REVISITING THE MOLLUSCAN FAUNA FROM THE CAMBRIAN (SERIES 2, STAGES 3–4) XINJI FORMATION OF NORTH CHINA

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Abstract: A diverse group of molluscs from the Cambrian Series 2, Stages 3–4 Xinji Formation of the North China Block (NCB) is described, based on more than 4500 specimens from three well-studied sections in Shaanxi and Henan provinces, along the southern and southwestern margin of the NCB. Twenty molluscan species are identified, including one bivalve, three stem group gastropods, and 16 additional helcionelloids. Among these, six helcionelloid species are reported from the NCB for the first time, and one new species, Parailsanella luonanensis sp. nov. is proposed. This diverse molluscan fauna shares a large number of species with contemporaneous faunas of South Australia (15), Antarctica (7), Laurentia (6), Siberia (3) and South China (1). Faunal similarities are even greater on a generic level. The striking similarities of the molluscan faunas of North China, South Australia and Antarctica strongly support the hypothesis that the NCB was situated close to Eastern Gondwana, most likely close to South Australia in the Cambrian Epoch 2. In addition, well-preserved shell attachment muscle scars were observed in the helcionelloid Figurina figurina, with two pairs of symmetrical, continuous, band-like muscle scars, which are obviously different from the musculature of both gastropods and monoplacophorans. Because of this unique musculature, these characteristic Cambrian cap-like molluscs are assigned to the Helcionelloida rather than to the Gastropoda or Monoplacophora.

Key words: Cambrian Series 2, North China, mollusc, taxonomy, muscle scar.

EARLY Cambrian skeletal fossil assemblages (small shelly fossils; SSFs) from the Cambrian Series 2 Xinji Formation of the North China Block (NCB) were intensively studied in the 1980s–1990s for the purpose of locating phosphorite mining deposits. This phosphatized skeletal assemblage provides an excellent archive of diverse biomineralizing animal groups, including sponges, brachiopods, molluscs, hyoliths, echinoderms and fossil sclerites of problematic biological function and affinity. Among them, the Mollusca represents a conspicuous element, and thus previously attracted much attention from palaeontologists. A number of papers have been published on the basis of abundant specimens from the Xinji Formation in Henan Province (He et al. 1984; Chen & Wang 1985; He & Pei 1985; Pei 1985, 1995; Li & Zhou 1986; Yu & Rong 1991), southern part of Shaanxi Province (Yi 1992), and equivalent strata of the Houjiashan Formation in Anhui Province (Zhou & Xiao 1984). More than 35 nominal molluscan taxa have been described, and many were named based on material from the NCB, e.g. Anhuiconus microtuberus Zhou & Xiao, 1984, Davidonia rostrata (Zhou & Xiao, 1984), Figurina nana (Zhou & Xiao, 1984), Pelagiella madianensis (Zhou & Xiao, 1984), Xingjsipra simplex (Zhou & Xiao, 1984), Yochelcionella chinensis Pei, 1985, Bemella xinjiensis (Feng et al., 1994) and Icorellina probosa Feng et al., 1994. The rich molluscan fauna from the NCB has dramatically improved our understanding of the evolution and radiation of early molluscs during the Cambrian explosion.

However, the molluscan fauna of the NCB has not been studied during the recent decades, as attention has mostly been focused on the Precambrian–Cambrian transition of South China, due to its well-exposed sections, excellent fossil record and rich phosphorite deposits.
Apistogramma aeques Discovered from the NCB for the first time, including have now been investigated, and many taxa have been dozen sections along the southern margin of the NCB 2018; Skovsted et al. 2016; Yun et al. 2016). More recently, Claybourn et al. (2019) described a diverse molluscan fauna with 12 species from the Shackle- ton Limestone of the Antarctic Platform. In light of these discoveries, the molluscan species from the Cambrian of North China have been partly re-evaluated (Parkhaev in Gravestock et al. 2001; Skovsted 2004), but insufficient illustrations, low-resolution images and poorly preserved specimens in older publications have made precise species-level identification and comparison difficult.

In recent years, the SSFs on the NCB have received renewed interest by many authors due to the unexpected high diversity and abundance of the assemblage, and the well-preserved shell microstructures of many fossils (Li et al. 2014, 2016, 2017, 2019a, b; Pan et al. 2015, 2017, 2018; Skovsted et al. 2016; Yun et al. 2016). More than a dozen sections along the southern margin of the NCB have now been investigated, and many taxa have been discovered from the NCB for the first time, including Apistogramma aeques Conway Morris in Bengstson et al., 1990, Cambroclavus absonus Conway Morris in Bengstson et al., 1990, Paterimitra pyramidalis Laurie, 1986 and Microdictyon sp. (Li et al. 2014, 2016; Pan et al. 2017, 2018). Ongoing work on this skeletal assemblage has yielded a rich molluscan fauna from multiple sections, allowing us to provide a comprehensive taxonomic revision of the Cambrian molluscan fossils of the NCB, and provide the tools for further comparison and biostatigraphical correlation with coeval faunas. In addition, some exceptionally well-preserved specimens provide new information on shell attachment muscle scars, and thus shed new light on Cambrian molluscan functional morphology, systematics and phylogeny.

**GEOLOGICAL SETTING AND AGE**

The NCB is bounded to the north by the Central Asian Orogenic Belt, to the south by the Qinling–Dabie Belt and the Su–Lu fault against the South China Block, and to the west by the Qilian Orogenic Belt against the Tarim Block (Stern et al. 2018) (Fig. 1A). The lithological sequences and sedimentary patterns through the Precambrian–Cambrian transition are consistent and can be precisely correlated along the southern margin, with sequences in ascending order: Luoquan, Dongpo, Xinji and Zhushadong formations. They are generally in conformable contact except for a distinct disconformity at the base of the Cambrian, with Terraneuviian strata completely absent. The Xinji Formation (equivalent to the Houjiashan Formation in the southeastern part of the NCB) is the oldest Cambrian deposit of the NCB. It is composed mainly of siliciclastic sediments intercalated with carbonate units, which generally rests disconformably on the upper Ediacaran Dongpo Shale, and is conformably overlain by the massive dolostones of the Zhushadong Formation. The carbonate rocks of the Xinji Formation, less than 5 m in thickness, yield an abundant and diverse assemblage of skeletal fossils (Fig. 1B).

The Xinji Formation also contains trilobites important for age constraints and intercontinental biostratigraphic correlation. This low diversity of trilobite assemblage has yielded two described genera: Estaingia and Redlichia (Zhang & Zhu 1979; Zhang et al. 1979). Fragments of Estaingia are very common, and several species have been identified, e.g. *E. luonanensis* Hsiang in Lu et al., 1965 and *E. houchiensis* Chang in Hsiang, 1963 (see review by Miao 2014). In contrast, Redlichia is extremely rare, but specimens of *Redlichia cf. nanjiangensis* Zhang & Lin in Lee, 1978 have been reported from the base of the Houjiashan Formation in Anhui Province, North China. The trilobite assemblage has long been correlated to the *Drepanuroidea* trilobite Biozone of the middle Tsanglangpuan Stage (Cambrian Stage 4) on the Yangtze Platform (Zhang & Zhu 1979; Zhang et al. 1979; He et al. 1984; He & Pei 1985; Miao 2014). In recent years, investigations on global palaeogeographical distribution and Cambrian SSF assemblages suggested that the NCB might have been very close to the northern or northeastern margin of Australia within Eastern Gondwana (Brock et al. 2000; Gravestock et al. 2001; Wrona 2003; Yun et al. 2016; Pan et al. 2018). From this perspective, restudy of the trilobite assemblage by Miao (2014) highlighted that the *Estaingia* trilobite assemblage from the Xinji Formation correlates well with the *Paraaraia janaec* trilobite Biozone of South Australia, and thus confirms the age of the Formation as latest Age 3 or early Age 4 of Cambrian Epoch 2.

**MATERIAL AND METHOD**

Rock samples were collected from the carbonate units of three well-known sections in Shaanxi and Henan provinces along the southern and southwestern margin of the NCB: (1) the Sanjianfang section (SJFH) in Baoan Town, Yexian County, Henan Province, the classical section for SSF investigations in NCB (He et al. 1984; Chen & Wang 1985; He & Pei 1985; Pei 1985, 1995; Li & Zhou 1986; Yu & Rong 1991); (2) the Shangyao section (SZW) in Shimen Town, Luonan County, Shaanxi Province, which has been widely studied (Yi 1992; Li et al.
collections come from the Chaijiawa section, providing the bulk of data for statistical analysis. Specimens were mounted, and sputter-coated with gold for examination with an FEI Quanta 400 FEG scanning electron microscope (SEM) at Northwest University and Hitachi S4300 SEM at the Swedish Museum of Natural History (SMNH). Microfossils described below are deposited at the Shaanxi Key Laboratory of Early Life and Environments (LELE), Northwest University, Xian, China.
Institutional abbreviations. ANU, Australian National University, Canberra, Australia; DGMRH, Regional Geological Survey Party, Department of Geology and Mineral Resources of Henan Province, Zhengzhou, China; GIA, Geological Institute, Anhui Province, China; LELE, Shaanxi Key Laboratory of Early Life and Environments, Northwest University, Xian, China; MGUH, Geological Museum of the University of Copenhagen, Denmark; NIGPAS, State Key Laboratory of Palaeoecology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China; NMV, National Museum of Victoria, Melbourne, Australia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; SAM, South Australian Museum, Adelaide, Australia; SMF, NaturMuseum und Forschungs-Institut Senckenberg, Frankfurt am Main, Germany.

DISCUSSION

Faunal composition and comparison

The Cambrian Series 2, Stages 3–4 Xinji Formation of North China yields one of the most diverse assemblages of molluscs in the early Cambrian. In our collections, an assemblage of 20 valid species is identified, encompassing one bivalve species: Pojetaia runnegari; three stem group gastropods: Pelagiella madianensis, Xinispira simplex and Protowenella flemingi; while the remaining 16 cap-shaped molluscan taxa are assigned to the Helcionelloidea (Table 1). Of these, six helcionelloid species, including Pararaconus paradoxus Runnegar in Bengtson et al., 1990, Horsegullia horsegulliensis (Parkhaev in Gravestock et al., 2001), Marocella mira Geyer, 1986, Bemella communis Parkhaev in Gravestock et al., 2001, Emargimantus? cf. E. tunuensis (Peel & Skovsted, 2005), and Truncatoconus? cf. T. yichangensis (Yu, 1979) are reported from the NCB for the first time, and in addition one new species, Parailsanella luonanensis sp. nov., is proposed (Table 1). Six species that have previously been described from the NCB: Humilispira adelocoma Parkhaev in Gravestock et al., 2001, Igelrella adunca Zhou & Xiao, 1984, Ilsanella reticulata Zhou & Xiao, 1984, Obtucoconus grossicostus Feng et al., 1994, Paraceratoconus ruidus Zhou & Xiao, 1984 and Purella sp. in Feng et al. (1994) are absent from our collections, although we recognize their presence in the Cambrian of the NCB as described in previous publications (Zhou & Xiao 1984; Feng et al. 1994). In addition, three species previously described as molluscs: Galeiscus theloides Zhou & Xiao, 1984, Ilsanella sp. (of Feng et al. 1994) and Scenella pyca Feng et al., 1994 should in our view be excluded from molluscan affiliation. These three fossils probably belong to larger scleritomes or represent fragments of other macroscopic organisms (Table 2).

