

# 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. bellerophonitids) 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,

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 2014a). 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 2014a). Pleurotomariida have an inner nacreous shell layer (Batten 1972a; 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 mantle 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 'Euomphalinae' 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 Bellerophonitida 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 mid-continent 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<sub>2</sub>O<sub>2</sub>) 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<sub>4</sub>) or methylene chloride (CH<sub>2</sub>Cl<sub>2</sub>) 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 deposited 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<sub>4</sub>Cl) 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).

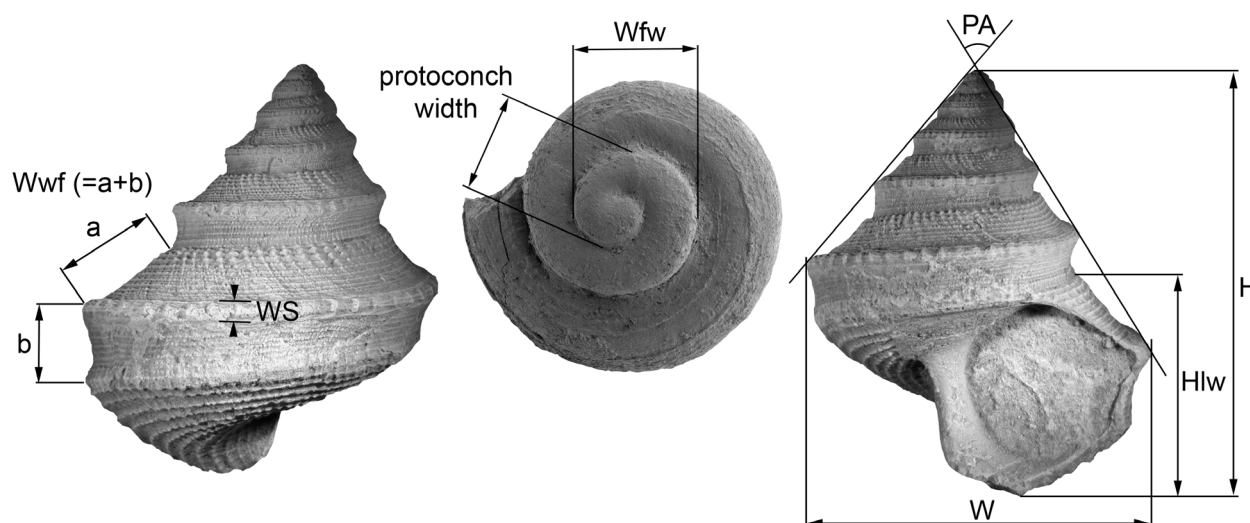


*Measurements & ratios used.* **H**, height of shell; **Hlw**, height of last whorl; **Nn**, number of nodes on last whorl; **PA**, pleural angle; **RSwh**, ratio of selenizone width to whorl height (=  $WS/Hlw$ ); **RSwf**, ratio of selenizone width to whorl face width (=  $WS/Wwf$ ); **W**, width of 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 1960a, 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 *Trepsira* Ulrich in Ulrich & Scofield, 1897
- Subfamily EOTOMARIINAE Wenz, 1938
- Genus *Baylea* de Koninck, 1883
- Genus *Glabrocingulum* Thomas, 1940a
- Subgenus *Glabrocingulum* Thomas, 1940a



**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 *Paragoniozonia* Nelson, 1947  
 Genus *Worthenia* de Koninck, 1883  
 Subgenus *Worthenia* de Koninck, 1883  
 Subgenus *Yochelsonospira* Thein & Nitecki, 1974  
 Genus *Borestus* Thomas, 1940a  
 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, 1960b  
 Superfamily ORTHONEMATOIDEA Nützel & Bandel, 2000  
 Family GONIASMATIDAE Nützel & Bandel, 2000  
 Genus *Peruvispira* Chronic, 1949  
 Genus *Platyzoa* Knight, 1945

## SYSTEMATIC PALAEOLOGY

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- 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. 1202).

*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 *Treospira*, *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 oklahomensis* 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 *Treospira* 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 *Treospira* and *Angyomphalus* as subgenera of *Treospira*. Later, both taxa were used

at the genus level (Shikama & Nishida 1968; Blodgett & Johnson 1992; Peel 2016). *Treospira* differs from *Angyomphalus* by having an umbilical callus. Both taxa share a similar shape and an ornament of subsutural nodes. *Angyomphalus* differs from *Treospira* 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.

*Treospira sphaerulata* (Conrad, 1842)

Figure 3

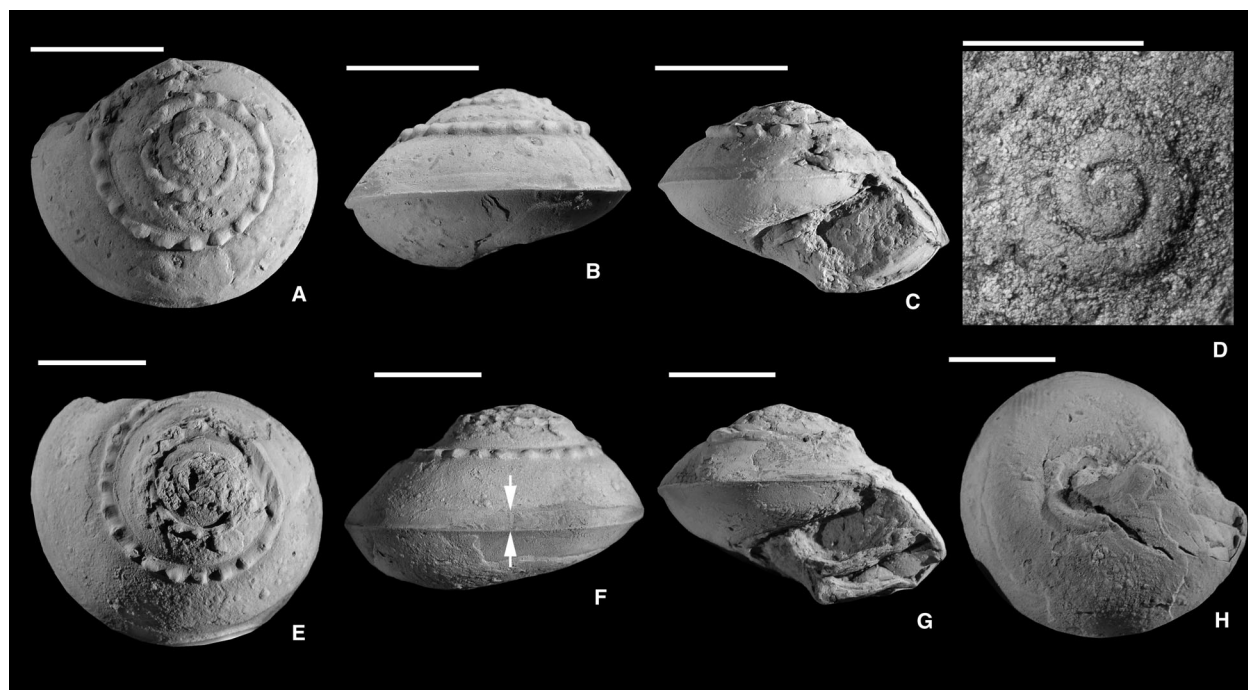
- \* 1842 *Pleurotomaria sphaerulata* Conrad, p. 272, pl. 16 fig. 12.  
1967 *Treospira (Treospira) sphaerulata* (Conrad); Yochelson & Saunders, p. 237 (for further synonymy).

**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 proscyrct on whorl face, strongly proscyrct 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.** *Treospira 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).

*Treospira* cf. *illinoensis* (Worthen, 1884)

Figure 4

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

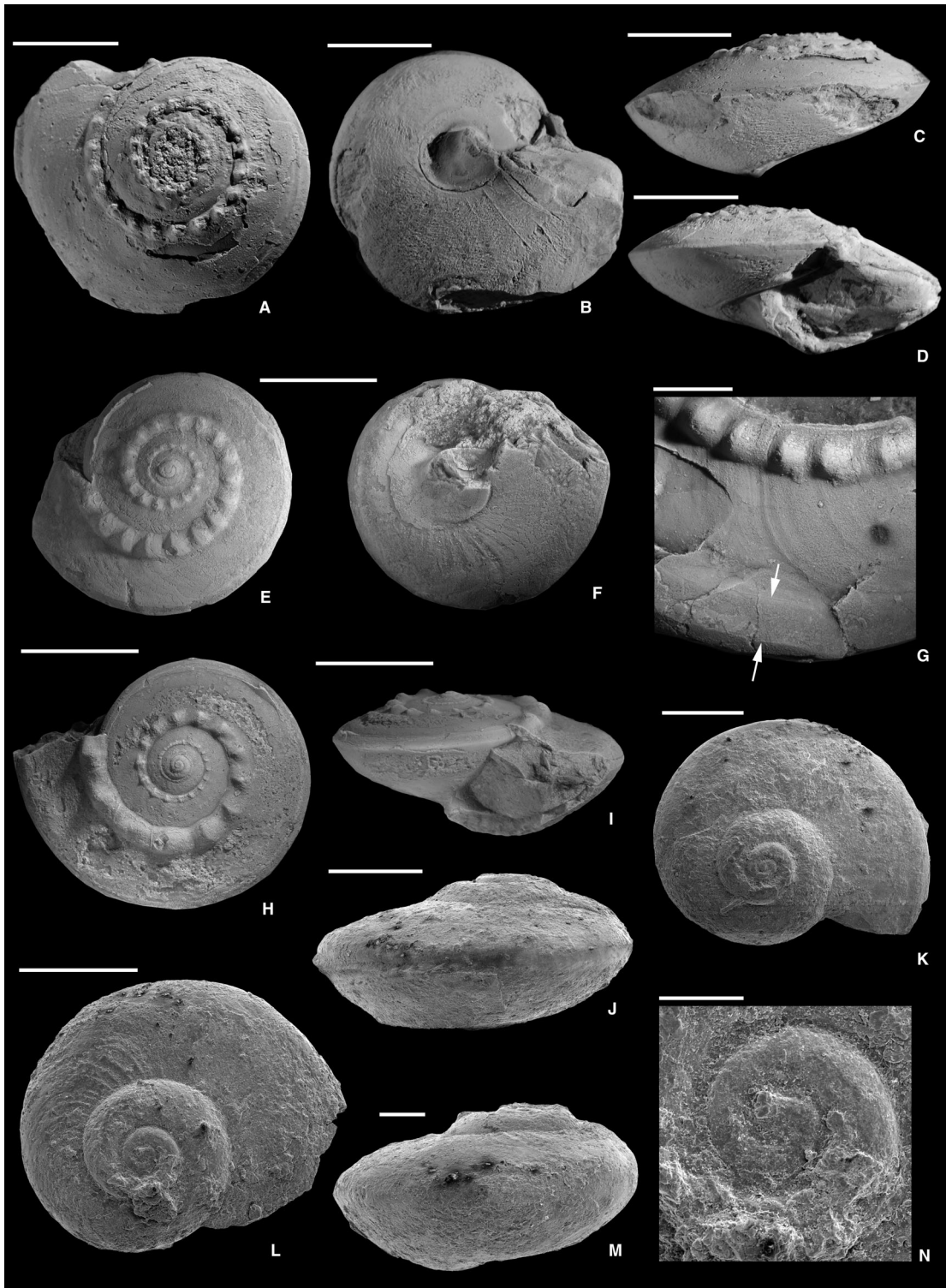
	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh	Nn
2020 LIX 2	11.7	21.8	126	–	9.5	8.0	1.6	0.20	0.17	21
2020 LX 2	13.3	22.7	120	–	9.5	8.15	1.6	0.20	0.17	24
2020 LX 3	14.0	24.2	128	–	11.3	8.5	1.8	0.21	0.16	23
2009 XXII 20	7.6	11.7	134	–	5.9	4.4	0.7	0.16	0.12	16
2020 XCI 8	11.3	22.2	134	0.2	9.1	8.2	1.5	0.18	0.16	16
2020 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-spined; 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 prosocyrct on whorl face, prosocyrct 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 (1964a, b) pointed out the complicated taxonomy of Pennsylvanian *Treospira* species from the USA. The *Treospira* 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 *Treospira illinoensis* 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 *Treospira* and included *Pleurotomaria depressa* and *Pleurotomaria illinoensis* as two separate members of the genus. Girty (1915) synonymized many species with *Treospira depressa* including *T. illinoensis*. 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 (1964b) figured the original material of Worthen (1884) and designated a lectotype for *T. illinoensis*. 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.

*Treospira depressa* (Cox). *Treospira 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 (1964b) stated, 'a comprehensive study of all available low-spined specimens of *Treospira* 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*.

*Treospira 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 *Treospira* 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* L veill , 1835 from the Carboniferous of Belgium; subsequent designation by Wenz (1938).

*Emended diagnosis.* Turbiniiform; 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 Gosseletinae 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-spined 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-spined 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.* (2020a), *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 (1972b) resembles *Baylea*, *Biarmeaspira* Mazaev, 2006, and *Pseudobaylea* Dickins, 1963 more than it resembles *Worthenia*. In the discussion of *Worthenia* cf. *schirjaevensis*, Batten (1972b) 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.
- 1964a *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 prosoclyt 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 opisthoclyt; 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 (1964a) 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 (1964a) 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.

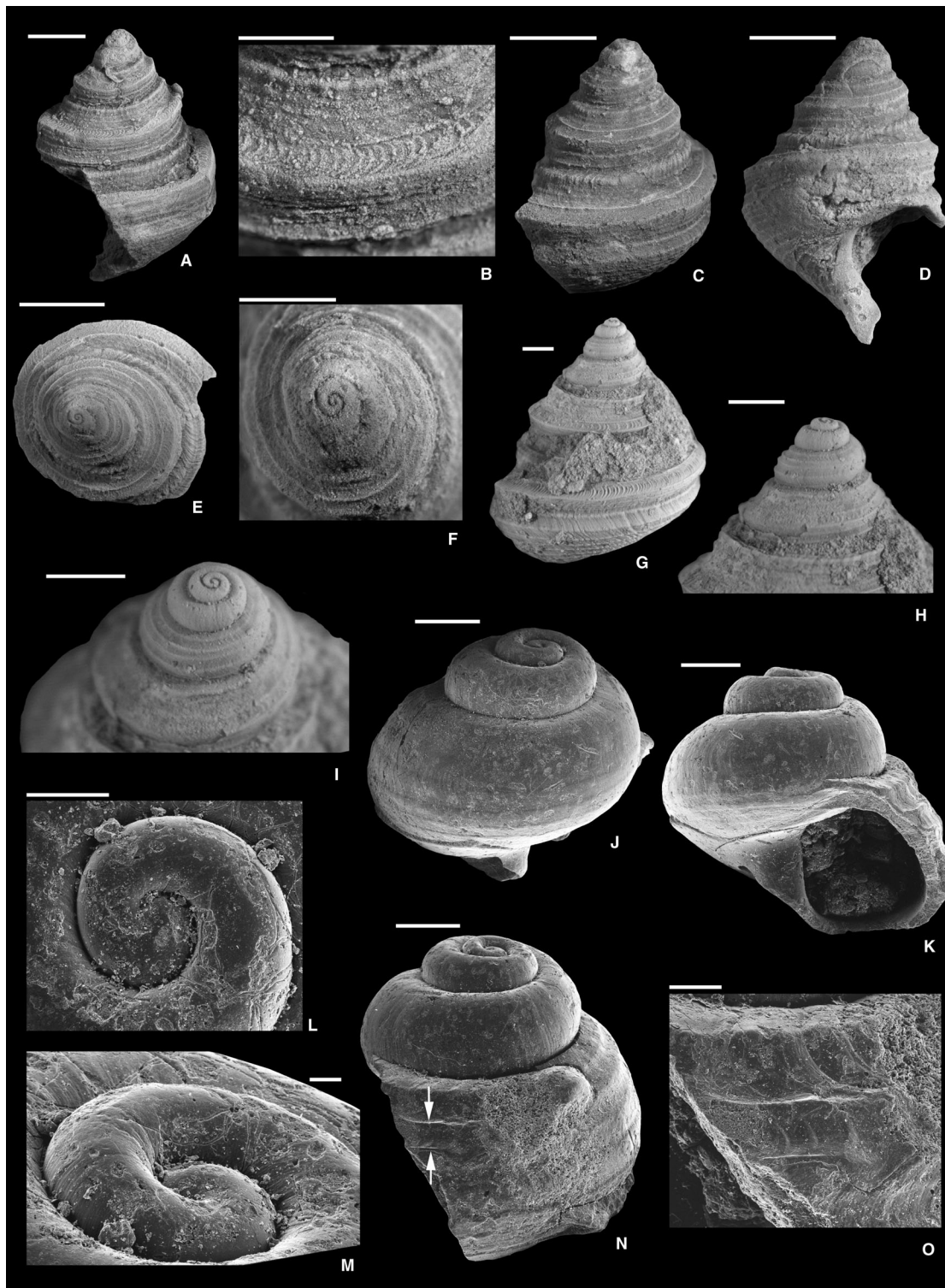
The growth line pattern of our material is the same as that reported by Weller (1929, pl. 3, fig. 1) for *Ba. giffordi* and Kues & Batten (2001, p. 23) for *Ba. kuesi*.

#### *Baylea gurleyi* (Meek, 1871)

##### Figure 6

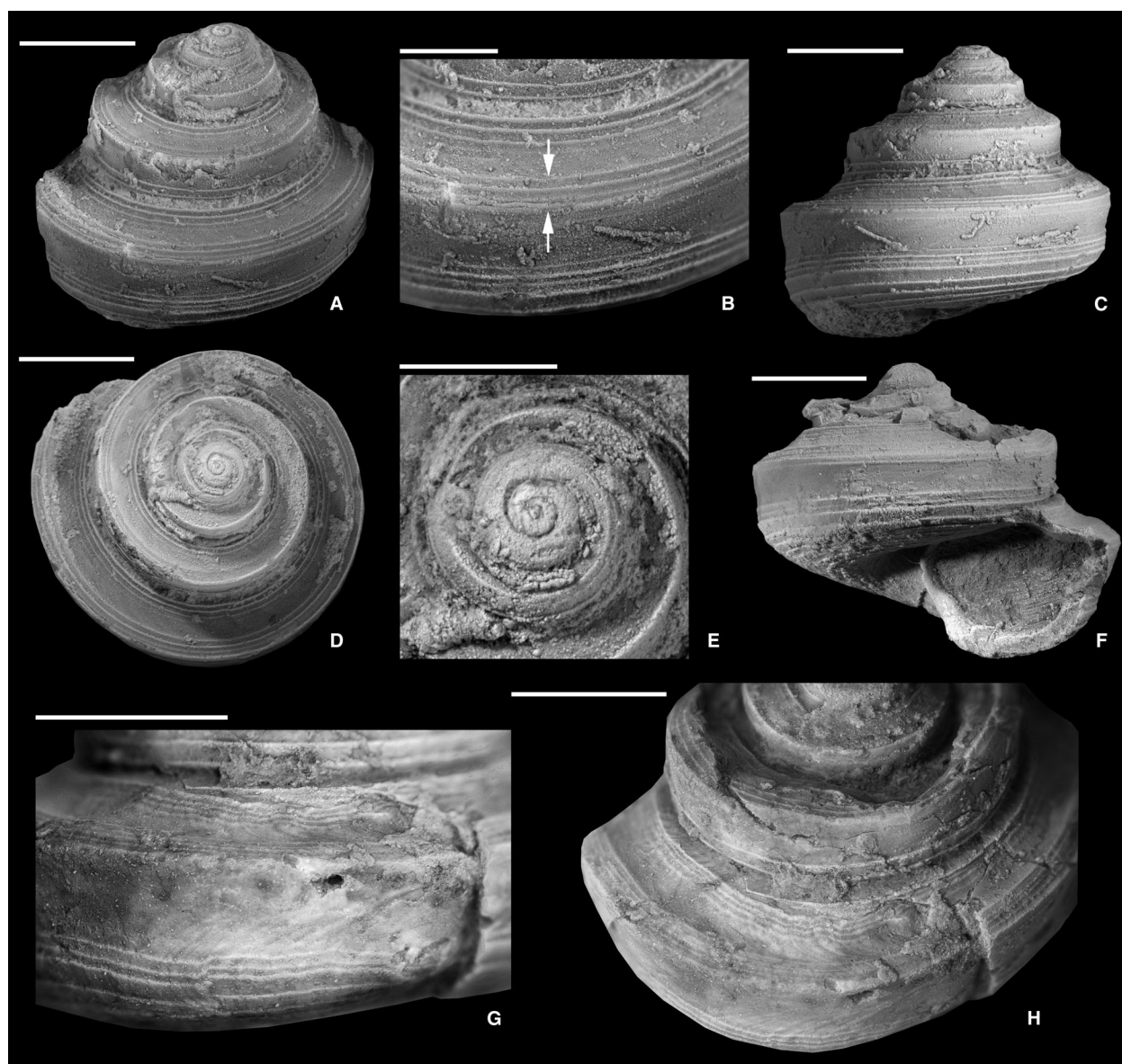
- \* 1871 *Pleurotomaria gurleyi* Meek p. 177.
- 1873 *Pleurotomaria gurleyi*; Meek & Worthen, pl. 30 figs 6a, b.
- 1929 *Yvania gurleyi* (Meek); Weller, p. 20, pl. 3 figs 1a–d, 7.
- 1967 *Baylea gurleyi* (Meek); Yochelson & Saunders, p. 35.





**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 prosocyrst with zenith point at adaxial half, growth lines at lateral whorl face asymmetrically prosocyrst 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*

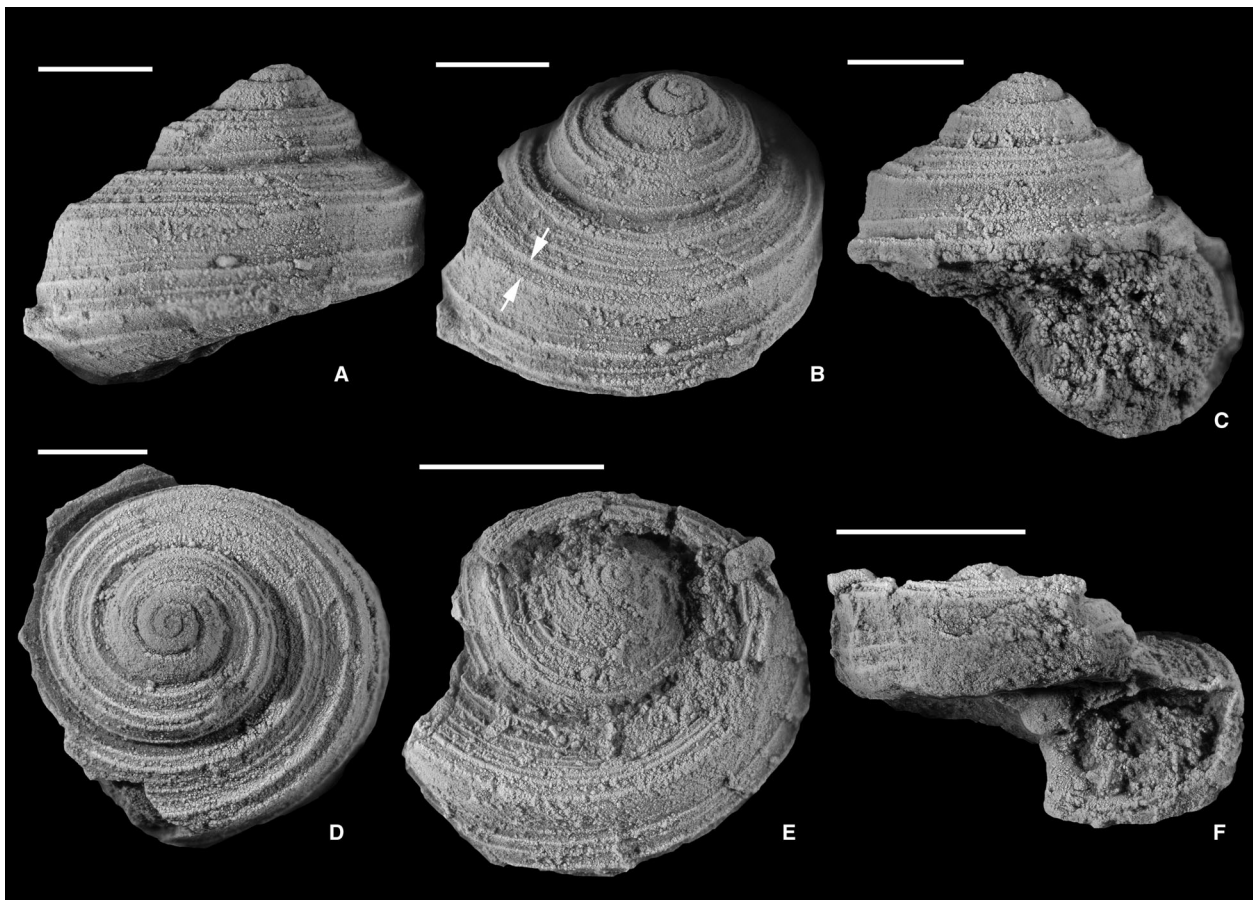
that agrees well with the specimens at hand. The ornamentation on the early whorl face is poorly preserved and barely visible. Therefore, the presence of six spiral lirae on the early whorls as described by Meek (1871) and Weller (1929) could not be observed. The spiral cords on the early whorl face 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.
- ? 2019a *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 (2019a) 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 (2019a) 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.

