° (very low spired)

Chr. 26.Inclination of ramp (App. 1-Fig. 1E; ordered character)
0. -16° – -45° (steeply climbing; as in *Schizogonium*)
1. -1° – -15°
2. 0° – 15° (horizontal lying to gently sloping)
3. 16° – 45° (steeply sloping)
4. 46° – 75° (very steeply sloping)

Chr. 27.Ontogenetic change of inclination of ramp
0. Increase in inclination (more steeply sloping or less steeply climbing)
1. No change
2. Decrease in inclination (e.g., *Shwedagonia*)

Chr. 28.Curvature (shape) of ramp
0. Strongly concave
1. Slightly concave to flat
2. Slightly convex to flat
3. Strongly convex or well-rounded

Chr. 29.Ontogenetic change in shape of ramp
0. Becoming more concave/ less convex
1. No change
2. Becoming less concave/ more convex

Chr. 30.Subsutural angulation (shoulder)

0. Absent
1. Present (e.g., *Sisenna*)

Chr. 31.Formation of subsutural angulation
0. Before onset of selenizone
1. With onset of selenizone
2. After onset of selenizone

Chr. 32.Median angulation
0. Absent
1. Present

Chr. 33.Position of median angulation
0. Positioned on lower edge of selenizone (e.g., *Baylea*, *Ananias*)
1. Positioned within selenizone (e.g., *Worthenia*, *Schizogonium*)
2. Positioned on upper edge of selenizone (e.g., *Tapinotomaria*, *Eymerella*, *Catazona*, *Kittlidiscus*)
3. Positioned above upper edge of selenizone (e.g., *Borestus*, *Phymatopleura*)

Chr. 34.Formation of median angulation
0. Before onset of selenizone
1. With onset of selenizone
2. After onset of selenizone

Chr. 35.Angulation on ramp (in addition to median angulation)
0. Absent
1. Present (e.g., *Bembexia*)

Chr. 36.Formation of ramp angulation
0. Before onset of selenizone
1. With onset of selenizone
2. After onset of selenizone

Chr. 37.Inclination of selenizone (angle between selenizone plane and horizontal plane perpendicular to shell axis) (App. 1-Fig. 1G; ordered character)
0. 0° – 30° (almost perpendicular to axis, facing adapically, e.g., *Baylea*)
1. 31° – 75°
2. 76° – 105° (almost parallel to axis, e.g., *Borestus*)
3. 106° – 150° (facing abapically)
4. 151° – 195° (facing basally)

Chr. 38.Whorl face below selenizone (lateral whorl face)
0. Absent (e.g., *Luciella*)
1. Present

Chr. 39.Inclination of lateral whorl face (App. 1-Fig. 1H; ordered character)
0. 0° – 45° (horizontally lying, perpendicular to axis)
1. 46° – 80° (steeply sloping)
2. 81° – 100° (subparallel to shell axis)
3. >100° (facing abapically)

Chr. 40.Curvature (shape) of lateral whorl face
0. Strongly concave
1. Slightly concave to almost flat
2. Slightly convex to almost flat
3. Strongly convex or well-rounded

Chr. 41.Ontogenetic change in shape of lateral whorl face
0. Becoming more concave/ less convex
1. No change
2. Becoming less concave/ more convex

Chr. 42.Ratio of width of lateral whorl face (WL) to width of whorl face above selenizone (Wu) in last whorl (=WL/Wu, App. 1-Fig. 1A; ordered character)
0. < 0.17
1. 0.17 – 0.50
2. 0.51 – 0.90
3. 0.91 – 1.10
4. 1.11 – 2.00
5. 2.01 – 5.00 (e.g., *Rhaphischisma*)

Chr. 43.Basal edge (transition to base)
0. Evenly convex
1. Angulated
2. Pronounced basal carina/keel (e.g., *Discotomaria*)
3. Basal carina/keel with hollow spines (e.g., *Schizogonium*)

Chr. 44.Position of basal edge with respect to center of whorl (App. 1-Fig. 1I; ordered character)
0. -6° – -30° (above mid-whorl)
1. -5° – 5° (at mid-whorl)
2. 6° – 30°
3. 31° – 60°
4. 61° – 90°

Chr. 45.Position of periphery
0. Below lower edge of selenizone
1. At lower edge of selenizone
2. Borders of selenizone or selenizone itself represent periphery
3. Upper edge of selenizone (e.g., *Luciella, Tapinotomaria*)

4. Above selenizone

Chr. 46.Curvature of base
0. Almost flat to slightly concave
1. Slightly convex
2. Convex or well-rounded

Chr. 47.Circumumbilical ridge
0. Present
1. Absent

Chr. 48.Inclination of columellar lip relative to shell axis
0. 0° – 15° (parallel to axis)
1. > 15°

Chr. 49.Curvature of columellar lip
0. Slightly concave
1. Straight
2. Slightly convex
3. Convex to rounded

Chr. 50.Umbilicus
0. Wide, phaneromphalous
1. Narrow, phaneromphalous
2. Anomphalous or pseudoumbilicate (columellar lip curved backwards)
3. Filled with callus

Apertural characters

Chr. 51.Alignment of inner and outer lips
0. Outer lip standing forward
1. Outer and inner lips are aligned
2. Inner lip standing forward

Chr. 52.Angle of aperture inclination
0. 0° – 15° (aperture straight)
1. 16° – 45° (oblique)
2. > 45° (strongly oblique)

Shell accretion (shape of growth lines, ornament)

Chr. 53.Shape of growth line on ramp
0. Orthocline (straight, sweep backwards just above selenizone)
1. Prosocline (slightly convex, maximum curvature near selenizone)

2. Prosocyrt, evenly convex
3. Prosocyrt, with maximum curvature at adapical (upper) half
4. Opisthocyrt just below suture than prosocline or prosocyrt

Chr. 54.Inclination of growth line on upper whorl face relative to shell axis (App. 1-Fig. 1J)
0. 0° – 15°
1. 16° – 30°
2. 31° – 45°
3. > 45°

Chr. 55.Curvature of growth lines on lateral whorl face
0. Orthocline, sweep backwards just below selenizone
1. Prosocyrt, with maximum curvature near selenizone
2. Prosocyrt evenly convex
3. Prosocyrt, with maximum curvature near abapical suture

Chr. 56.Inclination of growth line on lateral whorl face relative to shell axis (App. 1-Fig. 1J)
0. -45° – -6° (abapical portion stands forward)
1. -5° – 5° (parallel to shell axis)
2. 6° – 45° (adapical portion stands forward)

Chr. 57.Basal growth lines
0. Prosocyrt
1. Sinuous prosocyrt (prosocyrt near periphery then opisthocyrt near shell axis)
2. Opisthocyrt
3. Sinuous opisthocyrt (opisthocyrt near periphery then prosocyrt near shell axis)

Chr. 58.Thickening of columellar lip
0. Present (e.g., *Glabrocingulum*)
1. Absent

Chr. 59.Dominant ornament on early whorls
0. Smooth
1. Spiral threads or lirae
2. Axial ribs
3. Reticulate ornament

Chr. 60.Early whorl ornament appears
0. immediately after protoconch (within first whorl)
1. within second whorl
2. after third whorl (first three whorls smooth)

Chr. 61.Density of axial ornament on early whorls
0. Dense (width of interspace smaller than two times width of ornament)

1. Moderate (width of interspace two to three times width of ornament)
2. Sparse (width of interspace is more than three times width of ornament)

Chr. 62.Shape of axial ornament on early whorls before onset of selenizone
0. Orthocline
1. Prosocyrt
2. Sinuous opisthocyrt (opisthocyrt at adapical half then prosocyrt)

Chr. 63.Density of spiral ornament on early whorls
0. Dense (width of interspace smaller than two times width of ornament)
1. Moderate (width of interspace two to three times width of ornament)
2. Sparse (width of interspace is more than three times width of ornament)

Chr. 64.Dominant ornament on late whorls
0. Smooth
1. Spiral ornament dominant
2. Axial ornament dominant or rough growth lines
3. Spiral and axial ornament about equal in strength (reticulate)
4. Reticulate ornament with stronger spiral ornament
5. Reticulate ornament with stronger axial ornament

Chr. 65.Nodes at intersection of spiral and axial ornament (reticulate ornament)
0. Absent
1. Weak beads (e.g., *Nodocingulum*)
2. Prominent nodes (e.g., *Paragoniozona*)

Chr. 66.Spiral ornament type
0. Absent
1. Thread or cord
2. Sharp edge (crest)
3. Antimarginal (e.g., *Luciella*)

Chr. 67.Density of spiral ornament on late whorls
0. Dense (width of interspace smaller than two times width of ornament)
1. Moderate (width of interspace two to three times width of ornament)
2. Sparse (width of interspace is more than three times width of ornament)

Chr. 68.Spiral microornament
0. Absent
1. Pustules

Chr. 69.Axial ornament type
0. Absent
1. Striae or grooves

2. Thread or rib
3. Sharp projecting lamella (e.g., *Brachytomaria*)

Chr. 70.Density of axial ornament on late whorls
0. Dense (width of interspace smaller than two times width of ornament)
1. Moderate (width of interspace two to three times width of ornament)
2. Sparse (width of interspace is more than three times width of ornament)

Chr. 71.Subsutural nodes (e.g., *Wortheniella*)
0. Absent
1. Present

Chr. 72.Formation of subsutural nodes
0. With onset of selenizone
1. After onset of selenizone
2. Before the onset of selenizone

Chr. 73.Prominent axial folds or ribs on ramp
0. Absent
1. Present

Chr. 74.Formation of prominent axial folds or ribs on ramp
0. With onset of selenizone
1. After onset of selenizone
2. Before the onset of selenizone

Chr. 75.Nodes on whorl angulations (e.g., *Pleurotomaria*)
0. Absent
1. Present

Chr. 76.Formation of nodes on whorl angulations
0. With onset of selenizone
1. After onset of selenizone
2. Before the onset of selenizone

Chr. 77.Density or prominence of ornament through whorl face
0. Prominence or density of ornament same through whorl face
1. Prominence or density of ornament increase towards adapical suture
2. Prominence or density of ornament increase towards adapical suture and abapical suture (~basal edge)
3. Prominence increases towards whorl angulations (median angulation and basal edge)

Chr. 78.Prominence of lateral whorl face ornament
0. Equal to prominence of ornament on whorl face above selenizone
1. Stronger than prominence of ornament on whorl face above selenizone

2. Weaker than prominence of ornament on whorl face above selenizone

Chr. 79.Prominence of ornament on base
0. Basal ornament is weaker than ornament on whorl face
1. Ornament on base and whorl face are equally prominent
2. Spiral ornament is more prominent on base than whorl face (e.g., *Nodocingulum*)
3. Axial ornament is more prominent on base than whorl face (e.g., *Schizogonium*)

Chr. 80.Ornament on columellar lip
0. As ornament on base
1. Smooth (e.g., *Rhineoderma*)

Ontogeny

Chr. 81.Whorl expansion rate (change in shell width within last whorl) (=W1/W App. 1-Fig. 1C)
0. WER < 1.20 (very low)
1. 1.21 < WER < 1.50 (low)
2. 1.51 < WER < 1.90 (moderate)
3. 1.91 < WER (high)

Chr. 82.Whorl expansion rate through ontogeny
0. No change
1. Increases (e.g., *Shwedagonia*)

Chr. 83.Early whorl elevation
0. Sunken (slight change in coiling direction, e.g., *Wortheniella*)
1. Planispiral
2. Slightly elevated (low trochiform)
3. Strongly elevated

Chr. 84.Coiling mode of early whorls
0. Planispiral
1. Dextral

Chr. 85.Coiling mode of late teleoconch whorls
0. Sinistral
1. Planispiral
2. Dextral

Chr. 86.Open coiling
0. Absent
1. Present in first whorls
2. Present in last whorl

Chr. 87.Position of suture
0. Above basal edge
1. On basal edge

Chr. 88.Shift in position of suture during ontogeny
0. Position same throughout ontogeny
1. Gradually shift downwards
2. Deflected downwards in last whorl (e.g., *Glabrocingulum*)