The acid-resistant residues from the Xinji Formation of the Chaijiawa section yielded 3808 specimens belonging to 20 species. Pelagiella madianensis is the most conspicuous element, accounting for 52.52% of the total molluscan fauna, followed by Davidonia rostrata (13.13%), Anabarella australis Runnegar in Bengtson et al., 1990 (10.5%), Pojetaia runnegari (10.5%), Figurina figurina (3.41%) and Anhuiconus microtuberus (2.63%). The six most common species comprise 91.95% of all specimens, while none of the remaining 14 taxa is represented by more than 100 specimens (0.03–2.23% of the total fauna).

| Species (25) After revision (13 + 7 new findings*) | n | % |
|-----------------------------------------------|---|---|
| Aulriculaspira madianensis | Pelagiella madianensis | 2000 | 52.52 |
| Anulriculaspira adunca | Protowenella primaria | 1500 | 40.00 |
| Pojetaia runnegari | Figurina figurina | 130 | 3.41 |
| Securiconus vulgaris | Anhuiconus microtuberus | 100 | 2.63 |
| Anhuiconus microtuberus | Stenotheca drepanoida | 85 | 2.23 |
| Stenotheca drepanoida | Truncatoconus paradoxus* | 52 | 1.37 |
| Protowenella primaria | Pararaconus paradoxus* | 25 | 0.66 |
| Protowenella luonanensis* | Anabarella dumosa | 400 | 10.50 |
| Oryzoconcha prisca | Pojetaia runnegari | 400 | 10.50 |
| Pojetaia runnegari | Xinispira simplex | 20 | 0.53 |
| Xinispira simplex | Marocella mira* | 19 | 0.50 |
| Marocella mira* | Benella communis* | 18 | 0.47 |
| Anhuiconus microtuberus | Benella xinjensis | 16 | 0.42 |
| Protowenella drepanoida | Yochelcionella chinesis | 14 | 0.37 |
| Ostruconus rostritutae | Yochelcionella chinesis | 14 | 0.37 |
| Igelrella probosca | Igelrella probosca | 5 | 0.13 |
| Figurina nana | Figurina nana | 4 | 0.11 |
| E. tunuensis* | Emargimantus cf. E. tunuensis* | 2 | 0.05 |
| Parailsanella luonanensis* | Parailsanella luonanensis* | 2 | 0.05 |
| Truncatoconus? cf. T. yichangensis* | Truncatoconus? cf. T. yichangensis* | 1 | 0.03 |

SUM | 3808 | 100 |

n, number of specimens; %, proportion of the molluscan species.
Some molluscan species reported here are seemingly endemic to the Cambrian of North China, e.g. *Bemella xinjienesis*, *Igorellina probosa*, *Paraisanella luonanensis*, *Ilsanella reticulata*, but these account for a very low proportion of the total molluscan fauna in terms of specimens. Otherwise, most species, particularly the more common taxa, generally have a wider distribution among coeval molluscan faunas worldwide. The molluscan fauna of the NCB shares a majority of species (15) with contemporaneous fauna of South Australia, where they occur throughout the upper *Abadiella huoii* to lower *Pararaia janae* trilobite biozones, equivalent to the newly established *Dailyatia odyssei* Biozone (tommotiid) according to Betts et al. (2016, 2017, 2018). In particular, a highly comparable molluscan fauna was recovered from the upper Mernmerna Formation in Arrowie Basin and Parara Limestone in Stansbury Basin, South Australia. The close correlation to the *Dailyatia odyssei* Biozone in South Australia is strengthened by the shared presence of some key taxa, such as *Figurina figurina*, *Stenotheca drepanoidea*, *Horsegullia horsqulliensis*, *Bemella communis* and *Humilispira adelocosma* (Bengtson et al. 1990; Gravestock et al. 2001; Topper et al. 2009; Betts et al. 2016, 2017, 2018). This pattern is further corroborated by the presence of the comparable *Estingia* trilobite assemblage and many other key taxa such as *Cambroclavus absonus*, *Apistoconcha aphelae* and *Paterimitra pyramidalis* in both areas (Li et al. 2014, 2016; Pan et al. 2018).

In addition to South Australia, the faunal similarity to Antarctica is also notable, given that seven shared species such as *Davidonia rostrata*, *Pojetaia runnegari* etc. were recently described by Claybourn et al. (2019) from the Shackleton Limestone of the central Transantarctic Mountains. Among them, it is of great significance to highlight that the new finding of *Xinjispira simplex* in the Shackleton Limestone represents the first discovery of the species outside North China, and thus strengthen the links (Claybourn et al. 2019). Interestingly, the molluscan fauna of the NCB also shares some species with that of Laurentia, particularly the Cambrian Stage 4 Bastion Formation of North-East Greenland, with nine genera and five species in common, including *Davidonia rostrata*, *Anabarella australis*, *Anhuiconus microtuber* etc. (Gubanov et al. 2004; Skovsted 2004; Peel & Skovsted 2005). Some shared common taxa were also documented from equivalent strata along the continuous shelf margin of the Laurentian Platform: *Davidonia rostrata* and *A. microtuberus* from the Browns Pond Formation of the Taconic Allochthon of New York (Landing & Bartowski 1996); and *Yochelcionella chinensis* from the Forteau Formation of western Newfoundland and Kinzers Formation of Pennsylvania (Skovsted & Peel 2007, 2010; Atkins & Peel 2008). In contrast, similar molluscan species from North China are rarely found in Siberia and South China, which were geographically further from the NCB during this interval. Only three shared species (*Pojetaia runnegari*, *Marocella mira* and *Figurina nana*) were described in the Cambrian Series 2 Emyaksin Formation of northern Siberia (Kouchinsky et al. 2015), and one shared species (*Truncatoconus* cf. *T. yichangensis*) was known from the regional Meishucunian (Cambrian Fortunian) Tianzhushan (= Huangshandong) Member of the Dengying Formation and equivalent rocks of South China (Parkhaev & Demidenko 2010). Consequently, the striking similarities of the molluscan fauna from North China, South Australia and Antarctica strongly support the hypothesis that the NCB was situated close to Eastern Gondwana, most likely close to South Australia in the Cambrian (Table 3, Fig. 2).

**Muscle scars and their utility for Cambrian molluscan systematics**

Although the exceptional fossil record from North China and coeval faunas around the world indicates rapid radiation and speciation of mollusks in the early Cambrian, most of the recovered taxa cannot be easily assigned to any of the modern molluscan clades (Peel 1991; Skovsted 2004; Vendrasco 2012). This conundrum has been a longstanding palaeontological debate, because there is no direct anatomical evidence to infer the orientation of the shell (endogastric/exogastric) and torsion (torted/untorted) from phosphatized internal moulds, which are the most common type of fossils found. Moreover, rare morphological

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**Table 2.** Revision of molluscan species absent in Chajijiaowa section and problematic fossils excluded from molluscan affiliation.

| Species (10) | After revision (6 + 3) | References |
|-------------|------------------------|------------|
| Huijagouella shouxiangensis | Humilispira adelocosma | Zhou & Xiao (1984, pl. 2, fig. 12; pl. 3, figs 2, 3; pl. 6, figs 3–6) |
| Latouchella adelocosma | Igorellina adunca | Zhou & Xiao (1984, pl. 2, figs 7–11) |
| Latouchella adunca | Ilsanella reticulata | Zhou & Xiao (1984, pl. 2, figs 4–6) |
| Ilsanella reticulata | Obtusoconus grossicostus | Feng et al. (1994, pl. 2, figs 12, 13) |
| Obtusoconus grossicostus | Paraceratoconus ruidus | Zhuo & Xiao (1984, pl. 3, figs 12–14) |
| Purella sp. | Purella sp.? | Feng et al. (1994, pl. 1, figs 3–7) |
| Galeiscus theoides | Problematic taxon | Feng et al. (1994, pl. 6, figs 1–8) |
| Ilsanella sp. | Problematic taxon | Feng et al. (1994, pl. 1, figs 8, 9) |
| Scenella pygna | Cap-like taxon | Feng et al. (1994, pl. 1, figs 13–17) |
features of the external shell are also seemingly insufficient to deduce the specific configuration of soft body tissues in these animals (Skovsted 2004). Owing to these problems, Cambrian molluscs have been variously interpreted as monoplacophorans (Runnegar 1981), paragastropods (Linsley & Kier 1984) or referred to the extinct Class

| North China (26) | South Australia (15) | Antarctica (7) | Laurentia (6) | Siberia (3) | South China (1) |
|------------------|----------------------|----------------|---------------|-------------|-----------------|
| Pelagiella madianensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Davidenia rostrata ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Anabarella australis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Pojetaia runnegari ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Figurina figurina ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Anhuiconus microtuberosus ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Stenotheca drepanoidea ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Pararacoconus paradoxus ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Igorellina probosca ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Horsegullia horsegulliensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Xinjispira simplex ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Marcella mira ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Bemella communis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Bemella xinijiensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Protowenella flemingi ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Yochelionella chinensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Figurina nana ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Emarginimans? cf. E. tunuensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Parailsanella luumanensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Truncatoconus? cf. T. yichangensis ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Humilispira adelocosma ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Igorella adunca ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Ilsanella reticulata ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Obtusoconus grossicostus ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Paraceratoconus ruidus ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |
| Purella sp.? ✓ | ✓ | ✓ | ✓ | ✓ | ✓ |

**TABLE 3.** Occurrences of common species of early Cambrian molluscs between North China and other blocks.

![FIG. 2. Palaeogeographical reconstruction for the Cambrian Stage 3 and the position of the North China Block (modified from: Torsvik & Cocks 2013; Yang et al. 2015).]
Helcionelloida Peel, 1991 (or more informally as ‘helcionelloids’, Peel 1991; Skovsted 2004). However, see Parkhaev (2007, 2017a) for an alternative view of these taxa as endogastric and torted gastropods. Notwithstanding this debate, many authors agree that Cambrian helcionelloid molluscs constitute the stem to the Conchifera, a major group of the Mollusca that encompasses modern monoplacophorans, gastropods and other shell-bearing molluscan groups (Smith et al. 2011; Vinther 2015).

Parkhaev (2002, 2004a, 2006, 2014a) argued that regularly distributed polygonal textures on the surface of internal moulds are very likely to be left by shell attachment muscles, and accordingly, he reconstructed the dorsoventral muscular system of several molluscan species. However, other authors proposed an alternative interpretation regarding these delicate cell-like structures on mould surfaces, primarily as casts of prism-like microstructures in the external shells (Vendrasco et al. 2010, 2011, 2015; Vendrasco & Checa 2015). In our interpretation, the muscle scars of Cambrian helcionelloids would generally be too faint to be observed or preserved on phosphatized steinkerns after diagenesis and acid leaching. However, there is little doubt that shell attachment muscle scars would be the most reliable evidence for better understanding the molluscan body plan, and they may be preserved under exceptional circumstances. The localized delicate polygonal network on the mould surface of Figurina figurina herein, is confidently interpreted as muscle scars in terms of their regularity in distribution, consistent occurrence and distinct band-like pattern. This interpretation does not preclude the less localized polygonal patterns on other parts of mollusc shells representing casts of the shell microstructure.

The new muscle scars in Figurina figurina are almost identical to those illustrated by Parkhaev (2014a) from some Australian specimens of Bemella communis (synonymous to F. figurina, see below), but are more completely preserved. It is clear that F. figurina had a principal pair of elongated, symmetrical and continuous dorsoventral muscle scars and a tiny pair of muscle scars on the subapical wall. The symmetrical, continuous dorsoventral muscle scars are most closely comparable to the horseshoe-shaped musculature of some Palaeozoic limpet-type shells and modern limpet gastropods (Horný 1963; MacClintock 1963; Runnegar 1981; Harper & Rollins 1982; Peel & Horný 1999). However, some controversies regarding the phylogenetic significance of these scars remain given that the Palaeozoic limpets resemble monoplacophoran shells in general morphology, although they have continuous bands of shell attachment muscle scars rather than multiple, discrete scars as in living monoplacophorans. As a result, whether the Palaeozoic limpets represent ancestral monoplacophorans or primitive limpet gastropods is difficult to determine (Lindberg 2009). This controversy has lasted for more than half a century, and is far from resolved. The same problem applies to the interpretation of the muscle scars in Figurina figurina herein. In addition to the unique dorsoventral musculature, the function of the tiny pair of muscle scars on the subapical wall is not clear, given that similar muscle scars are rarely present in fossil or living molluscan representatives. As a consequence of these uncertainties, and the fact that the unique musculature of Figurina is obviously different from that of the postulated stem group gastropods discussed below, we assign Figurina figurina and all other examples of the characteristic Cambrian cap-like shells to the Class Helcionelloida Peel, 1991, and confirm the prediction that helcionelloids are not gastropods.