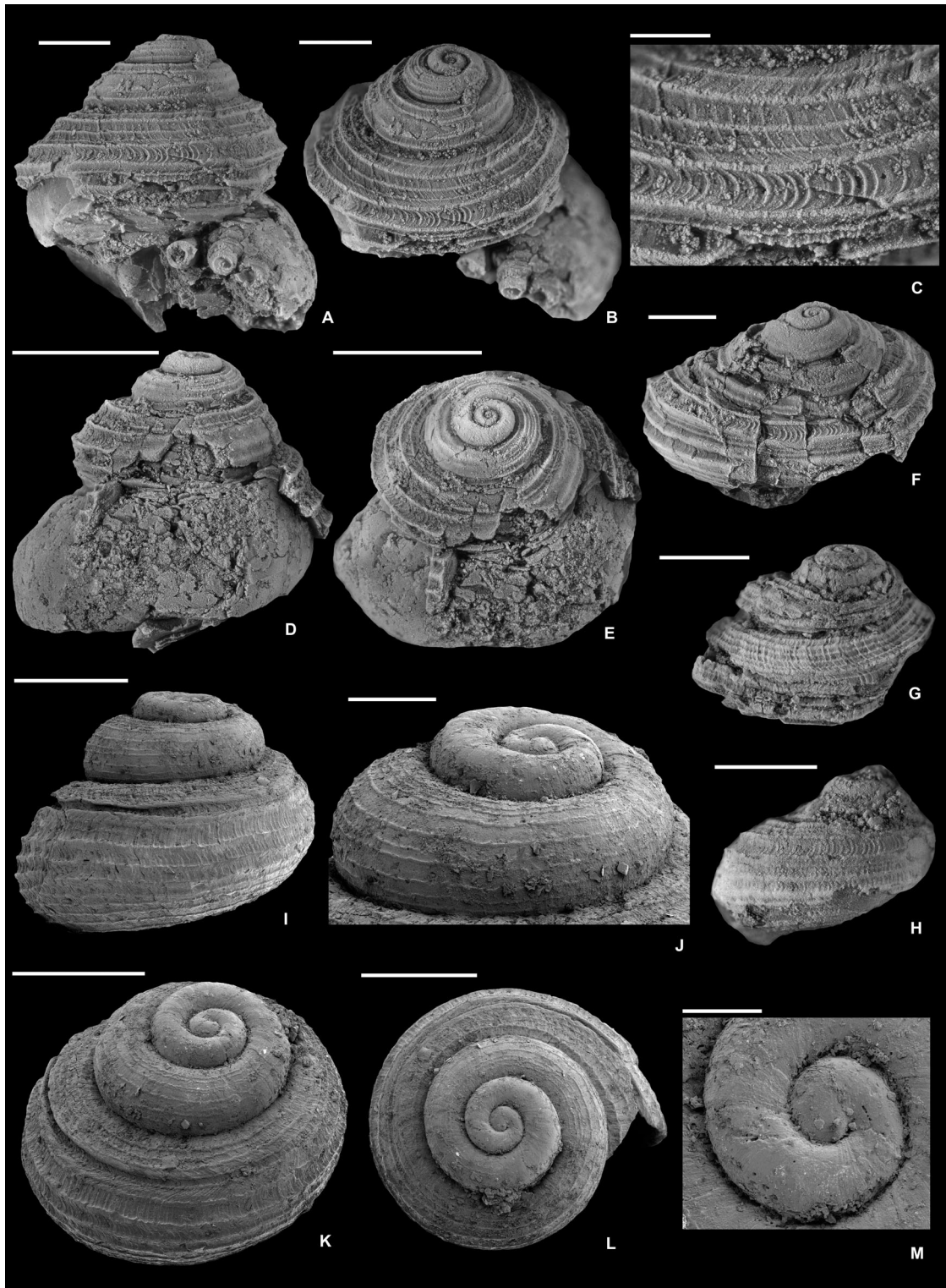
*Measurements (mm).*

	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

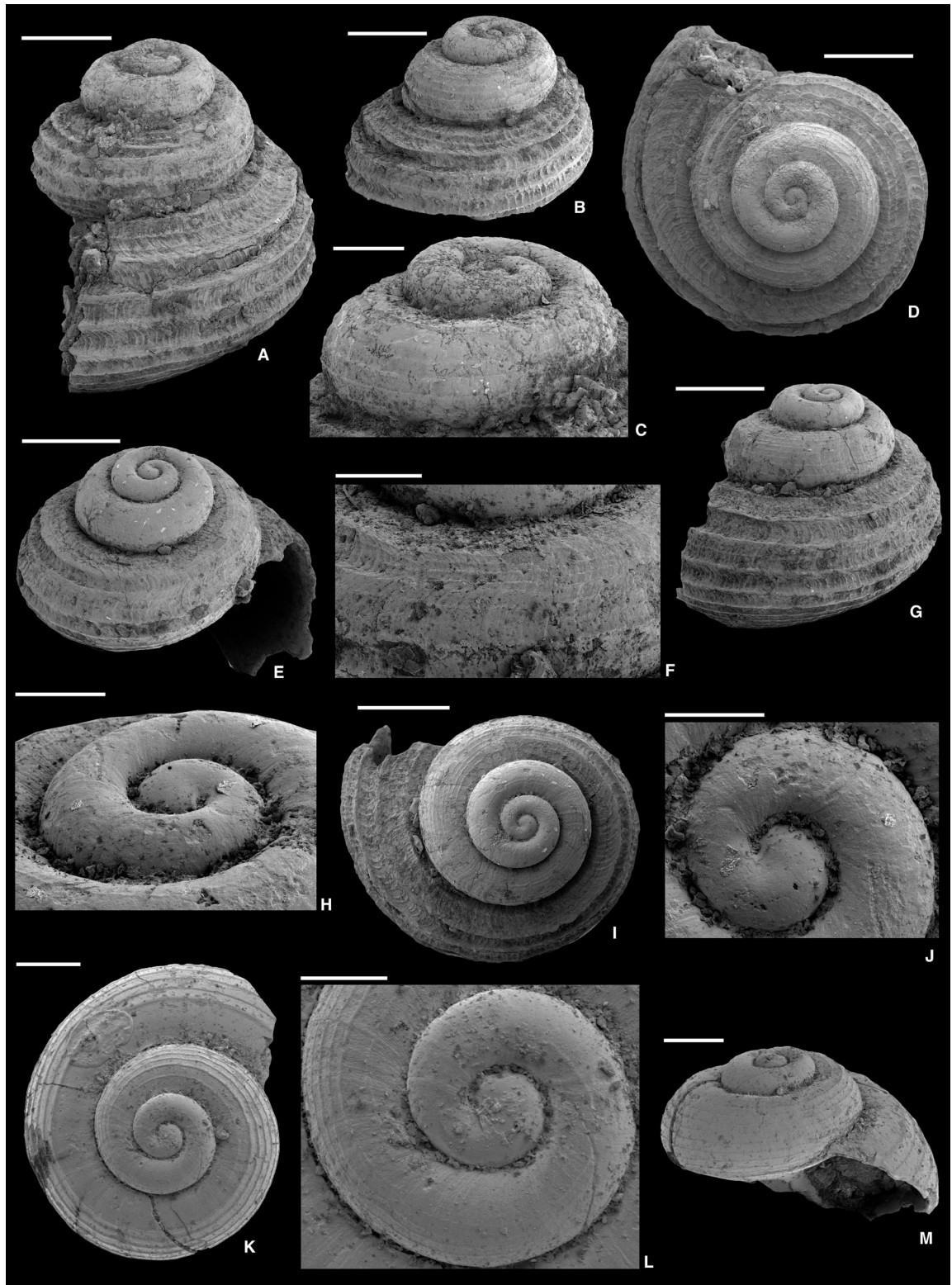
*Description.* Shell small, trochiform; largest specimen comprises five whorls; early whorls evenly rounded convex, with weak angulations at the borders of selenizone developing on latest preserved whorls; protoconch smooth, consisting of slightly less than one whorl, diameter c. 0.16 mm; first whorl 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 prosocyrct between subsutural cord and adapical edge of selenizone, prosocyrct between abapical edge of selenizone and fourth primary cord, opisthocyrct 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, prosocyrct near basal edge, then opisthocyrct; 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, 1940a 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, para-type; 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. yvannii*, 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 Fukui, 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 GLABROCIINGULUM Thomas, 1940a

*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 GLABROCIINGULUM Thomas, 1940a

*Type species.* *Glabrocingulum beggi* Thomas, 1940a 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 1964b, 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, 1866a) by Sturgeon (1964a, pl. 32 fig. 11) was included in the synonymy of *Gosseletina nodosa* (= *Glabrocingulum* (*Glabrocingulum*) *beedei*) by Hoare *et al.* (1997). Sturgeon's (1964a) specimen agrees well with the specimens assigned to *Gosseletina spironema* by Kues & Batten (2001, figs 7.2–7.4) and therefore Sturgeon's (1964a) 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 *Paragoniozonia*: *Paragoniozonia obesum* (Yoo, 1994) comb. nov. *Glabrocingulum pustulum* Yoo, 1994 (pl. 7, figs 1–4) likewise is herein assigned to *Paragoniozonia* (*Paragoniozonia*) *pustulum* (Yoo, 1994) comb. nov.) although its lunulae are not as prominent as in other members of *Paragoniozonia*. *Glabrocingulum* sp. in Yoo (1994, pl. 7 figs 1–4) should be assigned to *Rhineoderma* (see Remarks on *Paragoniozonia*, 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.
- 1972a *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.
- 2014b *Glabrocingulum grayvillense*; Nützel, fig. 1H.

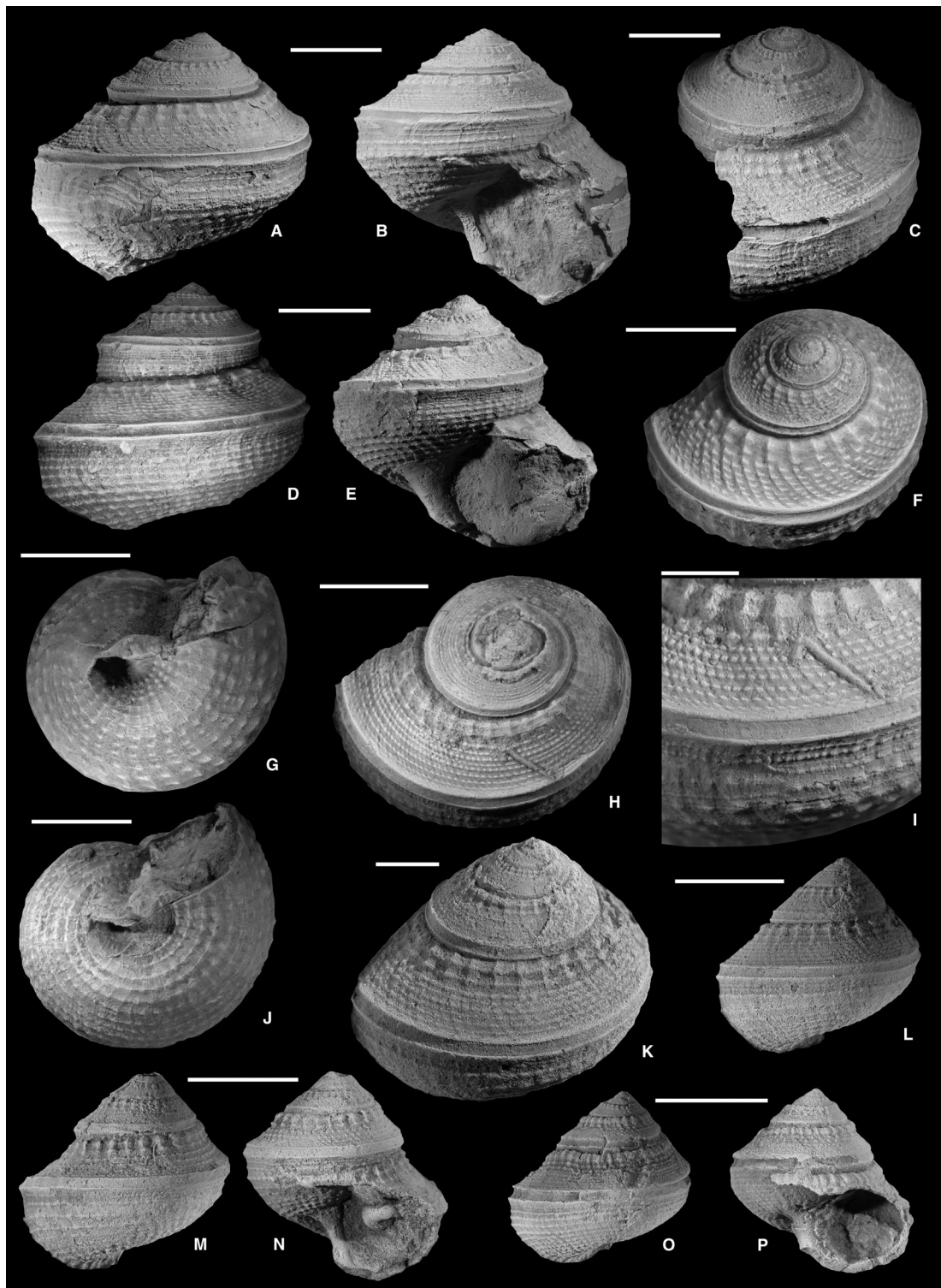
**Material.** A total of 2303 specimens. 3 from the Desmoinesian of Oklahoma (Wetumka Formation, OKD–15): SNSB-BSPG 2020 LXI. 526 from the Desmoinesian of Oklahoma (Wewoka Formation, OKD–11): SNSB-BSPG 2020 LXII 3–5, and a further 523 specimens (SNSB-BSPG 2020 LXII). 2 from the Desmoinesian of Oklahoma (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 prosocyrct 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 prosocyrct 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 opisthocyrct near basal edge, prosocyrct 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 2014a). 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-spined 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, prosocyrct 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 opisthocyrct near basal edge, prosocyrct near umbilicus; aperture subovate, as wide as high; outer lip angular, basal lip convex, columellar lip convex, callus-like thickened, curved backwards; base narrowly phanerocephalous.

**Remarks.** Gordon & Yochelson (1987) erected a new species based on the paratype of *Glabrocingulum quadrigatum* (Sadlick & Nielsen 1963, pl. 150 figs 5–8) and emended 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

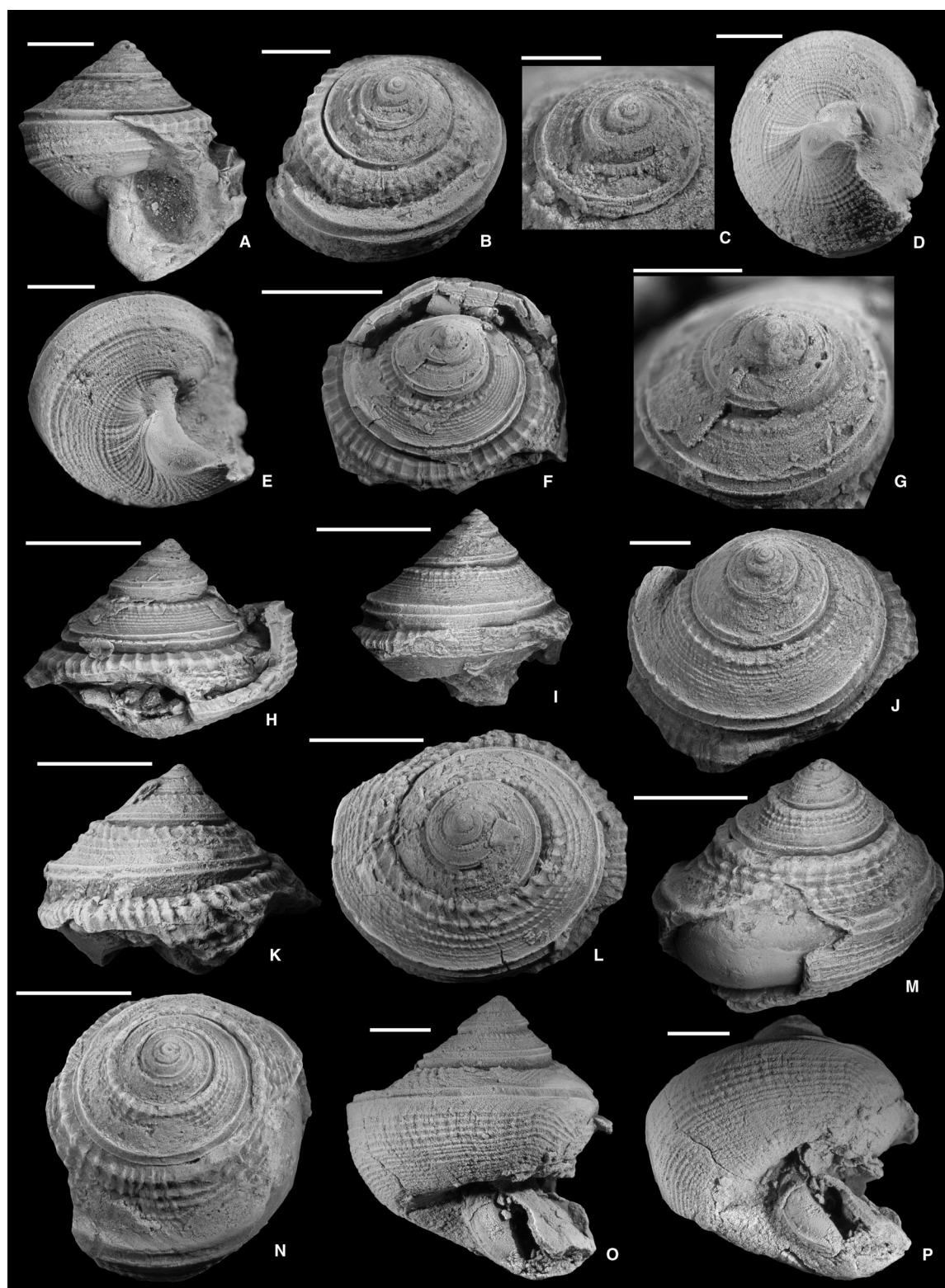
**Remarks.** *Glabrocingulum (Ananias)* can be differentiated from *Glabrocingulum (Glabrocingulum)* by its more high-spined shell and in having a well-developed vertical lateral whorl face in all teleoconch whorls. In *G. (Glabrocingulum)* whorls embrace just below the selenizone except on the last 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-spined in *G. (Glabrocingulum)*, more high-spined 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-spined 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*.

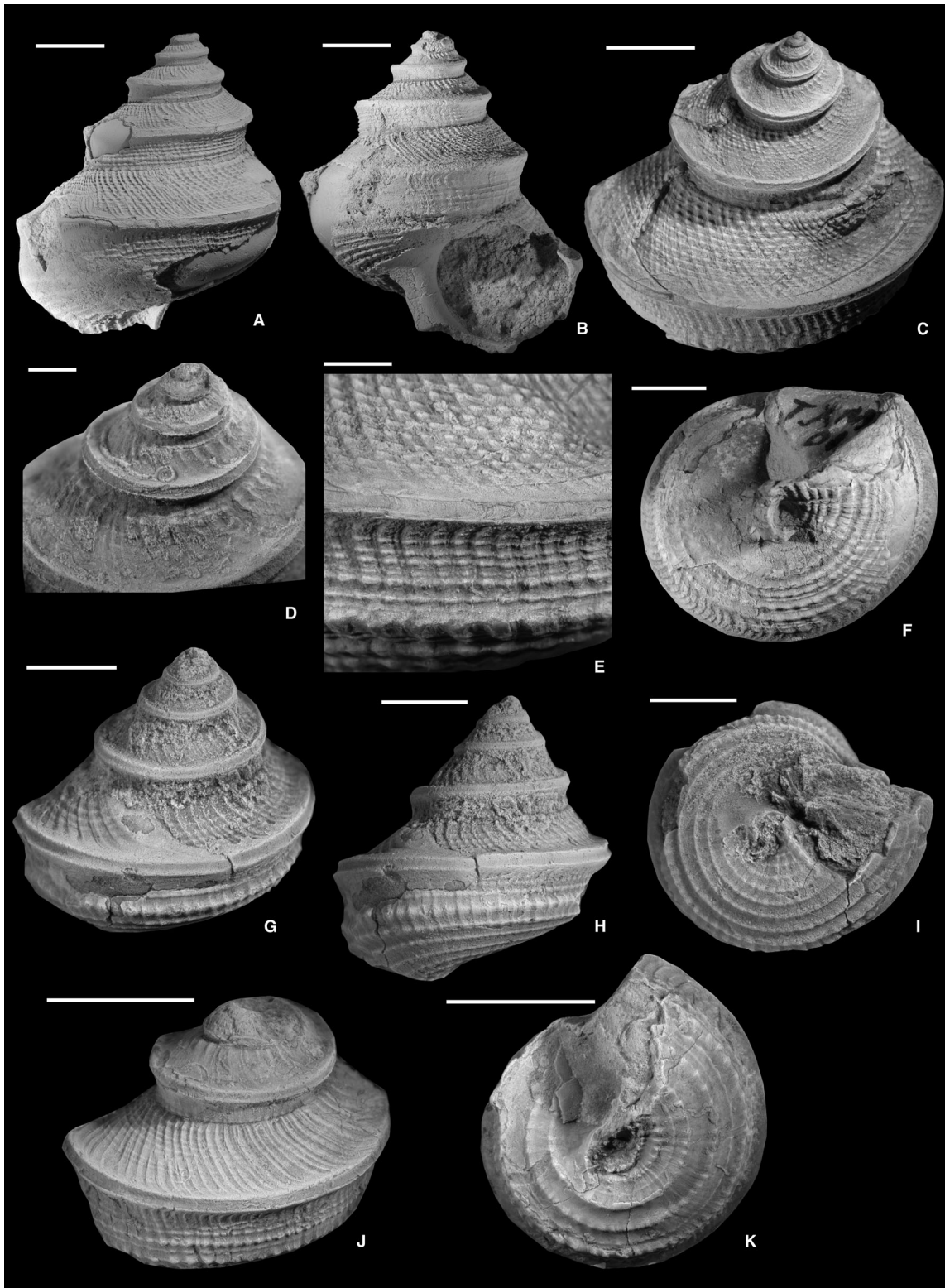
*Glabrocingulum (Ananias) welleri* (Newell, 1935)

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 proscoline 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 proscoline 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 prosclyrt below selenizone, slightly opisthoclyrt 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 opisthoclyrt near basal edge, slightly prosclyrt 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

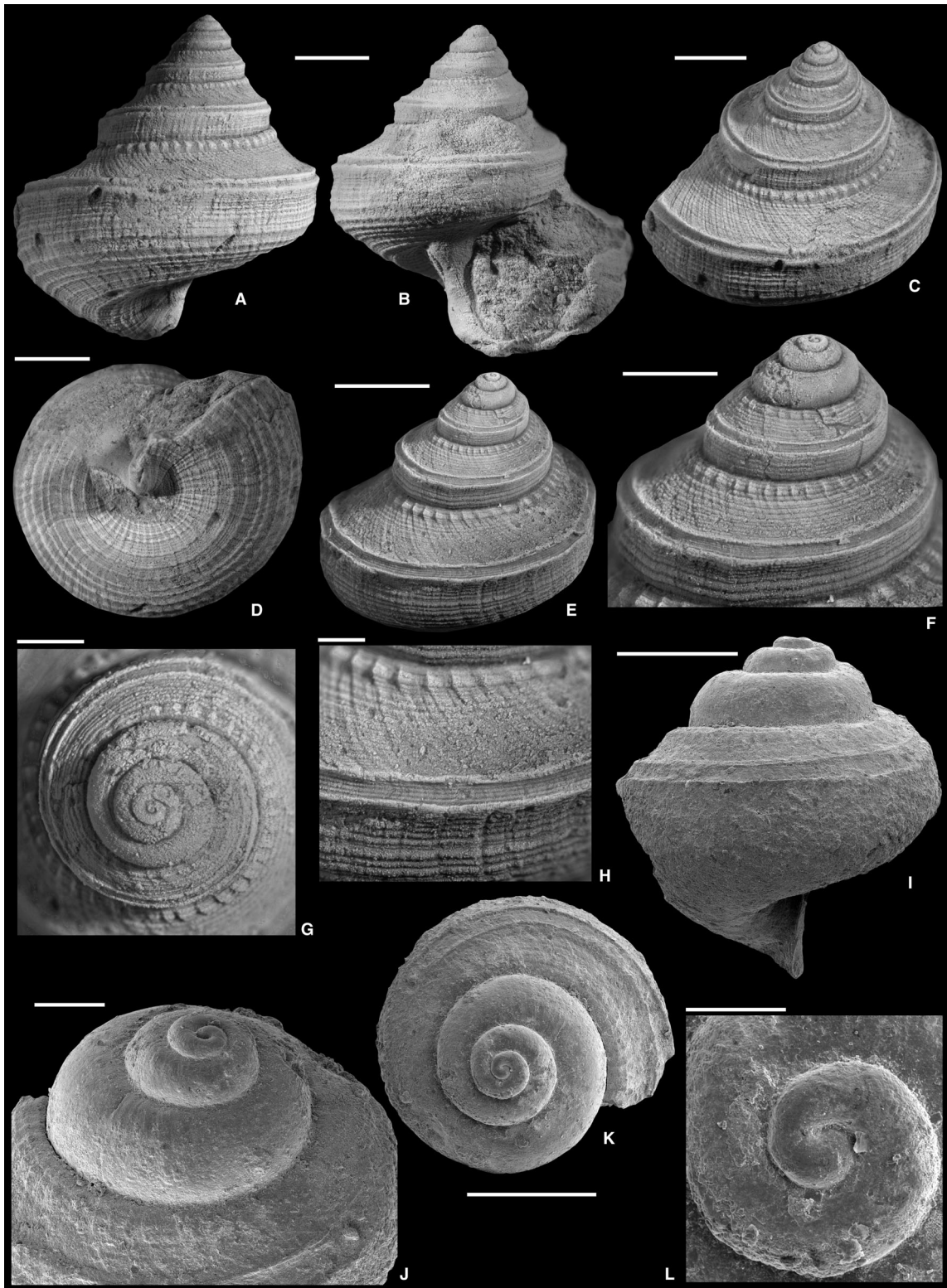
- ? 1866 *Pleurotomaria marcouiana* Geinitz, p. 10, table 1, fig. 10.  
 ? 1967 *Glabrocingulum (Ananias) marcouianum* (Geinitz); Yochelson & Saunders, p. 85.  
 1982 *Glabrocingulum (Ananias) welleri*; Schindel, figs 2b, 3.2a–c [non fig. 3.2d].  
 \* 2004 *Glabrocingulum (Ananias) tularosaensis* Kues,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