Chr. 89.Shell size (volume)
0. Very small (micro-mollusc: < 10 mm^3)
1. Small (10 –100 mm^3)
2. Moderate (100 –1000 mm^3)
3. Large (1000–10000 mm^3)
4. Huge (>10000 mm^3)

Chr. 90.Protoconch size (App. 1-Fig. 1B; ordered character)
0. 100 – 200 μm (small)
1. 201 – 300 μm (medium)
2. > 300 μm (large)

Chr. 91.First whorl width (Wfw, App. 1-Fig. 1B; ordered character)
0. 150 – 250 μm (small)
1. 251 – 350 μm (medium)
2. > 350 μm (large)

Chr. 92.Shell shape
0. Globular (e.g., *Gosseletina*)
1. Trochiform (convex whorl face)
2. Wortheniform (angular whorl face)
3. Conical (e.g., *Stuorella*)
4. Lenticular (e.g., *Trepospira*)
5. Evolute planispiral (e.g., *Porcellia*)

Appendix 3. Character matrix (in Nexus format)

```
#NEXUS

BEGIN DATA;
       DIMENSIONS  NTAX=109 NCHAR=93;
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         Baylea_giffordi
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;
END;
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Appendix 4. FAD and LAD of the taxa used in the analyses (in myr)

taxon	max	min
Trepospira_illinoiensis	313.80	298.90
Glabrocingulum_grayvillense	313.80	298.90
Ananias_tularosaensis	305.90	298.90
Baylea_giffordi	313.80	305.90
Spiroscala_shwedagoniformis	318.10	314.60
Eirlysella_buckhornensis	313.80	305.90
Phymatopleura_nodosa	313.80	305.90
Phymatopleura_brazoensis	305.90	298.90
Paragoniozona_paucinodosa	313.80	305.90
Worthenia_tabulata	303.40	298.90
Borestus_pagoda	318.10	314.60
Dictyotomaria_turrisbabel	303.40	298.90
Glyptotomaria_apiarium	303.40	298.90
Shansiella_carbonaria	313.80	298.90
Shansiella_globilineata	318.10	314.60
Proteomphalus_gracilis	237.00	230.50
Amplitomaria_spuria	237.00	230.50
Pseudoananias_subgranulata	237.00	230.50
Rhaphistomella_radians	237.00	230.50
Sisenna_venusta	237.00	230.50
Lineacingulum_texturatum	237.00	230.50
Rufilla_fasciolata	237.00	230.50
Temnotropis_carinata	237.00	230.50
Temnotropis_fuchsi	237.00	230.50
Pressulasphaera_pamphilus	237.00	230.50
Cancellotomaria_subcancellata	237.00	230.50
Zygites_subcancellata	237.00	230.50
Kokenella_costata	237.00	230.50
Lancedellia_costata	237.00	230.50
Acutitomaria_kustatscherae	237.00	230.50
Lineaetomaria_decorata	237.00	230.50
Kittlidiscus_bronni	237.00	230.50
Stuorella_tofanae	237.00	230.50
Stuorella_subconcava	237.00	230.50
Schizogonium_scalare	237.00	230.50
Schizogonium_subcostatum	237.00	230.50
Schizogonium_undae	237.00	230.50
Pseudowortheniella_rarissima	237.00	230.50
Wortheniella_coralliophila	237.00	230.50
Wortheniella_klipsteini	237.00	230.50
Bandelium_campense	237.00	230.50
Bandelium_ruedigeri	237.00	230.50
Nodocingulum_coronatum	237.00	230.50
Nodocingulum_granulosum	237.00	230.50
Nodocingulum_crenatum	237.00	230.50
Striacingulum_subcancellatum	237.00	230.50
Rinaldoella_rinaldoi	237.00	230.50
Rinaldoella_tornata	237.00	230.50
Pleurotomaria_anglica	190.80	182.70
Pleurotomaria_amalthei	190.80	182.70
Bathrotomaria_muensteri	163.50	157.30
Leptomaria_distinguenda	170.30	168.30
Pyrgotrochus_sp	170.30	168.30
Obornella_sp	170.30	168.30
Codinella_generelli	242.00	237.00
Eymarella_scalariformis	237.00	227.00
Eymarella_subscalariformis	237.00	227.00

taxon	max	min
Euryalox_subornatus	237.00	227.00
Euryalox_juvavica	247.20	242.00
Euzone_alauna	247.20	242.00
Sisenna_turbinata	237.00	227.00
Sisenna_daphne	237.00	227.00
Rufilla_densecincta	237.00	227.00
Lineacingulum_eremita	237.00	227.00
Trachybembix_junonis	242.00	237.00
Ptychomphalus_compressus	201.30	199.30
Ptychomphalus_politus	190.80	182.70
Angulomphalus_expansus	190.80	182.70
Cryptaenia_sp_	190.80	182.70
Kericserispira_faveolata	190.80	182.70
Trochotoma__Discotoma__auris	152.10	145.00
Valfinia_globulus	168.30	166.10
Neilsonia_sp_	346.70	330.90
Tapinotomaria_sp_	346.70	330.90
Borestus_sp_	346.70	330.90
Hesperiella_thomsoni	346.70	330.90
Hesperiella_sp	346.70	330.90
Sasakiella_ryckholtiana	346.70	330.90
Porcellia_puzo	358.90	346.70
Martinidiscus_woodwardii	346.70	330.90
Angyomphalus_desultoria	330.90	323.20
Baylea_yvanii	358.90	346.70
Gosseletina_callosa	346.70	330.90
Gosseletina_portlockiana	346.70	330.90
Mourlonia_carinata	346.70	330.90
Ptychomphalina_striata	346.70	330.90
Mourlonia_granulosa	346.70	330.90
Lunulazona_costata	346.70	330.90
Luciella_eliana	346.70	330.90
Rhineoderma_radula	358.90	346.70
Rhineoderma_wortheni	346.70	330.90
Dictyotomaria_sp	298.90	251.90
Dictyotomaria_sowerbyana	358.90	346.70
Eirlysia_lata	268.80	265.10
Apachella_thailandensis	272.95	268.80
Altotomaria_reticulata	272.95	268.80
Biarmeaspira_striata	268.80	265.10
Shwedagonia_pagoda	298.90	295.00
Calvibembexia_sulcomarginata	387.70	382.70
Euryzone_undulata	346.70	330.90
Euryzone_sp_	382.70	372.20
Bembexia_globosa	453.00	445.20
Clathrospira_trochiformis	458.40	453.00
Ruedemannia_thraivensis	453.00	445.20
Longstaffia_cyclonema	430.50	427.40
Bayerotrochus_midas	0.01	0.00
Eymarella_haueri	227.00	208.50
Kokenella_fischeri	227.00	208.50
Enantiostoma_perversum	227.00	208.50

Appendix 5. RevBayes code for the fossilized birth-death model

```
################################################################################################################
# This code is compiled by modifying the codes written by April M. Wright, Tracy A. Heath & Walker Pett
# The large part of the explanatory notes was written by these authors and kept without modification.
# The original codes can be reached from the following links:
# https://revbayes.github.io/tutorials/fbd/; https://revbayes.github.io/tutorials/morph_tree/V2.html
################################################################################################################

########################
# Reading in the Data #
########################

# Set working directory
setwd("C:\\Users\\Baran\\Baran\\Research\\Phylogeny of Pleurotomariida\\Data\\scripts")

# Import the taxa list
taxa <- readTaxonData("data/pleuro_age.tsv")

# Import the morphological character matrix
morpho <- readDiscreteCharacterData("data/pleuro.nex")

# helpers
n_taxa <- taxa.size()
moves = VectorMoves()

#############################################################################################
# Joint Fossilized Birth-Death Process prior on the topology and fossil occurrence times #
#############################################################################################

# Define exponential priors on the birth rate and death rate #
speciation_rate ~ dnExponential(10)
extinction_rate ~ dnExponential(10)

# Specify a scale move on the speciation_rate parameter #
# This move will be applied with 3 different tuning values (lambda) to help improve mixing #
moves.append( mvScale(speciation_rate, lambda=0.01, weight=1) )
moves.append( mvScale(speciation_rate, lambda=0.1,  weight=1) )
moves.append( mvScale(speciation_rate, lambda=1.0,  weight=1) )

# Specify a sliding-window move on the extinction_rate parameter #
# This move will be applied with 3 different window widths (delta) to help improve mixing #
moves.append( mvScale(extinction_rate, lambda=0.01, weight=1) )
moves.append( mvScale(extinction_rate, lambda=0.1,  weight=1) )
moves.append( mvScale(extinction_rate, lambda=1,    weight=1) )

# Create deterministic nodes for the diversification and turnover rates so that they can be monitored #
diversification := speciation_rate - extinction_rate
turnover := extinction_rate/speciation_rate

# Fix the probability of sampling parameter (rho) to 0.03 #
# because only one extant pleurotomariid species is included in this analysis #
rho <- 0.023

# Define an exponential prior on the rate of sampling fossils (psi) #
psi ~ dnExponential(10)

# Specify a scale move on the psi parameter #
```

```
# This move will be applied with 3 different tuning values (lambda) to help improve mixing #
moves.append( mvScale(psi, lambda=0.01, weight=1) )
moves.append( mvScale(psi, lambda=0.1,  weight=1) )
moves.append( mvScale(psi, lambda=1,    weight=1) )

# The FBD is conditioned on a starting time for the process, which is the origin time #
# Specify a uniform prior on the origin #
origin_time ~ dnUnif(460.0, 490.0)

# Specify a sliding-window move on the origin_time parameter #
# This move will be applied with 3 different window widths (delta) to help improve mixing #
moves.append( mvSlide(origin_time, delta=0.01, weight=5.0) )
moves.append( mvSlide(origin_time, delta=0.1,  weight=5.0) )
moves.append( mvSlide(origin_time, delta=1,    weight=5.0) )


### Define the tree-prior distribution as the fossilized birth-death process ###
fbd_tree ~ dnFBDRP(origin=origin_time, lambda=speciation_rate, mu=extinction_rate, psi=psi, rho=rho, taxa=taxa)

# Specify moves on the tree and node times #
# These moves update the tree topology
moves.append( mvFNPR(fbd_tree, weight=15.0) )
moves.append( mvCollapseExpandFossilBranch(fbd_tree, origin_time, weight=6.0) )

# These moves update the node ages #
# Because we are conditioning on the origin time, we must also sample the root node age #
moves.append( mvNodeTimeSlideUniform(fbd_tree, weight=40.0) )
moves.append( mvRootTimeSlideUniform(fbd_tree, origin_time, weight=5.0) )


### Create deterministic nodes to monitor various tree statistics ###
# Monitor the number of sampled ancestors in the FBD-tree #
num_samp_anc := fbd_tree.numSampledAncestors();


# Monitor the age of the extant pleurotomariids #
clade_extant = clade("Bayerotrochus_midas")
age_extant := tmrca(fbd_tree, clade_extant)

################################################################
# Branch rates #
################################################################

################################################################
# Uncorrelated lognormal model on morphological branch rates #
################################################################

### get the number of branches in the tree
n_branches <- 2 * n_taxa - 2

### the rate along each branch is assigned a lognormal prior
### the expectation of the lognormal is the ucln_mean, and will be given an exponential hyperprior
ucln_mean ~ dnExponential(2.0)
### we will also estimate the standard deviation of the lognormal (ucln_sigma) with an exponential hyperprior
ucln_sigma ~ dnExponential(3.0)
### we can create deterministic nodes for the variance and mu of the lognormal
ucln_var := ucln_sigma * ucln_sigma
ucln_mu := ln(ucln_mean) - (ucln_var * 0.5)
```

```
### both the ucln_mean and ucln_sigma will be operated on by scale moves
moves.append(mvScale(ucln_mean, lambda=1.0, tune=true, weight=4.0))
moves.append(mvScale(ucln_sigma, lambda=0.5, tune=true, weight=4.0))