In contrast to the unique musculature of the helcionelloid Figurina, muscle scars in postulated ancestral gastropods such as Pelagiella seem to be less controversial. The anisometrically coiled Pelagiella is known to have a pair of kidney-shaped, asymmetrical muscle scars with a larger right adaxial and smaller left abaxial (Runnegar 1981; Landing et al. 2002). This pattern is considered to reflect the torsion of the animal, and thus Pelagiella is generally regarded as a primitive, torted (at least partly) gastropod. The radial ridges or channels along the circumbilical shoulder of the moulds in Pelagiella (Isakar & Peel 2007), Xinjispira and Protowenella (herein) are interpreted to be formed during ontogeny by spirally migrating muscle scars. These muscle scars are more or less comparable to the colulmellar muscles of modern gastropods (Price 2003). Based on these observations, we regard all these three species as stem group members of the Gastropoda.

**SYSTEMATIC PALAEONTOLOGY**

Phylum MOLLUSCA Cuvier, 1797  
Class HELCIONELLOIDA Peel, 1991  
Order HELCIONELLIDAE Geyer, 1994  
Family HELCIONELLIDAE Wenz, 1938  
Genus TRUNCATOCONUS Yu, 1979

**Type species.** *Truncatoconus yichangensis* Yu, 1979.

**Species included.** Type species and *Truncatoconus campylurus* (Jiang, 1980).

*Truncatoconus*? cf. *T. yichangensis* Yu, 1979  
Figure 3A–H

**Synonyms.** See review by Parkhaev & Demidenko (2010).

**Holotype.** NIGPAS 54428 from the Cambrian Fortunian Tianzhushan (= Huangshandong) Member of the
Dengying Formation, Yichang, Hubei Province, South China (Yu 1979, pl. 1, figs 27, 28).

**Material.** One specimen (LC03-32-01) from the Cambrian Stages 3–4 Xinji Formation of the Chaijiaawa section in Shaanxi Province, and one specimen (SJFH-03-05) from the Sanjianfang section in Henan Province, North China.

**Description.** The shell is cap-shaped, depressed, height/length ratio c. 0.4 (Fig. 3A–E). The aperture is subrectangular or ovoid in outline, with blunt subcentral apex. Lateral profile triangular with flattened margin, except for shallow emargination on sub-apical field (Fig. 3F–H). External shell ornamentation consists of fine radiating striations (Fig. 3C, D).

**Remarks.** The type species *Truncatoconus yichangensis* Yu, 1979 was originally described by Yu (1979) from the Cambrian Fortunian Tianzhushan (= Huangshandong) Member of the Dengying Formation of Yichang, South China, and is characterized by a simple conical shell, triangular lateral profile with shallow emargination on the sub-apical surface. In contrast, *Truncatoconus campylurus* (Jiang, 1980) from the regional Meishucunian Stage (Cambrian Stage 2) of the Zhujiaqing Formation of South China has a lower shell and distinctive lateral profile, given that its subapical margin is obviously concave, in contrast to the convex margin of the supra-apical field (Parkhaev 2008; Parkhaev & Demidenko 2010). Specimens from North China are clearly comparable to *T. yichangensis* in general morphology, particularly in terms of the lower triangular lateral profile of the moulds. Similar shells were described from Cambrian Stages 3–4 Bastion Formation of North-East Greenland as Helcionelloid indet. by Skovsted.

**FIG. 3.** *Truncatoconus?* cf. *T. yichangensis* Yu, 1979 from the Cambrian Series 2 Xinji Formation of North China. A–E, LC03-32-01, internal mould with fine ornaments of radiating striations: A, apical; B, lateral; C, subapical; D, supra-apical; E, lateral view. F–H, SJFH-03-05, internal mould with distinct triangular lateral profile: F, apical; G, subapical; H, lateral view. Scar bars represent 200 μm (A–E); 100 μm (F–H).
stem lineage (Vendrasco et al., 2004, fig. 7K, O, P), and these may represent the same taxon as the material from North China.

**Occurrence.** Xinji Formation in Shaanxi and Henan provinces, North China; possibly Bastion Formation in the Albert Helm Bierge, North-East Greenland, Cambrian Series 2, Stages 3–4; Cambrian Fortunian Tianzhushan (= Huangshandong) Member of the Dengying Formation, Yichang, Hubei Province, South China.

**Genus EMARGINMANTUS Skovsted et al., 2012**

**Type species.** Emarginmantus angulatus Skovsted et al., 2012.

**Species included.** See review by Skovsted et al. (2012).

**Remarks.** Skovsted et al. (2012) established the genus *Emarginmantus* to encompass a group of enigmatic orthoconic fossils that develop a high, erect shell with the subapical wall drawn out into an apron that bears a shallow median emargination. The morphologically similar *Ocruranus* tunuensis (Jiang, 1980), *Ocruranus septentrionalis* Peel & Skovsted, 2005, *Ocruranus tunuensis* Peel & Skovsted, 2005, and possibly *Ocruranus* sp. in Peel & Skovsted (2005) were reassigned to *Emarginmantus*, and tentatively reinterpreted as helcionelloid molluscs (Skovsted et al. 2012). In contrast, other shells referred to *Ocruranus*, with moderately high cap-shaped shells and a distinctive upfolded subapical margin are likely to belong to a larger scleritome that consists of multiple skeletal elements such as *Eohalobia* Jiang, 1982 and some intermediates illustrated as *Stephaconus trulliformis* Jiang, 1980, considered synonymous to *Ocruranus trulliformis* by Qian & Bengtson (1989) and referred to *E. trulliformis* by Skovsted et al. (2012), from Terreneuvian strata of South China in terms of shell height and curvature (Qian & Bengtson 1989, fig. 69A, B). However, our specimens differ from *E. trulliformis* by the presence of the broad fold on the subapical field of the shell.

**Occurrence.** Xinji Formation in Shaanxi and Henan provinces, North China; Bastion Formation in Albert Helm Bierge, North-East Greenland. Cambrian Series 2, Stages 3–4.

**Genus PARARACONUS Runnegar in Bengtson et al., 1990**

**Type species.** Pararaconus staitorum Runnegar in Bengtson et al., 1990.

**Species included.** Type species and *Pararaconus paradoxus* Parkhaev in Gravestock et al. (2001).

**Pararaconus paradoxus** Parkhaev in Gravestock et al., 2001.

**Figure 5A–F**

2001 *Pararaconus paradoxus* Parkhaev in Gravestock et al., p. 157, pl. 31, figs 2–11.

**Holotype.** PIN 4664/323 from sample HG6, Cambrian Stages 3–4 Mernmerna Formation, Horse Gully, Yorke Peninsula, South Australia (Parkhaev in Gravestock et al. 2001, pl. 31, figs 2a–d).

**Material.** LC03-21-08, LC03-28-07, LC03-30-03, and 49 additional specimens from the Cambrian Stages 3–4 Xinji...
Formation of Chaijiawa section in Shaanxi Province, 14 specimens from the Sanjianfang section in Henan Province, five specimens from the Shangzhangwan section in Shaanxi Province, North China.

**Description.** The shell is cap-shaped, tall, highly compressed laterally, height/length ratio $c. 0.8$ (Fig. 5A–C). The apex is blunt, slightly inclined (Fig. 5F). Subapical field is almost straight or slightly concave, supra-apical field is convex (Fig. 5C, D). The aperture is elongated, elliptical in outline, and bears a shallow ring-like depression adjacent to the apertural margin (Fig. 5F). One specimen shows a distinct constriction between the protoconch and the rest of the mould (Fig. 5G).

**Remarks.** The characters distinguishing the two known species, the type species *Pararaconus staitorum* and *P. paradoxus* from South Australia, relate to the presence/absence of lateral depressions and buttress near the apertural margin (Bengtson et al. 1990; Parkhaev in Gravestock et al. 2001). The specimens from North China are placed in *P. paradoxus* based on the absence of a characteristic buttress on the lateral field of internal moulds and the general morphology of the material. The only slight difference is that the apertural rim of those South Australian materials of the species is more strongly flaring in contrast to the convex shell wall of North China specimens, but this may represent intraspecific variation or a preservation artefact. In addition, similar specimens assigned to *Pararaconus* sp. have previously been illustrated from contemporaneous rocks of Antarctica (Wrona 2003) and the Emyaksin Formation of Northern Siberia (Kouchinsky et al. 2015).

**Occurrence.** Xinji Formation in Shaanxi and Henan provinces, North China; Uppermost Kulpara Formation and Parara Limestone of Yorke Peninsula, South Australia, Cambrian Series 2, Stages 3–4.

**Genus PARAILSANELLA Zhegallo in Voronova et al., 1987**

**Type species.** Parailsanella acris Zhegallo in Voronova et al., 1987.

**Species included.** See review by Parkhaev (2004b).
**Parailsanella luonanensis** sp. nov.

Figure 6A–G

*LSID. urn:lsid:zoobank.org:act:2BCB18CB-A31C-4492-8B7C-0002251DE5CB*

**Holotype.** LELE SZW-06-19 from the Cambrian Stages 3–4 Xinji Formation of Shangzhangwan section, Luonan County, Shaanxi Province, North China (Fig. 6A–D).

**Derivation of name.** From Luonan County where the holotype was collected.

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**FIG. 5.** *Pararaconus paradoxus* Parkhaev in Gravestock *et al.*, 2001 from the Cambrian Series 2 Xinji Formation of North China. A–E, LC03-28-07, internal mould without ‘buttress’ on lateral field: A, apical; B, subapical; C, supra-apical view; D–E, lateral view. F, LC03-30-03, internal mould. G, LC03-21-08, internal mould with globose apex, apical view. Scale bars represent 100 μm.
Material. LC03-18-02, LC-04-01 from the Cambrian Stages 3–4 Xinji Formation of the Chaijiawa section in Shaanxi Province, SZW-06-19, SZW-08-03, SZW-05-01, SZW-04-10 and 15 additional specimens from the Shangzhangwan section in Shaanxi Province, North China.

Diagnosis. Conical shell, laterally compressed with prominent globose protoconch. Aperture narrow, elongated elliptical. External ornamentation of shell consisting of numerous sharp concentric ribs separated by broad grooves that bear reticulate microsculpture.

Description. The shell is cap-shaped, tall, highly compressed laterally, height/length ratio c. 0.6–0.8 (Fig. 6A). Subapical field is concave, supra-apical field convex, lateral surface is straight or slightly concave in early growth stages, but progressively flaring towards the aperture (Fig. 6B–D). Protoconch is globose, large (200 µm in diameter), smooth, inclined, and overhanging the subapical margin. The aperture is narrow, elongated elliptical in outline with length/width ratio c. 2 (Fig. 6A–D). External shell ornamentation of the largest specimen consists of 7–8 sharp concentric ribs separated by broad grooves (Fig. 6F, G). Some well-preserved specimens express an exquisite reticulate microsculpture within the grooves, formed by intersecting transverse and radiating striations (Fig. 6E).