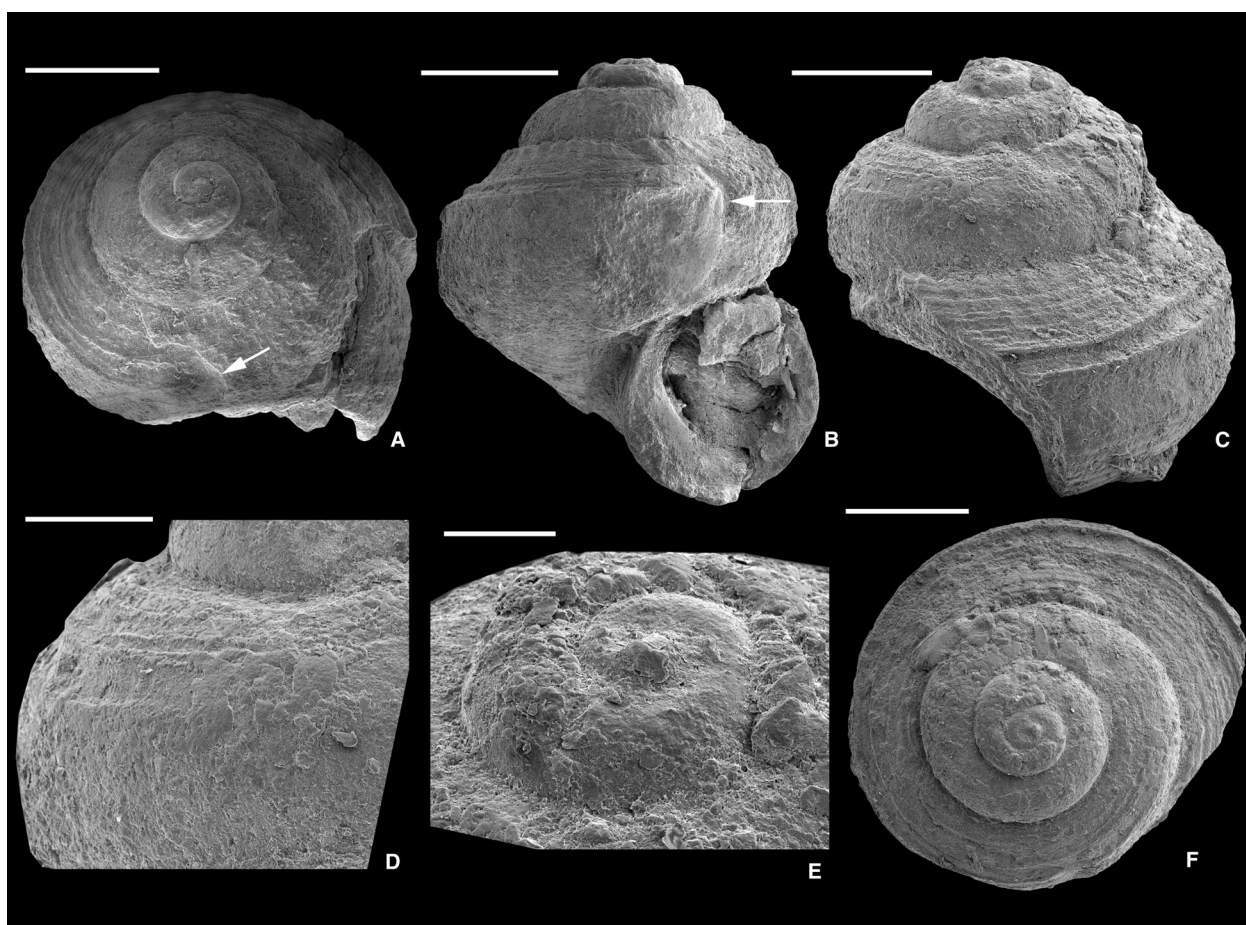
	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 7	8.9	8.4	87	0.23	4.7	3.9	0.3	0.09	0.07
2009 XXII 18	8.9	7.8	88	–	4.6	3.8	0.4	0.10	0.08
2020 XCI 28	6.2	6.1	82	0.20	3.3	2.8	0.3	0.11	0.09

**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 prosocyrst 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 prosocyrst 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 opisthocyrst near basal edge, prosocyrst 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.

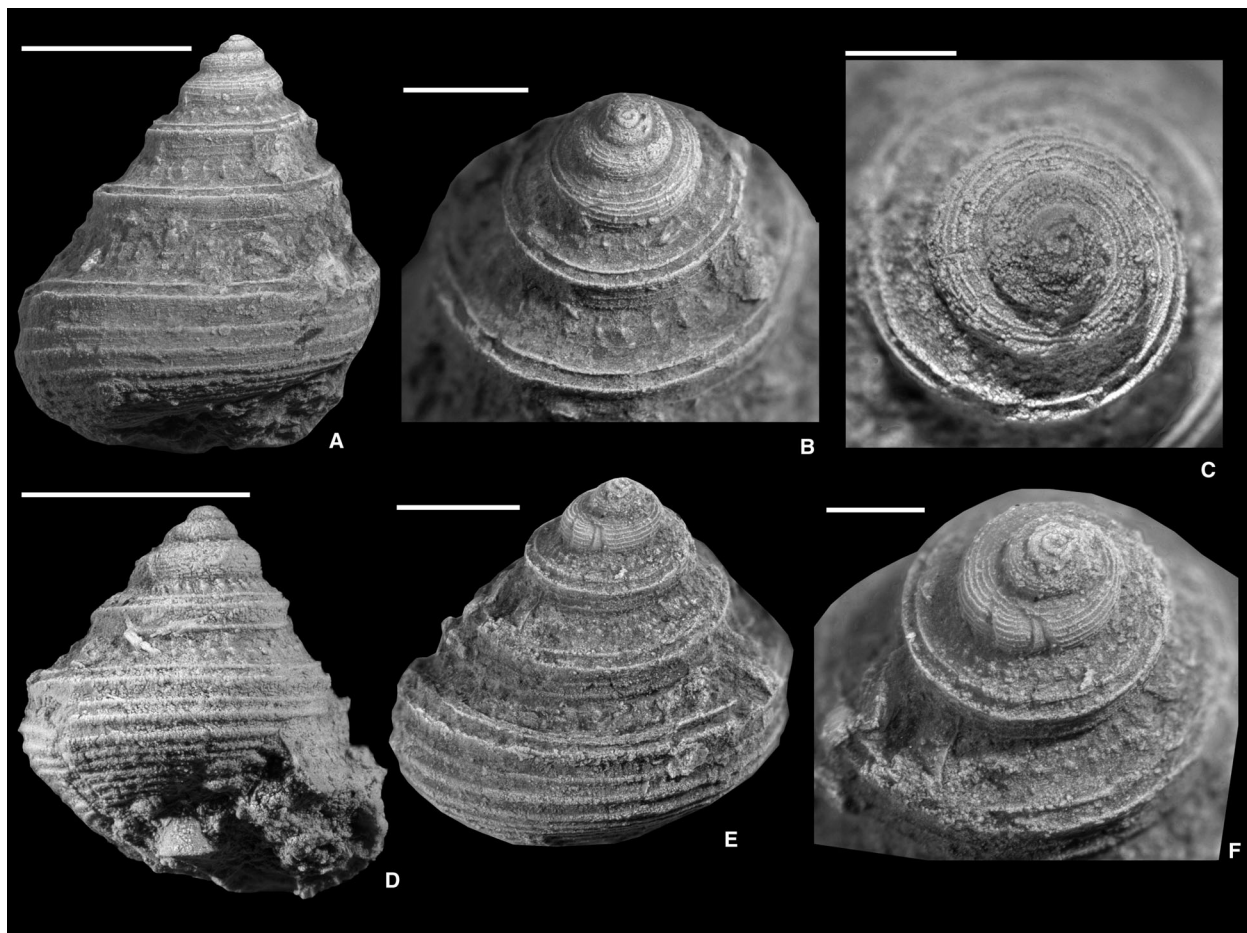
*Measurements (mm).*

	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 prosocyrts, 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, 1940a, 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.

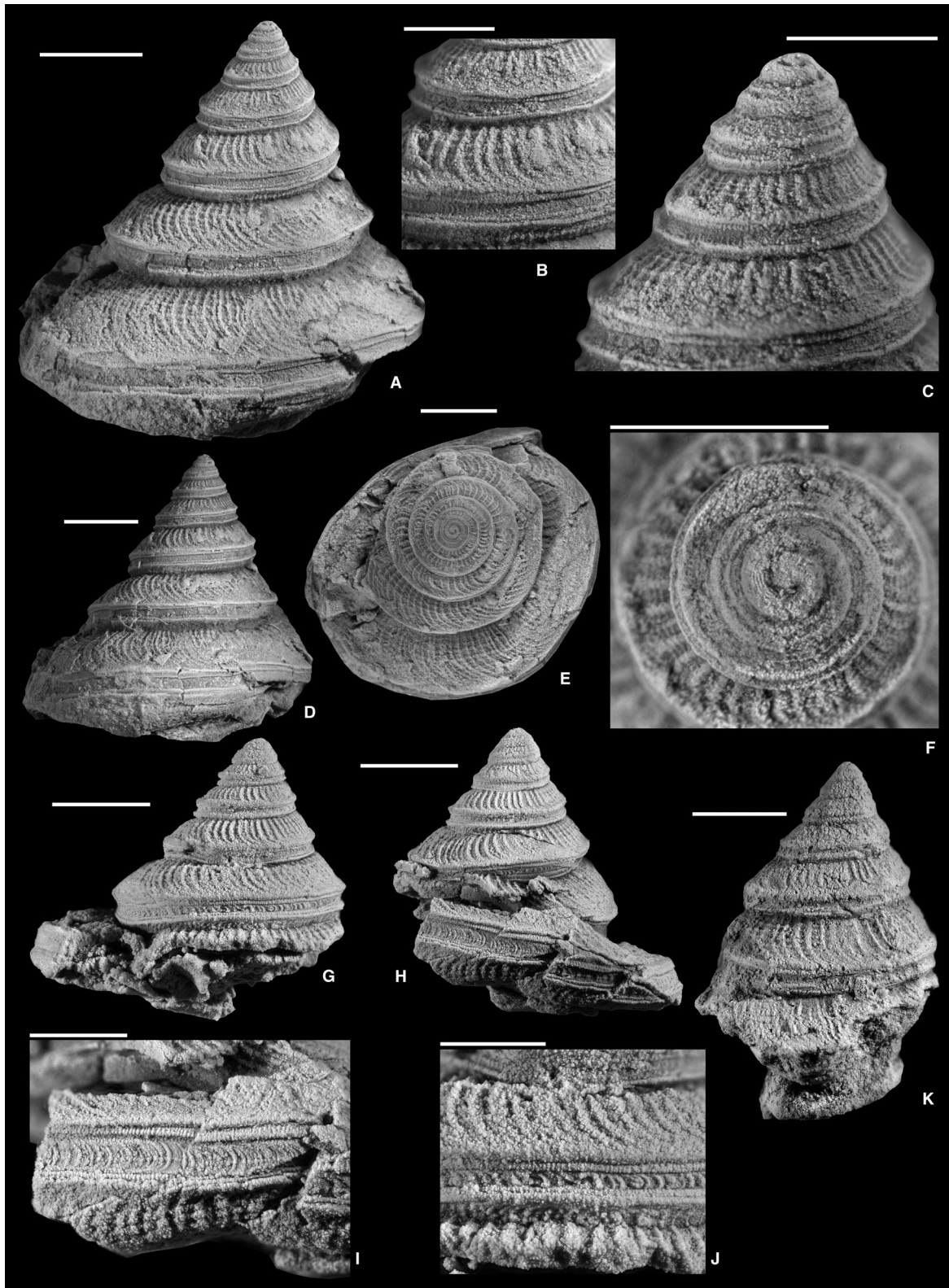
The selenizone of *Spiroscala* is not only bordered by spiral ridges but also develops vertical plate-like extensions (Batten 1958) between the prominent spiral ridges; the selenizone is bordered by these plates. This morphological character is also shared with the eotomariid genera *Oehlertia* Perner, 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 (2019a) 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 (2019a), all the above-mentioned characters are lumped into *Shwedagonia* and the depth of slit becomes the only criterion to differentiate the two genera. Mazaev (2019a) 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, 1866a from the Pennsylvanian of Illinois was previously assigned to *Spiroscala* by Knight (1945) but is herein placed in *Euconospira*. *Euconospira conoides* (Meek & Worthen, 1866a) comb. nov. has a non-graduate 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-spined 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.

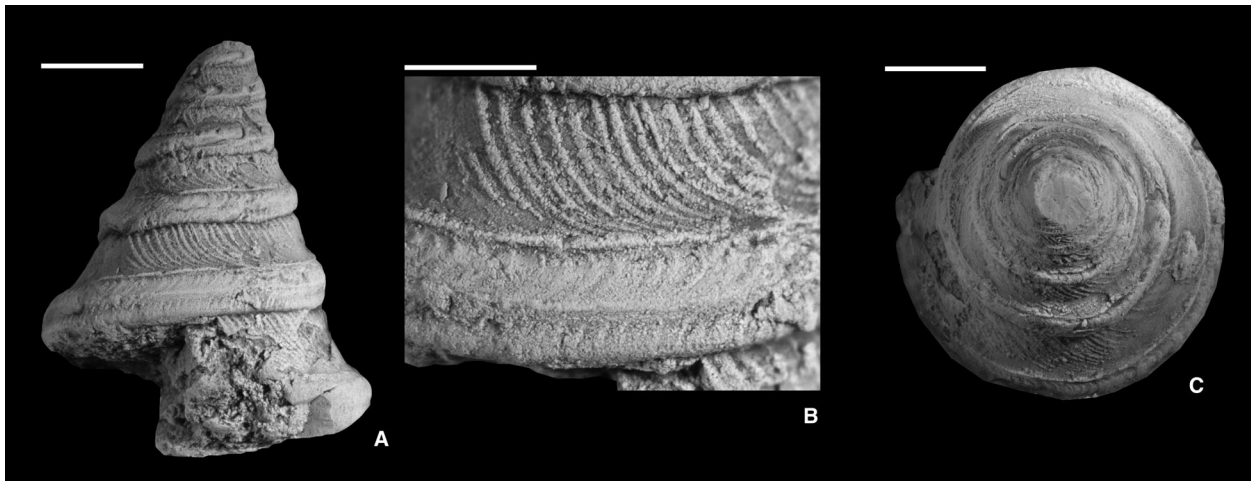
*Material.* 1 specimen from the Missourian of Texas (Placid Shale Member, TXM-14): SNSB-BSPG 2020 LXXI 1.

*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-spined; 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	–	–	–

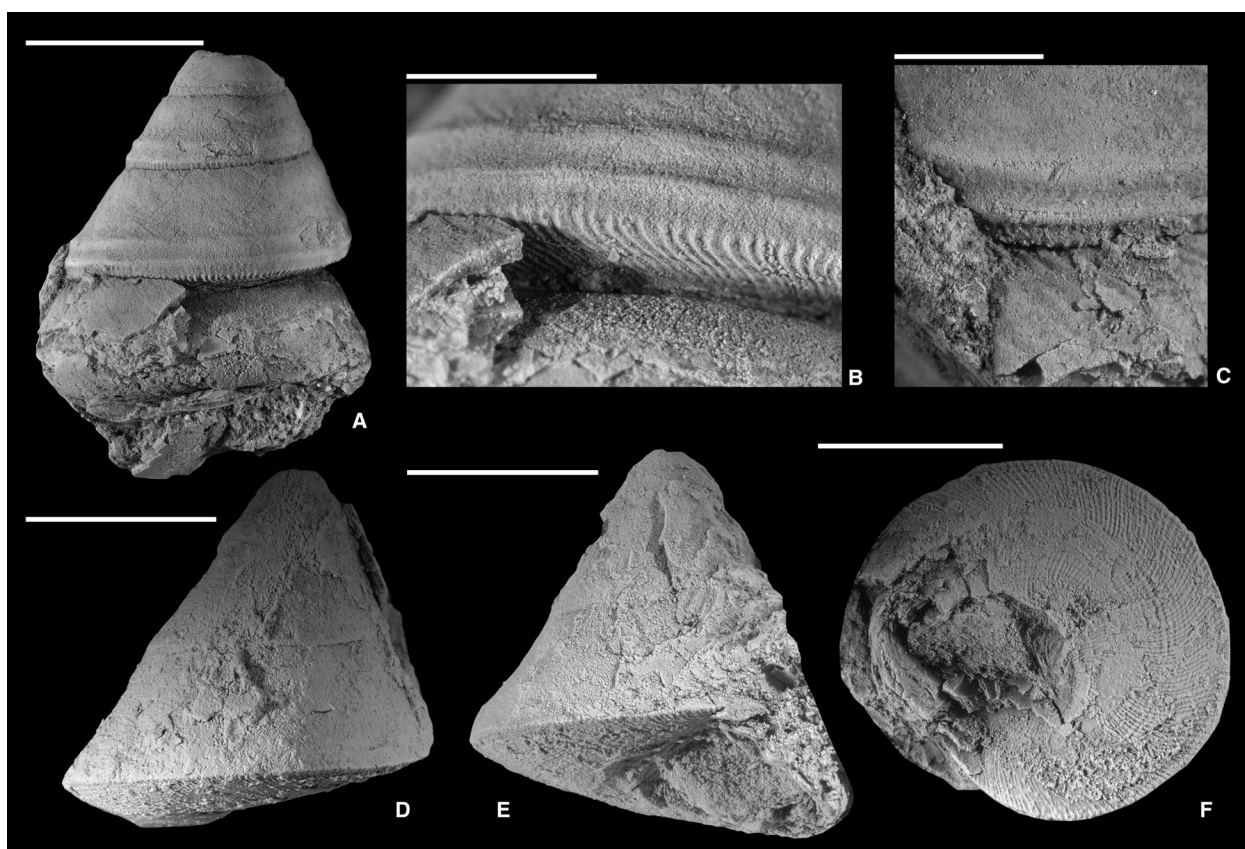
*Description.* Shell conical, with a pleural angle of 60°; suture slightly incised; early whorls not preserved; largest specimen with four whorls; whorl profile with weak angulation at adapical edge of selenizone; sutural ramp steeply inclining, almost straight to slightly convex, slightly concave near 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, 1866a). *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, 1866a) 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 Lucellidae 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 Lucellidae; 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 occultabanda* 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* from 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.

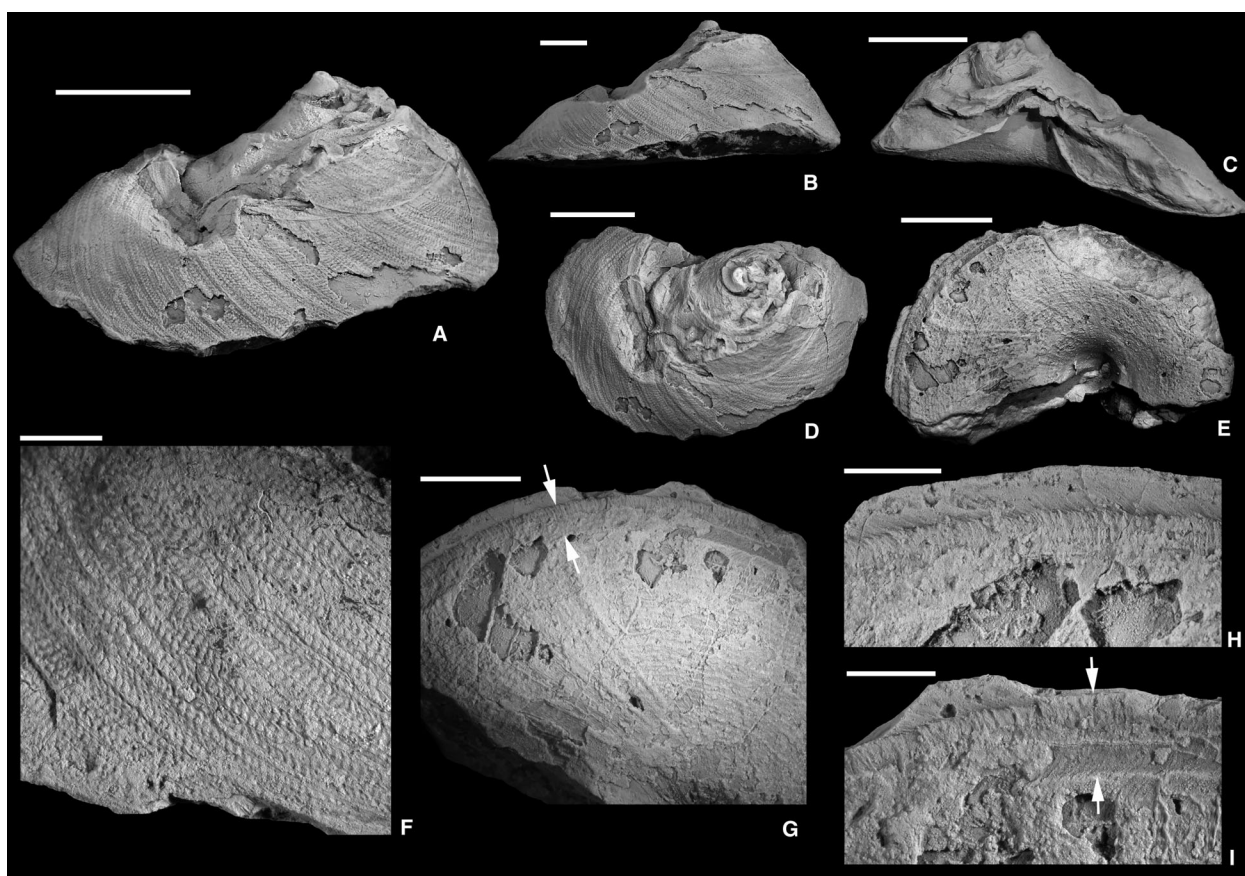
*Material.* 1 specimen from the Virgilian of Texas (Finis Shale Member, TXV–54): SNSB-BSPG 2020 LXXIX 1.

##### *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 anti-marginal, 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 1940b, 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.* *Eirlysellia 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 *Eirlysellia* and hence Lucieliidae 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, *Eirlysellia* 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-spined, 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 (1940b) proposed a new genus *Brookesella* (type species *Trochus hissingierianus* de Koninck, 1843) in her PhD thesis. Since this thesis has not been published, *Brookesella* is not a valid name. Here, we include *Trochus hissingierianus* 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 hissingierianus* de Koninck, 1843 [= *Eirlysella hissingieriana* (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 Bogy 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 prosocyr growth lines; later whorl face slightly convex to flat, with narrow subsutural shoulder, ornamented with oblique prosocline/prosocyr 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 prosocyr near selenizone, orthocline or slightly prosocyr near umbilical region; base anomphalous with smooth, callous columellar region; aperture subquadrate.