### now we will create a vector of stochastic nodes
### each element in the vector represents a branch rate
### the indices of the vector correspond to branch indices in the tree
### using a for-lop initialize the branch rates and assign a move to each one
for(i in 1:n_branches){
   branch_rates[i] ~ dnLnorm(ucln_mu, ucln_sigma)
   moves.append(mvScale(branch_rates[i],lambda=1.0,tune=true,weight=2.0))
}
### add 2 more moves on the branch rate vector
moves.append(mvVectorScale(branch_rates,lambda=1.0,tune=true,weight=2.0))
moves.append(mvVectorSingleElementScale(branch_rates,lambda=30.0,tune=true,weight=1.0))

### a helpful parameter to monitor
mean_rt := mean(branch_rates)


###########################################
# Site rate model #
###########################################

#Set up Gamma-distributed rate variation.
alpha_morpho ~ dnExponential( 1.0 )
rates_morpho := fnDiscretizeGamma( alpha_morpho, alpha_morpho, 4 )

#Moves on the parameters to the Gamma distribution.
moves.append( mvScale(alpha_morpho, lambda=0.01, weight=5.0) )
moves.append( mvScale(alpha_morpho, lambda=0.1,  weight=3.0) )
moves.append( mvScale(alpha_morpho, lambda=1,    weight=1.0) )

###########################################
# Morphological substitution model #
###########################################

n_max_states <- 7
idx = 1
morpho_bystate[1] <- morpho
for (i in 2:n_max_states) {
morpho_bystate[i] <- morpho                    # make local tmp copy of data
morpho_bystate[i].setNumStatesPartition(i)          # only keep character blocks with state space equal to size i
nc = morpho_bystate[i].nchar()                 # get number of characters per character size with i-sized states
if (nc > 0) {q[idx] <- fnJC(i)                 # make i-by-i rate matrix

                    m_morph[idx] ~ dnPhyloCTMC ( tree=fbd_tree, Q=q[idx], nSites=nc, branchRates=branch_rates,
siteRates=rates_morpho, type="Standard")

                    m_morph[idx].clamp(morpho_bystate[i])

                    idx = idx + 1

                    idx}
}

########
# MCMC #
```

```
########

# initialize the model object #
mymodel = model(fbd_tree)

monitors = VectorMonitors()

# Create a vector of monitors #
# 1. for the full model #
monitors.append( mnModel(filename="output/pleuro_lnormal.log", printgen=10) )

# 2. the tree #
monitors.append( mnFile(filename="output/pleuro_lnormal.trees", printgen=10, fbd_tree) )

# 3. and a few select parameters to be printed to the screen #
monitors.append( mnScreen(printgen=10, num_samp_anc, origin_time) )

# Initialize the MCMC object #
mymcmc = mcmc(mymodel, monitors, moves)

# Run the MCMC #
mymcmc.run(generations=500000)

trace = readTreeTrace("output/pleuro_lnormal.trees")
mccTree(trace, file="output/pleuro_lnormal.mcc.tre" )

# Quit RevBayes #
q()
```

Appendix 6. Stratigraphic congruence metrics

Table 1. Stratigraphic congruence metrics for the most parsimonious trees (see App. 7-Figure 1 for the consensus tree)

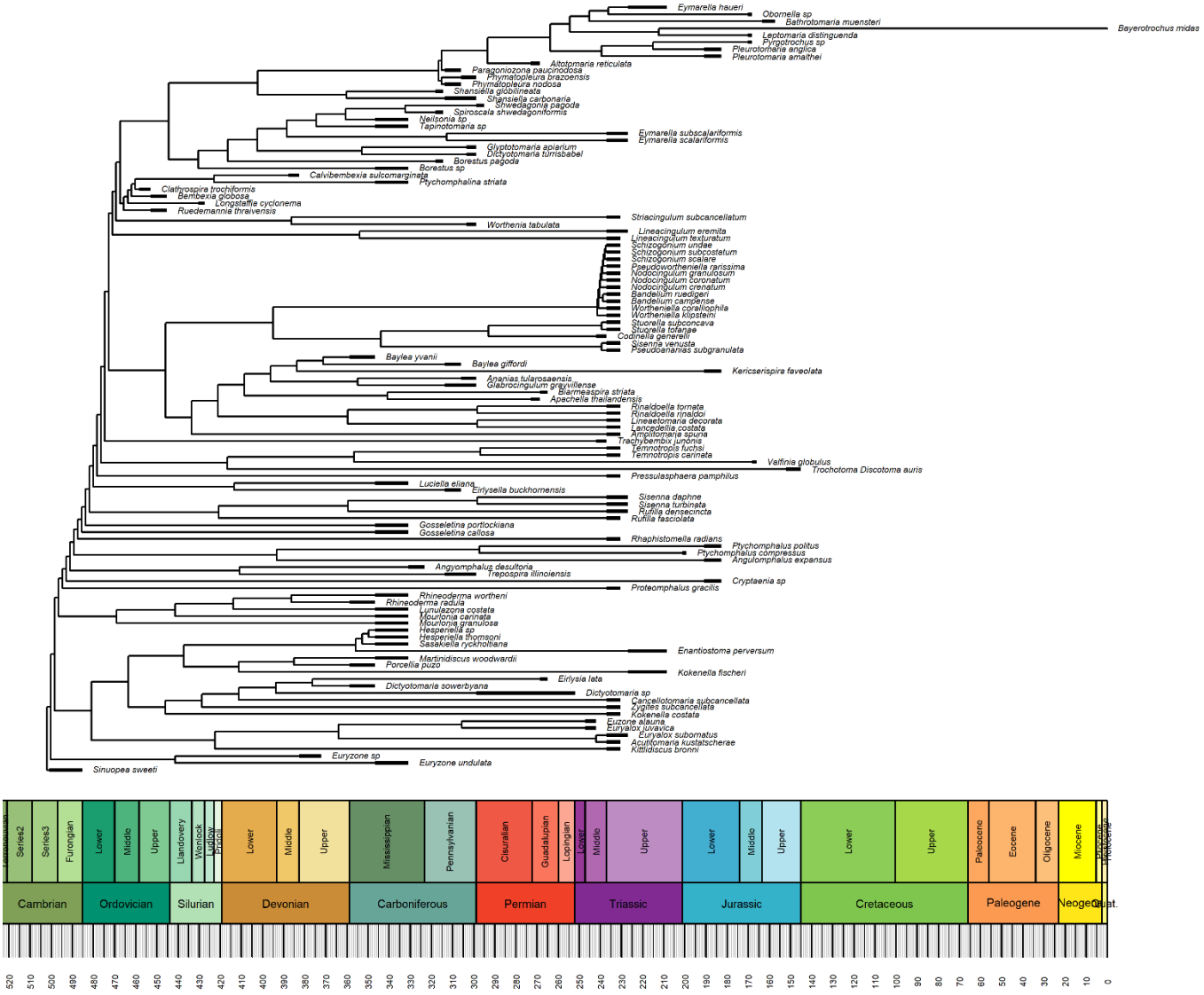
	SCI	RCI	GER	MSM*	est.p.SCI	est.p.RCI	est.p.GER	est.p.MSM*	MIG
tree_1	0.50	-530.21	0.77	0.08	9.30E-08	9.50E-14	1.80E-09	1.80E-16	6162.89
tree_2	0.51	-523.34	0.77	0.08	1.10E-08	8.30E-14	9.90E-10	3.70E-17	6095.69
tree_3	0.51	-529.14	0.77	0.08	1.10E-08	9.30E-14	1.60E-09	1.40E-16	6152.39
tree_4	0.50	-524.41	0.77	0.08	9.30E-08	8.50E-14	1.10E-09	4.80E-17	6106.19
tree_5	0.52	-516.31	0.77	0.08	1.20E-09	7.20E-14	5.30E-10	6.80E-18	6026.99
tree_6	0.51	-523.19	0.77	0.08	1.10E-08	8.30E-14	9.70E-10	3.60E-17	6094.19
tree_7	0.50	-518.79	0.77	0.08	9.30E-08	7.50E-14	6.60E-10	1.30E-17	6051.19
tree_8	0.50	-530.21	0.77	0.08	9.30E-08	9.50E-14	1.80E-09	1.80E-16	6162.89
tree_9	0.51	-529.14	0.77	0.08	1.10E-08	9.30E-14	1.60E-09	1.40E-16	6152.39
tree_10	0.51	-511.92	0.78	0.08	1.10E-08	6.60E-14	3.60E-10	2.30E-18	5983.99
tree_11	0.52	-522.11	0.77	0.08	1.20E-09	8.10E-14	8.90E-10	2.80E-17	6083.69
tree_12	0.51	-517.71	0.77	0.08	1.10E-08	7.40E-14	6.00E-10	9.60E-18	6040.69
tree_13	0.51	-517.39	0.77	0.08	1.10E-08	7.30E-14	5.80E-10	8.90E-18	6037.49
tree_14	0.50	-512.99	0.77	0.08	9.30E-08	6.70E-14	3.90E-10	3.00E-18	5994.49
tree_15	0.52	-522.11	0.77	0.08	1.20E-09	8.10E-14	8.90E-10	2.80E-17	6083.69
tree_16	0.52	-504.89	0.78	0.08	1.20E-09	5.70E-14	1.90E-10	3.80E-19	5915.29
tree_17	0.51	-511.76	0.78	0.08	1.10E-08	6.50E-14	3.50E-10	2.20E-18	5982.49
tree_18	0.51	-523.19	0.77	0.08	1.10E-08	8.30E-14	9.70E-10	3.60E-17	6094.19
tree_19	0.50	-518.79	0.77	0.08	9.30E-08	7.50E-14	6.60E-10	1.30E-17	6051.19
tree_20	0.51	-517.71	0.77	0.08	1.10E-08	7.40E-14	6.00E-10	9.60E-18	6040.69
tree_21	0.52	-510.69	0.78	0.08	1.20E-09	6.40E-14	3.20E-10	1.70E-18	5971.99
tree_22	0.51	-505.96	0.78	0.08	1.10E-08	5.80E-14	2.10E-10	5.00E-19	5925.79
tree_23	0.52	-510.69	0.78	0.08	1.20E-09	6.40E-14	3.20E-10	1.70E-18	5971.99
tree_24	0.51	-511.76	0.78	0.08	1.10E-08	6.50E-14	3.50E-10	2.20E-18	5982.49

Table 2. Stratigraphic congruence metrics for the bayesian tree calculated with 95 taxa recovered at the tips (see App. 7-Figure 2 for the MSACCT)

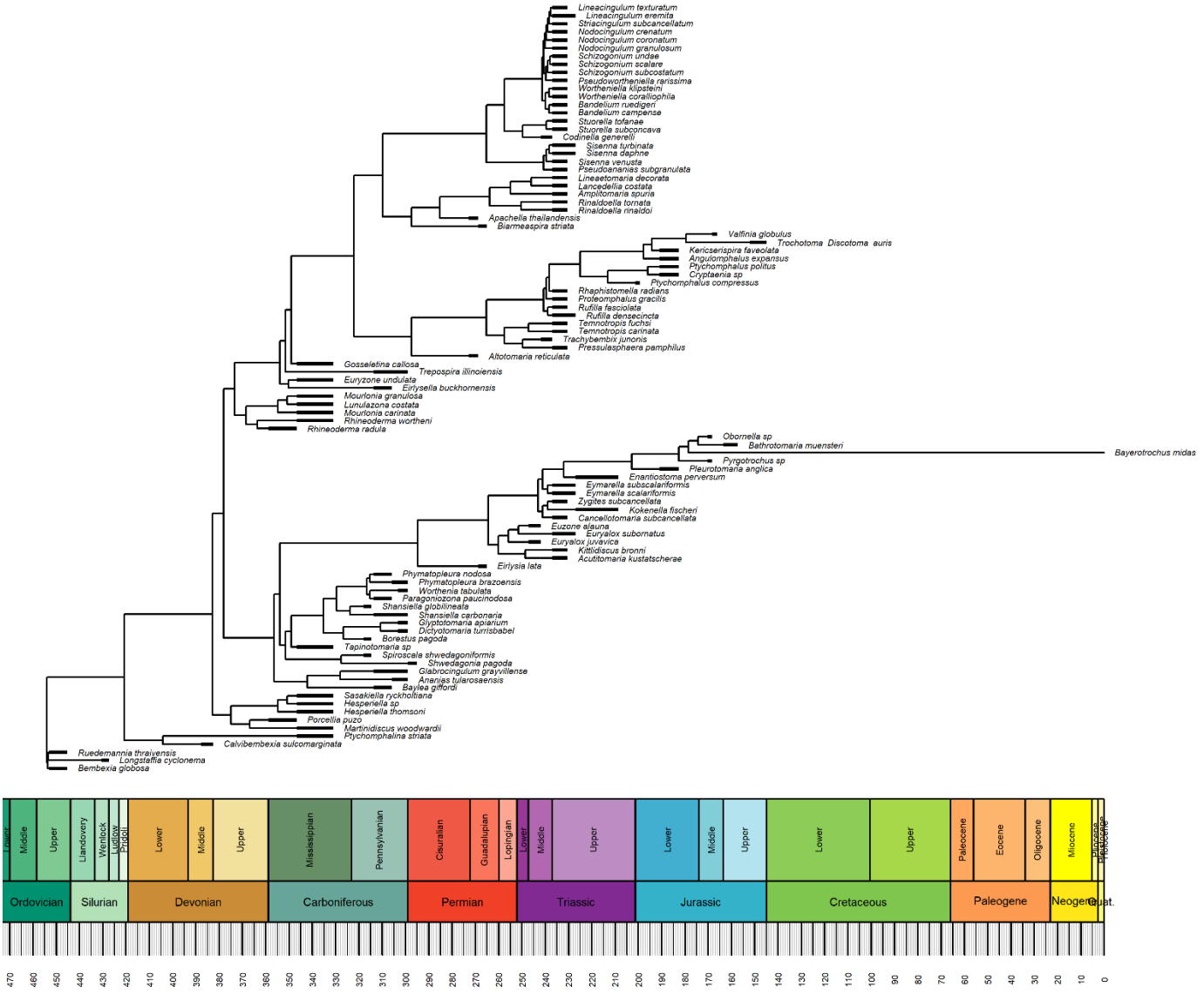
	SCI	RCI	GER	MSM*	est.p.SCI	est.p.RCI	est.p.GER	est.p.MSM*	MIG
bayes_tree_1	0.71	-48.30	0.96	0.40	1.70E-58	1.22E-21	6.27E-75	0	1140.44

Table 3. Stratigraphic congruence metrics for the bayesian tree, calculated with all 109 taxa, by supposing all taxa were recovered at the tips (see App. 7-Figure 3 for the MSACCT)

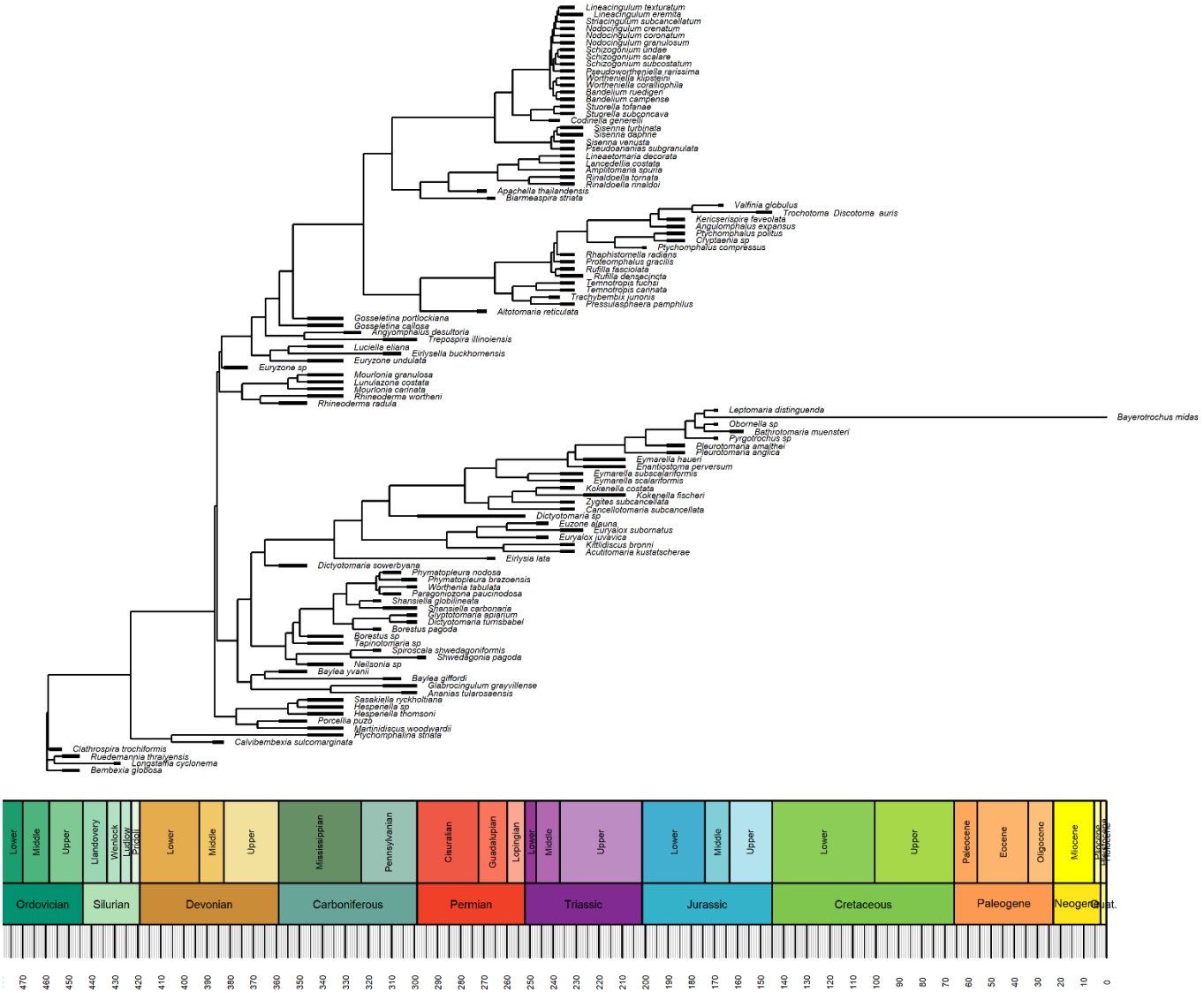
	SCI	RCI	GER	MSM*	est.p.SCI	est.p.RCI	est.p.GER	est.p.MSM*	MIG
bayes_tree_1	0.74	-43.34	0.95	0.33	1.20E-69	3.24E-21	1.02E-64	0	1379.34



App. 6-Figure 1: Time-scaled consensus tree of 24 MPTs.



App. 6-Figure 2: Time-scaled Bayesian tree only with 95 taxa recovered at the tips (i.e., without sampled ancestors).



App. 6-Figure 3: Time-scaled Bayesian tree with all 109 taxa. The sampled ancestors are treated as tip taxa to draw this tree.

#The code used in the R package "strap" (Bell & Lloyd 2015)