Remarks. This species resembles to some degree specimens referred to Capitoconus artus Skovsted, 2004 from the Cambrian Stages 3–4 Bastion Formation of North-East Greenland (Skovsted 2004, fig. 5J, K), but the latter has a much larger and more elongated protoconch, wider aperture and more prominent ribs of the external shell. Parailsanella luonanensis sp. nov. is very similar to one internal mould described as Parailsanella sp. 2 from the Cambrian Series 2 Emyaksin Formation of Northern Siberia (Kouchinsky et al. 2015, fig. 7), but the poorly preserved Siberian specimen shows no trace of external shell ornamentalations. Parailsanella luonanensis sp. nov. is readily distinguishable from the other seven species of the genus (Parailsanella acris Zhegallo in Voronova et al., 1987, P. dzhargalantica Zhegallo in Esakova & Zhegallo, 1996, P. murenica Zhegallo in Esakova & Zhegallo, 1996, P. recta (Missarzhevsky, 1989), Parailsanella lata Parkhaev in Gravestock et al., 2001, P. khairkhanica Zhegallo in Esakova & Zhegallo, 1996 and Parailsanella sayutinae Parkhaev, 2004b) by the presence of a distinct globose protoconch and reticulate, net-like micro-ornament of the external shell.

Occurrence. Xinji Formation (Chaijiawa and Shangzhangwan sections) in Shaanxi province, North China, Cambrian Series 2, Stages 3–4.

**FIG. 6.** Parailsanella luonanensis sp. nov. from the Cambrian Series 2 Xinji Formation of North China. A–D, SZW-06-19, phosphate coating with concentric rugae and globose apex: A, lateral; B, apical; C, obliquely apical view; D, amplification of boxed area in A, showing distinct net-like microsculptures within the inter-rugae grooves. E, SZW-08-03, phosphate coating with concentric rugae, lateral view. F, SZW-05-01, lateral view. G, SZW-04-10, lateral view. Scale bars represent: 100 µm (A–C, E–G); 50 µm (D).
**BEMELLA** Missarzhevsky in Rozanov et al., 1969

*Type species.* *Bemella jactica* Missarzhevsky in Rozanov & Missarzhevsky, 1966.

**Species included.** See reviews by Parkhaev & Demidenko (2010) and Devaere et al. (2013).

**Remarks.** Three species of *Bemella*, including *B. obscuricosta* Zhou & Xiao, 1984, *B. costa* Zhou & Xiao, 1984 and *B. anhuiensis* Zhou & Xiao, 1984, were previously described from the Houjiashan Formation in Anhui Province (Zhou & Xiao 1984) and the Xinji Formation in Henan Province (Feng et al. 1994). The latter two were revised as *Davidonia rostrata* (Zhou & Xiao, 1984) by Parkhaev (2001). Furthermore, our new observations suggest that specimens with the same morphology as *B. obscuricosta* described by Zhou & Xiao (1984, pl. 2, figs 1–3) and Feng et al. (1994, pl. 2, figs 1, 2) might also represent incomplete specimens of *D. rostrata* (see Discussion below). However, two species that can be confidently assigned to the genus, *B. communis* Parkhaev in Gravestock et al., 2001 and *B. xinjiensis* (Feng et al., 1994), were recovered in our material and are described herein.

*Bemella communis* Parkhaev in Gravestock et al., 2001

**Figure 7A–I**

2001 *Bemella communis* Parkhaev in Gravestock et al., p. 273, pl. 28, figs 4–10, p. 275, pl. 29, figs 1–6 (non pl. 28, figs 6, 8, pl. 29, figs 3, 5).

2002 *Bemella communis* Parkhaev in Gravestock et al.; Parkhaev, p. 455, pl. 3, figs 1, 2.

2009 *Bemella communis* Parkhaev in Gravestock et al.; Topper et al. p. 232, fig. 11A–F.

**Holotype.** PIN 4664/1331 from the Cambrian Stage 2 Sellick Hill Formation, Myponga Beach, Fleurieu Peninsula, South Australia (Parkhaev in Gravestock et al. 2001, pl. 29, fig. 2a–c).

**Material.** LC03-24-08, LC03-30-06, LC03-A-63, LC02-B-135, and 14 additional specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, one specimen (SZW-07-06) from the Shangzhangan section in Shaanxi Province, six specimens from the Sanjianfang section in Henan Province, North China.

**Description.** The shell is cap-shaped, of medium height, moderately compressed laterally with height/length ratio c. 0.6. Subapical field is slightly concave, supra-apical field is well rounded and convex (Fig. 7B, C). The apex is blunt, inclined, and reaching the margin of the aperture (Fig. 7D–F). Aperture is planar, ovoid in outline. Exterior of internal moulds is smooth or sometimes covered by ornaments of fine, densely distributed pits (Fig. 7A).

**Remarks.** In contrast to the abundant specimens documented by Parkhaev in Gravestock et al. (2001) from the Sellick Hill Formation, Mernmerna Formation and equivalent strata in South Australia, specimens of *Bemella communis* are relative rare in our molluscan collections from North China. The internal moulds from North China generally have a smooth surface, which differs from the characteristic concentric folds in specimens of South Australia. However, this morphology is comparable to some specimens of *B. communis* from South Australia, and the difference is probably related to individual variability or taphonomic factors. Two specimens previously described as *Bemella communis* by Parkhaev (2014a) from the Yorke Peninsula of South Australia are almost identical to *Figurina figurina* as defined below, in general morphology, particularly in terms of their characteristic pitted ornamentations, and are consequently placed in *F. figurina*.

**Occurrence.** Xinji Formation in Shaanxi and Henan provinces, North China; Parara and Ramsay Limestones in Yorke Peninsula, and Mernmerna Formation in Flinders Ranges, South Australia, Cambrian Series 2, Stages 3–4; Cambrian Stage 2 Sellick Hill Formation in Fleurieu Peninsula, South Australia.

*Bemella xinjiensis* (Feng et al., 1994)

**Figure 8A–G**

1984 *Spatulocomus* sp. cf. He et al., p. 357, pl. 2, fig. 5.

1994 *Repenoconus xinjiensis* Feng et al., p. 19, pl. 1, figs 13–17.

**Holotype.** NIGPAS 116909 from the Cambrian Stages 3–4 Xinji Formation of Yexian County, Henan Province, North China (Feng et al. 1994, pl. 1, figs 15–17).

**Material.** LC03-07-14, LC03-14-14, LC03-16-04, LC0616-04, LC0618-22, LC0620-13, LC0620-11 and nine additional specimens from the Xinji Formation of Chaijiawa section in Shaanxi Province, two specimens (SZW-07-18 and SZW-14-19) from the Shangzhangan section in Shaanxi Province, eight specimens from the Sanjianfang section in Henan Province, North China.

**Description.** The shell is cap-shaped, extremely depressed, moderately compressed laterally, with height/length ratio c. 0.3. In internal moulds subapical field very short, transiting into a parietal train at an acute angle; supra-apical field is convex,
longitudinally elongated (Fig. 8B–E). The apex is acute, recurved, slightly projecting over the margin of the aperture and hooked downward. Aperture is simple, elongated oval in outline with length/width ratio c. 2 (Fig. 8F, G). Surface of internal moulds is generally smooth, but one large specimen bears three to four broad rugae separated by shallow grooves. The rugae appear to increase in amplitude during ontogeny (Fig. 8A).

Remarks. This species was originally described by Feng et al. (1994) as *Repenoconus xinjiensis* from the Xinji Formation in Henan Province, North China. The species was later transferred to *Bemella* by Parkhaev *in* Gravestock et al. (2001), and this interpretation has been accepted in subsequent literature (Parkhaev & Demidenko 2010; Devaere et al. 2013). The combination of an extremely low cap-shaped shell, elongated oval aperture and short subapical field distinguishes *B. xinjiensis* from other species of the genus. A specimen described as *Spatuloconus* sp. by He et al. (1984, pl. 2, fig. 5) from the Xinji Formation in Henan Province may also belong to *B. xinjiensis*. 
Occurrence. Xinji Formation in Shaanxi and Henan provinces, North China, Cambrian Series 2, Stages 3–4.

Genus ANABARELLA Vostokova, 1962

Type species. Anabarella plana Vostokova, 1962.

Species included. See review by Claybourn et al. (2019); Li et al. (2019b).

Anabarella australis Runnegar in Bengtson et al., 1990.

Figure 9A–H

Synonyms. See review by Li et al. (2019b).

Holotype. SAMP29017 from UNEL1761, the base of the Cambrian Stages 3–4 Mernmerna Formation, Horse Gully, Yorke Peninsula, South Australia (Bengtson et al. 1990, fig. 164D).

Material. LC0603-02, LC0618-09, LC0625-04, LC0626-04 and more than 400 additional specimens from the Xinji Formation of Chaijiawa section in Shaanxi Province, SZW-02-12, SZW-03-14 and 26 additional specimens from the Shangzhangwan section in Shaanxi Province, 10 specimens from the Sanjianfang section in Henan Province, North China.

Description. See Li et al. (2019b).

Remarks. Specimens preserving phosphatized coatings of the shell are obviously identical to Anabarella australis from South Australia (Bengtson et al. 1990; Gravestock et al. 2001). The shell is small, univalve, rapidly expanding, bilaterally symmetrical and highly compressed laterally. Shells are coiled throughout about one whorl, with the apical part tightly coiled and projecting beyond the apertural margin (Fig. 9B, E–H). The protoconch is hemispherical, clearly separated from the teleoconch by a slightly circumferential ridge and the initiation of growth lines (Fig. 9A). In contrast, associated internal moulds are morphologically very similar to a different helcionelloid genus, Planutenia Elicki, 1994, with the initial part of the mould weakly bent through about half a whorl (Fig. 9D). Interestingly, the Anabarella-type external coating and Planutenia-shaped internal mould may be observed in the same specimen, with a distinct void chamber in the initial part of the shell (Fig. 9A, C). This observation provides
convincing evidence that Planutenia is a subjective junior synonym of Anabarella.

Occurrence. Xinji Formation in Shaanxi and Henan provinces, North China; Görlitz syncline, Eastern Germany; Yorke Peninsula (Kulpara Formation and Parara Limestone) and the Flinders Ranges (Ajax Limestone and Mernmerna Formation), South Australia; Bastion Formation, North-East Greenland, Cambrian Series 2, Stages 3–4.

Genus STENOTHECA Salter in Hicks, 1872

Type species. Stenotheca cornucopia Salter in Hicks, 1872.

Species included. The type species, Stenotheca acutacosta Walcott, 1890 and Stenotheca drepanoida (He & Pei in He et al., 1984). See review by Parkhaev in Gravestock et al. (2001).

Stenotheca drepanoida (He & Pei in He et al., 1984)

Figure 10A–C

1984 Anabarella drepanoida He & Pei in He et al., p. 351, pl. 2, figs 1–7 (non fig. 8).
1984 Anabarella drepanoida He & Pei in He et al.; Zhou & Xiao, p. 1333, pl. 3, figs 15–17.
1987a Anabarella drepanoida He & Pei in He et al.; Yu, pl. 68, figs 7–8.
1990 Stenotheca cf. drepanoida He & Pei in He et al.; Bengtson et al., p. 244, fig. 163b–g, m, n.
1994 Stenotheca drepanoida He & Pei in He et al.; Feng et al., p. 8, pl. 3, figs 3, 6, 7, 14, 15.
1996 Mellopegma absida Li & Ding, p. 60, 63, pl. 1, figs 14, 15.
2001 Stenotheca drepanoida He & Pei in He et al.; Parkhaev in Gravestock et al. p. 189, pl. 42, figs 1–9.
2009 Stenotheca drepanoida He & Pei in He et al.; Topper et al. p. 229, fig. 10A–D.
Material. LC0627-04 and more than 85 additional specimens from the Xinji Formation of Chaijiawa section in Shaanxi Province, SJFH-01-12, SJFH-03-08 and 17 additional specimens from the Sanjianfang section in Henan Province, two specimens (SZW-01-20, SZW-10-19) from the Shangzhangwan section in Shaanxi Province, North China.