**Remarks.** We have not studied the type material of *Eirlysella hissingierianus* (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 (1940b) of an *E. hissingierianus* specimen from the Isle of Man. *Eirlysella hissingierianus* seems to be coelocoid 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

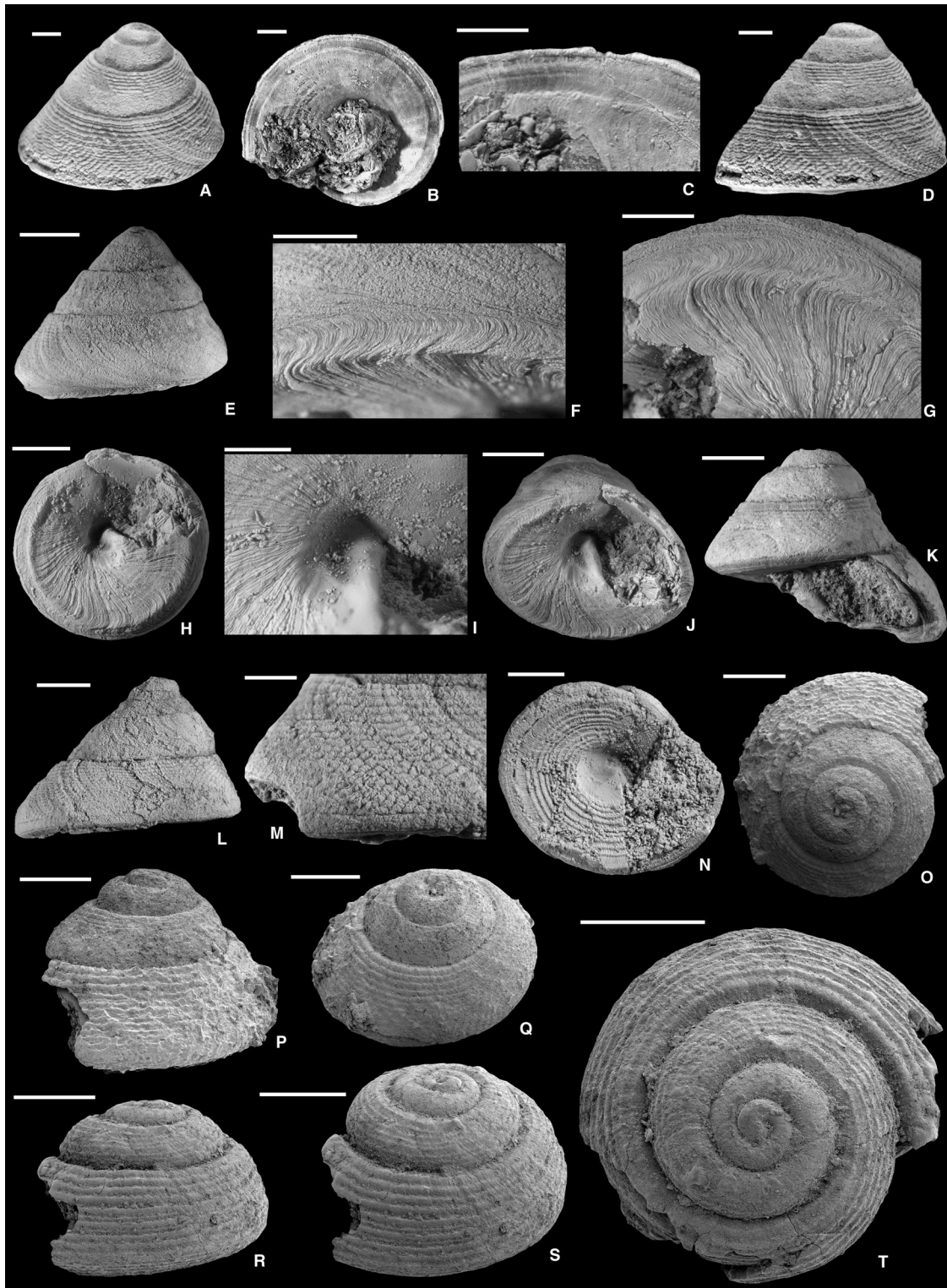
Family PHYMATOPLEURIDAE Batten, 1956

**Original diagnosis.** 'Discoïd 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 (2014a, 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 (2019b) 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 (2019b) included the species *Paragoniozonia 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.
- 1964a *Phymatopleura nodosus* (Girty); Sturgeon, p. 215, pl. 33 figs 23–26. pl. 36 fig. 11.
- 1967 *Phymatopleura nodosus* (Girty); Yochelson & Saunders, p. 165.
- 1972a *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):

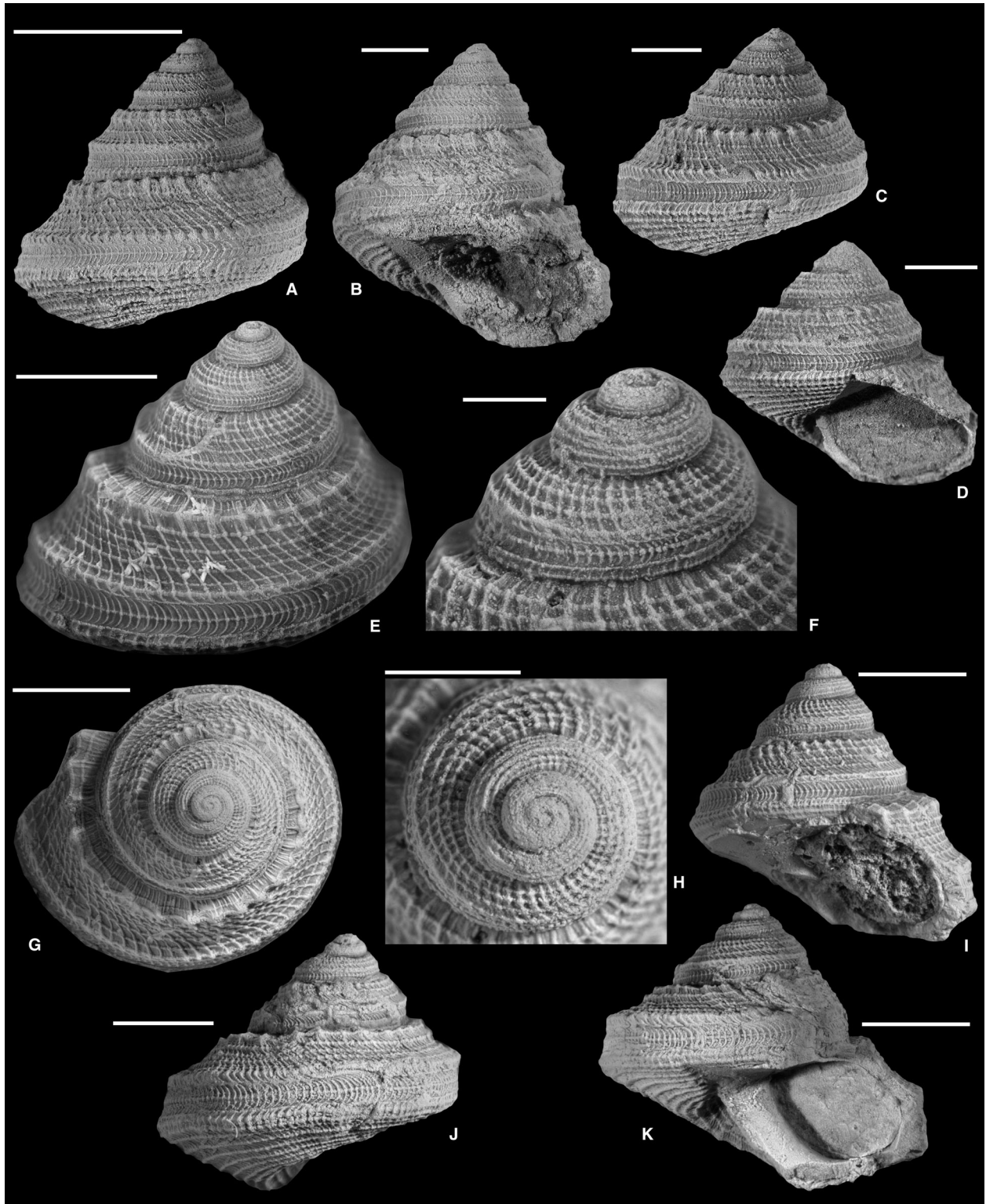
SNSB-BSPG 2020 LXVIII 1. 4 from the Desmoinesian of Oklahoma (Holdenville Formation, OKD–01): SNSB-BSPG 2020 LXIII 1, and a further 3 specimens (SNSB-BSPG 2020 LXIII).

#### 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. 22), 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 *Paragoniozonia*, and seems more persistent than other characters (i.e. adult shell morphology and ornamentation). Knight (1945) also noted that the vertical position 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.
- 2014b *Phymatopleura* sp.; Nützel, p. 68, fig. 1E.

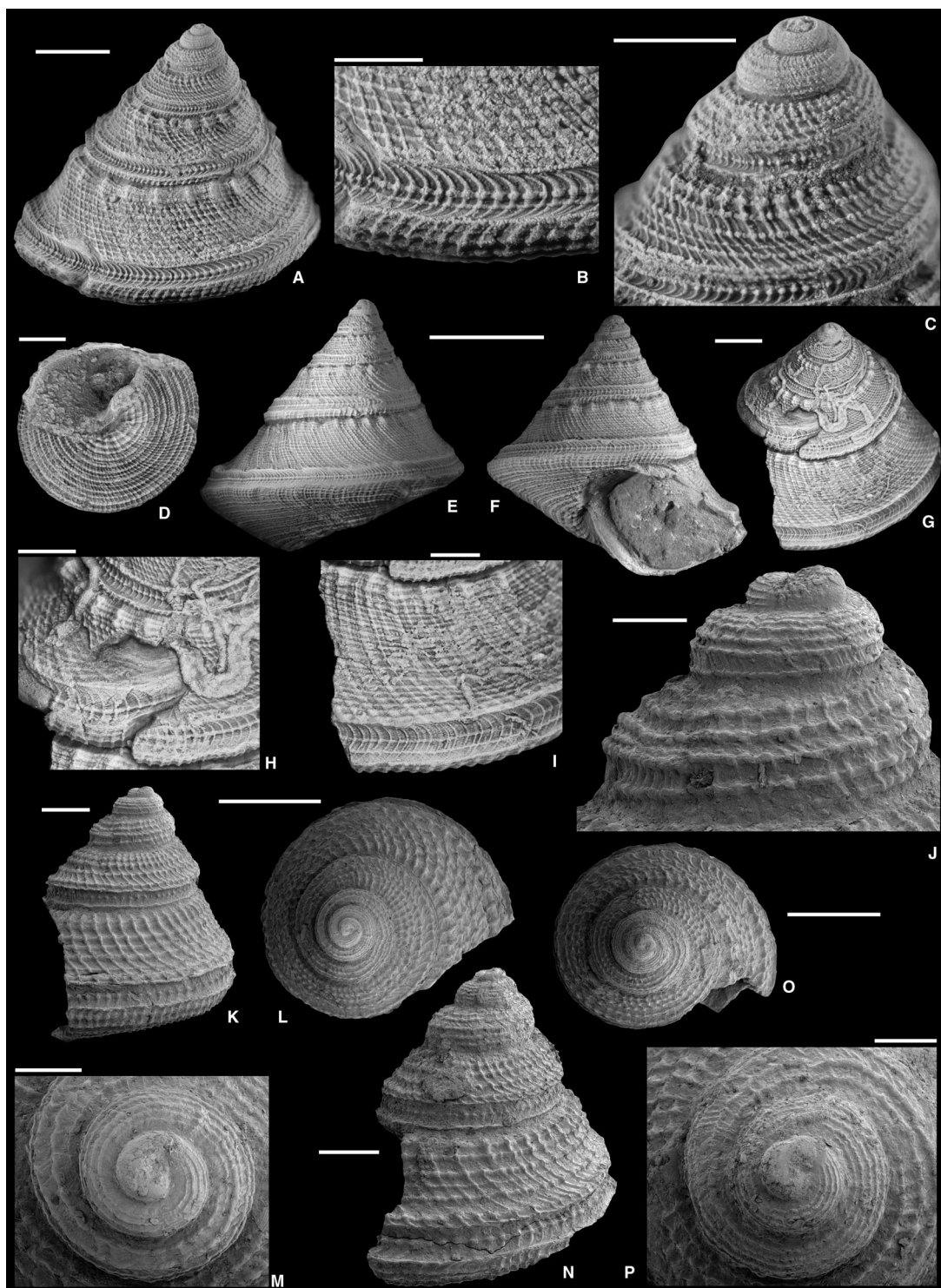
**Material.** A total of 322 specimens. 8 from the Missourian of Texas (Placid Shale Member, TXM–14): SNSB-BSPG 2020 LXXI. 71 from the Virgilian of Texas (Colony Creek Shale Member, TXV–46): SNSB-BSPG 2009 XXII 6, and a further 70 specimens (SNSB-BSPG 2009 XXII). 123 from the Virgilian of Texas (Finis 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).

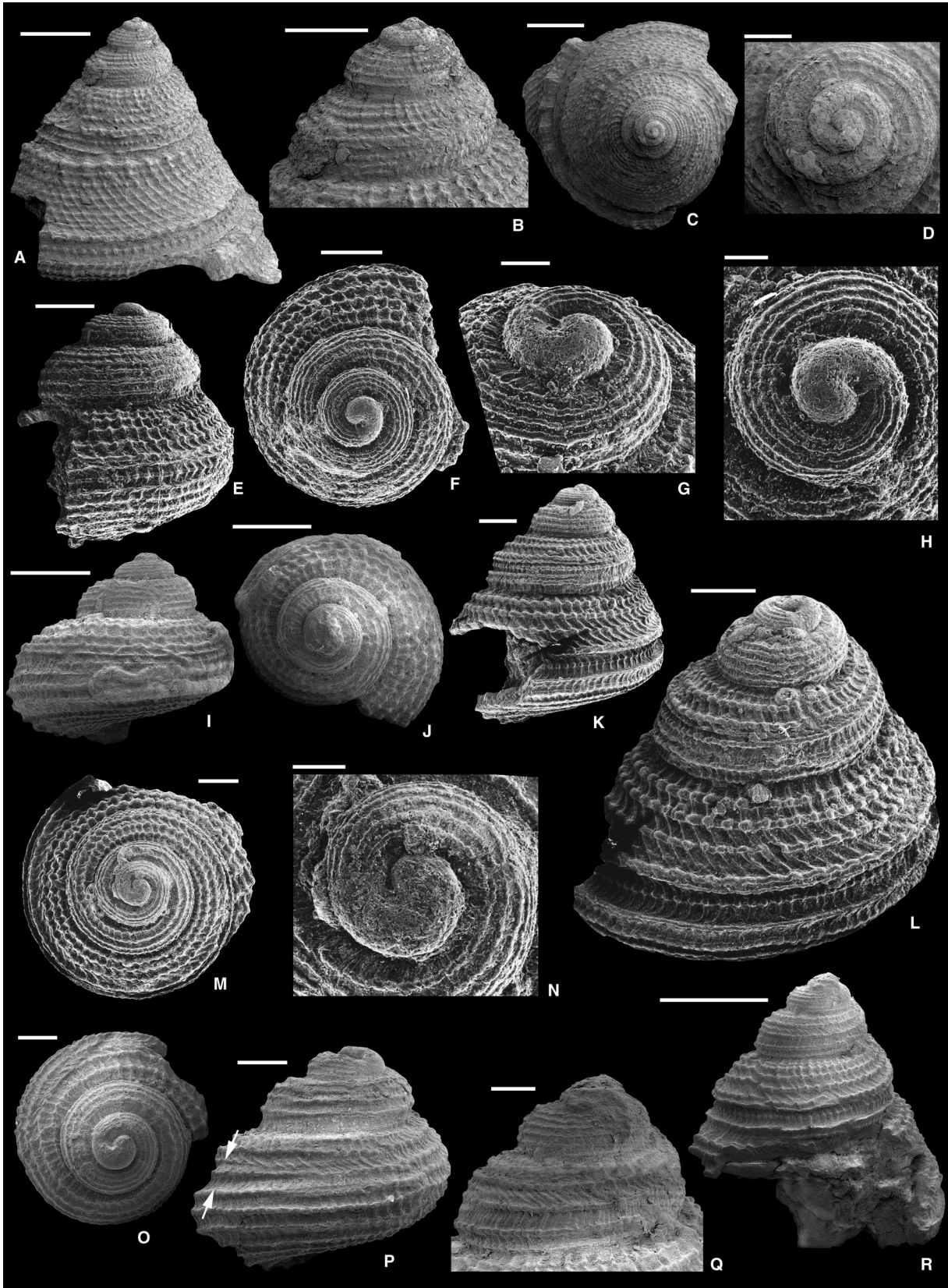
	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2009 XXII 6	11.0	10.9	74	0.30	5.0	3.6	0.8	0.21	0.16
2020 XCI 5	10.9	10.4	74	0.34	4.8	3.5	0.7	0.21	0.15
2020 LXXIV 1	9.3	10.4	76	–	4.2	4.0	0.8	0.19	0.18
2020 LXXVI 1	8.3	8.0	72	0.33	3.8	3.2	0.6	0.20	0.17
2020 LXXVIII 1	11.6	11.8	78	–	5.4	4.2	1.1	0.26	0.20

**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/prosocyrct 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, prosocyrct 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 prosocyrct just below periphery, then turning into opisthocyrct; aperture subquadrate, oblique, slightly wider than high; outer lip concave, basal lip flatly concave, columellar lip straight, oblique.

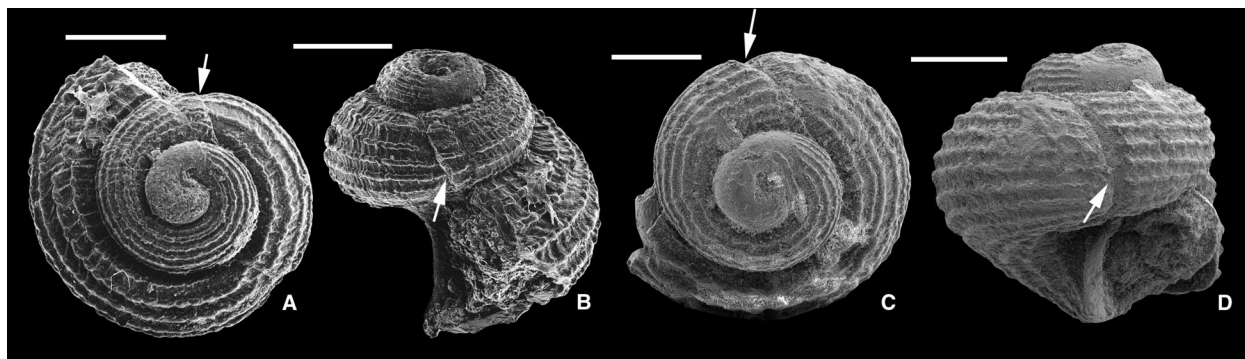


**FIG. 23.** *Phymatopleura brazoensis* (Shumard, 1860). A–D, SNSB-BSPG 2020 LXXVI 1, from the Finis Shale Member (Virgilian, Texas); B, oblique apical view, detail of ornament. E–F, SNSB-BSPG 2020 LXXVIII 1, from the Finis Shale Member (Virgilian, Texas). G–I, SNSB-BSPG 2020 LXXIV 1, from the Finis 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.





**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); 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 phaneroomphalous. 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 phaneroomphalous 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 *Pl. 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

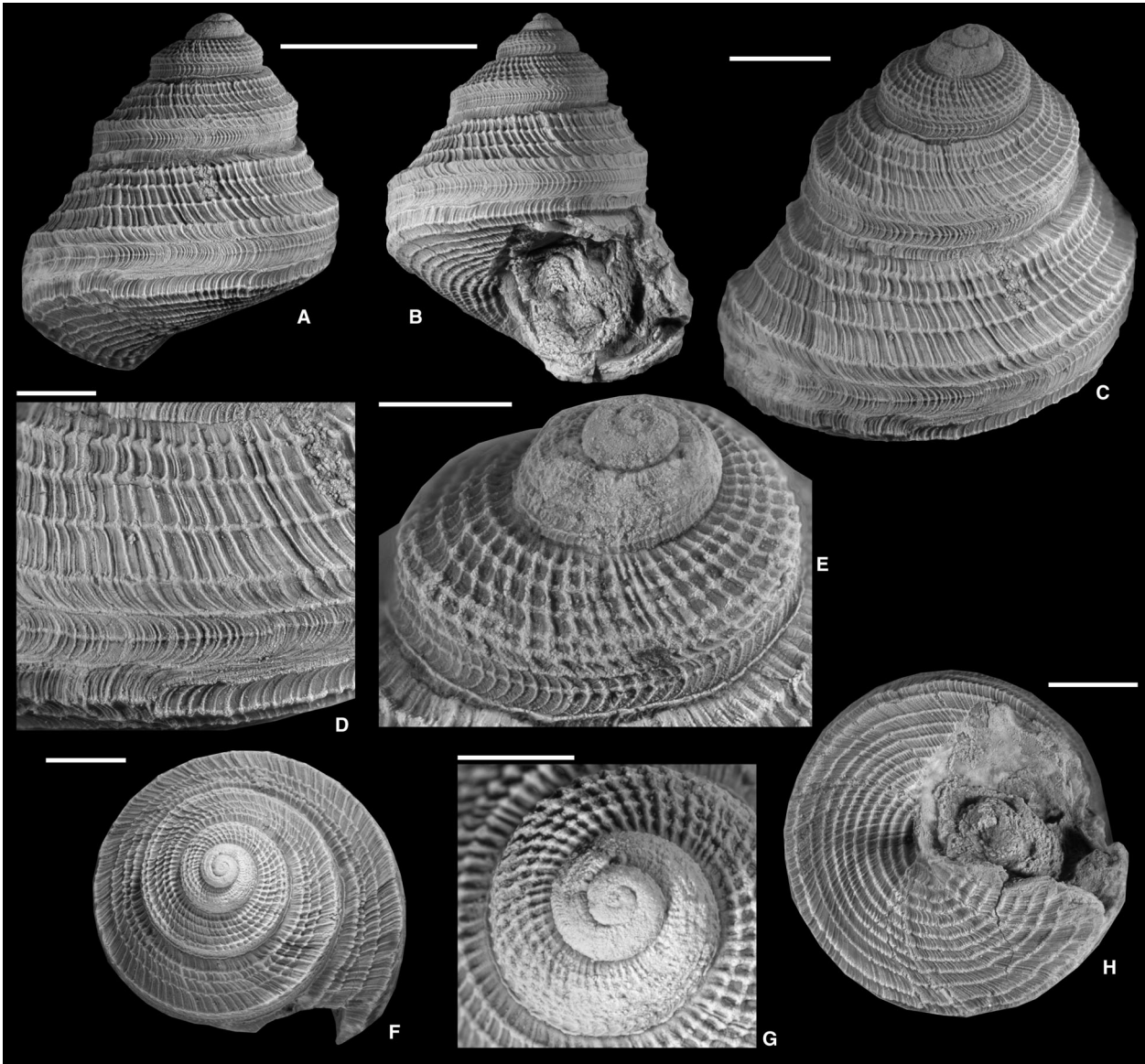
? 1915 *Orestes nodosus*; Girty, p. 320, pl. 22 figs 7–7a (non figs 8–10).

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**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	RSwf
2020 I 22	9.6	8.2	59	0.37	4.7	4.3	0.9	0.21	0.19

*Description.* Shell small, trochiform, cyrtocoid, 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 prosocyrct 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 opisthocyrct 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,  $\times 3$ , 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, NW $\frac{1}{4}$ , NW $\frac{1}{4}$ , SW $\frac{1}{4}$ , sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7 $\frac{1}{2}$ ' 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).*

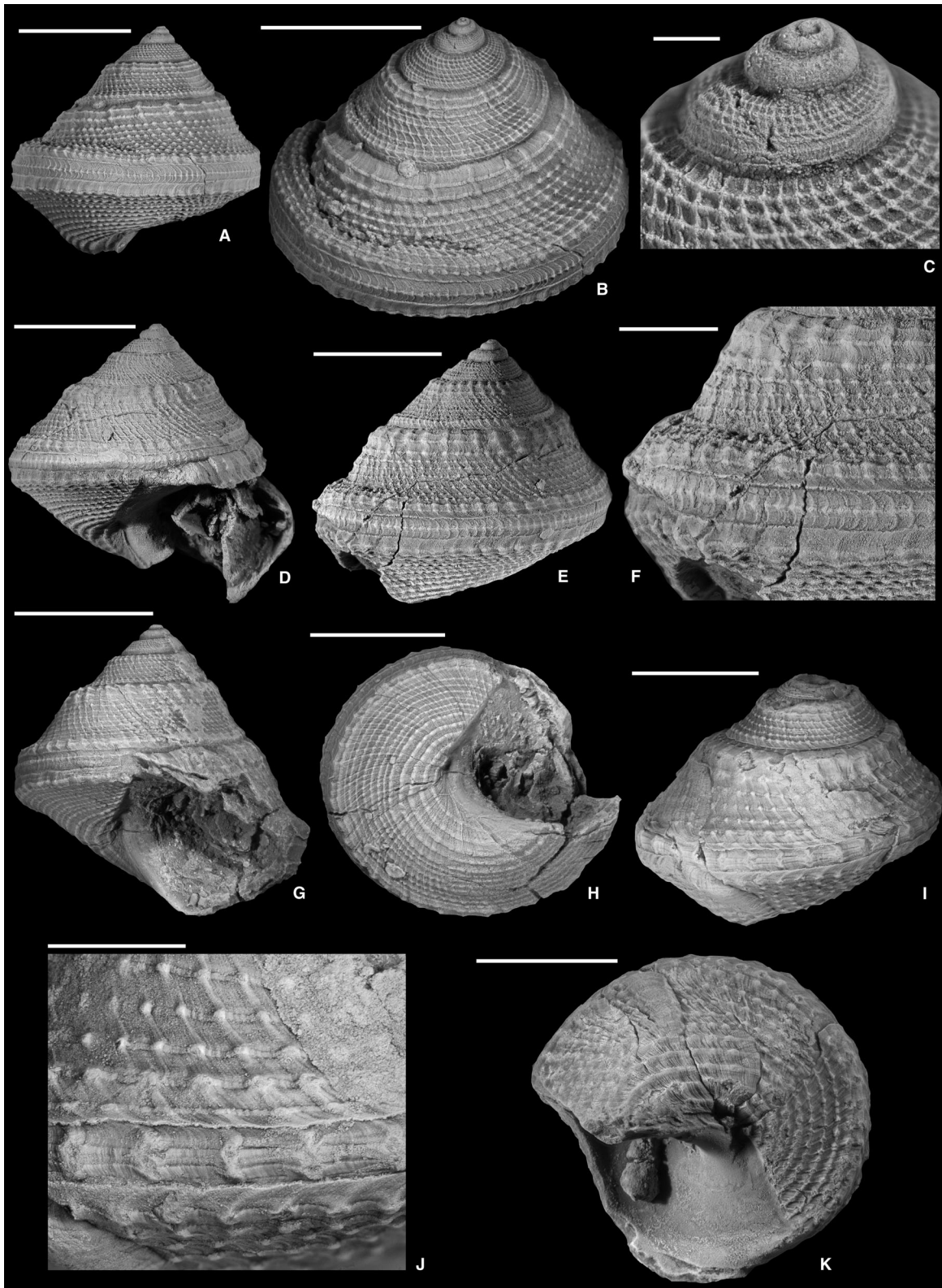
	H	W	PA	Wfw	Hlw	Wwf	WS	RSwf	RSwh
2020 LVIII 1	10.8	11.4	86	0.36	5.6	5.2	0.8	0.16	0.15
2020 LVIII 2	10.7	11.0	87	–	6.8	5.5	0.9	0.16	0.13
2020 LVIII 3	11.7	11.6	83	0.39	7.0	5.6	0.9	0.15	0.12

*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 prosocyrct 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 suprasutural 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 opisthocyrct 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, 1964a (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 *Rhinoederma* de Koninck. Unlike the type species of *Rhinoederma*, *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 (2019b) 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.