```
install.packages(c("geoscale", "strap"), dependencies=TRUE)
install.packages("paleotree" , dependencies=TRUE)
library(strap)
library(paleotree)
setwd("C:/Users/Baran/Baran/Research/Phylogeny of Pleurotomariida/Phd thesis/strap")

#Parsimony
pleuro.ages <- read.table("pleuro_age.txt", header=T)
pleuro.trees <- read.tree("24MPT.txt")
pleuro.tree <- DatePhylo(pleuro.trees[[1]], pleuro.ages, method="equal", rlen=1)
tiff("parsimony.tiff", units="in", width=7, height=6, res=600)
geoscalePhylo(ladderize(pleuro.tree, right=FALSE), pleuro.ages, cex.ts=0.4,
units=c("Period","Epoch"), vers="ICS2015")
dev.off()

Y <- StratPhyloCongruence(pleuro.trees, pleuro.ages, hard=FALSE,
randomly.sample.ages=TRUE, fix.topology=TRUE, fix.outgroup=TRUE)
Y$input.tree.results
write.table(Y$input.tree.results, "pleuro_strat_congruence.csv", sep=",")

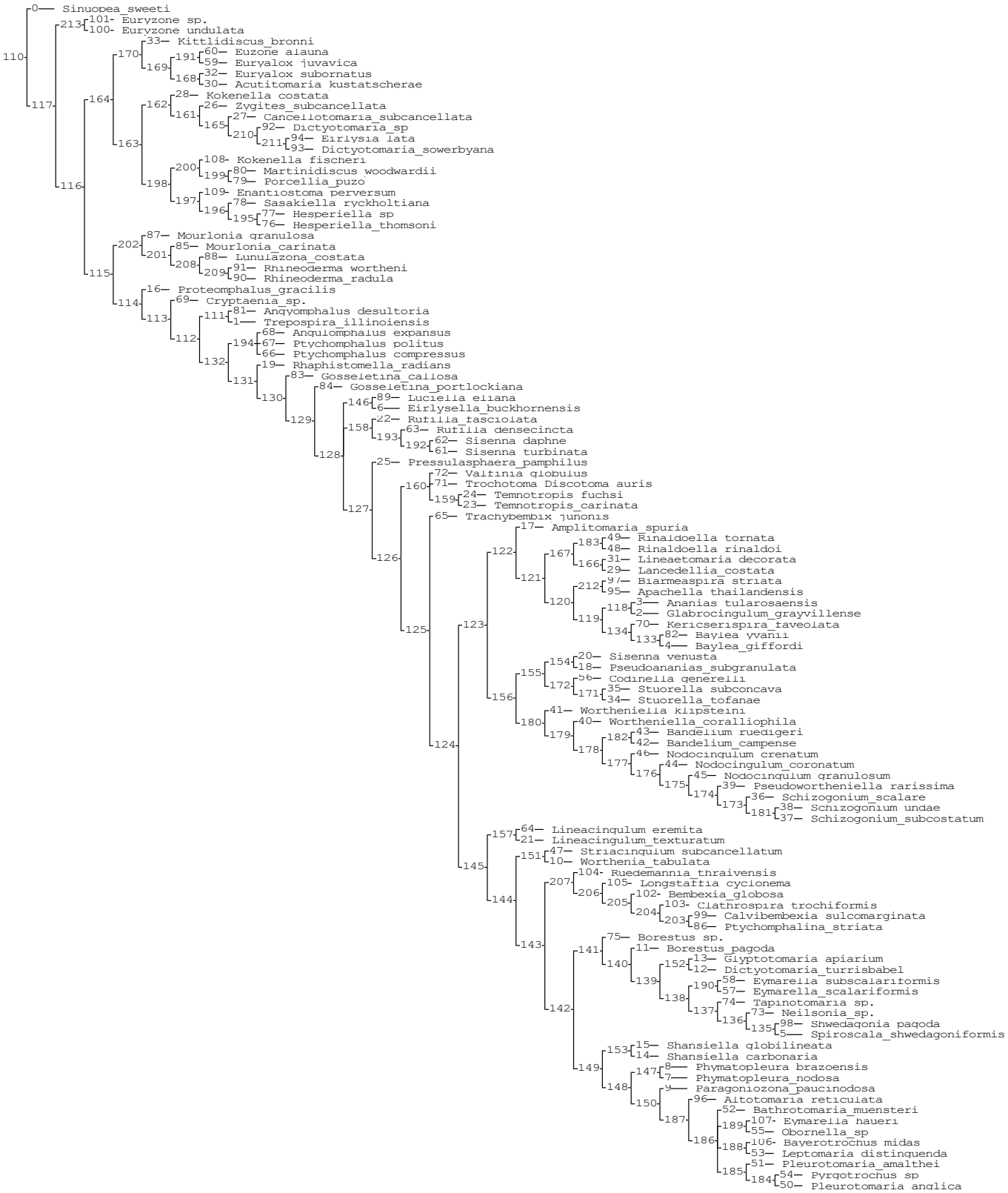
#Bayesian_without branch taxa
bayes.ages <- read.table("bayes_age.tsv", header=T)
bayes.tree <- read.tree("bayes.txt")
bayes.tree <- DatePhylo(bayes.tree, bayes.ages, method="equal", rlen=1)
tiff("bayesian_only_tips.tiff", units="in", width=7, height=6, res=600)
geoscalePhylo(ladderize(bayes.tree, right=FALSE), bayes.ages, cex.ts=0.4,
units=c("Period","Epoch"), vers="ICS2015")
dev.off()