Description. The shell is extremely compressed laterally with height/length ratio c. 0.7–0.8. Subapical field is strongly concave, forming a circular or subcircular shape; supra-apical field is evenly rounded. The initial shell is strongly recurved, projecting over the rear margin of the aperture, with pointed apex hooked downwards or backwards. Aperture is extremely narrow and elongated (Fig. 10A). Some specimens preserve polygonal textures on the mould surface, which generally cover the whole surface of the internal moulds (Fig. 10C). In addition, some specimens bear numerous faint comarginal ribs (Fig. 10B).

Remarks. This species was originally described as *Anabarella drepanoida* by Zhou & Xiao (1984) from the Cambrian Houjiashan Formation of Anhui Province, North China, but was later revised as *Stenotheca drepanoida* by Runnegar in Bengtson et al. (1990). In general morphology, specimens of *S. drepanoida* from North China are strikingly similar to *Anabarella australis*, particularly the *Planutenia*-type internal moulds described above in terms of their general morphology (Fig. 9D and see Li et al. 2019b, figs 3A–C, 4). However, *S. drepanoida* has a much narrower aperture and a higher shell with polygonal network on the internal mould surface, which is different to the surface ornaments of moulds from *A. australis*.

Occurrence. Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Parara Limestone in Yorke Peninsula and Mernmerna Formation in Flinders Ranges, Cambrian Series 2, Stages 3–4; Sellick Hill Formation in Fleurieu Peninsula, South Australia, Stage 2.

Genus DAVIDONIA Parkhaev, 2017b

Type species. *Mellopegma rostrata* Zhou & Xiao, 1984.

Species included. See review by Claybourn et al. (2019).

*Davidonia rostrata* (Zhou & Xiao, 1984). Figure 11A–N

Synonyms. See review by Claybourn et al. (2019).

Holotype. GIA 800059 from the Cambrian Stages 3–4 Houjiashan Formation (equivalent to Xinji Formation) of Huoqiu, Anhui Province, North China (Zhou & Xiao 1984, pl. 3, fig. 7a–c).

Material. LC03-09-03, LC03-12-06, LC03-12-07, LC03-13-12, LC03-15-02 and more than 500 additional specimens from the Xinji Formation of Chaijiawa section, Shaanxi Province, SJFH-04-19, SJFH-11-07, SJFH-13-20, SJFH-19-18, SJFH-20-20 and more than 150 additional specimens from the Sanjianfang section in Henan Province, SZW-03-06, SZW-06-21 and 80 additional specimens from the Shangzhangwan section in Shaanxi Province, North China.

Description. The shell is cap-shaped, of medium height (average length/height ratio, 1.8) and moderately compressed laterally. The apex is blunt, recurved and projecting over the margin of the aperture. The subapical field is smooth, short and gently concave, forming a sharp angle with the short parietal train from which it is separated by a deep comarginal groove (Fig. 11A–D). The aperture is ovoid in outline, tapering towards the subapical field (Fig. 11M, N). Surface of internal moulds with distinct, coarse concentric folds, up to 6–7 in large shells, generally present from mid-height of the moulds and towards the aperture (Fig. 11G–L). These folds are generally wider and more prominent on the anterior part of the moulds and taper towards the subapical field (Fig. 11D–F, K, L).

Remarks. This species was originally described as *Mellopegma rostata* by Zhou & Xiao (1984) and Feng et al.
(1994), but following Parkhaev in Gravestock et al. (2001), has most often been described as *Mackinnonia rostrata* (Skovsted 2004; Vendrasco & Checa 2015; Jackson & Claybourn 2018). However, the generic name *Mackinnonia* Runnegar in Bengtson et al., 1990 is a junior synonym of *Mackinnonia* Janiszewska, 1963 and the new name *Davidonia* Parkhaev, 2017 was introduced to replace *Mackinnonia* Runnagar in Bengtson et al., 1990.
(Parkhaev 2017b). *Davidonia rostrata* is very common in our molluscan collections and has a wide range of morphological variations through ontogeny. Recently, Jackson & Claybourn (2018) used geometric morphometric methods, a combination of elliptical Fourier and multivariate analysis, to investigate the intra- and interspecific variations of the protoconch and teleoconch of *D. rostrata* and *D. tacomica* (Skovsted, 2004) from the Cambrian Series 2 of Greenland, South Australia and Antarctica. They found that ontogenetic sequences of outline curves, truncated at successive rugae, significantly discriminate between the two species (Jackson & Claybourn 2018). Specimens described as *Bemella obscursa*, *B. costa*, *B. anhuiensis* as well as *Helcionella sidingshanensis* Zhou & Xiao, 1984 from the Xinji Formation in Anhui Province and equivalent Houjiashan Formation in Anhui Province (Zhou & Xiao 1984) are very likely to represent juvenile shells and incomplete specimens of *D. rostrata*.

**Occurrence.** Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Yorke Peninsula (Kulpara Formation and Parara Limestone), Flinders Ranges (Mernmerna Formation and Ajax Limestone, South Australia; Shackleton Limestone, Antarctica; Bastion Formation, North-East Greenland, Cambrian Series 2, Stages 3–4; Stage 2 Sellick Hill Formation in Fleurieu Peninsula of South Australia.

**Genus FIGURINA Parkhaev in Gravestock et al., 2001**

**Type species.** *Figuurina figurina* Parkhaev in Gravestock et al., 2001.

**Species included.** Type species, *Figuurina nana*, Zhou & Xiao, 1984, *Figuurina groenlandica* Skovsted, 2004.

**Figuurina figurina** Parkhaev in Gravestock et al., 2001

Figures 12A–I, 13A–H, 14A–G, 15A–G

1994: *Securiconus vulgaris* cf. Feng et al. p. 18, pl. 2, figs 3, 4.

2001: *Figuurina figurina* Parkhaev in Gravestock et al., p. 288, pl. 36, figs 1–3.

2001: *Figuurina capitata* Parkhaev in Gravestock et al., p. 288, pl. 36, figs 4–7.

2001: *Bemella communis* Parkhaev in Gravestock et al., pl. 28, figs 6, 8, pl. 29, figs 3, 5.

2014a: *Bemella communis* Parkhaev in Gravestock et al.; Parkhaev, p. 19, pl. 3, figs 1, 2.

2014b: *Figuurina capitata* Parkhaev in Gravestock et al.; Parkhaev p. 374, pl. 3, fig. 12.

**Holotype.** PIN 4664/237 from the Cambrian Stages 3–4 Mernmerna Formation of Horse Gully, Yorke Peninsula, South Australia (Parkhaev in Gravestock et al. 2001, pl. 36, figs 2a–e).

**Material.** LC03-04-16, LC03-21-03, LC03-22-05, LC03-23-02, LC03-24-05, LC03-28-01, LC03-28-05, LC03-29-05, LC03-33-03, LC03-33-04, and more than 130 additional specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, five specimens from the Shangzhangwan section in Shannxi Province, SJFH-01-12, SJFH-02-01, SJFH-02-05, SJFH-02-6 and 16 additional specimens from the Sanjianfang section in Henan Province, North China.

**Description.** The shell is cap-shaped, of medium height, expands rapidly and is moderately compressed laterally. Subapical field is very short, strongly concave; supra-apical field is gently convex. The apex is recurved, overhanging the subapical field, and strongly hooked. The aperture is simple, ovoid in outline. Surface of internal moulds is smooth or with faint concentric rugae. In addition, the mould surface is generally covered by a fine micro-ornament of densely distributed narrow, deep pits. Moulds of the apical part of the shells are usually smooth (without pits) and spheroid shaped. The apex of the juvenile shells is recurved, but rarely reaches the margin of the aperture (Fig. 12A–I). In specimens of intermediate size, the shell expands rapidly, is moderately compressed laterally, with elongated elliptical aperture (Fig. 13F–H) and lateral fields slightly convex, flattened, or even concave. The shell of larger specimens is increasingly flaring towards the aperture, which is generally wider ovoid in outline (Fig. 13A–E).

In some specimens well-preserved muscle scars are easily discernible, usually represented by delicate polygonal textures on the mould surface. Polygons consist of cellular imprints (10 μm in average diameter) delimited by slightly elevated ridges. Two pairs of muscle scars are present. One tiny pair of scars occurs on the subapical surface of the mould, immediately adjacent to the apex and extending downwards towards the apertural margin (Fig. 14A–D). These scars are narrow, slightly diverging, band-like structures with a width of c. 40–50 μm (Fig. 14E–G). The other pair of scars is larger, forming narrow, continuous bands along the dorsolateral margin of the moulds (Fig. 15D–G). The scars expand anteriorly with terminal ending on the anterolateral fields (Fig. 15A–C).

**Remarks.** Specimens described as *Securiconus vulgaris* by Feng et al. (1994) from the Xinji Formation of Henan Province are very likely to belong to *F. figurina*. Parkhaev in Gravestock et al. (2001, p. 167) erected this new genus and species based on specimens from South Australia, and noted that ‘It differs from a similar genus *Trenella* Parkhaev, 2001 by a small parietal train and small siphonal groove.’ The subapical train and siphonal groove, however, are absent in our collections, and in material of the same genus from Greenland described by Skovsted (2004). Despite this discrepancy, the specimens from North China appear identical to some of the described...
specimens of *F. figurina* (Parkhaev in Gravestock et al. 2001, pl. 36, figs 1, 3) from the Cambrian Stages 3–4 Mernemrna Formation and equivalent strata of South Australia. Moreover, observations of the new specimens from North China indicate that Australian material referred to a second species, *Figurina capitata* Parkhaev in Gravestock et al., 2001, probably represent juvenile specimens of *F. figurina*, indicating that *F. capitata* is a junior synonym of *F. figurina*. In addition, some specimens assigned to *Bemella communis* by Parkhaev in Gravestock et al. (2001, pl. 28, figs 6, 8, pl. 29, figs 3, 5) appear to fit the diagnosis of *F. figurina*, and were thus referred to this species by Skovsted (2004). The internal moulds of *F. figurina* from North China are also comparable with *F. groenlandica* from the Cambrian Stages 3–4 Bastion Formation of North-East Greenland in general morphology (Skovsted 2004), except that the latter shows additional radial ridge-like ornaments on the lateral surface of the moulds, a feature that is absent in specimens from North China and South Australia.

**Occurrence.** Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Parara Limestone of Yorke Peninsula, South Australia, Cambrian Series 2, Stages 3–4.