*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/prosocyrct 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 opisthocyrct 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 nodolirata* Nelson, 1947

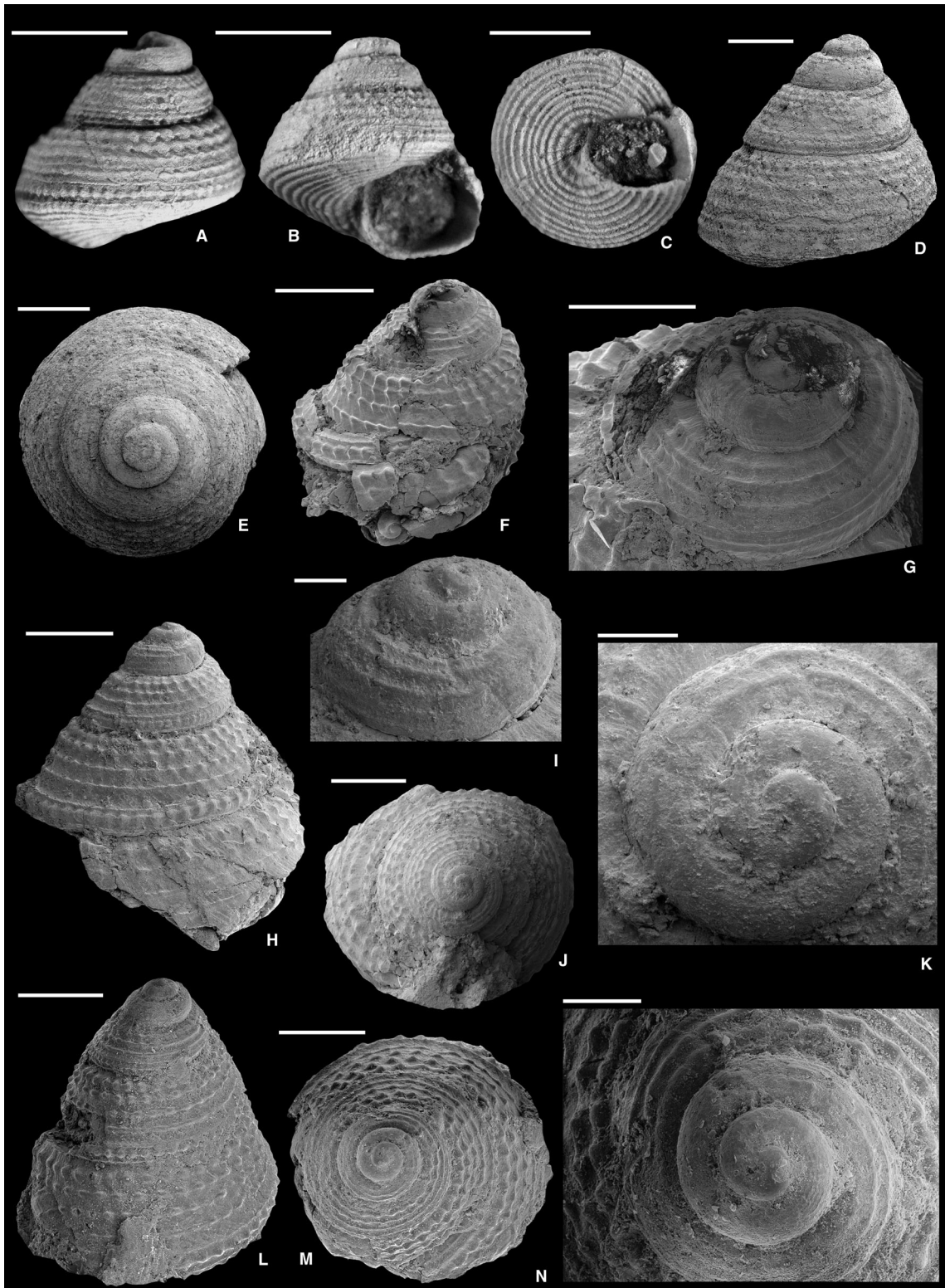
Figure 28

- \* 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.

*Paragoniozona paucinodosa* Nelson, 1947

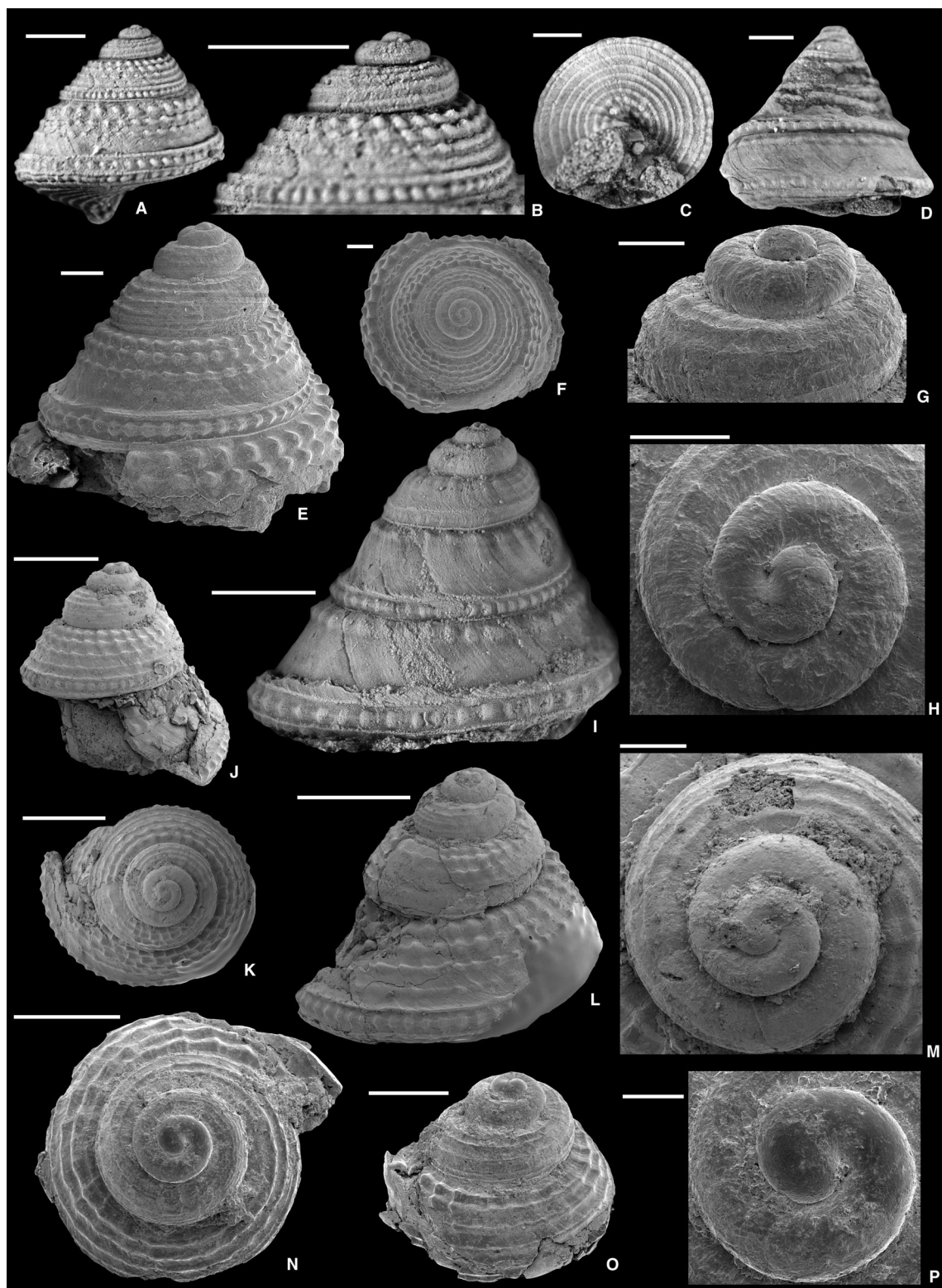
Figures 29, 30

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

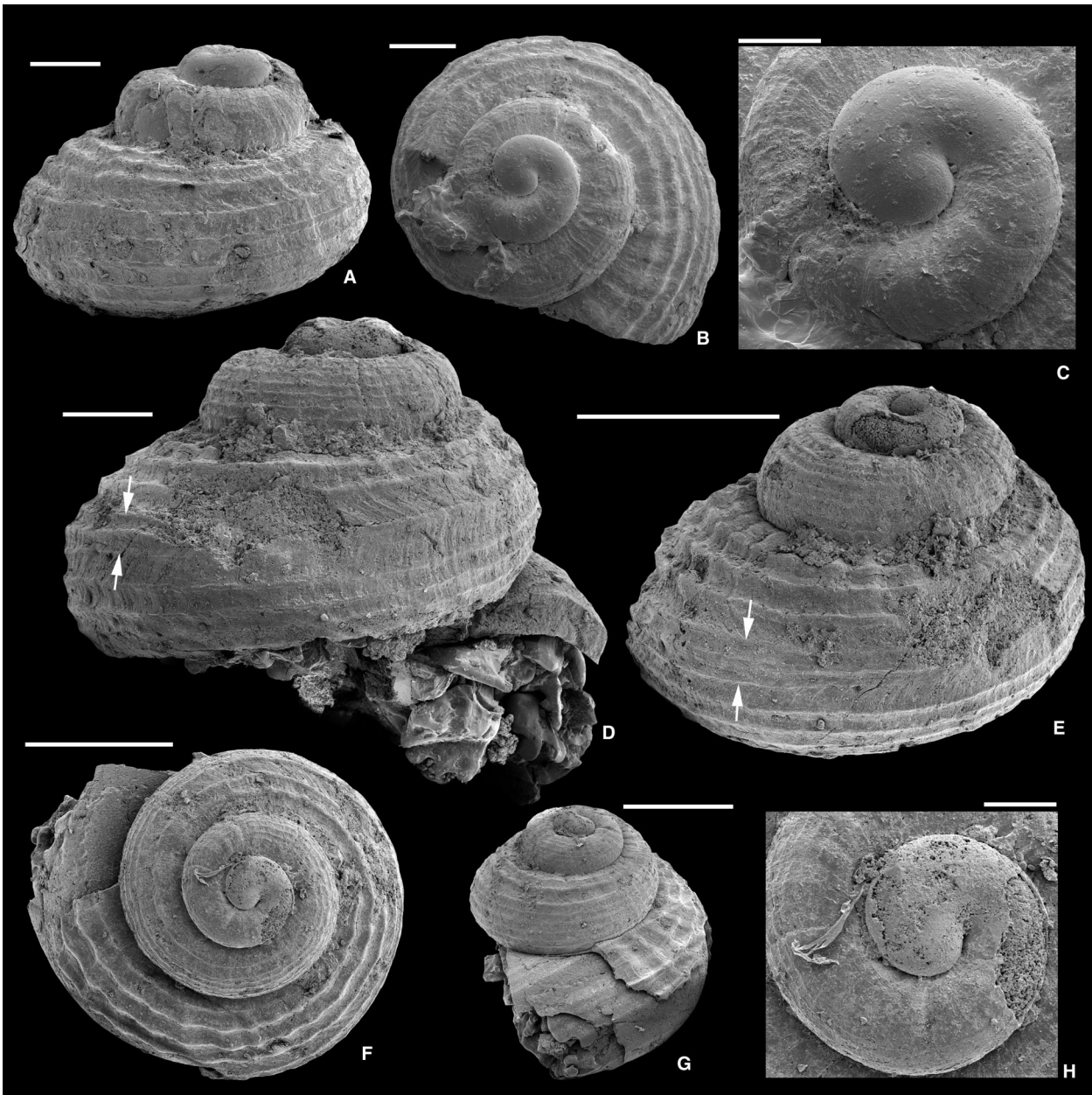


**FIG. 28.** *Paragoniozona nodolirata* Nelson, 1947, from the Buckhorn Asphalt (Desmoinesian, Oklahoma). A–C, SNSB-BSPG 2011 X 77. D–E, SNSB-BSPG 2011 X 262. F–G, SNSB-BSPG 2011 X 260; G, oblique apical view, detail of early whorls. H–K, SNSB-BSPG 2011 X 263; I, oblique apical view, detail of early 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.
- ? 1964a *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 cyrtocoid, 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 prosoclyt 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 opisthoclyt 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)

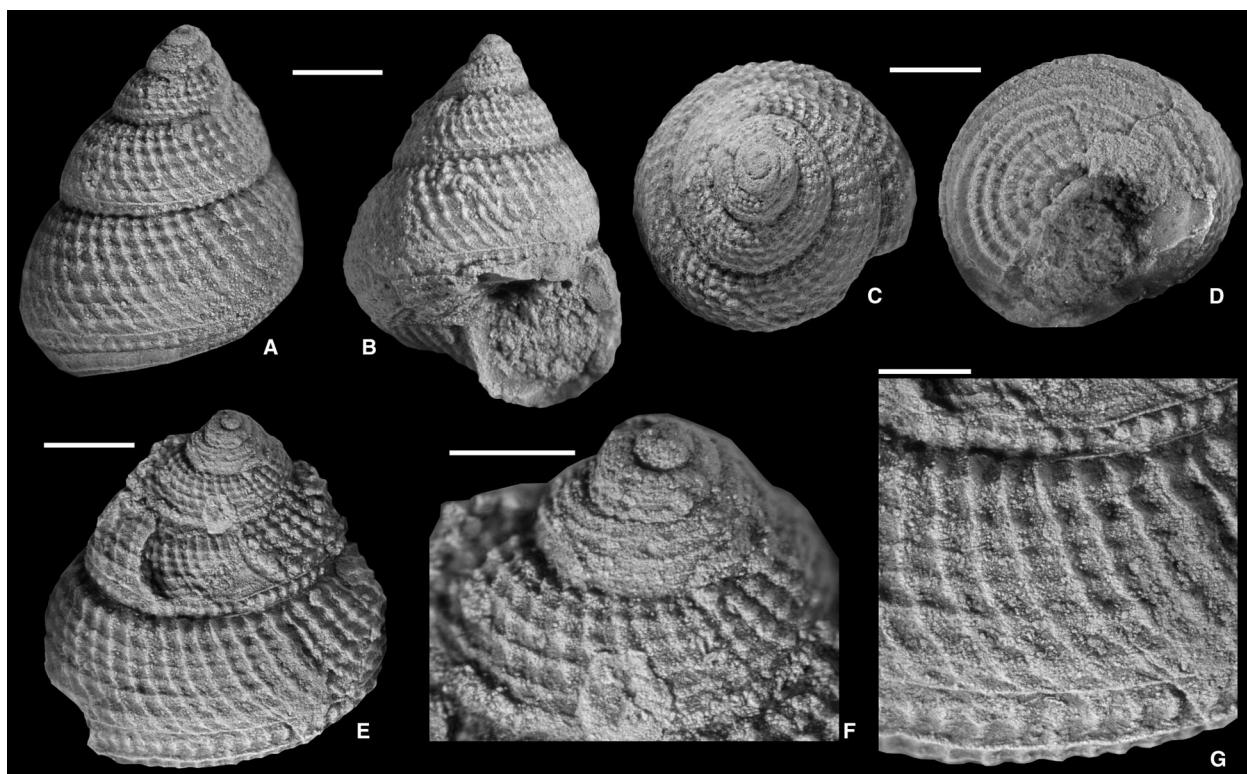
Figure 32

- 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  $c. 80^{\circ}$ – $85^{\circ}$ ; early whorl face convex, ornamented with spiral threads; later whorl face convex to slightly convex, ornamented with spiral cords and prosocline to slightly prosoclyrt 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 opisthoclyrt 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  $65^{\circ}$  (from illustration;  $60^{\circ}$  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 ( $80^{\circ}$ ) 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

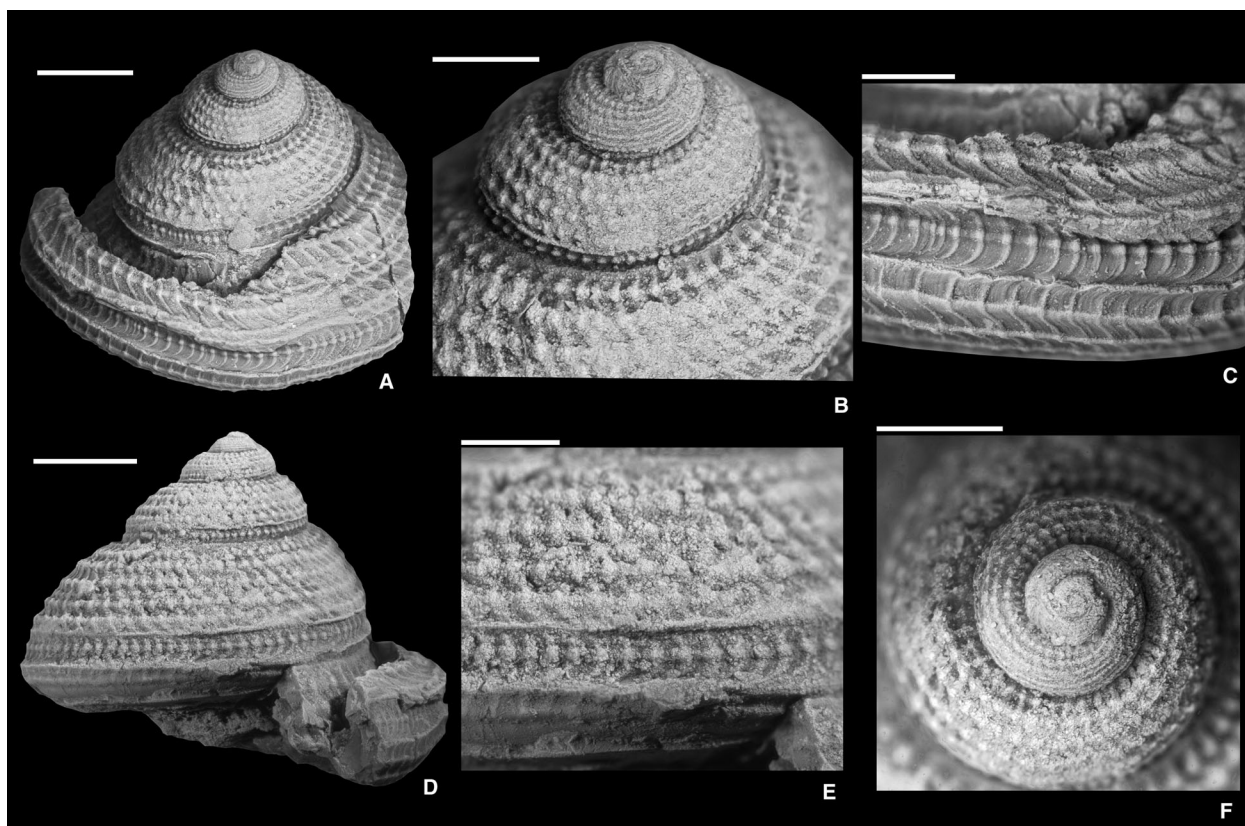
*Derivation of name.* After the geologist and palaeontologist Thomas E. Yancey, for his work on late Palaeozoic invertebrate faunas.

*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 ( $34^{\circ}26'44''N$ ;  $96^{\circ}57'41''W$ ), 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 prosoclyrt 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.