X <- StratPhyloCongruence(bayes.tree, bayes.ages, hard=FALSE,
randomly.sample.ages=TRUE, fix.topology=TRUE, fix.outgroup=TRUE)
X$input.tree.results
write.table(X$input.tree.results, "bayes_strat_congruence_only_tip.csv", sep=",")

#Bayesian_taxa within branches as tips
bayes.ages <- read.table("bayes_age_all.tsv", header=T)
bayes.tree <- read.tree("bayes_tip.txt")
bayes.tree <- DatePhylo(bayes.tree, bayes.ages, method="equal", rlen=1)
tiff("bayesian_all.tiff", units="in", width=7, height=6, res=600)
geoscalePhylo(ladderize(bayes.tree, right=FALSE), bayes.ages, cex.ts=0.4,
units=c("Period","Epoch"), vers="ICS2015")
dev.off()

Z <- StratPhyloCongruence(bayes.tree, bayes.ages, hard=FALSE,
randomly.sample.ages=TRUE, fix.topology=TRUE, fix.outgroup=TRUE)
Z$input.tree.results
write.table(Z$input.tree.results, "bayes_strat_congruence_all.csv", sep=",")
```

Appendix 7. The list of apomorphies in the consensus tree of MPTs



App. 7-Figure 1: The consensus tree of 24 MPTs, with node numbers.

Sinuopea_sweeti
  No autapomorphies
Trepospira_illinoiensis
  Char. 0: 2 --> 3
  Char. 16: 1 --> 2
  Char. 37: 1 --> 0
  Char. 58: 1 --> 0
  Char. 71: 0 --> 1
  Glabrocingulum_grayvillense
  Char. 25: 2 --> 3
  Char. 48: 0 --> 1
  Char. 58: 1 --> 0
  Char. 69: 1 --> 2
  Char. 70: 0 --> 1
  Char. 87: 1 --> 0
  Char. 88: 0 --> 2
Ananias_tularosaensis
  Char. 24: 0 --> 3
  Char. 43: 1 --> 0
  Char. 46: 2 --> 1
  Char. 78: 0 --> 1
  Char. 89: 3 --> 2
Baylea_giffordi
  Char. 8: 1 --> 2
  Char. 18: 0 --> 5
  Char. 22: 3 --> 2
  Char. 28: 1 --> 0
  Char. 30: 0 --> 1
  Char. 84: 1 --> 0
  Char. 89: 3 --> 1
Spiroscala_shwedagoniformis
  Char. 4: 2 --> 3
  Char. 26: 4 --> 3
  Char. 39: 2 --> 3
  Char. 40: 3 --> 0
  Char. 42: 1 --> 0
  Char. 90: 1 --> 2
  Char. 91: 1 --> 2
Eirlysella_buckhornensis
  Char. 4: 4 --> 6
  Char. 8: 2 --> 3
  Char. 15: 1 --> 3
  Char. 16: 1 --> 3
  Char. 25: 3 --> 2
  Char. 26: 3 --> 4
  Char. 37: 3 --> 4
  Char. 43: 0 --> 1
  Char. 44: 1 --> 2
  Char. 46: 2 --> 0
  Char. 49: 2 --> 1
  Char. 79: 1 --> 0
  Char. 84: 1 --> 0
Phymatopleura_nodosa
  Char. 30: 0 --> 1
  Char. 32: 0 --> 1
  Char. 52: 1 --> 2
  Char. 53: 2 --> 3
  Char. 67: 0 --> 1
  Char. 70: 0 --> 1
  Char. 77: 0 --> 1
  Char. 91: 1 --> 2
Phymatopleura_brazoensis
  Char. 1: 0 --> 1
  Char. 24: 1 --> 2
  Char. 39: 2 --> 1
  Char. 40: 2 --> 3
  Char. 55: 4 --> 1
  Char. 92: 2 --> 3
Paragoniozona_paucinodosa
  Char. 4: 2 --> 1
  Char. 10: 1 --> 2
  Char. 13: 0 --> 1
  Char. 17: 2 --> 3
  Char. 18: 15 --> 3
  Char. 26: 3 --> 4
  Char. 39: 2 --> 3
  Char. 45: 0 --> 2
  Char. 54: 2 --> 3
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Node 138
  Char. 10: 2 --> 3
  Char. 15: 2 --> 3
  Char. 16: 2 --> 3
  Char. 33: 3 --> 2
Node 139
  Char. 26: 3 --> 4
  Char. 28: 1 --> 2
  Char. 81: 2 --> 1
Node 140
  Char. 0: 2 --> 1
  Char. 34: 2 --> 1
  Char. 91: 1 --> 2
Node 141
  Char. 10: 1 --> 2
  Char. 14: 1 --> 0
  Char. 79: 2 --> 1
Node 142
  Char. 4: 3 --> 2
  Char. 15: 01 --> 2
  Char. 16: 1 --> 2
  Char. 33: 1 --> 3
  Char. 45: 2 --> 0
  Char. 46: 2 --> 1
  Char. 65: 0 --> 1
Node 143
  Char. 42: 2 --> 1
  Char. 67: 1 --> 2
Node 144
  Char. 20: 0 --> 1
  Char. 54: 2 --> 1
Node 145
  Char. 17: 0 --> 1
  Char. 18: 0 --> 1
  Char. 39: 1 --> 2
  Char. 45: 0 --> 2
  Char. 64: 1 --> 3
  Char. 69: 01 --> 2
Node 146
  Char. 12: 0 --> 1
  Char. 18: 0 --> 1
  Char. 37: 1 --> 3
  Char. 38: 1 --> 0
  Char. 57: 2 --> 1
  Char. 66: 1 --> 3
  Char. 80: 0 --> 1
  Char. 92: 0 --> 3
Node 147
  Char. 48: 0 --> 1
  Char. 60: 1 --> 0
  Char. 71: 0 --> 1
Node 148
  Char. 17: 1 --> 2
  Char. 19: 0 --> 1
  Char. 29: 1 --> 0
  Char. 67: 2 --> 0
Node 149
  Char. 23: 0 --> 1
  Char. 32: 1 --> 0
  Char. 40: 1 --> 2
  Char. 54: 1 --> 2
  Char. 70: 1 --> 0
Node 150
  Char. 16: 2 --> 1
  Char. 28: 1 --> 2
  Char. 56: 0 --> 1
  Char. 63: 0 --> 1
Node 151
  Char. 8: 2 --> 1
  Char. 23: 0 --> 1
  Char. 29: 1 --> 0
  Char. 41: 1 --> 0
  Char. 77: 0 --> 2
  Char. 78: 0 --> 1
Node 152
  Char. 37: 2 --> 1
  Char. 39: 2 --> 3
  Char. 40: 1 --> 0
  Char. 43: 1 --> 2
  Char. 70: 1 --> 0
  Char. 77: 0 --> 2
Node 153
  Char. 8: 2 --> 1
  Char. 25: 2 --> 3
  Char. 28: 1 --> 3
  Char. 43: 1 --> 0
  Char. 58: 1 --> 0
  Char. 66: 1 --> 2
  Char. 79: 2 --> 0
  Char. 92: 2 --> 1
Node 154
  Char. 8: 2 --> 1
  Char. 25: 2 --> 3
  Char. 53: 2 --> 3
Node 155
  Char. 28: 0 --> 1
  Char. 46: 2 --> 1
  Char. 48: 0 --> 1
Node 156
  Char. 56: 0 --> 1
  Char. 60: 1 --> 0
  Char. 74: 1 --> 2
Node 157
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  Char. 1: 0 --> 1
  Char. 16: 1 --> 0
  Char. 21: 0 --> 1
  Char. 26: 3 --> 4
  Char. 47: 1 --> 0
  Char. 50: 2 --> 0
  Char. 59: 1 --> 0
  Char. 79: 2 --> 0
Node 158
  Char. 42: 1 --> 23
  Char. 50: 2 --> 1
  Char. 67: 0 --> 1
  Char. 78: 0 --> 2
Node 159
  Char. 0: 2 --> 1
  Char. 16: 1 --> 2
  Char. 53: 2 --> 1
  Char. 58: 1 --> 0
Node 160
  Char. 34: 0 --> 2
  Char. 41: 1 --> 0
  Char. 49: 2 --> 3
  Char. 52: 1 --> 2
Node 161
  Char. 27: 1 --> 0
  Char. 38: 0 --> 1
  Char. 81: 3 --> 2
Node 162
  Char. 3: 0 --> 1
  Char. 16: 3 --> 2
  Char. 60: 1 --> 0
Node 163
  Char. 8: 2 --> 1
  Char. 49: 2 --> 3
  Char. 57: 2 --> 0
Node 164
```

```