**FIG. 12.** Juvenile shell of *Figurina figurina* Parkhaev in Gravestock et al., 2001 from the Cambrian Series 2 Xinji Formation of North China. A–D, LC03-24-05, internal mould of the juvenile shell: A, apical; B, lateral; C, subapical; D, obliquely lateral view. E, LC03-29-05, internal mould with a fine ornament with densely distributed pits, apical view. F, LC03-28-01, apical view. G–H, LC03-33-04: G, apical; H, obliquely lateral view. I, LC03-33-03, apical view. Scale bars represent 100 μm.
FIG. 13. Mature shell of *Figurina figurina* Parkhaev in Gravestock et al., 2001 from the Cambrian Series 2 Xinji Formation of North China. A–E, LC03-28-05, internal mould with a fine ornament of densely distributed pits: A, apical; B, lateral; C, lateral; D, subapical; E, supra-apical view. F–H, SJFH-02-01, internal mould with a fine ornament with densely distributed pits: F, apical; G, lateral; H, sub-apical view. Scale bars represent 200 μm.
FIG. 14. Muscle scars of *Figurina figurina* Parkhaev in Gravestock *et al.*, 2001 from the Cambrian Series 2 Xinji Formation of North China. A–D, LC03-22-05, internal mould with elongated, continuous, symmetrical and band-like muscle scars along the dorsolateral margin of the moulds: A, apical; B, lateral; C, lateral; D, obliquely apical view with muscle scar on dorsolateral margin indicated (white arrow). E, SJFH-02-05, internal mould with two pairs of muscle scars on the subapical wall (black arrow) and dorsolateral margin (white arrow), lateral view. F, SJFH-02-6, obliquely apical view with two pairs of muscle scars on the subapical wall (black arrow) and dorsolateral margin (white arrow). G, LC03-04-16, lateral view with muscle scars on the subapical wall (black arrow) and dorsolateral margin (white arrow). Scale bars represent: 200 μm (A–D); 100 μm (F); 50 μm (E, G).
FIG. 15. Muscle scars of *Figurina figurina* Parkhaev in Gravestock et al., 2001 from the Cambrian Series 2 Xinji Formation of North China. A, LC03-21-03, internal mould with a pair of elongated, continuous, symmetrical muscle scars along the dorsolateral margin of the moulds, apical view. B–C, SJFH-01-12, muscle scars with polygonal cell-like structure, apical view. D, LC03-23-02, internal mould with dorsoventral muscle scars. E, amplification of boxed area in D showing muscle scars consisting of polygonal texture, lateral view. F–G, LC03-04-16, internal mould, lateral view. Scale bars represent: 100 μm (A, B, D, F); 50 μm (C, E, G).
**Figurina nana** (Zhou & Xiao, 1984)

Figure 16A–E

1984 *Mellopegma nanum* Zhou & Xiao, 1984, p. 132, pl. 4, fig. 11.

2001 *Figurina nana* Parkhaev in Gravestock et al., p. 169, pl. 35, figs 4–8.

**Holotype.** GIA 800063 from the Cambrian Series 2 Houjiashan Formation (equivalent to Xinji Formation) of Huoqiu, Anhui Province, North China (Zhou & Xiao 1984, pl. 3, fig. 11).

**Material.** Four specimens (LC03-01-03, LC03-11-22, LC03-13-22, LC03-14-11) from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, one specimen (SJFH-02-06) from the Sanjianfang section in Henan Province, North China.

**Description.** The shell is cap-shaped, of medium height (average length/height ratio, 2.7), expanding rapidly and moderately compressed laterally. Subapical field is short, strongly concave, separated by a sharp angle and a deep comarginal groove from the parietal train; supra-apical field is evenly convex, elongated longitudinally. The apex is blunt, recurved, projecting over the margin of the aperture. The aperture is elongated ovoid, tapering towards subapical side with length/width ratio c. 2 (Fig. 16A–E). Exterior of internal moulds bears faint concentric rugae, and is sometimes covered by a micro-ornament of densely distributed pits (Fig. 16F).

**Remarks.** Internal moulds of *Figurina nana* are strikingly similar to juvenile shells of *Davidonia rostrata* described above in general morphology. However, recovered specimens of *F. nana*, are of the same size as adult shells of *D. rostrate* (Table 4), and also develop a much wider aperture and distinctive morphology of their internal moulds. This species was originally described as *Mellopegma nanum* by Zhou & Xiao (1984) from the Cambrian Stages 3–4 Houjiashan Formation of Anhui Province, North China. Parkhaev in Gravestock et al. (2001) revised this species as *Figurina nana* based on its

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**Fig. 16.** *Figurina nana* (Zhou & Xiao, 1984) from the Cambrian Series 2 Xinji Formation of North China. A–D, SJFH-02-06, internal mould: A, apical; B, obliquely lateral; C, lateral; D, subapical view. E, LC03-01-03, internal mould with subapical train and comarginal groove, lateral view. F, amplification of E showing fine ornaments of densely distributed pits. Scale bars represent: 200 μm (A–E); 20 μm (F).
diagnostic characters of the small parietal train and comarginal groove as well as short subapical wall. Similar specimens were previously documented from Cambrian Stages 3–4 Mernmerna Formation and Stage 2 Sellick Hill Formation of South Australia (Parkhaev in Gravestock et al. 2001) and the uppermost Emyaksin Formation of Siberia (Kouchinsky et al. 2015).

Occurrence. Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Parara Limestone, Yorke Peninsula, South Australia; Emyaksin Formation, Northern Siberia, Cambrian Series 2, Stages 3–4; Stage 2 Sellick Hill Formation, Fleurieu Peninsula, South Australia.

Genus ANHUICONUS Zhou & Xiao, 1984

Type species. Anhuiconus microtuberus Zhou & Xiao, 1984.

Species included. The type species only.

Anhuiconus microtuberus Zhou & Xiao, 1984

Figure 17A–J

1984 Anhuiconus microtuberus Zhou & Xiao, p. 139, pl. 1, figs 1–6.
1994 Anhuispira microtuberus Zhou & Xiao; Feng et al., p. 4, pl. 1, figs 1, 2.
1996 Asperconella troyensis Landing & Bartowski, p. 746, figs 5.1–5.4, 5.6.

TABLE 4. Height and length measurements of selected specimens of Davidonia rostrata (Zhou & Xiao, 1984) and Figurina nana (Zhou & Xiao, 1984).

| Specimen ref. | Length (μm) | Height (μm) | L/H ratio |
|---------------|-------------|-------------|-----------|
| Davidonia rostrata | | | |
| LC03-06-09 | 1169 | 651 | 1.8 |
| LC03-06-13 | 810 | 485 | 1.7 |
| LC03-08-17 | 1002 | 568 | 1.8 |
| LC03-08-18 | 937 | 561 | 1.7 |
| LC03-09-03 | 1191 | 681 | 1.7 |
| LC03-11-19 | 686 | 331 | 2.1 |
| LC03-13-12 | 1217 | 705 | 1.7 |
| LC03-13-02 | 1424 | 740 | 1.9 |
| SJFH-18-14 | 1165 | 665 | 1.8 |
| SJFH-20-15 | 1188 | 649 | 1.8 |
| SJFH-20-20 | 1422 | 786 | 1.8 |
| Figurina nana | | | |
| LC03-1-03 | 1973 | 767 | 2.6 |
| SJFH-2-6 | 2188 | 790 | 2.8 |

2001 Anhuiconus microtuberus Zhou & Xiao; Parkhaev in Gravestock et al. p. 164, pl. 30, figs 1–7.
2004 Asperconella troyensis Landing & Bartowski; Skovsted, p. 26, fig. 7H–J, L.

Holotype. GIA 800057 from the Cambrian Stages 3–4 Houjiashan Formation (equivalent to Xinji Formation) of Huoqiu, Anhui Province, North China (Zhou & Xiao 1984, pl. 1, fig. 1a–d).

Material. LC03-22-06, LC03-23-05, LC03-27-07, LC03-29-04, and more than 100 additional specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, 22 specimens from the Shangzhangwan section in Shaanxi Province, SJFH-01-02, SJFH-2-7-35, SJFH-22-01, and 12 additional specimens from the Sanjianfang section in Henan Province, North China.

Description. Cyrtococonic shell of medium height, slightly compressed laterally with rapidly expanding whorls. Initial shell recurved, with blunt apex hooked downward and projected beyond the apertural margin. Supra-apical field is well rounded in a distinct circular lateral profile; subapical wall is short, strongly concave. The aperture is subcircular in outline. The largest specimen (Fig. 17H–J; length, 1800 μm; height, 1100 μm; width, 1000 μm) is planispirally coiled, consisting of 0.75 whors. Surface of internal moulds ornamented by regularly distributed nodules or tubercles aligned in distinct V-shaped rows on the dorsum (Fig. 17A, B, G).

Remarks. Anhuiconus and a few similar Cambrian genera e.g. Asperconella Landing & Bartowski, 1996 and Daedalia Parkhaev in Gravestock et al., 2001, have relatively open coiled, bilaterally symmetrical shells with delicate ornamentations of tubercles or nodules on internal moulds, and can thus be easily distinguished from other helcionelloids (Skovsted 2004). Among them, Anhuiconus is extremely similar to Asperconella in general morphology. Parkhaev in Gravestock et al. (2001) noted that Anhuiconus differs from Asperconella by smaller tubercles on internal mould surface. However, Skovsted (2004) suspected the two genera to be conspecific, but the insufficient illustration of Anhuiconus microtuberus from North China and South Australia, particularly lacking details of the diagnostic tuberculate ornament, initially made comparison difficult. New collections of A. microtuberus from North China show that the nodes or tubercles are arranged in a typical V pattern on the dorsum, and are effectively identical to Asperconella. In addition, we argue that the size differences of the tubercles are not distinct and are seemingly a consequence of preservational artefacts. Consequently, we consider Asperconella troyensis as a subjective junior synonym of Anhuiconus microtuberus.
Occurrence. Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; South Australia, Parara Limestone in Yorke Peninsula and Mernmerna Formation in Flinders Ranges; Bastion Formation of North-East Greenland and Browns Pond Formation of New York State, USA, Cambrian Series 2, Stages 3–4.

Genus HORSEGULLIA Parkhaev, 2004c

Type species. Horsegullia horsegulliensis Parkhaev in Gravestock et al., 2001.

Species included. The type species only.

Horsegullia horsegulliensis Parkhaev in Gravestock et al., 2001

Figure 18A–I

2000 Igoellina sp. Parkhaev, pl. 5, fig. 5a, b.
2001 Yorkiella horsegulliensis Parkhaev in Gravestock et al., p. 172, pl. 33, fig. 1.
2008 Horsegullia horsegulliensis (Parkhaev); Parkhaev, p. 52, fig. 3.15F.
**Holotype.** PIN 4664/1499 from the Cambrian Stages 3–4 Mernmerna Formation of Horse Gully, Yorke Peninsula, South Australia (Parkhaev in Gravestock et al. 2001, pl. 33, fig. 1a, b).

**Material.** LC02-02-09, LC03-12-18, LC03-32-02, LC03-32-09, and 21 additional specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijawa section in Shaanxi Province, two specimens (SZW-07-21 and SZW-10-23) from the Shangzhangwan section in Shangxi Province, 26 specimens from the Sanjianfang section in Henan Province, North China.

**Description.** The cyrtoconic shell is of medium height and moderately compressed laterally. Initial shell is strongly recurved, with blunt apex hooked downwards, strongly projecting beyond the apertural margin (Fig. 18A–C). Supra-apical field is well rounded, elongated longitudinally, lateral fields are evenly convex and rapidly flaring towards the aperture, and subapical field is elongated, extremely concave, passing into a very short parietal train at an acute angle (Fig. 18D–F). Aperture is tear drop shaped, tapering towards the subapical side with length/width ratio c. 1.2 (Fig. 18H). Exterior of internal moulds is covered by a fine micro-ornament of densely distributed flat-bottomed shallow pits, and one large specimen bears faint comarginal rugae separated by wide, shallow grooves (Fig. 18G, I).

**Remarks.** This species was originally described as Yorkiella horsegulliensis by Parkhaev in Gravestock et al. (2001) from the Cambrian Stages 3–4 Mernmerna Formation of South Australia, but was later renamed Horsegullia horsegulliensis by Parkhaev (2004c). In our molluscan collections from North China, this species is very similar to Anhuiconus microtuberus and Igorellina probosca Feng et al., 1994 in the elongated shell with rapidly expanding whors. However, the presence of a distinct tear drop-shaped aperture, extremely overhanging apex, elongated subapical wall and pitted micro-ornament of H. horsegulliensis clearly distinguishes this species from species of Anhuiconus and Igorellina as well as from other helcionelloids.