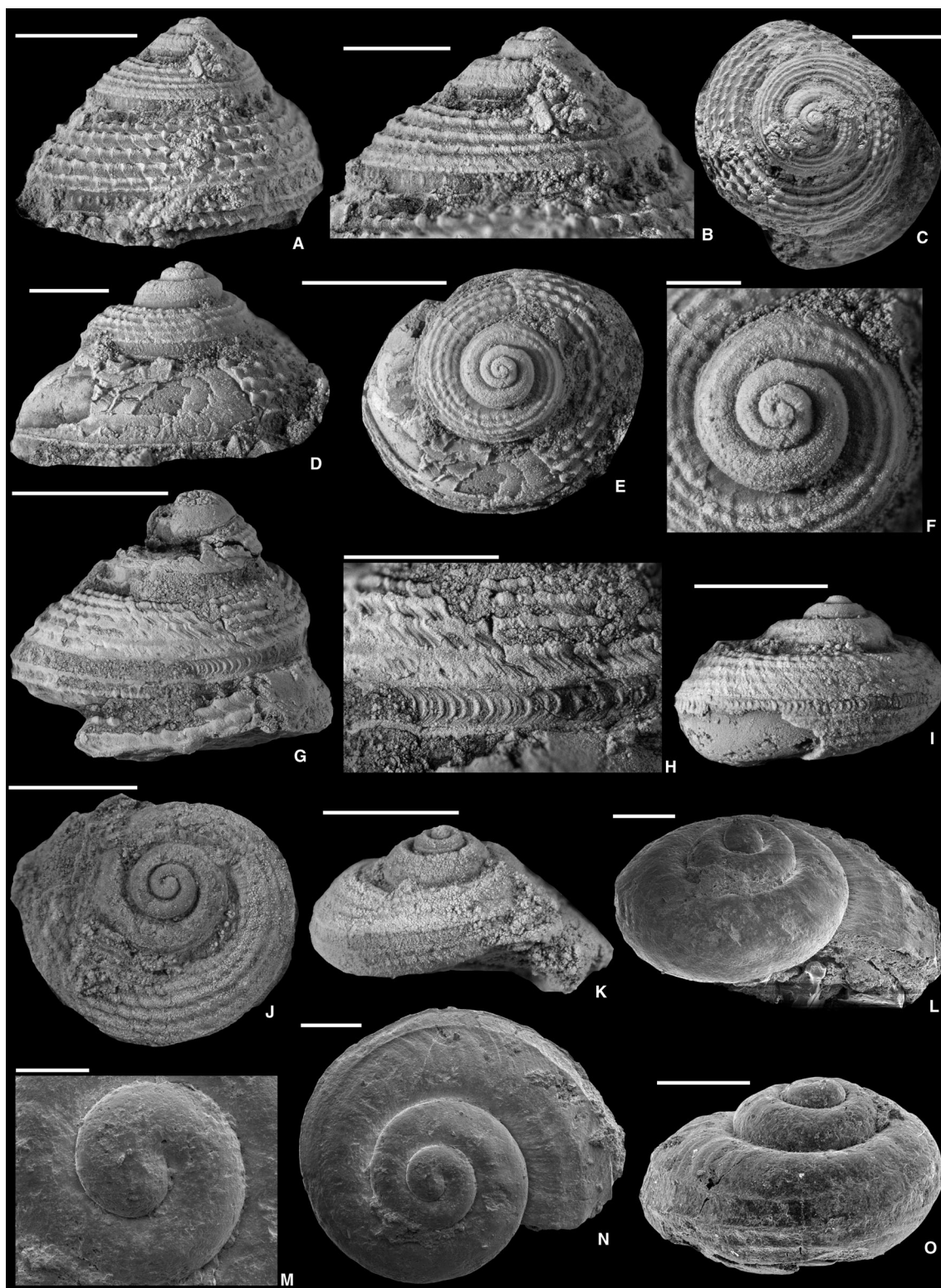
*Remarks.* The specimens at hand resemble the monotypic Carboniferous genus *Hammatozospira* Gordon & Yochelson, 1983 and

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. 1209) 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.*, 2020b, 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.*, 2020b) 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

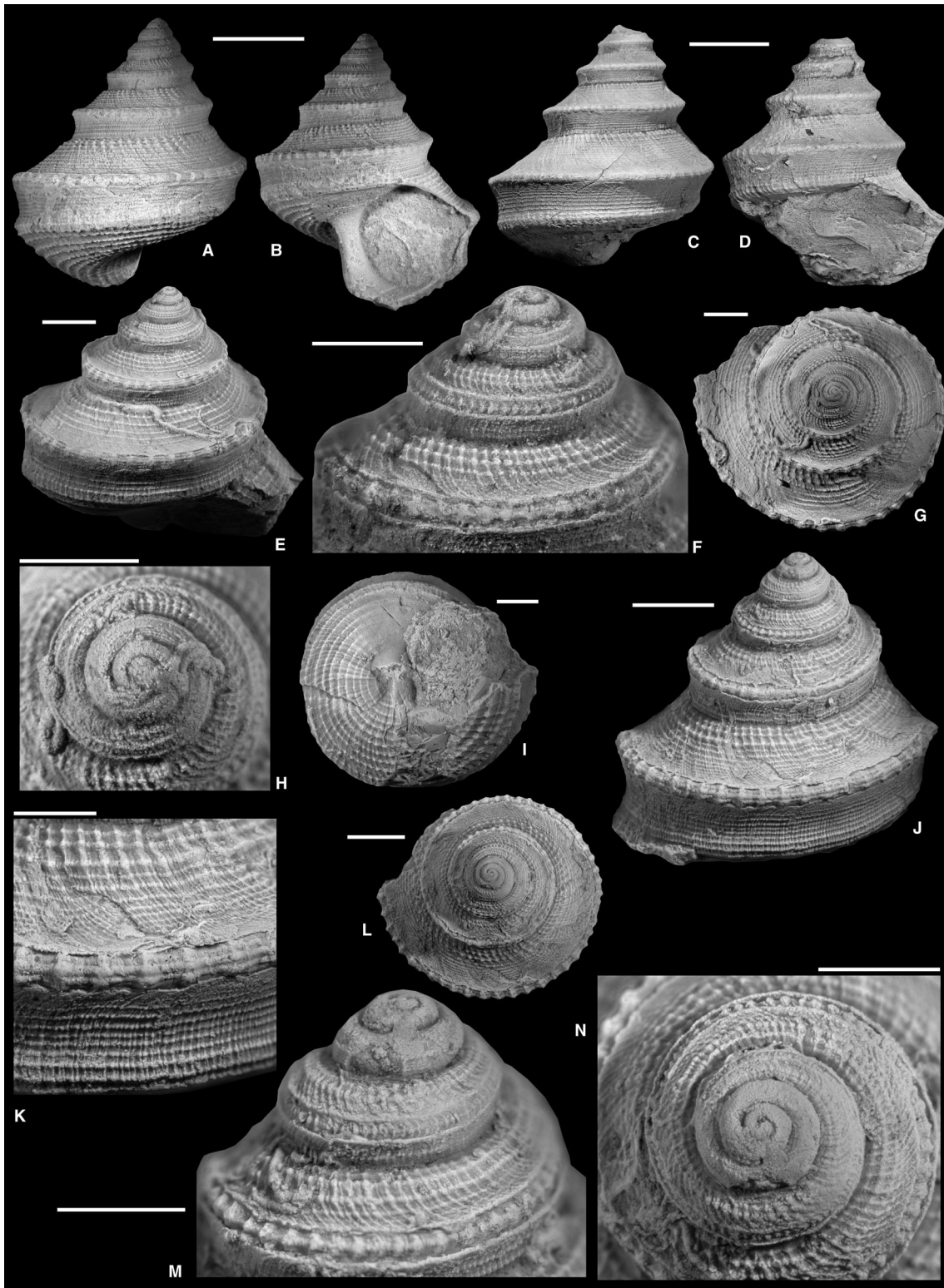
lophospirids in having a concave selenizone low on the whorl face at mid height of the whorl.

*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

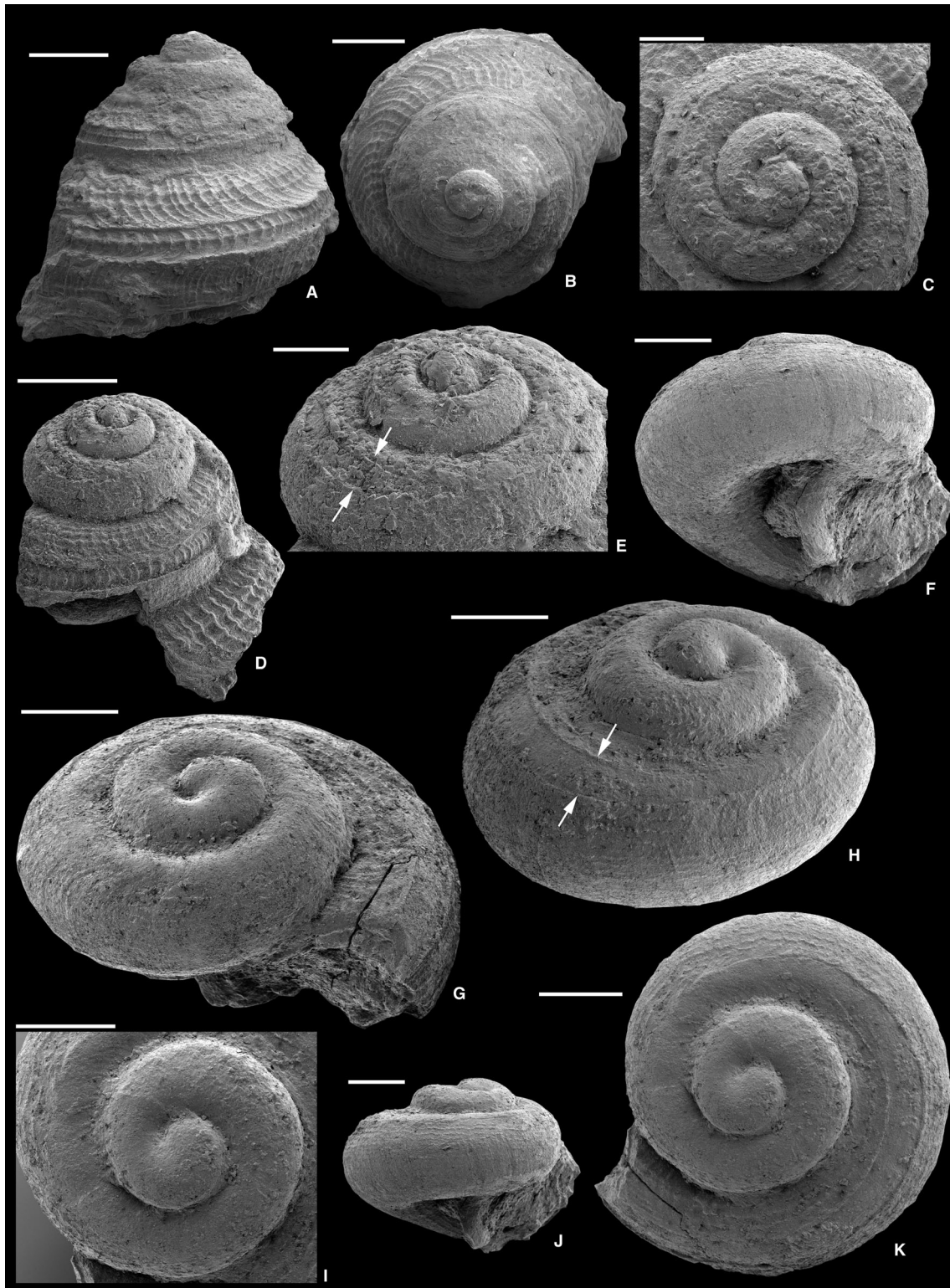
- \* 1835 *Turbo tabulatus* Conrad, p. 267, pl. 12 fig. 1.
- 1915 *Worthenia tabulata* Conrad; Girty, p. 152, pl. 22 figs 1–4a.
- 1922 *Worthenia tabulata*; Plummer & Moore, pl. 22 figs 17–19 [non pl. 19 fig. 25].
- 1941 *Worthenia tabulata* (Conrad); Knight, p. 385. pl. 34 fig. 1a–c.
- 1967 *Worthenia tabulata* (Conrad); Yochelson & Saunders, p. 243 (for further synonymy).
- 1972a *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 prosocline 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

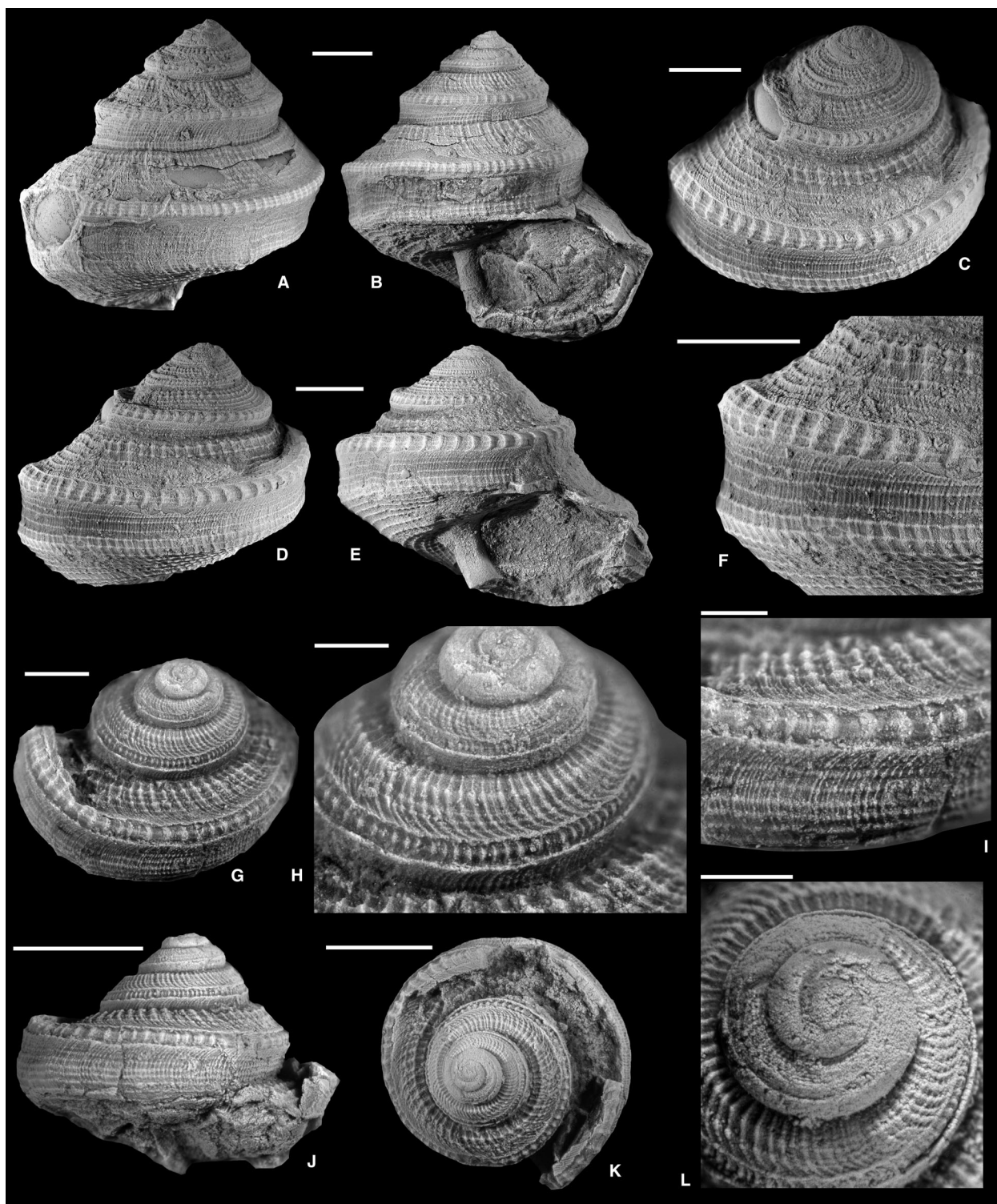
- 1964a *Worthenia* cf. *W. tabulata* (Conrad); Sturgeon, p. 209, pl. 32 fig. 6.  
 1996 *Worthenia tabulata* (Worthen); Hoare & Miller, p. 154, fig. 13-3.9.  
 \* 1997 *Worthenia parvula* Hoare et al., p. 1031, figs 4.11–4.15.

**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 prosocline axial threads and nodes at intersections; transition to base with rounded basal edge; base convex, ornamented with opisthoclyt radial growth lines/threads and node-bearing spiral cords; aperture slightly wider than high; base narrowly phaneromphalous.

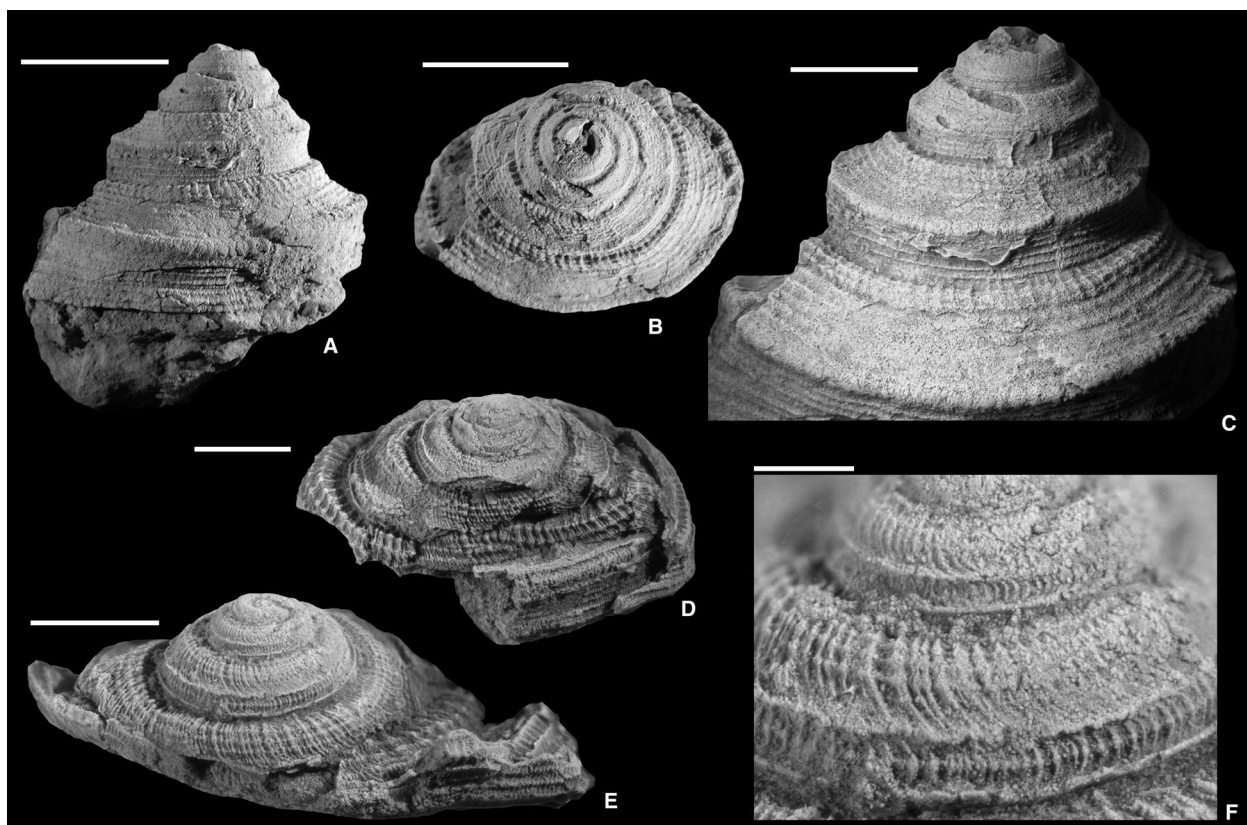
*Remarks.* *Worthenia (W.) parvula* has only been reported from the Allegheny Formation of Ohio. The small specimens assigned herein to *W. (W.) parvula* from the Holdenville Formation of Oklahoma record the only occurrence outside Ohio.

*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  | <i>Pleurotomaria speciosa</i> Meek & Worthen, p. 461.                            |
|     | 1866b | <i>Pleurotomaria speciosa</i> M. & W.; Meek & Worthen, p. 352, pl. 28 figs 5a–c. |
|     | 1967  | <i>Worthenia speciosa</i> (Meek & Worthen); Yochelson & Saunders, p. 242.        |
|     | 1989  | <i>Worthenia speciosa</i> (Meek & Worthen); Batten, pl. 9 figs 10–12.            |
| non | 1995  | <i>Worthenia speciosa</i> (Meek & Worthen); Batten, p. 19 fig. 25.               |
|     | 2001  | <i>Worthenia speciosa</i> (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-spined; 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 prosoclyt 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 opisthoclyt 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. 2020a 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-spined and with wider interspace between the lunulae; it probably represents *W.* (*W.*) *legrandi* Kues & Batten, 2001.

## Subgenus YOCHELSONOSPIRA Thein &amp; 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

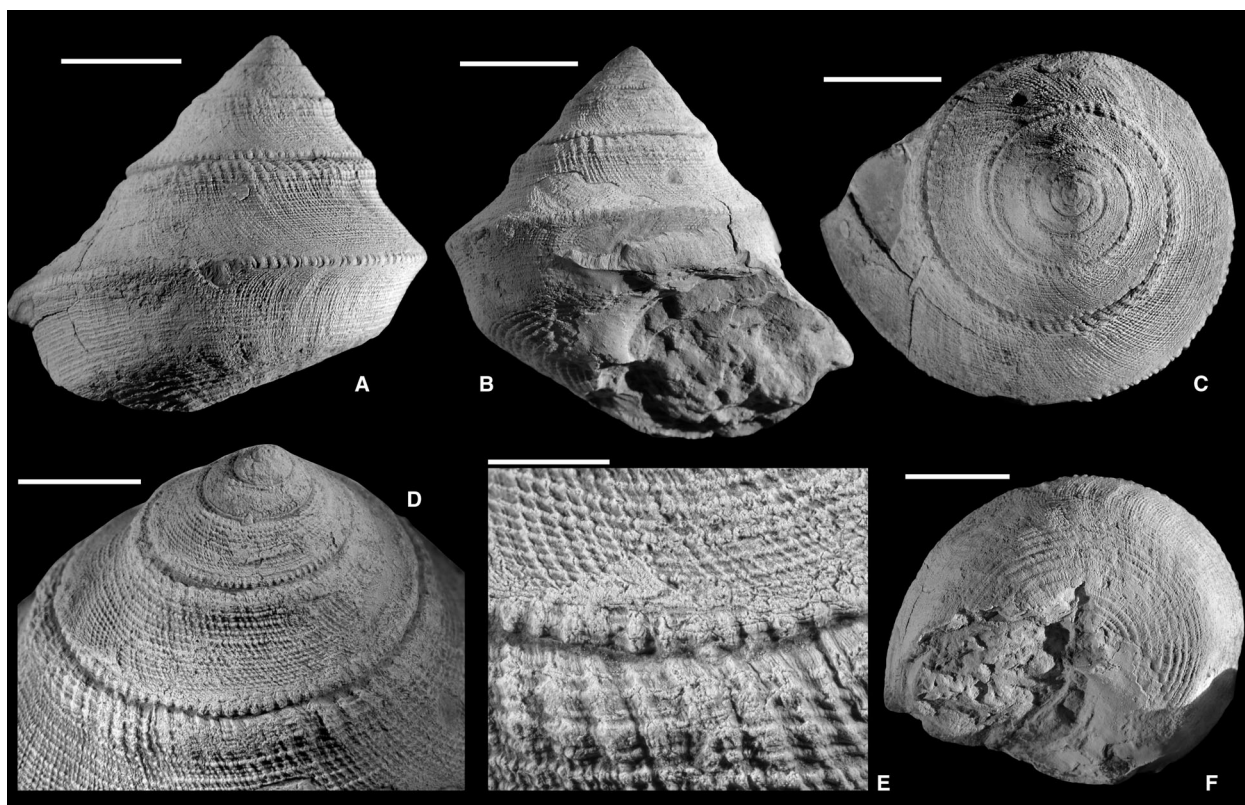
**LSID.** urn:lsid:zoobank.org:act:37B96178-5D2D-4A0A-A46E-38CD2DFF50EF

**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, prosocyrct 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 opisthocyrct 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 textiliger* Meek, 1871 in general shell morphology. However, the figure later provided by Meek (1875, p. 314, pl. 13 fig. 7a–b) suggests that *Ple. textiliger* 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. textiliger* 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. textiliger* 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, 1940a

*Type species.* *Borestus wrighti* Thomas, 1940a 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-spined 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 & Heidelberg (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.
- ? 1940a *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.

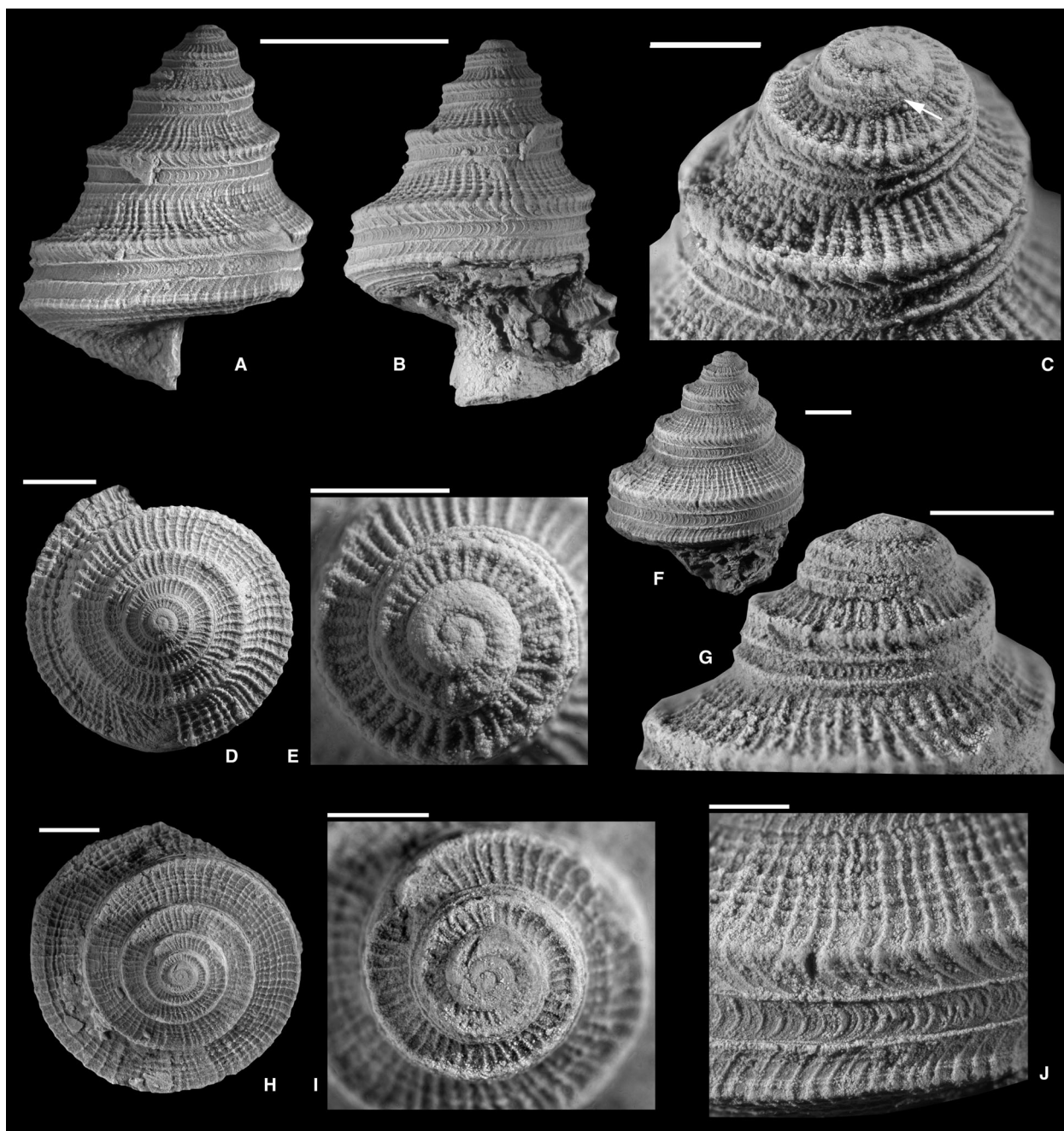
*Measurements (mm).*

	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-spined 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, prosoclyrt 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 opisthoclyrt 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, 1940a) 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 (1866b, 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 Karapınar & 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 (Karapınar & Nützel 2021). Its type species, *Stuorella subconca* (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

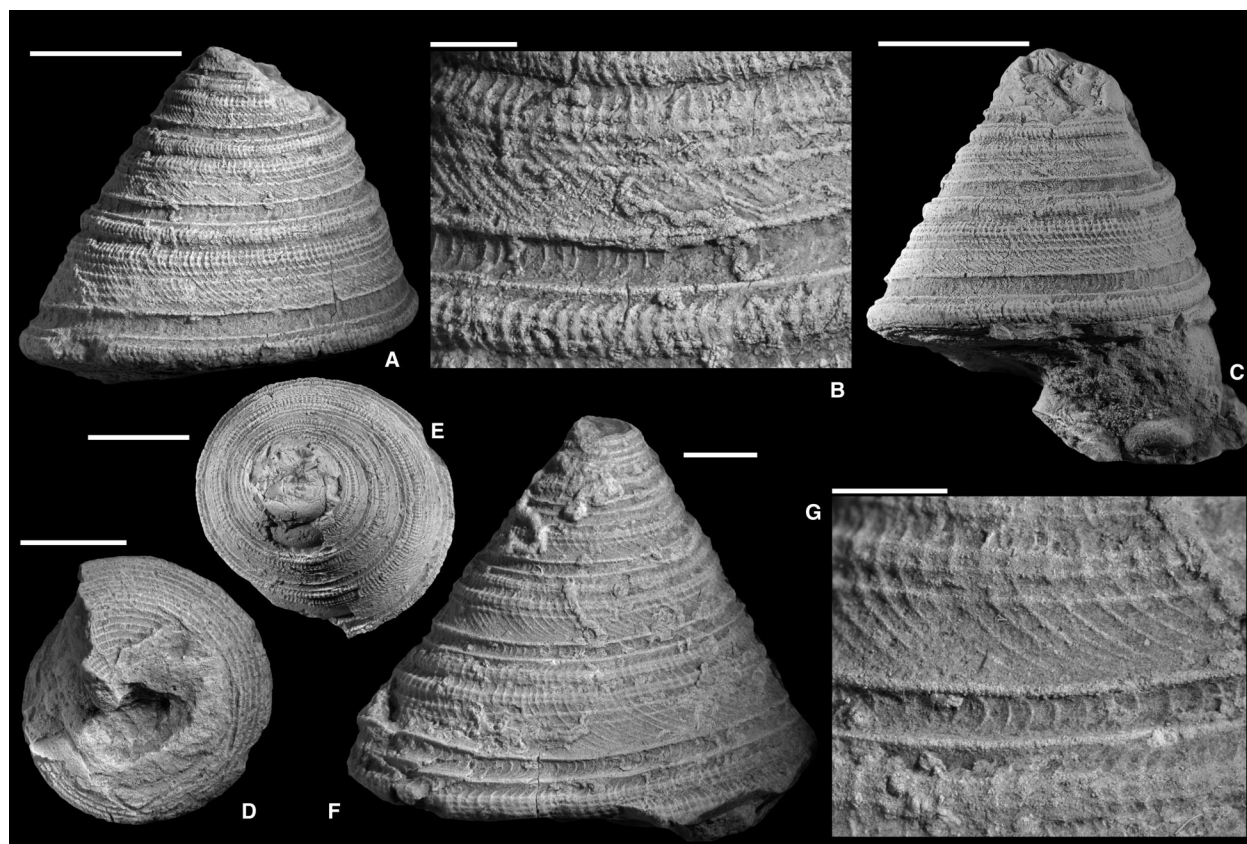
- \* 1945 *Glyptotomaria apiarium* Knight, p. 577, pl. 79 fig. 4a–c.
- 1967 *Glyptotomaria (Glyptotomaria) apiarium* (Knight); Yochelson & Saunders, p. 90.