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  Char. 16: 1 --> 3
  Char. 17: 0 --> 1
  Char. 50: 12 --> 0
  Char. 59: 0 --> 2
  Char. 64: 2 --> 3
Node 165
  Char. 4: 2 --> 3
  Char. 25: 3 --> 2
  Char. 50: 0 --> 1
  Char. 59: 2 --> 3
  Char. 78: 0 --> 2
Node 166
  Char. 8: 2 --> 1
  Char. 9: 1 --> 2
  Char. 40: 1 --> 0
  Char. 55: 4 --> 0
  Char. 59: 1 --> 2
  Char. 84: 0 --> 1
Node 167
  Char. 14: 1 --> 0
  Char. 42: 2 --> 34
  Char. 56: 0 --> 2
  Char. 69: 1 --> 2
  Char. 89: 1 --> 0
Node 168
  Char. 9: 2 --> 1
  Char. 25: 23 --> 1
  Char. 28: 3 --> 2
  Char. 42: 1 --> 2
  Char. 81: 3 --> 1
Node 169
  Char. 14: 1 --> 2
  Char. 15: 3 --> 2
  Char. 38: 0 --> 1
  Char. 45: 2 --> 1
  Char. 64: 3 --> 4
Node 170
  Char. 10: 1 --> 3
  Char. 61: 1 --> 2
  Char. 63: 01 --> 2
  Char. 84: 0 --> 1
Node 171
  Char. 4: 3 --> 1
  Char. 17: 0 --> 3
  Char. 28: 1 --> 2
  Char. 40: 1 --> 2
  Char. 50: 2 --> 1
  Char. 64: 1 --> 2
  Char. 67: 1 --> 0
Node 172
  Char. 26: 3 --> 4
  Char. 32: 1 --> 0
  Char. 57: 2 --> 3
  Char. 81: 2 --> 0
  Char. 92: 2 --> 3
Node 173
  Char. 9: 1 --> 2
  Char. 43: 1 --> 3
Node 174
  Char. 0: 3 --> 2
  Char. 41: 0 --> 1
  Char. 59: 3 --> 2
  Char. 62: 1 --> 0
  Char. 64: 4 --> 2
  Char. 67: 1 --> 0
  Char. 79: 2 --> 1
  Char. 81: 2 --> 3
Node 175
  Char. 4: 3 --> 4
  Char. 8: 2 --> 1
  Char. 50: 2 --> 1
  Char. 91: 0 --> 1
Node 176
  Char. 25: 2 --> 3
  Char. 46: 2 --> 1
  Char. 61: 1 --> 0
  Char. 68: 1 --> 0
  Char. 70: 1 --> 0
  Char. 83: 0 --> 1
Node 177
  Char. 41: 1 --> 0
  Char. 69: 0 --> 2
Node 178
  Char. 55: 4 --> 1
  Char. 56: 1 --> 2
Node 179
  Char. 17: 0 --> 3
  Char. 20: 0 --> 1
  Char. 39: 1 --> 2
  Char. 83: 1 --> 0
Node 180
  Char. 18: 0 --> 3
Node 181
  Char. 8: 1 --> 0
  Char. 26: 3 --> 2
  Char. 28: 2 --> 1
  Char. 39: 2 --> 1
Node 182
  Char. 4: 3 --> 4
  Char. 61: 1 --> 2
  Char. 66: 1 --> 0
  Char. 89: 1 --> 0
Node 183
  Char. 27: 1 --> 0
  Char. 29: 1 --> 0
  Char. 43: 1 --> 0
  Char. 44: 2 --> 3
  Char. 50: 2 --> 1
Node 184
  Char. 28: 2 --> 1
  Char. 56: 1 --> 0
  Char. 65: 1 --> 0
Node 185
  Char. 16: 1 --> 0
  Char. 75: 0 --> 1
Node 186
  Char. 0: 2 --> 1
  Char. 3: 0 --> 1
  Char. 20: 1 --> 0
  Char. 32: 0 --> 1
  Char. 39: 2 --> 1
  Char. 60: 1 --> 0
  Char. 61: 0 --> 1
  Char. 89: 1 --> 4
Node 187
  Char. 4: 2 --> 3
  Char. 23: 1 --> 0
  Char. 42: 01 --> 2
  Char. 59: 1 --> 3
  Char. 91: 1 --> 2
Node 188
  Char. 27: 1 --> 0
  Char. 64: 4 --> 3
  Char. 65: 1 --> 2
Node 189
  Char. 8: 2 --> 1
  Char. 18: 5 --> 0
  Char. 24: 1 --> 0
  Char. 42: 2 --> 1
  Char. 53: 2 --> 1
  Char. 56: 1 --> 0
Node 190
  Char. 17: 1 --> 2
  Char. 34: 1 --> 2
  Char. 47: 1 --> 0
  Char. 48: 0 --> 1
  Char. 49: 2 --> 0
  Char. 50: 12 --> 0
  Char. 54: 1 --> 2
  Char. 59: 1 --> 3
Node 191
  Char. 55: 0 --> 1
  Char. 61: 2 --> 0
  Char. 83: 1 --> 2
  Char. 91: 1 --> 2
Node 192
  Char. 2: 1 --> 0
  Char. 16: 1 --> 0
  Char. 28: 2 --> 1
  Char. 32: 0 --> 1
  Char. 42: 23 --> 4
  Char. 59: 1 --> 0
  Char. 81: 3 --> 2
  Char. 83: 2 --> 1
  Char. 84: 1 --> 0
  Char. 89: 1 --> 2
  Char. 92: 0 --> 2
Node 193
  Char. 9: 1 --> 0
  Char. 23: 0 --> 1
  Char. 24: 0 --> 1
  Char. 44: 1 --> 2
  Char. 91: 1 --> 2
Node 194
  Char. 33: 1 --> 0
  Char. 49: 2 --> 3
  Char. 90: 1 --> 2
  Char. 91: 1 --> 2
Node 195
  Char. 50: 0 --> 2
  Char. 84: 0 --> 1
Node 196
```
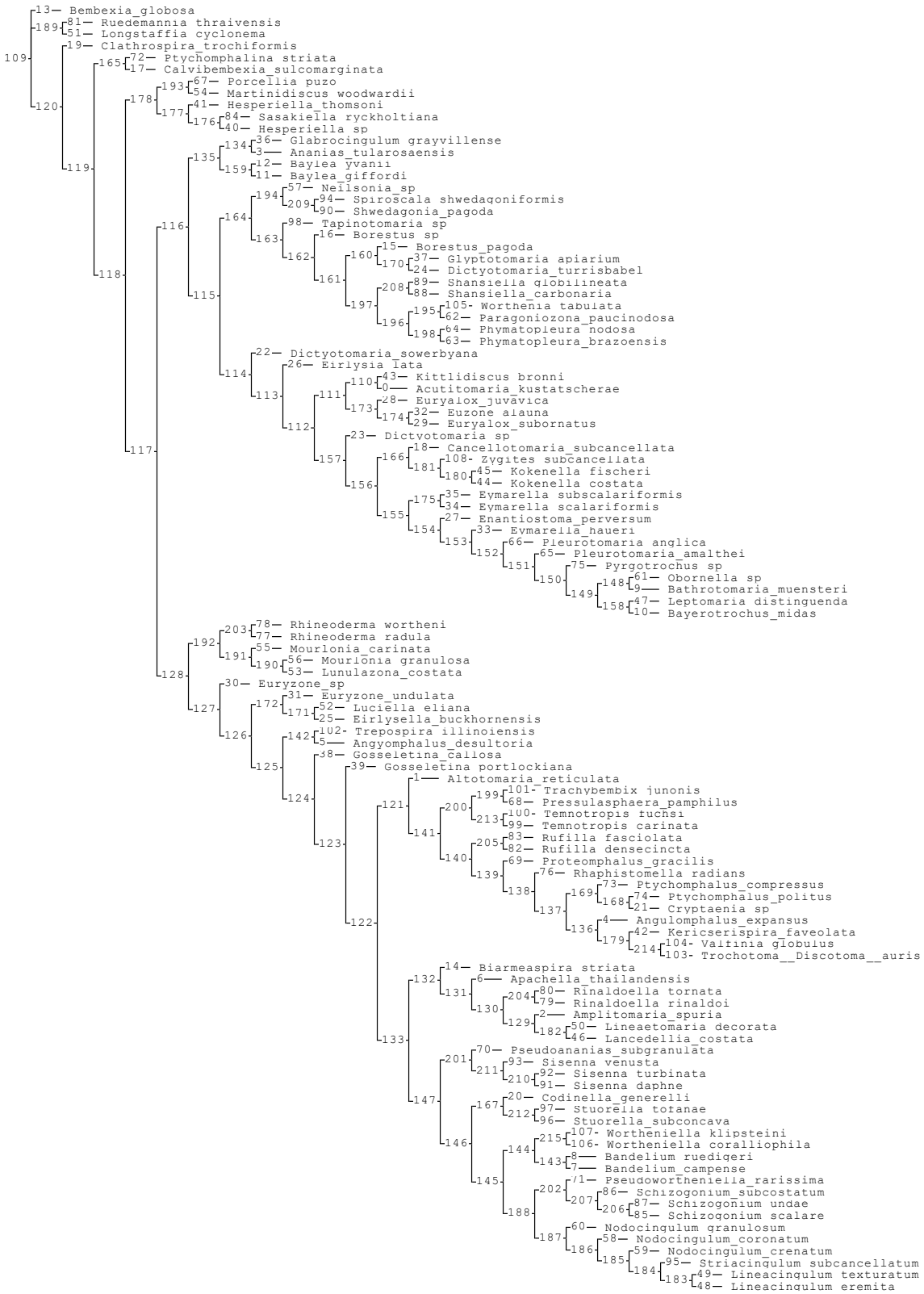

```
  Char. 13: 0 --> 1
  Char. 26: 3 --> 4
  Char. 44: 2 --> 3
  Char. 46: 2 --> 1
  Char. 66: 1 --> 0
  Char. 91: 1 --> 2
Node 197
  Char. 4: 2 --> 1
  Char. 27: 1 --> 0
  Char. 37: 2 --> 3
  Char. 81: 3 --> 2
Node 198
  Char. 20: 2 --> 1
  Char. 61: 1 --> 0
  Char. 67: 2 --> 0
Node 199
  Char. 8: 1 --> 0
  Char. 18: 1 --> 0
  Char. 26: 2 --> 1
  Char. 27: 1 --> 2
  Char. 54: 2 --> 1
  Char. 84: 0 --> 1
Node 200
  Char. 25: 3 --> 4
  Char. 26: 3 --> 2
  Char. 44: 2 --> 1
  Char. 92: 1 --> 5
Node 201
  Char. 84: 0 --> 1
Node 202
  Char. 9: 2 --> 1
  Char. 46: 2 --> 1
  Char. 53: 2 --> 3
  Char. 65: 0 --> 2
Node 203
  Char. 8: 2 --> 1
  Char. 17: 1 --> 0
  Char. 25: 2 --> 3
  Char. 49: 2 --> 1
  Char. 59: 2 --> 0
  Char. 81: 2 --> 3
  Char. 87: 1 --> 0
Node 204
  Char. 4: 3 --> 2
  Char. 39: 2 --> 3
  Char. 46: 2 --> 1
Node 205
  Char. 14: 1 --> 2
  Char. 16: 1 --> 3
  Char. 33: 1 --> 0
  Char. 66: 1 --> 0
  Char. 89: 2 --> 3
Node 206
  Char. 45: 2 --> 1
  Char. 70: 1 --> 0
  Char. 79: 2 --> 1
Node 207
  Char. 10: 1 --> 3
  Char. 35: 0 --> 1
  Char. 43: 1 --> 0
  Char. 92: 2 --> 3
Node 208
  Char. 28: 3 --> 2
  Char. 45: 2 --> 3
Node 209
  Char. 4: 2 --> 1
  Char. 10: 1 --> 3
  Char. 19: 0 --> 1
  Char. 24: 0 --> 2
  Char. 29: 1 --> 0
  Char. 53: 3 --> 2
  Char. 59: 0 --> 3
  Char. 64: 2 --> 4
  Char. 80: 0 --> 1
Node 210
  Char. 9: 2 --> 1
  Char. 10: 1 --> 2
  Char. 20: 2 --> 0
  Char. 28: 3 --> 2
  Char. 55: 0 --> 4
  Char. 56: 1 --> 0
  Char. 67: 2 --> 1
  Char. 70: 2 --> 1
  Char. 83: 1 --> 2
  Char. 84: 0 --> 1
Node 211
  Char. 0: 1 --> 2
  Char. 13: 0 --> 1
  Char. 48: 1 --> 0
  Char. 61: 1 --> 0
  Char. 77: 0 --> 2
  Char. 79: 1 --> 0
Node 212
  Char. 25: 2 --> 1
  Char. 54: 2 --> 1
Node 213
  Char. 3: 0 --> 1
  Char. 27: 1 --> 0
  Char. 28: 3 --> 2
  Char. 45: 2 --> 1
```