**Occurrence.** Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Camrian Parara Lime-stone in Yorke Peninsula, Horse Gully, South Australia, Cambrian Series 2, Stages 3–4.

**Genus IGORELLINA Missarzhevsky, 1989**

**Type species.** Igorellina monstrosa, Missarzhevsky in Rozanov et al., 1969.

**Species included.** The type species and Igorellina probosca Feng et al., 1994.

**Igorellina probosca** Feng et al., 1994

**Figures** 19A–K, 20A–C

1994 Igorellina probosca Feng et al., p. 6, pl. 5, figs 1–19.
1994 Igorellina proboscis Feng et al., p. 17 (unintentional spelling mistake in English abstract).

**Holotype.** NIGPAS 116950 from the Cambrian Stages 3–4 Xinji Formation, Yexian County, Henan Province, North China (Feng et al. 1994, pl. 4, figs 16–18).

**Material.** Five specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijawa section in Shaanxi Province, SJFH-01-01, SJFH-01-03, SJFH-01-04, SJFH-01-20, SJFH-02-09, SJFH-03-05, SJFH-05-02, SJFH-08-09, and 27 additional specimens from the Sanjianfang section in Henan Province, North China.

**Description.** Cyrtococonic shell of medium height, moderately compressed laterally, elongated longitudinally with rapidly expanding whors. Aperture is simple, ovoid in outline, tapering towards the subapical side (Fig. 19F, H). The initial shell is recurved, with apex hooked downwards (Fig. 19A–D). In larger specimens, the shell wall is flaring rapidly towards the aperture and the initial shell is projecting strongly beyond the apertural margin (Fig. 19I–K). Protoconch is elongated, bulbous and relatively large (200 μm in diameter), separated from the teleoconch by a distinct circumferential constriction (Fig. 19D–G). Exterior of internal moulds is smooth or ornamented by faint comarginal rugae (Fig. 19A–D). One large specimen (length, 2000 μm; width, 1000 μm) exhibits narrow, sharp plications separated by wide shallow grooves in later formed parts of the shell (Fig. 20A–C).

**Remarks.** This species was originally described by Feng et al. (1994) from the Cambrian Stages 3–4 Xinji Formation of Henan Province, North China. Parkhaev in Gravestock et al. (2001) erected a new genus, Fenqiaronia on the basis of one large specimen from the Cambrian Stages 3–4 Mernmerna Formation of South Australia (Parkhaev in Gravestock et al. 2001, pl. 35, figs 1–3), and argued that Igorellina probosca from North China might represent a juvenile form of this taxon. New collections of I. probosca from North China express a wide range of morphological variation and a gradual ontogenetic series. In particular, the largest recovered I. probosca specimen (Fig. 20A–C) differs dramatically from the conical shells of Fenqiaronia, which have a coiled initial part (Gravestock et al. 2001, pl. 35, figs 1–3). According to these observations, we exclude I. proboscis from Fenqiaronia and confirm the validity of the species as originally defined.

**Occurrence.** Xinji Formation in Shaanxi, Henan and Anhui provinces, North China, Cambrian Series 2, Stages 3–4.
Family YOCHELCIONELLIDAE Runnegar & Jell, 1976

Genus YOCHELCIONELLA Runnegar & Pojeta, 1974

Type species. Yochelcionella cyrano Runnegar & Pojeta, 1974.

Species included. See reviews by Atkins & Peel (2004, 2008).

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FIG. 18. Horsegullia horseguliensis (Parkhaev in Gravestock et al. 2001) from the Cambrian Series 2 Xinji Formation of North China. A–C, LC03-32-09, internal mould with initial part extremely recurved: A, lateral; B, dorsal; C, dorsal view. D–E, LC03-32-07, internal mould: D, obliquely lateral; E, apical view. F, LC03-12-18, lateral view. G, LC02-02-09, internal mould with comarginal faint rugae. H, LC03-32-02, internal mould with ovoid shaped aperture, apertural view. I, amplification of H showing a fine ornament of densely distributed pits. Scale bars represent: 200 μm (A–H); 20 μm (I).
FIG. 19. *Igorellina probosca* Feng *et al.*, 1994 from the Cambrian Series 2 Xinji Formation of North China. A, SFH-01-20, lateral view. B, SFH-03-05, lateral view. C, SFH-01-03, lateral view. D, SFH-08-09, lateral view. E, SFH-01-04, lateral view. F, SFH-01-01, apertural view. G, SFH-05-02, lateral view. H, SFH-04-01, internal mould with globose protoconch that is separated from the teleoconch by a distinct circumferential constriction, apertural view. I–K, SFH-02-09, internal mould with strongly recurved apex: I, dorsal; J, apical; K, lateral view. Scale bars represent: 100 μm (A–F); 200 μm (G–K).
Description. The shell is tall, highly compressed laterally with a prominent subapical tubular snorkel that points obliquely upward in adult shells (Fig. 21B, D, E). The initial shell is smooth, rapidly expanding, inclined through about a quarter of one whorl with apex overhanging the subapical field. Subapical field is concave, while supra-apical field is well rounded (Fig. 21A, C). In larger specimens, the shell wall below the snorkel expands slowly and coils in opposite direction to the coiling of early growth stages, and thus results in a distinct sigmodal lateral profile (Fig. 21C, G). Mould ornaments consist of comarginal rugae separated by broad shallow grooves (110 μm in width). In addition, well-preserved specimens are covered with fine micro-ornaments of densely distributed pits (Fig. 21F).

Remarks. This species was originally described by Pei (1985) based on one internal mould from the Cambrian Stages 3–4 Xinji Formation of Henan Province, North China. Later, two incomplete specimens of the species were reported by Runnegar in Bengtson et al. (1990) from the Cambrian Stage 4 Oraparinna Shale of South Australia. During the last decade, abundant specimens of Yochelcionella were recovered from numerous localities in Eastern Laurentia, particularly in the Cambrian Stage 4 Forteau Formation of western Newfoundland and Kinzers Formation of Pennsylvania. Some of these specimens have been assigned to Y. chinensis based on the similar morphology of the initial shell (Skovsted & Peel 2007, 2010; Atkins & Peel 2008).

Occurrence. Xinji Formation in Shaanxi and Henan provinces, North China; Oraparinna Shale, Flinders Ranges, South Australia; Forteau Formation, Newfoundland, Canada; lowest Kinzers Formation, Thomasville, Pennsylvania, USA. Early Cambrian (Cambrian Series 2, Stages 3–4).

Family MAROCELLIDAE Topper et al., 2009
Genus MAROCCELLA Geyer, 1986

Type species. Maroccella mira Geyer, 1986.

Species included. See review by Topper et al. (2009).

Maroccella mira Geyer, 1986

Holotype. SMF34844 from the Lemdad-Mulde, Hoher Atlas, Morocco (Geyer 1986, pl. 6, fig. 83).

Material. LC03-12-05, LC03-12-08, LC03-21-05, LC03-14-16, LC03-33-01, LC05-26-02, and 13 additional fragments from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, North China.
Description. The juvenile shell (specimens with maximum length c. 1 mm, 0.5 mm in width) is smooth, moderately compressed laterally, recurved, with truncated apex overhanging the subapical wall, and a simple, elongated ovoid aperture. In larger internal moulds, the shell develops coarse comarginal and radial folds separated by narrow grooves resulting in a coarse cancellate pattern (Fig. 22B, G, H). Supra-apical surface becomes evenly convex, subapical area is initially more concave, but progressively flare towards the aperture. Incomplete internal moulds of the initial teleoconch preserve exquisite replications of the interior compartmental structures of the original shells. Moulds of individual compartments are subquare in shape and slightly inclined towards the apex (Fig. 22A, C–E). However, it is obvious that the size and shape of compartments can vary extensively, being bifurcated by secondary partitions along comarginal and radiating directions (Fig. 22F). In addition, well-preserved moulds express very fine pits covering the mould surface (Fig. 22H).

Remarks. Marocella is an enigmatic Cambrian helcionelloid macromollusc, reaching up to 18 mm in length.

FIG. 21. Yochelcionella chinensis Pei, 1985 from the Cambrian Series 2 Xinji Formation of North China. A–F, LC03-24-02, internal mould with subapical tubular snorkel, comarginal rugae, distinct sigmodal lateral profile: A, lateral; B, subapical; C, lateral; D, apical; E, supra-apical view; F, close-up showing fine ornament of densely distributed pits. G, LC0620-90, internal mould, lateral view. Scale bars represent: 100 μm (A–E, G); 20 μm (F).
(Skovsted et al. 2007), which is characterized by a unique structure of the interior of the shell with a network pattern of subquadrate compartments formed by intersecting concentric and radiating partitions formed by narrow internal walls. This genus has been documented from numerous localities of Cambrian Stage 3 to Wuliuan of South Australia, Spain, Siberia, Morocco, South China and Antarctica (Topper et al. 2009). Interestingly, *Marocella* seems to be more common in, and perhaps better adapted to, siliciclastic depositional environments in comparison with millimetre-sized micromolluscs that are commonly found in carbonate facies (Skovsted et al. 2007; Topper et al. 2009; Jacquet & Brock 2016). Consequently, phosphatized internal moulds of *Marocella* have rarely been studied. The characteristic morphology of the specimens from North China described here is interpreted to reflect internal moulds of the complicated interior shell surface of *Marocella*. Parkhaev in Gravestock et al. (2001) described several internal moulds of similar morphology as *Marocella australensis* from the upper Mermernna Formation and lower Minlaton Formation of the Stansbury Basin, South Australia. The specimens have ‘strongly smoothed ornamentation of the anterior part of the mould surface’ (Parkhaev in Gravestock et al. 2001, p. 160). However, Topper et al. (2009) argued that this feature of the juvenile shell has little taxonomic significance and that the poor preservation of the specimens hampers further comparison. Observations of new collections from North China provide new morphological details for *M. mira*, including a distinct smooth initial

**FIG. 22.** *Marocella mira* Geyer, 1986 from the Cambrian Series 2 Xinji Formation of North China. A, LC05-26-02, internal mould with compartments formed by intersecting concentric and radiating partitions, apical view. B, LC03-12-05, internal mould with smooth juvenile shell, apical view. C–E, LC03-21-05: C–D, lateral; E, supra-apical view. F, LC03-12-08, fragment with sub-rectangular compartments. G–H, LC03-33-01: G, subapical; H, lateral view. Scale bars represent: 200 μm (A–E); 500 μm (F); 100 μm (G, H).
shell followed by the formation of the diagnostic compartmental structures of the adult shell, and hence support the hypothesis that *M. australensis* is a subjective junior synonym of *M. mira*.

**Occurrence.** Xinji Formation in Shaanxi and Henan provinces, North China; Flinders Ranges, Arrowie Syncline (Mernmera Formation in the Bunkers Range, Elder Range, Chace Range, Bunyeroo Gorge and Steptoe Syncline; Oraparinna Shale in the Bunkers Range, Elder Range, and Erengunda Creek tributary) and Yorke Peninsula (Parara Limestone and Minlaton Formation), South Australia; central Transantarctic Mountains (Shackleton Limestone), Antarctica; High Atlas Mountains (Tatelt Formation and Jebel Wawrmast Formation), Morocco; Anabar Anticline, Siberian Platform. Cambrian Series 2 (Stage 3) to Miaolongian (Wulian).

**Type species.** *Cyrtolithes atlantoides* Matthew, 1894.

Species included. See review by Parkhaev in Gravestock et al. (2001).

*Pelagiella madianensis* (Zhou & Xiao, 1984)

**Figures 23A–I, 24A–H**

2001 *Pelagiella madianensis* (Zhou & Xiao); Parkhaev in Gravestock et al., p. 195, pl. 46, figs 1–12, pl. 47, figs 1–8.