**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 slightly 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 1964b, 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 (1964b), 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 *Devonrhineoderma*: *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* (Karapınar & Nützel 2021).

#### *Dictyotomaria turrisbabel* sp. nov.

##### Figure 41

2014b 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

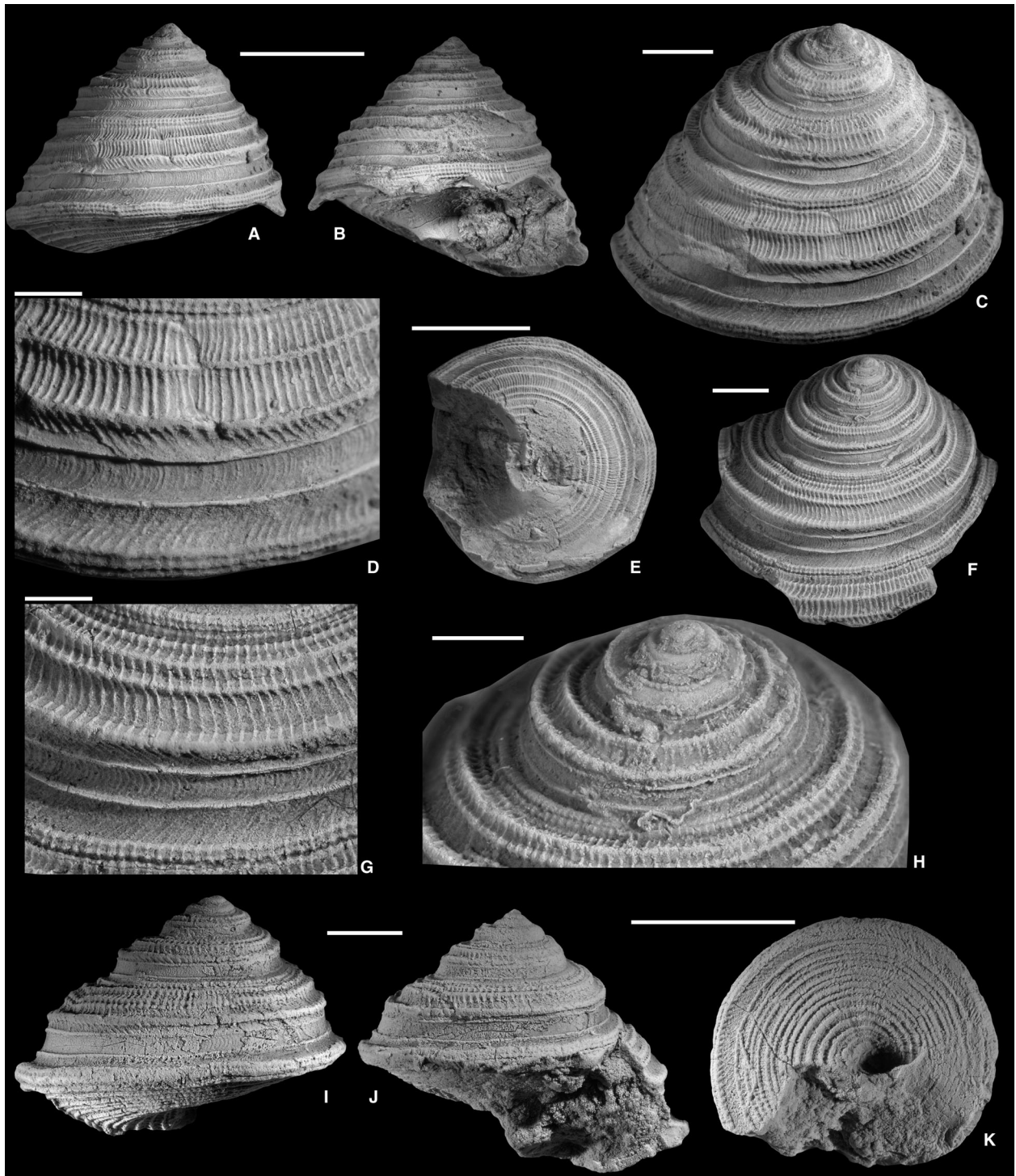
*Type location & age.* Virgilian, Colony Creek Shale Member (Caddo Creek Formation), Lake Brownwood 7½ Quadrangle, Brown County, Texas; hillside exposure (AMNH locality 5500; 31°50′25.33″N, 99°01′51.79″W).

*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 cyrtocoid, 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 colabral axial threads; 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 1964b, 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, 1940a 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 kentuckyensis* (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, 1964a. 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)

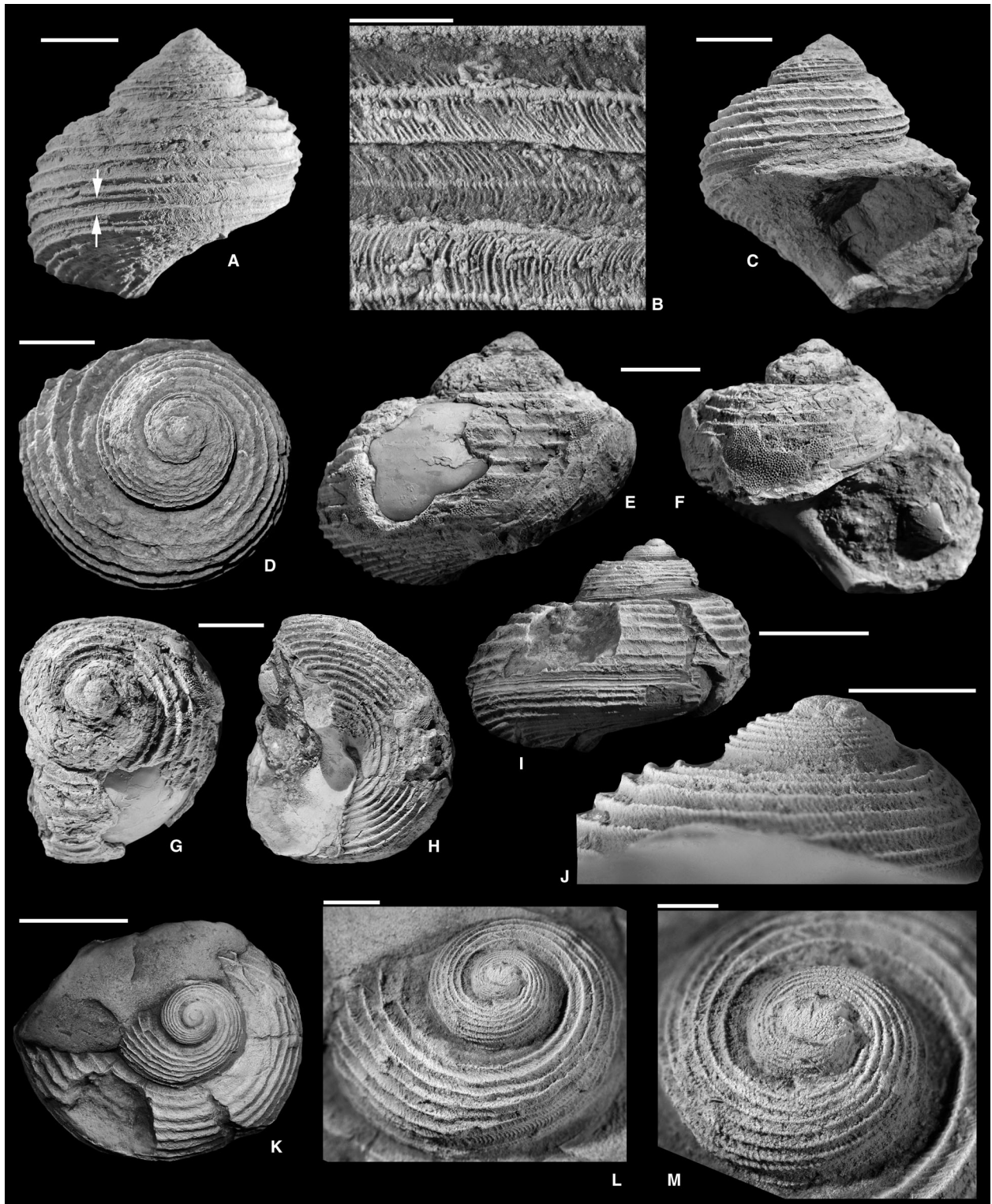
##### Figure 42

- \* 1855 *Pleurotomaria carbonaria* Norwood & Pratten, p. 75, pl. 9 fig. 8.
- 1964a *Shansiella carbonaria* (Norwood & Pratten); Sturgeon, p. 209, pl. 32 figs 18–21.
- 1967 *Shansiella carbonaria* (Norwood & Pratten); Yochelson & Saunders, p. 201.
- 1972a *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 prosocyrte above selenizone, prosocyrte 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 opisthocyrte 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.

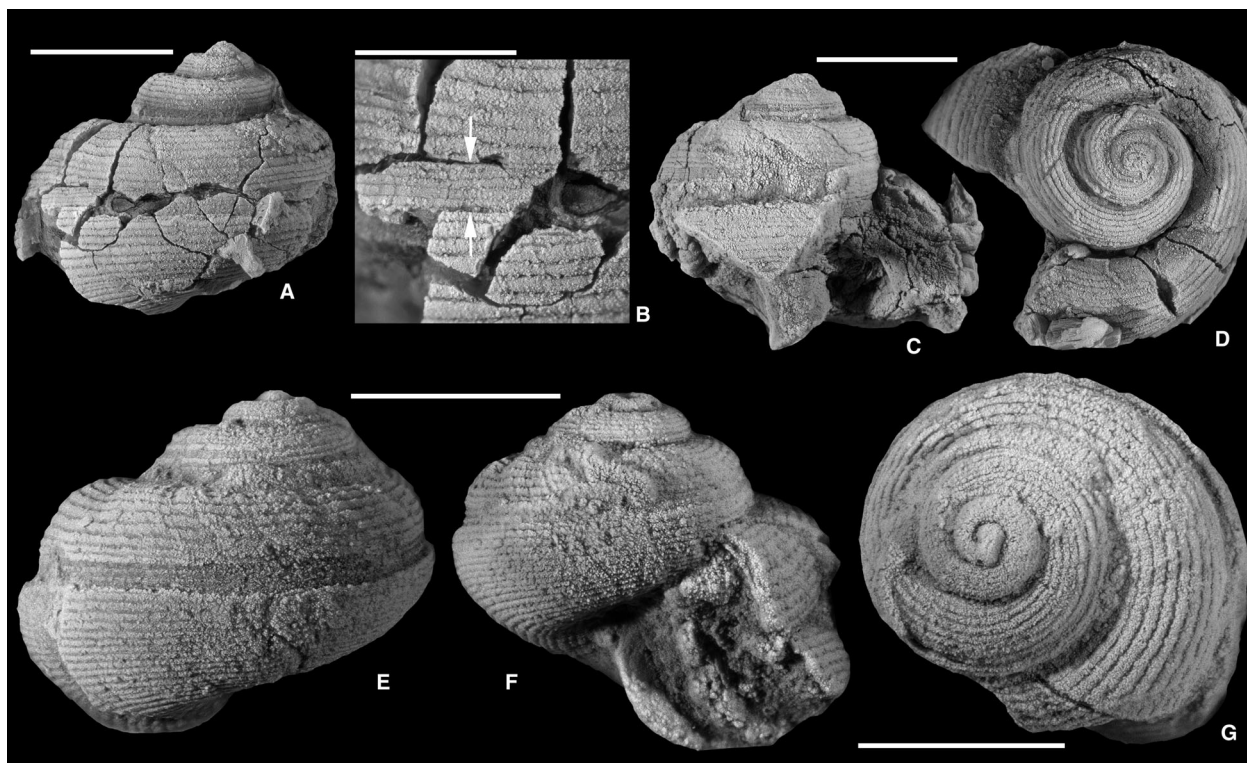
**Remarks.** Two of the studied specimens from TXV–36 are encrusted by sponges (?*Chaetetes* sp.) around the selenizone. In one specimen (2020 LXXVI 3) the sponge has grown just on the selenizone in a small spot (2 mm in diameter) next to the broken aperture. In another specimen (2020 LXXVI 2) the sponge 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.
- 1964a *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 prosoclyt growth lines/striae; base convex, ornamented as whorl face and with opisthoclyt 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

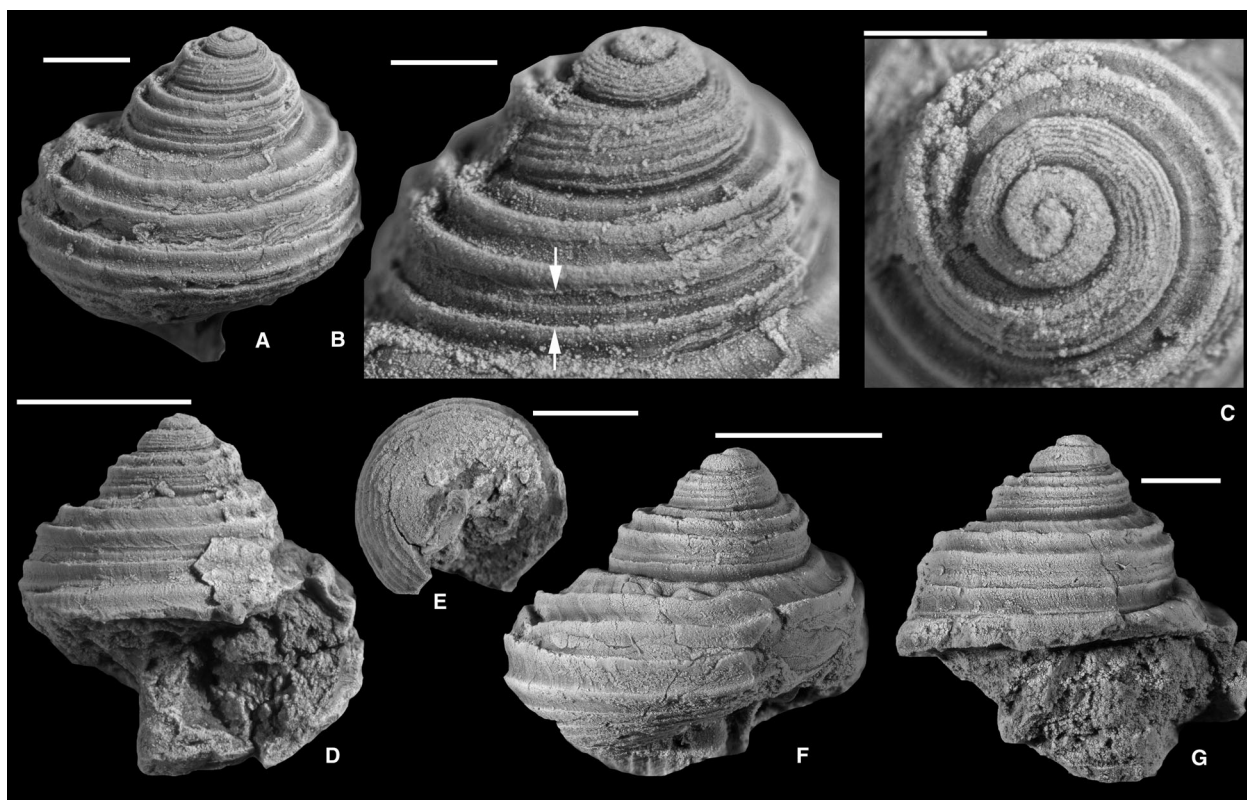
**Type location & age.** Morrowan, Gene Autry Formation exposed in gullies on east side of unnamed tributary of Sycamore Creek on the Daube Ranch, NW¼, NW¼, SW¼, sec. 3, T. 4 S., R. 4 E., Johnson Co., Ravia 7½' Quadrangle, Oklahoma (AMNH locality 5270; 34°14'13.76"N, 96°52'42.02"W).

**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, slightly 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, 1940a) 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.) altispinalis* Yin, 1932, the type species of *Shansiella (Shansiella)* from the Carboniferous of Shanxi, is larger and has more spiral cords.

Subclass CAENOGASTROPODA Cox, 1960b

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

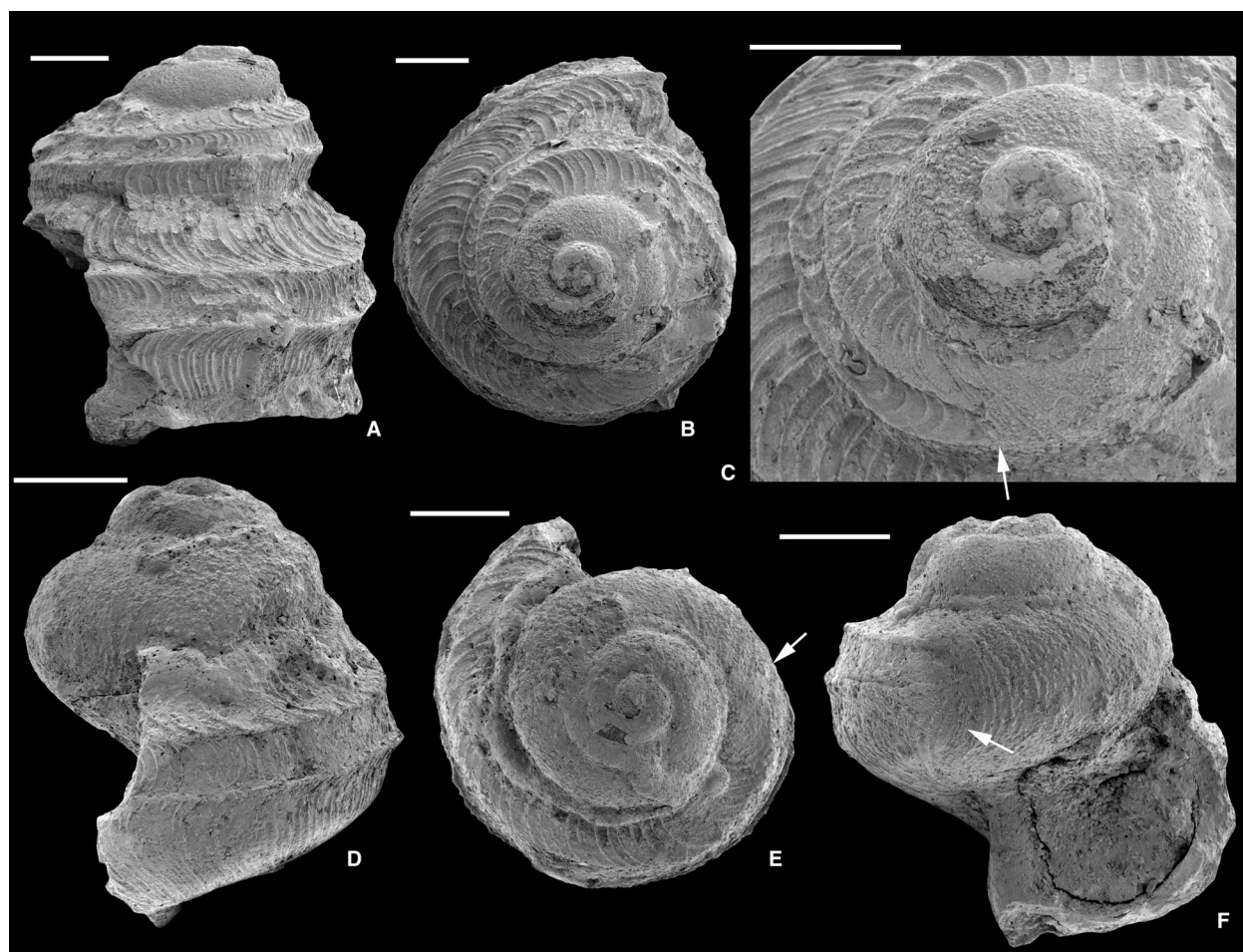
Carboniferous of Xinjiang, very closely resembles *Peruvispira* and might represent a younger synonym of *Peruvispira*.

*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. canningensis* from the lower Permian of Australia. *Peruvispira canningensis* 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. canningensis* 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.