Appendix 8. The list of apomorphies in the Bayesian (MSACC) tree



App. 8-Figure 1: The bayesian (MSACC) tree, with node numbers. The sampled ancestors are reconstructed as terminal taxa.

Acutitomaria_kustatschera
  Char. 7: 0 --> 1
  Char. 10: 3 --> 1
  Char. 20: 2 --> 1
  Char. 44: 2 --> 3
  Char. 50: 0 --> 2
  Char. 64: 3 --> 5
  Char. 77: 0 --> 1
  Char. 84: 1 --> 0
Altotomaria_reticulata
  Char. 15: 1 --> 3
  Char. 18: 0 --> 1
  Char. 24: 0 --> 1
  Char. 27: 1 --> 0
  Char. 40: 2 --> 3
  Char. 42: 1 --> 4
  Char. 48: 1 --> 0
  Char. 49: 2 --> 3
  Char. 53: 2 --> 0
  Char. 55: 4 --> 0
  Char. 59: 1 --> 3
  Char. 63: 0 --> 1
  Char. 64: 1 --> 4
  Char. 65: 0 --> 1
  Char. 67: 0 --> 1
  Char. 69: 0 --> 2
  Char. 78: 0 --> 1
  Char. 79: 1 --> 0
  Char. 81: 3 --> 1
  Char. 92: 0 --> 1
Amplitomaria_spuria
  Char. 2: 1 --> 0
  Char. 14: 0 --> 2
  Char. 21: 0 --> 1
  Char. 24: 0 --> 3
  Char. 25: 2 --> 3
  Char. 28: 2 --> 3
  Char. 34: 1 --> 0
  Char. 42: 4 --> 1
  Char. 73: 0 --> 1
  Char. 77: 0 --> 2
  Char. 87: 1 --> 0
Ananias_tularosaensis
  Char. 24: 0 --> 3
  Char. 67: 1 --> 0
  Char. 78: 0 --> 1
Angulomphalus_expansus
  Char. 14: 1 --> 2
  Char. 24: 0 --> 3
  Char. 42: 1 --> 2
  Char. 67: 0 --> 1
Angyomphalus_desultoria
  Char. 28: 2 --> 1
  Char. 47: 1 --> 0
Apachella_thailandensis
  Char. 26: 3 --> 4
  Char. 41: 1 --> 0
  Char. 45: 0 --> 1
  Char. 49: 2 --> 1
  Char. 78: 0 --> 2
  Char. 81: 2 --> 1
Bandelium_campense
  Char. 26: 3 --> 2
  Char. 42: 2 --> 5
  Char. 73: 0 --> 1
  Char. 79: 2 --> 1
  Char. 81: 2 --> 1
  Char. 92: 2 --> 1
Bandelium_ruedigeri
  Char. 2: 0 --> 1
  Char. 3: 0 --> 1
  Char. 4: 4 --> 5
  Char. 27: 1 --> 2
  Char. 57: 2 --> 3
  Char. 58: 1 --> 0
Bathrotomaria_muensteri
  Char. 58: 1 --> 0
Bayerotrochus_midas
  Char. 0: 1 --> 0
  Char. 16: 1 --> 2
  Char. 25: 2 --> 3
  Char. 41: 1 --> 2
  Char. 44: 2 --> 1
  Char. 49: 2 --> 1
  Char. 54: 2 --> 3
Baylea_giffordi
  Char. 8: 1 --> 2
  Char. 18: 0 --> 5
  Char. 22: 3 --> 2
  Char. 28: 1 --> 0
  Char. 30: 0 --> 1
  Char. 43: 0 --> 1
  Char. 50: 1 --> 2
  Char. 84: 1 --> 0
Baylea_yvanii
  Char. 40: 1 --> 2
  Char. 49: 2 --> 1
  Char. 78: 0 --> 1
  Char. 81: 2 --> 1
Bembexia_globosa
  Char. 58: 1 --> 0
Biarmeaspira_striata
  Char. 21: 0 --> 1
  Char. 24: 0 --> 1
  Char. 45: 0 --> 2
  Char. 53: 2 --> 4
  Char. 55: 4 --> 1
  Char. 69: 0 --> 1
  Char. 89: 1 --> 2
Borestus_pagoda
  Char. 83: 2 --> 1
  Char. 84: 1 --> 0
Borestus_sp
  Char. 55: 4 --> 3
Calvibembexia_sulcomarginata
  Char. 29: 1 --> 0
  Char. 35: 0 --> 1
  Char. 41: 1 --> 0
  Char. 43: 0 --> 1
  Char. 55: 4 --> 3
  Char. 57: 2 --> 3
  Char. 58: 1 --> 0
  Char. 77: 0 --> 3
  Char. 78: 0 --> 2
  Char. 91: 1 --> 0
  Char. 92: 1 --> 4
Cancellotomaria_subcancellata
  Char. 4: 2 --> 3
  Char. 37: 2 --> 1
  Char. 49: 3 --> 2
  Char. 61: 0 --> 1
  Char. 63: 0 --> 1
Clathrospira_trochiformis
  Char. 24: 0 --> 3
  Char. 78: 0 --> 2
Codinella_generelli
  Char. 15: 1 --> 2
  Char. 16: 1 --> 3
  Char. 23: 0 --> 1
  Char. 42: 2 --> 4
  Char. 44: 2 --> 1
  Char. 54: 2 --> 0
  Char. 78: 0 --> 2
  Char. 79: 2 --> 0
Cryptaenia_sp
  Char. 9: 1 --> 2
  Char. 28: 2 --> 3
  Char. 32: 1 --> 0
  Char. 37: 1 --> 3
  Char. 38: 1 --> 0
  Char. 44: 1 --> 2
  Char. 83: 2 --> 1
  Char. 84: 1 --> 0
Dictyotomaria_sowerbyana
  Char. 4: 2 --> 3
  Char. 57: 3 --> 0
Dictyotomaria_sp
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  Char. 57: 3 --> 0
  Char. 61: 0 --> 1
  Char. 63: 0 --> 1
Dictyotomaria_turrisbabel
  Char. 20: 1 --> 0
  Char. 27: 1 --> 0
  Char. 30: 0 --> 1
  Char. 55: 4 --> 3
Eirlysella_buckhornensis
  Char. 15: 1 --> 3
  Char. 16: 1 --> 3
  Char. 26: 3 --> 4
  Char. 43: 0 --> 1
  Char. 44: 1 --> 2
  Char. 46: 2 --> 0
  Char. 49: 2 --> 1
Eirlysia_lata
  Char. 8: 2 --> 1
  Char. 23: 0 --> 1
  Char. 37: 2 --> 1
  Char. 39: 2 --> 1
  Char. 41: 1 --> 0
  Char. 43: 0 --> 2
  Char. 45: 1 --> 0
Enantiostoma_perversum

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Char. 28: 2 --> 3
Char. 38: 1 --> 0
Char. 45: 1 --> 3
Char. 53: 2 --> 3
Char. 54: 2 --> 3
Char. 57: 3 --> 0
Char. 85: 2 --> 0
Char. 88: 0 --> 1
Euryalox_juvavica
Char. 26: 3 --> 4
Char. 65: 0 --> 1
Euryalox_subornatus
Char. 4: 2 --> 3
Char. 37: 2 --> 1
Char. 45: 1 --> 0
Char. 53: 2 --> 0
Char. 61: 0 --> 2
Euryzone_sp
Char. 0: 2 --> 1
Char. 3: 0 --> 1
Char. 27: 1 --> 0
Char. 67: 0 --> 2
Euryzone_undulata
Char. 3: 0 --> 1
Char. 27: 1 --> 0
Char. 77: 0 --> 1
Euzone_alauna
Char. 0: 4 --> 3
Char. 40: 2 --> 1
Char. 67: 2 --> 1
Eymarella_haueri
Char. 9: 1 --> 2
Char. 53: 2 --> 1
Char. 63: 0 --> 2
Eymarella_scalariformis
Char. 25: 2 --> 1
Char. 79: 1 --> 0
Char. 89: 2 --> 3
Eymarella_subscalariformis
Char. 18: 1 --> 5
Char. 29: 1 --> 0
Glabrocingulum_grayvillense
Char. 25: 2 --> 3
Char. 43: 0 --> 1
Char. 58: 1 --> 0
Char. 70: 0 --> 1
Char. 87: 1 --> 0
Char. 88: 0 --> 2
Glyptotomaria_apiarium
Char. 32: 1 --> 0
Char. 54: 1 --> 2
Char. 56: 0 --> 1
Char. 92: 2 --> 3
Gosseletina_callosa
Char. 42: 1 --> 2
Char. 81: 3 --> 2
Char. 84: 0 --> 1
Gosseletina_portlockiana
Char. 53: 2 --> 1
Hesperiella_sp
Char. 20: 1 --> 0
Hesperiella_thomsoni
Char. 19: 0 --> 1
Char. 25: 23 --> 1
Char. 79: 1 --> 0
Char. 89: 2 --> 1
Kericserispira_faveolata
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Char. 42: 1 --> 3
Char. 44: 1 --> 2
Char. 48: 1 --> 0
Char. 49: 3 --> 2
Char. 69: 0 --> 1
Char. 77: 0 --> 1
Char. 78: 0 --> 2
Char. 80: 0 --> 1
Char. 81: 3 --> 2
Char. 92: 4 --> 2
Kittlidiscus_bronni
Char. 8: 2 --> 3
Char. 9: 1 --> 0
Char. 14: 0 --> 1
Char. 28: 2 --> 1
Char. 30: 0 --> 1
Char. 32: 0 --> 1
Char. 38: 1 --> 0
Char. 43: 0 --> 1
Char. 45: 1 --> 2
Char. 53: 2 --> 3
Char. 65: 0 --> 1
Char. 92: 1 --> 4
Kokenella_costata
Char. 54: 2 --> 1
Char. 61: 0 --> 1
Kokenella_fischeri
Char. 14: 0 --> 1
Char. 20: 2 --> 1
Char. 28: 3 --> 2
Char. 32: 0 --> 1
Char. 44: 2 --> 1
Char. 65: 0 --> 1
Char. 67: 2 --> 1
Char. 70: 2 --> 1
Char. 75: 0 --> 1
Char. 85: 2 --> 1
Lancedellia_costata
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Char. 42: 4 --> 3
Char. 54: 2 --> 3
Char. 61: 1 --> 2
Char. 66: 1 --> 0
Leptomaria_distinguenda
Char. 26: 3 --> 4
Char. 32: 1 --> 0
Char. 58: 1 --> 0
Lineacingulum_eremita
Char. 8: 2 --> 3
Char. 9: 1 --> 0
Char. 27: 1 --> 0
Char. 30: 1 --> 0
Char. 39: 2 --> 3
Char. 46: 2 --> 1
Char. 48: 0 --> 1
Char. 57: 2 --> 3
Char. 67: 1 --> 0
Char. 88: 0 --> 2
Char. 91: 1 --> 2
Lineacingulum_texturatum
Char. 43: 1 --> 0
Char. 53: 2 --> 4
Char. 55: 1 --> 4
Char. 56: 2 --> 0
Char. 83: 1 --> 2
Char. 84: 0 --> 1
Lineaetomaria_decorata
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Char. 17: 0 --> 1
Char. 18: 0 --> 1
Char. 28: 2 --> 1
Char. 30: 0 --> 1
Char. 41: 1 --> 0
Char. 53: 2 --> 0
Char. 64: 2 --> 4
Char. 68: 1 --> 0
Longstaffia_cyclonema
Char. 8: 2 --> 1
Char. 20: 1 --> 0
Char. 28: 1 --> 2
Char. 40: 1 --> 2
Char. 42: 1 --> 3
Char. 92: 3 --> 1
Luciella_eliana
Char. 8: 3 --> 1
Char. 17: 0 --> 1
Char. 24: 0 --> 3
Char. 27: 1 --> 2
Char. 84: 0 --> 1
Lunulazona_costata
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Char. 13: 0 --> 2
Char. 14: 1 --> 2
Char. 20: 0 --> 2
Char. 25: 3 --> 2
Char. 44: 2 --> 1
Char. 57: 2 --> 1
Char. 58: 1 --> 0
Char. 66: 1 --> 0
Char. 70: 0 --> 1
Char. 77: 0 --> 1
Char. 92: 1 --> 3
Martinidiscus_woodwardii
Char. 32: 0 --> 1
Char. 47: 1 --> 0
Mourlonia_carinata
Char. 13: 0 --> 1
Char. 54: 2 --> 3
Char. 89: 2 --> 4
Mourlonia_granulosa
Char. 3: 0 --> 1
Char. 24: 0 --> 2
Char. 27: 1 --> 0
Char. 64: 2 --> 5

Char. 79: 1 --> 0
Char. 83: 2 --> 1
Char. 84: 1 --> 0
Neilsonia_sp
Char. 37: 2 --> 1
Char. 55: 4 --> 3
Char. 66: 1 --> 0
Char. 70: 1 --> 2
Char. 79: 1 --> 0
Nodocingulum_coronatum
Char. 49: 2 --> 1
Char. 60: 0 --> 1
Char. 77: 0 --> 1
Nodocingulum_crenatum
Char. 42: 2 --> 1
Char. 44: 2 --> 3
Char. 53: 2 --> 3
Char. 68: 0 --> 1
Char. 73: 0 --> 1
Char. 83: 1 --> 0
Nodocingulum_granulosum
Char. 18: 3 --> 5
Char. 27: 1 --> 0
Char. 40: 1 --> 2
Char. 54: 2 --> 3
Char. 63: 2 --> 1
Obornella_sp
Char. 8: 2 --> 1
Char. 18: 5 --> 0
Char. 25: 2 --> 4
Char. 26: 3 --> 2
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Char. 41: 1 --> 0
Char. 43: 1 --> 2
Char. 44: 2 --> 1
Char. 53: 2 --> 1
Char. 64: 4 --> 5
Paragoniozona_paucinodosa
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Char. 17: 2 --> 3
Char. 26: 3 --> 4
Char. 28: 1 --> 2
Char. 39: 2 --> 3
Char. 55: 4 --> 1
Char. 56: 0 --> 1
Char. 64: 3 --> 4
Char. 65: 1 --> 2
Char. 81: 2 --> 1
Char. 92: 2 --> 3
Phymatopleura_brazoensis
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Char. 24: 1 --> 2
Char. 39: 2 --> 1
Char. 40: 2 --> 3
Char. 55: 4 --> 1
Char. 92: 2 --> 3
Phymatopleura_nodosa
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Char. 52: 1 --> 2
Char. 53: 2 --> 3
Char. 91: 1 --> 2
Pleurotomaria_amalthei
Char. 53: 2 --> 1
Char. 67: 0 --> 1
Pleurotomaria_anglica
Char. 23: 0 --> 1
Char. 28: 2 --> 1
Char. 69: 2 --> 0
Porcellia_puzo
Char. 29: 1 --> 2
Char. 73: 0 --> 1
Char. 89: 2 --> 4
Pressulasphaera_pamphilus
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Chapter 7. Conclusion

Pleurotomariida represent the most diversified and abundant gastropod group in the studied Carboniferous (Late Palaeozoic) locations (chapter 2, Karapunar et al. 2022). Their diversity and abundance in gastropod faunas gradually decreased towards the end of the Palaeozoic and they represented smaller fraction of the Permian gastropod faunas (chapter 3, Ketwetsuriya et al. 2020; chapter 4, Karapunar et al. 2022b; chapter 5, Karapunar & Nützel 2021, fig. 95). As in all other gastropods, their diversity dropped abruptly at the end-Permian mass extinction (chapter 5, Karapunar & Nützel 2021). They show a remarkable diversification during the Triassic, reflected by numerous new genera and families but their recovery within the Triassic was interrupted during the Carnian (chapter 5, Karapunar & Nützel 2021). The phylogenetic analyses suggest the most of the supraspecific taxa of Pleurotomariida are paraphyletic or polyphyletic and need reconsideration (chapter 6, Karapunar & Nützel in prep.). Phylogenetic analyses further indicate that the survival of Pleurotomariida from mass extinctions does not depend on the speciation rate of a lineage (chapter 6, Karapunar & Nützel in prep.).