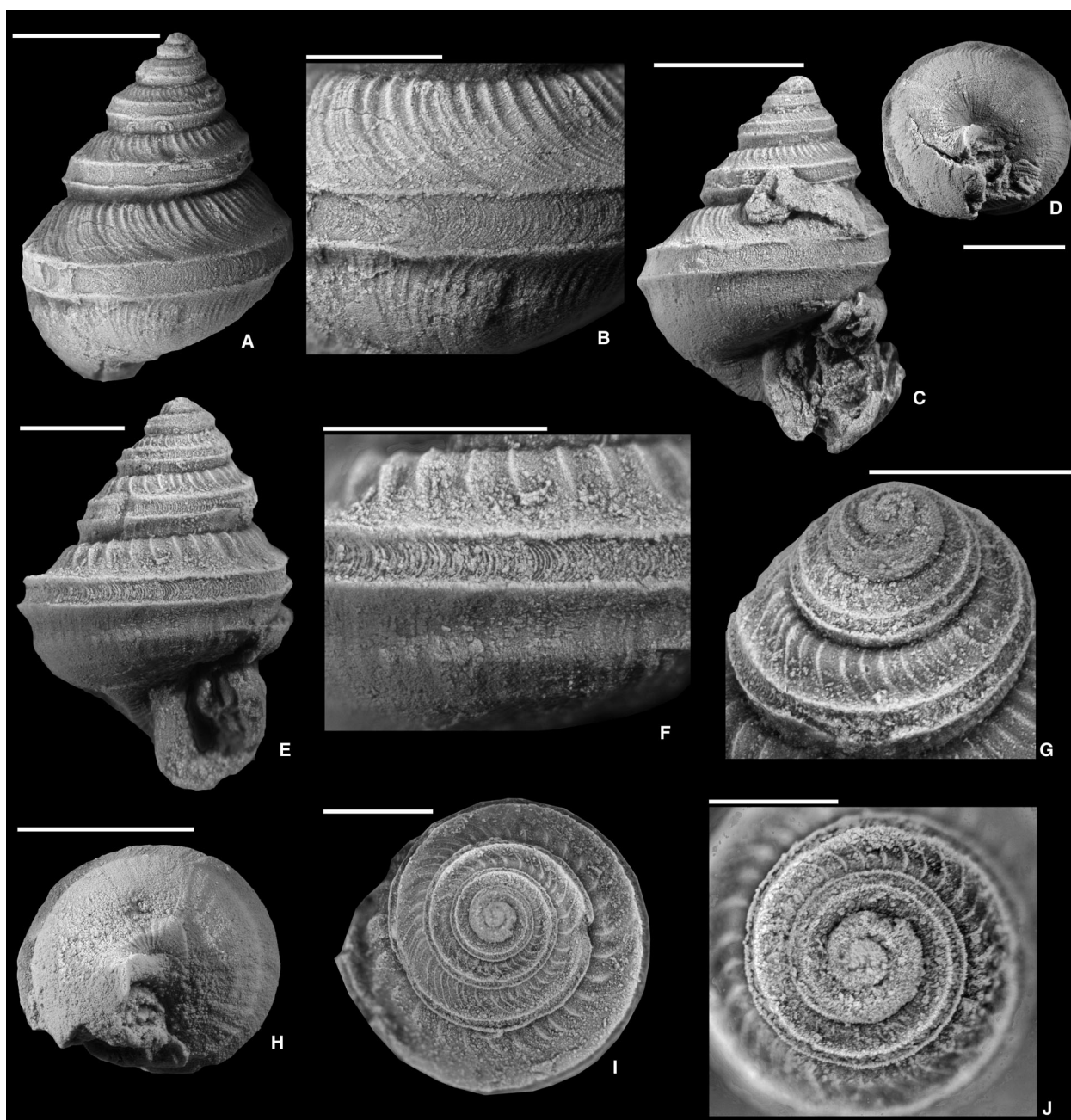
*Measurements (mm).*

	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-spined; 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 *Peruvispira* 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-spined, 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 spined 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.* (2020a) 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.* 2020a, 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, 1940a, are axial ribs that fade towards selenizone. Axial ribs are present in most of the *Peruvivispira* species including its type species. The main difference between *Neilsonia* and *Peruvivispira* 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 *Peruvivispira* because the abapical suture is situated well below the selenizone in both species. The holotype of *Peruvivispira 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. *Peruvivispira 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 *Peruvivispira* 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 subsutural 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 Gosseletiniidae (Batten 1966; Batten 1972b; 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 *Peruvivispira*.

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-spined 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 (1940b) recognized this genus before Knight (1945) proposed the name *Platyzona* and she proposed *Semestrophia* 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, *Semestrophia* is not a valid name. *Helix? striatus* was later assigned to *Platyzona* by Batten (1966).

As mentioned by Batten (1972b), 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, 2019a 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.

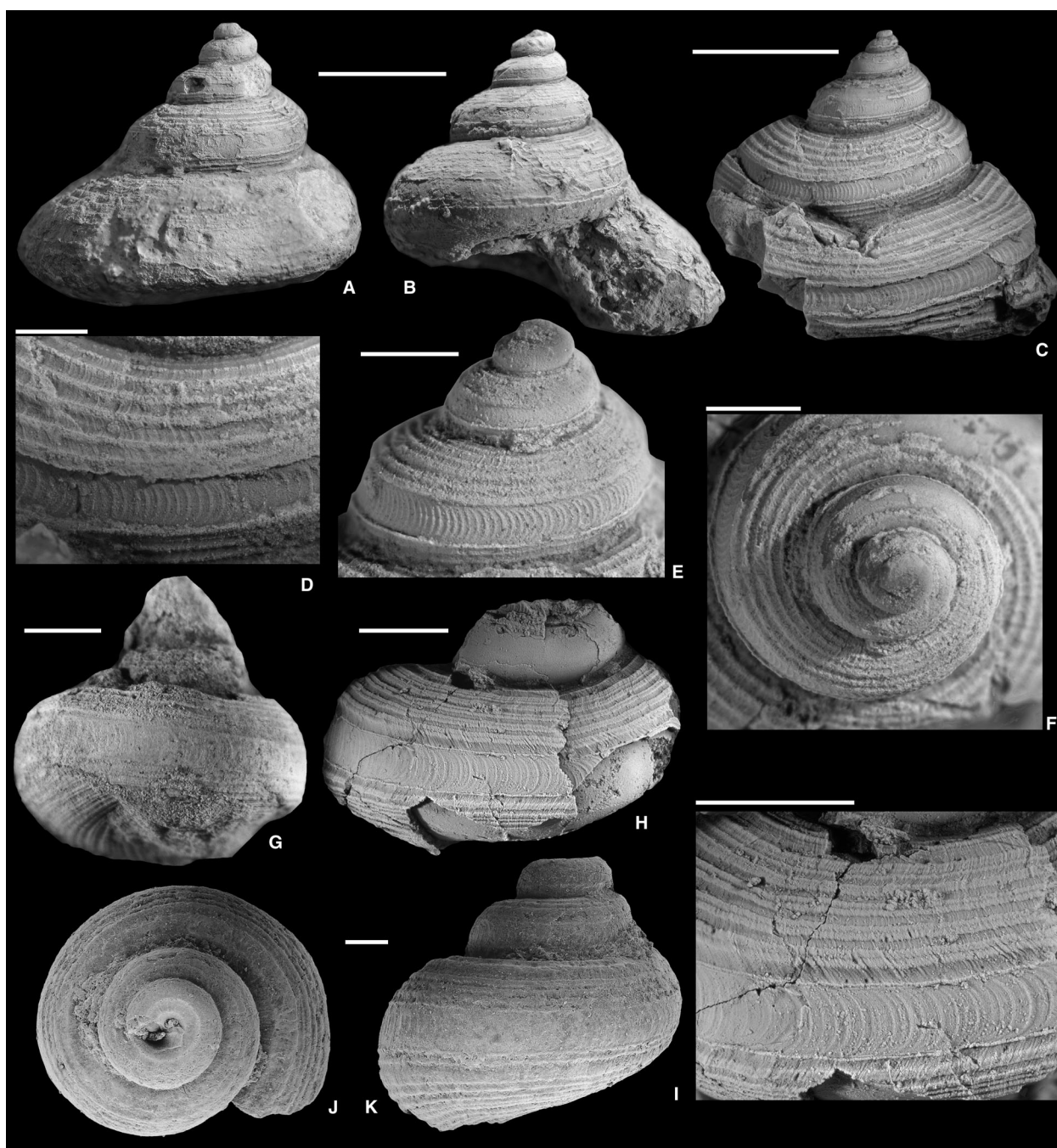
*Material.* A total of 11 specimens. 1 from the Virgilian of Texas (Colony Creek Shale Member, TXV-46): SNSB-BSPG 2009 XXII 19. 1 from the Virgilian of Texas (Finis Shale Member, TXV-56): SNSB-BSPG 2020 LXXX 4. 9 from the Buckhorn Asphalt Quarry (Desmoinesian, Oklahoma): SNSB-BSPG 2011 X 82, 248–251,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

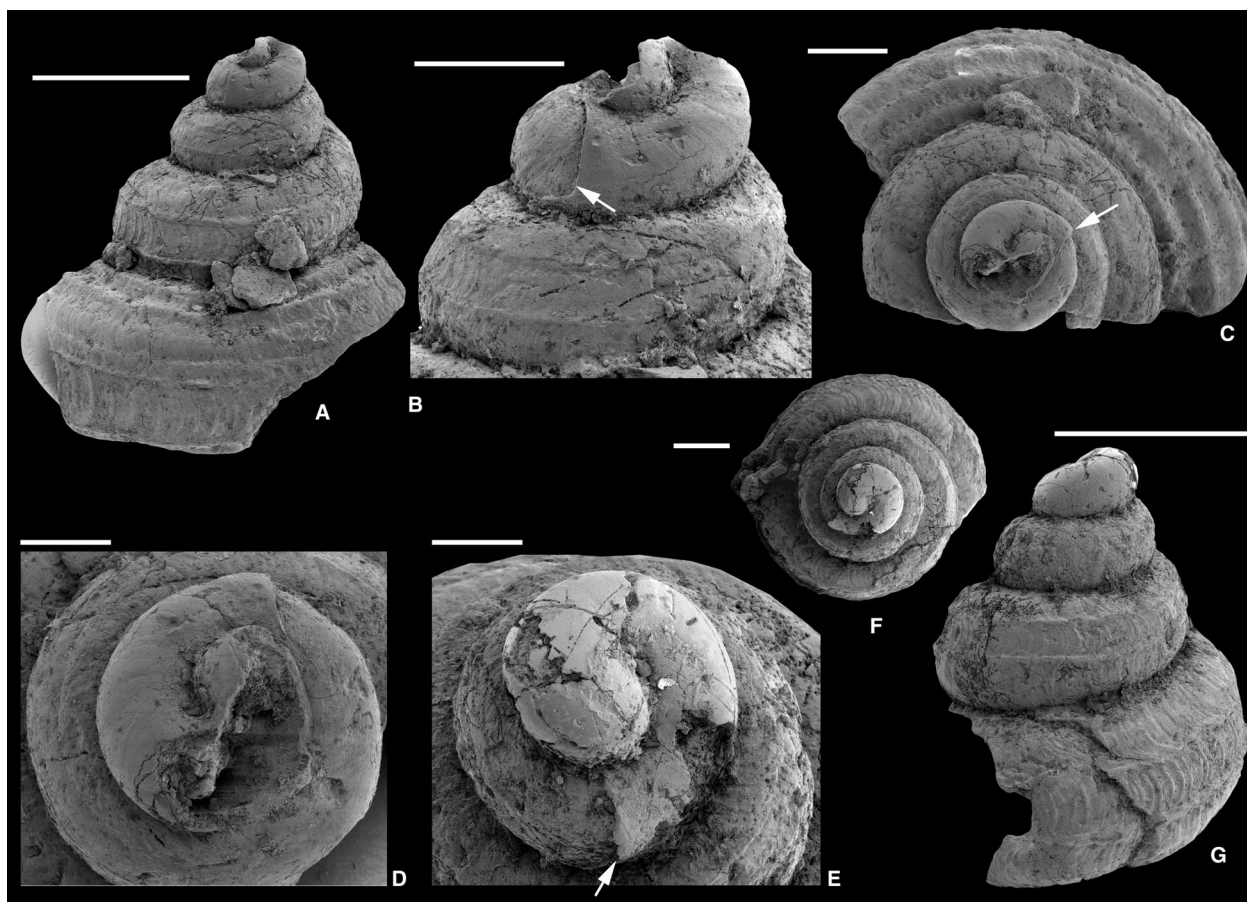




**FIG. 47.** *Platyzona hespera* Kues & Batten, 2001. A–B, SNSB-BSPG 2020 LXXX 4, from the Finis Shale Member (Virgilian, Texas). C–F, SNSB-BSPG 2009 XXII 19, from the Colony Creek Shale (Virgilian, Texas); D, lateral view, detail of surface ornament and selenizone; E, oblique apical view, detail of 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: *Treospira 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 *Treospira* 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 *Treospira* shows lower SBF compared to other genera such as *Glabrocingulum* and they concluded that *Treospira* was less resistant to durophagous predation due to having a relatively lower spire height. Unlike most other pleurotomariid genera with reported SBF, *Treospira* develops an infilling (callus) in its umbilicus. Most of the crushed *Treospira* cf. *illinoensis* 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 *Treospira* 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 2014a). 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).

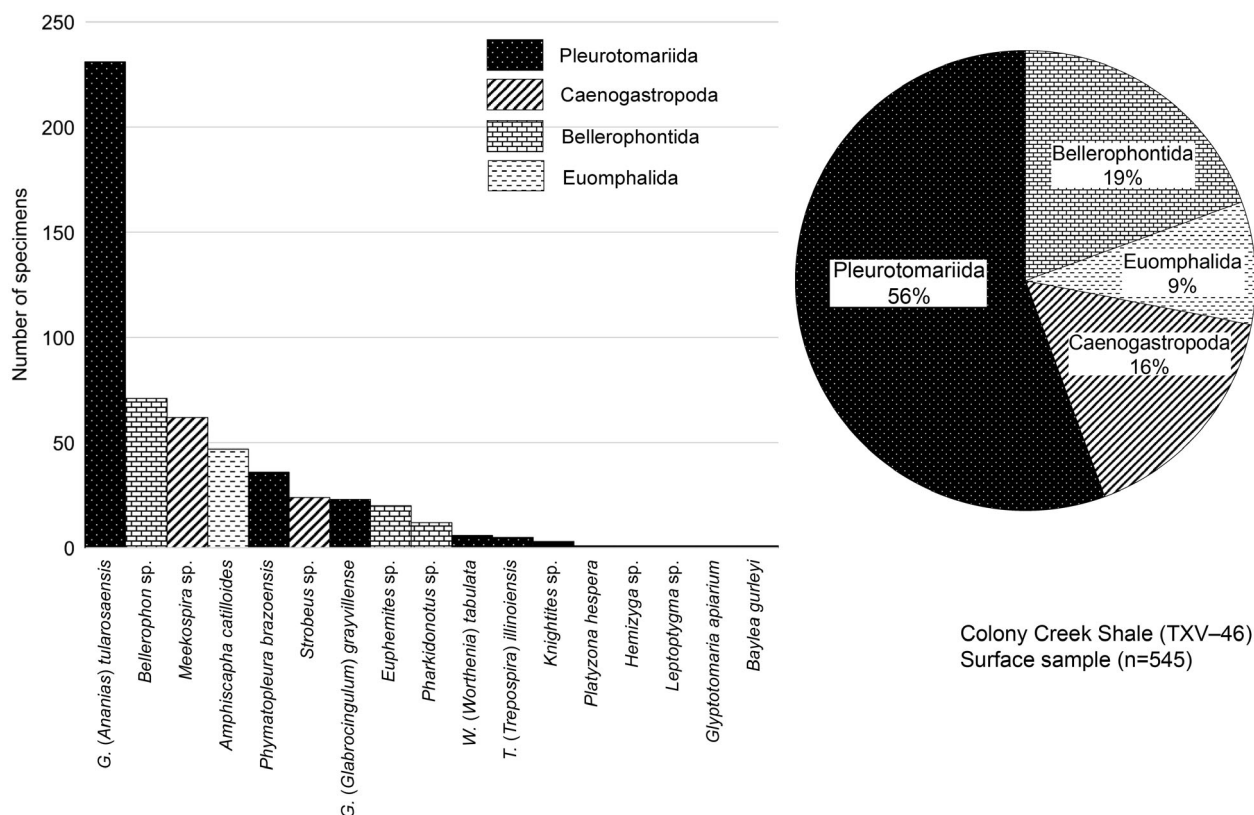
In the surface samples gathered from the Colony Creek Shale at locality TXV–46, Pleurotomariida constitute 41% of the gastropod species (17 species) and 56% of the

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 anachronistic; it has not been observed in post-Triassic assemblages.

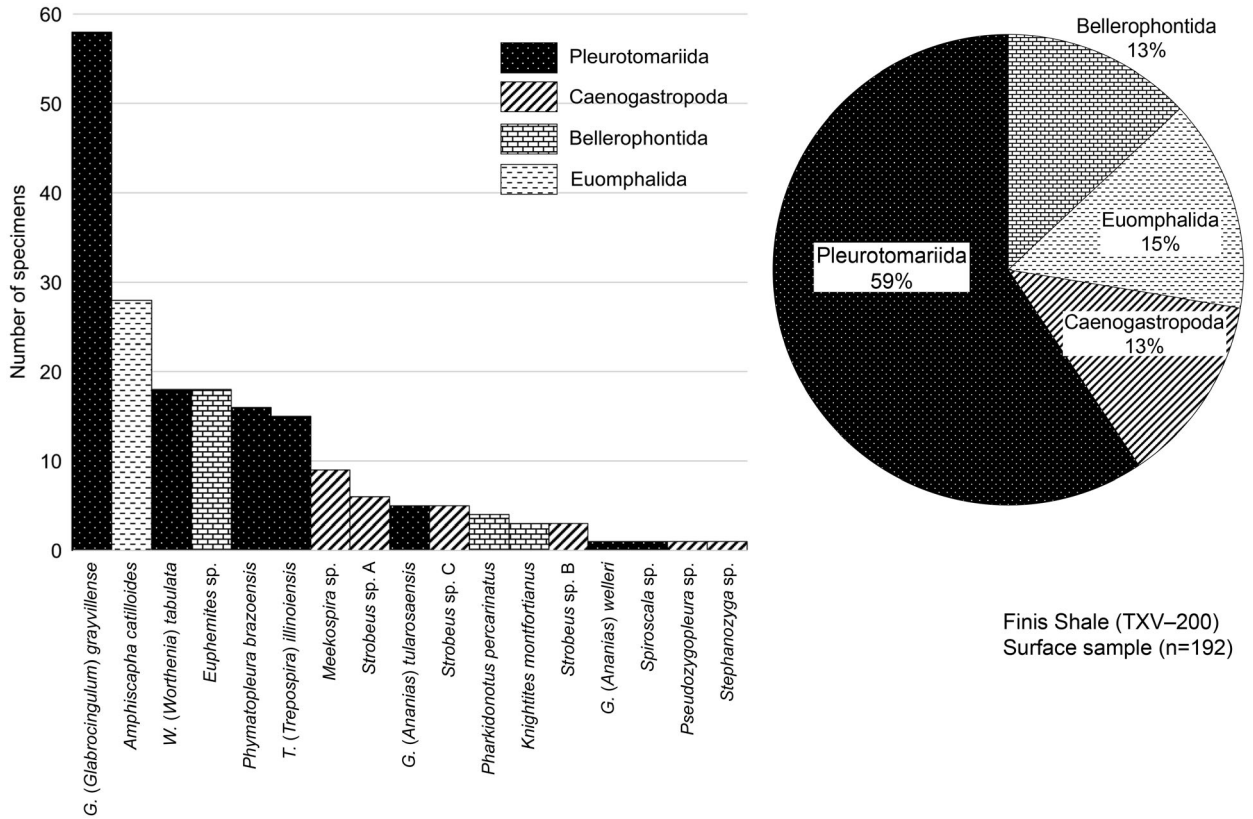
For the fauna from the Finis Shale Member, the surface sampling method neglects the small specimens (both, juveniles of larger growing species and small species), which can be only obtained by bulk sampling. Therefore, any conclusion drawn from only surface samples is biased. The relative abundance of 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.

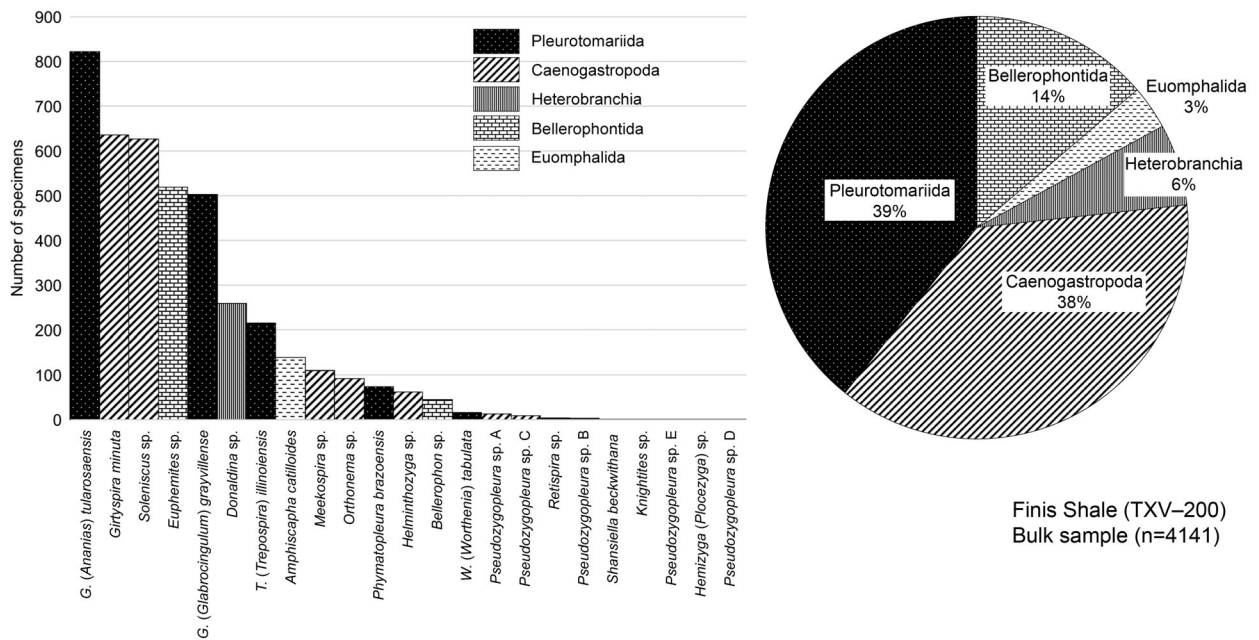
Species with a short life span (often small-bodied) or juveniles of the same species are expected to be more abundant in an assemblage than large-bodied, long-lived species or adult specimens of the same species (Kidwell 2001; Vermeij & Herbert 2004; also see Kidwell & Rothfus 2010). However, the size 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.

	<i>Trepsira</i>	<i>G. (Glabrocingulum)</i>	<i>G. (Ananias)</i>	<i>Phymatopleura</i>	<i>Worthenia</i>
<b>Finis Shale Member (TXV–200)</b>					
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
<b>Finis Shale Member (TXV–56)</b>					
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.* 2020b). 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.* 2020a). 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 (Goniatidae). 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

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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. 1972a. The ultrastructure of five common Pennsylvanian pleurotomarian gastropod species of eastern United States. *American Museum Novitates*, **2501**, 1–34.
- BATTEN, R. L. 1972b. 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, Lophospiridae, 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. 1960a. 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. 1960b. 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 mollusques 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 Leopoldinisch- 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 Scienze 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. Spargen 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 Strep-toneura. *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 GOUEMAND, 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., CHAROEN-TITIRAT, T. and NÜTZEL, A. 2020a. 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. 2020b. 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'Académie 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 Bellerophonina and suborder Neritopsina) from the Upper Paleozoic of southern Fergana. *Trudy Vsesouznogo Nauchno-Issledovatel'skogo Geologicheskogo Instituta Biostratigraficheskij 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 Gastropoda. *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 Syncline. *Paleontological Journal*, **40**, 42–53.
- MAZAEV, A. V. 2011. Pennsylvanian gastropods of the suborder 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. 2019a. Lower Permian gastropods of Shakh-tau (Asselian–Sakmarian boundary beds, southern Cisuralia). *Paleontological Journal*, **53**, 1237–1345.
- MAZAEV, A. V. 2019b. Morphology and systematics of the late Paleozoic Gastropods *Deseretospira* Gordon and Yochelson and *Terrihabena* 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. 1866a. 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. 1866b. 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. 2014a. Larval ecology and morphology in fossil gastropods. *Palaeontology*, **57**, 479–503.
- NÜTZEL, A. 2014b. 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 GRÄDINARU, 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. *Système silurien du centre de la Bohême, par Joachim Barrande. 1ère 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. *Palaentology*, **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. 1964a. Allegheny fossil invertebrates from Eastern Ohio - Gastropoda. *Journal of Paleontology*, **38**, 189–226.
- STURGEON, M. T. 1964b. New descriptions of hitherto inadequately 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 Permians du Djebel Tébagá (sud Tunisie). *Palaentographica, 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. 1940a. Revision of the Scottish Carboniferous Pleurotomariidae. *Geological Society of Glasgow Transactions*, **20**, 30–72.
- THOMAS, E. G. 1940b. 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 PALAEOLOGY (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 Turbiniidae) 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. I. 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, Scaphopoda, 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, 1866a) comb. nov. [*Spiroscala conoides*]

*Lamellospira catherinae* (Gemmellaro, 1889) comb. nov. [*Luciella catherinae*]

*Eirlysella hissingiana* (de Koninck, 1843) comb. nov. [*Trochus hissingianus*]

*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 2019b]

*Ruedemannia crenilunula* (Yoo, 1994) comb. nov. [*Worthenia crenilunula*]

*Yiningicus waterhousei* (Ketwetsuriya *et al.*, 2020b) 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 & Heidelberg, 2003) comb. nov. [*Dictyotomaria eurocapillaria*]

*Lukesispira gundyensis* (Yoo, 1988) comb. nov. [*Austroneilsonia gundyensis*]

*Peruwispira? insculpta* (Hall, 1858) comb. nov. [*Murchisonia insculpta*]

*Peruwispira invisitata* (Hoare *et al.*, 1997) comb. nov. [*Neilsonia invisitata*]

*Peruwispira welleri* (Thein & Nitecki, 1974) comb. nov. [*Neilsonia welleri*]

*Peruwispira coatesi* (Peel, 2016) comb. nov. [*Neilsonia coatesi*]

*Peruwispira ganneyica* (Peel, 2016) comb. nov. [*Neilsonia ganneyica*]

*Erwinispira? luculenta* (Pan & Erwin, 2002) comb. nov. [*Platyzoona 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*) *bee-dei* (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.