In agreement with the previous estimates on the generic diversity, Pleurotomariida is found to be the most diverse and abundant gastropod group in the studied Carboniferous shallow water deposits (chapter 2, Karapunar et al. 2022a). However, their relative abundance is dependent on the studied size ranges and significantly decreases in smaller size fractions. Generally, shells larger than 5 mm are recovered in the surface collection method. Hence the diversity estimates based on surface collections are biased favoring large-sized species. Surface collection is a traditional method, on which a large part of the knowledge on past diversity of molluscs is built. If the diversity estimates on the fossil assemblage/community level and at a larger scale are biased by collection methods, then the diversity of Pleurotomariida might have been incorrectly estimated and might differ if specimens in smaller size ranges are included. An overall increase in predation pressure in marine environments throughout the Phanerozoic has been suggested (e.g., Vermeij 1977). It seems to be plausible that shell slit weakens the shell and makes the animal more prone to durophagous predation. The absence of Pleurotomariida in the Recent shallow water environments and their diversity decrease through time was explained by Harasewych (2002) with their weaker shell (due to the presence of slit). The finding of repaired shell fractures at the shell size of 1 mm shows that the predation was present starting from the benthic settlement (post-metamorphosis) onwards and the predatory pressure

was much higher in the Late Palaeozoic than previously estimated. Hence it weakens the hypothesis that the predation was the primary driver of their diversity decline. Early ontogenetic shells, including the protoconch and early teleoconch (e.g., onset, ornament of selenizone, coiling and ornamentation of shell before onset of selenizone) were documented for the first time for many Palaeozoic taxa. The study of early ontogenetic shells revealed previously unknown shell features, helped to improve diagnoses of several globally distributed Palaeozoic genera and advanced comparisons of Palaeozoic taxa with post-Paleozoic taxa.

The study of a new gastropod fauna from the Permian Thailand (chapter 3, Ketwetsuriya et al. 2020) improved and complemented the knowledge on the Permian gastropod diversity which is especially important because this region was likely a diversity hot spot and data form this region are scarce. This example and several previous studies on Permian gastropod assemblages suggest that Pleurotomariida was still dominant in middle Permian shallow water settings, but less diverse compared to their diversity in Carboniferous faunas. The new classification of Palaeozoic Pleurotomariida based on the study of early shell characters (chapter 2, Karapunar et al. 2022a) revealed that the oldest collection of the Permian gastropod fauna from Thailand (chapter 4, Karapunar et al. 2022b) lacks Pleurotomariida entirely. However, this seems to be a local ecological effect because this unusual marine gastropod assemblage is almost monospecific.

According to the current knowledge, the family diversity of Pleurotomariida peaked in the Triassic in its entire evolutionary history. Almost all of the newly evolved Triassic pleurotomariidan families have their type genera from the Upper Triassic St. Cassian Formation (i.e., Schizogoniidae (=Pseudoschizogoniidae), Stuorellidae, Wortheniellidae, Kittlidiscidae, Zygitidae, Lancedellidae, Rhaphistomellidae, Temnotropidae; and the seguenzioid family Laubellidae). However, the type specimens of numerous taxa had not been properly documented and had been known only from their often poor initial descriptions and inadequate figures due to the technical limitations at that time. This and the failure to study type material led to misidentifications by some subsequent authors and further complicated the assessment of the diversity of Pleurotomariida from the St. Cassian Formation. The comprehensive study of the St. Cassian fauna (chapter 5, Karapunar & Nützel 2021) revealed that more than half of the species identifications in subsequent works (especially the ones published during the 20th and 21st centuries) are wrong. As a result of a thorough revision and a detailed study of all type specimens and newly collections, nine new genera and eight new

species were described. Some of the genera previously described from the St. Cassian Formation (e.g., *Wortheniella*, *Rinaldoella*) were differentiated from the Palaeozoic taxa based on characters of the early shell although the early shell characters of Palaeozoic taxa had not been unknown at the time. The detailed study of the Palaeozoic Pleurotomariida (chapter 2, Karapunar et al. 2022a) allowed to compare the previously described and newly erected St. Cassian taxa with the Palaeozoic ones. Furthermore, this study helped to assess whether some of the St. Cassian species represent Palaeozoic genera as proposed in the early works. Consequently, none of the St. Cassian pleurotomariidan genera were found to represent Palaeozoic genera, all evolved during the recovery period in the Triassic according to the current knowledge. However, re-study of the Palaeozoic species might reveal that some of these Triassic genera originated during the Palaeozoic. Although no new family evolved during the Permian, the origination of several new families during the Triassic is remarkable and reflects the high morphological disparity of Pleurotomariida during the Triassic. However, the recovery of Pleurotomariida from the end-Permian mass extinction event was less successful compared with other gastropod groups, especially that of Caenogastropoda, and was interrupted during the Carnian. All gastropod groups experienced a diversity loss during the Carnian Pluvial Episode (CPE), but the loss was more severe in Pleurotomariida indicating that they were more vulnerable to the environmental changes and faunal turnovers happened during this event. The diversity loss might be due to their ecology (e.g., feeding and habitat preferences), geographical distribution (being mostly restricted to the tropical zone) and anatomy (poor handling of high sediment load).

The present phylogenetic analyses suggest that most supraspecific taxa of Pleurotomariida are paraphyletic or polyphyletic. Thus, a further revision of the classification is necessary (chapter 6, Karapunar & Nützel in prep.). However, different methods (Parsimony and Bayesian) produce significantly different phylogenies and supports are very low for the majority of the recovered clades. Therefore, a revision should not be based solely on the reconstructed phylogenies. The Parsimony analysis produced ghost ranges and hence the evolutionary relationship reconstructed with this method does not agree with the stratigraphical record of the analyzed taxa. Bayesian analysis (Fossilized Birth Death method) produced a tree agreeing more with the stratigraphical information because it integrates the stratigraphical age in the analysis. The Bayesian phylogeny indicates two splitting events within the Devonian producing three major lineages. Among them, two lineages survived the end-Permian. One surviving

lineage (Worthenielliini) proliferated more than the other lineage (Pleurotomariini) within the Triassic. However, only Pleurotomariini could persist to the Recent. This suggests that other aspects than evolutionary or speciation rates played a role in the survival or extinction of pleurotomariidan lineages. Considering the new findings (chapter 2, Karapunar et al. 2022a; chapter 5, Karapunar & Nützel 2021; chapter 6, Karapunar & Nützel in prep.) ecology, habitat preference and geographical range seem to be more likely reasons behind the dwindling of Pleurotomariida through time.

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ARTICLES IN PEER-REVIEWED JOURNALS

Karapunar, B., Nützel, A., & Ketwetsuriya, C. (2022b). *Peruvispira*-dominated low-diversity gastropod assemblage from the Middle Permian Ratburi Limestone of Central Thailand. Alcheringa, 1–9, https://doi.org/10.1080/03115518.2022.2050814.

Karapunar, B., Nützel, A., Seuss, B., & Mapes, R. H. (2022a). Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) and some slit bearing Caenogastropoda from the Pennsylvanian of the USA. Papers in Palaeontology, 8(2): 1–95 (e1417), https://doi.org/10.1002/spp2.1417.

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

Karapunar, B., Werner, W., Fürsich, F. T., & Nützel, A. (2021). The earliest example of sexual dimorphism in bivalves – evidence from the astartid *Nicaniella* (Lower Jurassic, southern Germany). Journal of Paleontology, 95, 1216–1225, https://doi.org/10.1017/jpa.2021.48.

Karapunar, B., Werner, W., Fürsich, F. T., & Nützel, A. (2021). Predatory drill holes in the oldest thyasirid bivalve, from the Lower Jurassic of South Germany. Lethaia, 54, 229–244, https://doi.org/10.1111/let.12399.

Fürsich, F. T., **Karapunar, B.**, Werner, W., & Nützel, A. (2020). Ecology of the Early Jurassic bivalve *Harpax spinosus* (J. Sowerby, 1819). Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen, 297(2): 227–243, https://doi.org/10.1127/njgpa/2020/0923.

Karapunar, B., Werner, W., Fürsich F. T., & Nützel, A. (2020). Taxonomy and palaeoecology of the Early Jurassic (Pliensbachian) bivalves from Buttenheim, Franconia (Southern Germany). Palaeontographica Abteilung A, 318: 1–127, https://doi.org/10.1127/pala/2020/0098.

Ketwetsuriya, C., **Karapunar, B.**, Charoentitirat, T., & Nützel, A. (2020). Middle Permian (Roadian) gastropods from the Khao Khad Formation, Central Thailand: Implications for palaeogeography of the Indochina Terrane. Zootaxa, 4766(1): 1–47, https://doi.org/10.11646/zootaxa.4766.1.1.

CONFERENCE PRESENTATIONS

Karapunar B. (2021). Phylogeny, classification and palaeodiversity of Pleurotomariida (Gastropoda). Annual Munich Earth Science PhD Conference, October 22-24, 2021, Hinterriß, Austria.

Karapunar B., & Nützel A. (2021). The extinction and recovery of Pleurotomariida (Gastropoda) across the Permian–Triassic – how taxonomic and ecological studies improve our knowledge. 92nd Annual Meeting of the Paläontologische Gesellschaft, September 27–30, 2021, Vienna, Austria (online).

Karapunar B., & Nützel A. (2019). The life history traits of five common pleurotomariid (gastropoda) taxa from the Pennsylvanian of Texas. 90th Annual Meeting of the Paläontologische Gesellschaft, September 15–18, 2019, Munich, Germany.

Karapunar B., & Nützel A. (2018). Diversity dynamics of slit band gastropods (order Pleurotomariida) at the Paleozoic - Mesozoic transition. 5th International Palaeontological Congress, July 8–13, 2018, Paris, France.

Karapunar B., Nützel A., & Werner W. (2017). Taxonomy and Paleoecology of bivalves prior to the Pliensbachian-Toarcian extinction in Franconia. 88th Annual Meeting of the Paläontologische Gesellschaft, March 26–30, 2017, Münster, Germany.

POSTER PRESENTATIONS

Karapunar B., Werner W., & Fürsich, F. (2019). Diversity and palaeoecology of the bivalve fauna from the Pliensbachian (Lower Jurassic) of Buttenheim, Franconia. 90th Annual meeting of the Paläontologische Gesellschaft, September 15–18, 2019, Munich, Germany.

POPULAR SCIENCE ARTICLES

Werner, W., & **Karapunar, B.** (2021). Die Muschelfauna des Amaltheentons von Buttenheim. Fossilien, Sonderheft 2021, 35–44.