2003 *Pelagiella madianensis* Zhou & Xiao; Wrona, fig. 13C–E.

2008 *Pelagiella madianensis* Zhou & Xiao; Parkhaev 2008, p. 54, fig. 3.17E, F.

2016 *Pelagiella madianensis* Zhou & Xiao; Yun et al., p. 95, fig. 5.

2017 *Pelagiella madianensis* Zhou & Xiao; Li et al., p. 2, figs 1a, d, p. 3, fig. 1a–c.

**Holotype.** GIA 801051 from the Cambrian Stages 3–4 Houjiashan Formation (equivalent to Xinji Formation) of Huoqiu, Anhui Province, North China (Zhou & Xiao 1984, pl. 4, fig. 14a–d).

**Material.** LC0601-05, LC0630-58, LC0630-65, LC0635-05, LC0632-69, LC0632-71, LC0632-75, LC0632-78, LC06019, LC06139, and more than 2000 additional specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, SJFH-05-01 and more than 300 additional specimens from the Sanjianfang section in Henan Province, North China.

**Description.** Anisometrically coiled shell, expands rapidly from apex to aperture and becomes strongly asymmetrical (Fig. 23A–C). The aperture of the last whorl is elongated, rectangular or triangular in outline. The peripheral margin is rounded, the lateral margin is convex and a projecting wing or ear is developed at the side of the aperture. The lateral surface bears a spiral carina along the circumbilical shoulder on internal moulds (Fig. 23D–F). The protoconch is bulb like, 100–120 μm in diameter, and is separated from the teleoconch by a distinct circumferential constriction. The teleoconch is slightly compressed laterally with lateral field depressed in contrast to the well-rounded dorsum (Fig. 23G–I).

The shell exterior is ornamented by distinct microsculptures, although no trace of growth lines was observed. The initial shell is characterized by a smooth surface, which usually develops numerous pustules (20 μm in diameter), regularly aligned in radial rows (Fig. 24A). These pustules may fuse into ridges with interspace occupied by fine, parallel ribs (Fig. 24A–C). In mature specimens, the ribs are inclined in relation to the larger ridges with an angle gradually increasing to 40° (Fig. 24D–H).

**Remarks.** *Pelagiella* is a common and useful fossil for international biostratigraphic correlation and the species *P. subangulata* (Tate, 1892) has been suggested as a potential index fossil for defining the base of the Cambrian Series 2, Stage 3 in terms of its narrow stratigraphical range and almost global distribution (Steiner 2007; Zhang et al. 2017). However, *Pelagiella* exhibit a considerable morphological diversity with up to 30 named species, although not all of these are likely to be valid (see review...
by Parkhaev in Gravestock et al. 2001). Unfortunately, most reported specimens are internal moulds lacking information on shell ornament etc., and comparative information for species-level classification is rarely preserved. Inevitably, many named species may be synonymous and assemblages consisting of internal moulds without details of shell ornament are generally undiagnostic and should be treated with caution, at least without a detailed analysis of variability (Bengtson et al. 1990; Gravestock et al. 2001; Skovsted 2006).

**FIG. 23.** *Pelagiella madianensis* (Zhou & Xiao, 1984) from the Cambrian Series 2 Xinji Formation of North China. A, LC0635-05, phosphate coating showing ear-like lateral profile. B, LC0632-71, internal mould, obliquely apertural view. C, LC0632-78, lateral view. D, LC0601-05, apertural view. E, LC0632-69, lateral view. F, LC06019, lateral view. G, LC06139, internal mould with rounded dorsum, dorsal view. H, LC0630-58, lateral view. I, LC0632-75. Scale bars represent: 100 μm (A–F); 200 μm (G–I).
Parkhaev in Gravestock et al. (2001) regarded *Pelagiella madianensis* from the Xinji Formation of North China and equivalent strata in South Australia and *P. subangulata* as ‘twin-species’ in terms of their similar gross appearances. However, our material of *P. madianensis* from North China can be easily distinguishable from *P. subangulata* by its elongated aperture, open umbilicus and distinct radial ornaments. In contrast, *P. subangulata* has an open oval aperture, narrow deep umbilicus and distinctive sculptures that form a V pattern on the dorsum. Our material of *P. madianensis* differs from *P. adunca* Rozanov & Missarzhevsky, 1966 from the strata of Cambrian Stages 3–4 of the Malyi Karatau Range, Altai-Sayan fold belt and Transbaikalia of Siberian Platform (Parkhaev 2004b) by its more depressed lateral surface and an extremely elongated aperture (length/width, 2.3), in contrast to the equally rounded lateral wall of *P. adunca*. Specimens of *Pelagiella* from the contemporaneous Tal Formation of the Ganga Valley, Lesser Himalaya, India were referred to *P. madianensis* by Kumar et al. (1987, fig. 3O, P). However, the described specimens are incomplete and the external shell is absent and thus, the affinity to *P. madianensis* of the Indian specimens is uncertain until more convincing evidence has been presented. Specimens from the Cambrian Stage 4 Emyaksin Formation of Siberia described as *Pelagiella* sp. 1 by Kouchinsky et al. (2015, fig. 17A–D) exhibit distinctive sculptures of fine radial striations and transverse ribs on the surface of internal moulds, which can easily be discriminated from the ornament of *P. madianensis* herein.
Occurrence. Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Yorke Peninsula (Parara, Ramsay, Stansbury and Coobowie limestones) and the Flinders Ranges (Ajax, Wirrealpa and Willkawillina limestones and Mernmerna Formation), South Australia; Glacial erratics of King George Island, West Antarctica, Cambrian Series 2, Stages 3–4.

Order & Family UNCERTAIN
Genus PROTOWENELLA Runnegar & Jell, 1976

Type species. Protowenella flemingi Runnegar & Jell, 1976.

Species included. See review by Brock (1998).

Protowenella flemingi Runnegar & Jell, 1976
Figure 25A–J

Holotype. ANU 29107 from L128, Currant Bush Limestone, post-Templetonian, western Queensland, Australia (Runnegar & Jell 1976, fig. 7B–F).

Material. Fifteen specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, SJFH-01-22, SJFH-03-07, SJFH-05-23, SJFH-08-11, SJFH-10-12, SJFH-13-16, SJFH-16-07, SJFH-18-12, SJFH-20-08, SJFH-20-14, and more than 100 additional specimens from the Sanjianfang section in Henan Province, North China.

Description. Internal moulds of planispiral, bilaterally symmetrical, globose and smooth shell. The juvenile shell has a relatively large protoconch (200 μm in diameter) and aperture, but a very short subapical wall (Fig. 25A–D). In more mature specimens, the shell is openly coiled, reaching one full whorl. Aperture is simple, circular or subcircular and of constant proportions through ontogeny. The circumbilical shoulders bear a pair of prominent helical channels that originate immediately below the apex and extend towards the aperture. As a result, a pair of notches is clearly visible on the subapical side of the aperture (Fig. 25E–J).

Remarks. Specimens assigned to Protowenella are characterized by a planispirally coiled shell with a pair of prominent channels along the circumbilical shoulders. This genus has been widely documented from the Miaoaligian, Wuiluan strata of New Zealand (MacKinnon 1985), Australia (Runnegar & Jell 1976; Brock 1998), Bornholm (Berg-Madsen & Peel 1978), Morocco (Geyer 1986), Siberia (Gubanov et al. 2004) and Spain (Wotte 2006). In contrast, material of Cambrian Series 2 has rarely been illustrated but sporadic reports from the Siberian Platform (regional Botomian Stage) and the roughly coeval strata in Maly Karatau of Kazakhstan (Missarzhevs’kyi & Mambetov 1981; Missarzhevs’kyi 1989; Brock 1998), Northern Territories of Australia (Smith et al. 2015) and the Shackelton Limestone of Antarctica (Claybourn et al. 2019) have been published. However, given that almost all known specimens are internal moulds, comparative features for classification are rare, making precise species identification and comparison difficult. As a result, specimens have most often been retained in open nomenclature (Brock 1998; Claybourn et al. 2019). Zhou & Xiao (1984) erected two new species of Protowenella as P. primaria and P. huainanensis from the Cambrian Stages 3–4 Houjiashan Formation of Anhui Province, North China. The stated distinguishable feature of the two species is that P. primaria is less involute, i.e. openly coiled, compared to P. huainanensis (Zhou & Xiao 1984). However, our new collections from North China exhibit a wide range of morphological variation through ontogeny, and suggest that the two forms represent intraspecific variation. Furthermore, in our interpretation, both of the described specimens as well as our new collections are identical to the type species, P. flemingi Runnegar & Jell, 1976 from the Miaolingian Currant Bush Limestone, post-Templetonian, Australia (Runnegar & Jell, 1976, fig. 6B–I), and Bornholm (Berg-Madsen & Peel 1978, fig. 6A–E). Consequently, we assign the North China material to this long ranging species.

Genus XINJISPIRA Yu & Rong in Yu, 1987a

Type species. Xinjispira simplex Zhou & Xiao, 1984.

Species included. The type species only.

Xinjispira simplex (Zhou & Xiao, 1984)
Figure 26A–H

1984 Barskoviia simplex Zhou & Xiao, p. 135, pl. 4, figs 6–12.
1987b Xinjispira simplex Zhou & Xiao; Yu, p. 54, pl. 4, figs 14–16.
1987a Xinjispira simplex Zhou & Xiao; Yu, p. 210, pl. 68, figs 1–6, text-fig. 62.
1990 Xinjispira simplex Zhou & Xiao; Yu, p. 146, fig. 4.
1991 Xinjispira simplex Zhou & Xiao; Yu & Rong, p. 341, 342, pl. 1, figs 10–13.
1994 Xinjispira simplex Zhou & Xiao; Feng et al., p. 13, pl. 2, figs 14–18.
FIG. 25. Protowenella flemingi Runnegar & Jell, 1976 from the Cambrian Series 2 Xinji Formation of North China. A, SJFH-13-16, internal mould with extremely short subapical field, apertural view. B, SJFH-10-12, internal mould, apertural view. C, SJFH-01-22, internal mould, apertural view. D, SJFH-05-23, internal mould, apertural view. E, SJFH-08-11, internal mould with a pair of prominent channels along circumbilical shoulders, apertural view. F, SJFH-20-14, apertural view. G, SJFH-18-12, apertural view. H, SJFH-16-07, apertural view. I, SJFH-03-07, lateral view. J, SJFH-20-08, supra-apical view. Scale bars represent: 50 μm (A–D); 100 μm (E–J).
Holotype. GIA 80096 from the Cambrian Stages 3–4 Houjiashan Formation (equivalent to the Xinji Formation) in Houqiu, Anhui Province, North China (Zhou & Xiao 1984, pl. 4, fig. 7a–d).

Material. Twenty specimens from the Cambrian Stages 3–4 Xinji Formation of Chaijiawa section in Shaanxi Province, SJFH-03-12, SJFH-05-03, SJFH-05-09, SJFH-19-09, SJFH-17-19, SJFH-19-10, SJFH-19-12, SJFH-19-13, and more than 100 additional specimens from the Sanjianfang section in Henan Province, North China.

Description. Internal moulds of sinistral, globose, loosely coiled shell with open umbilicus reaching about one whorl (Fig. 26A, B). The spire is slightly projecting above the upper surface of the whorl. The shell periphery is well rounded; the base is flattened or slightly convex (Fig. 26C, D). A pair of prominent helical channels occurs on umbilical shoulders, which originate immediately below the apex and extend towards the aperture (Fig. 26E–H). Aperture is circular or subcircular. Mould surface is ornamented by fine concentric ribs, presumably reflecting external growth lines.

Remarks. Xinjispira is an enigmatic mollusc genus known only from North China (Zhou & Xiao 1984; Feng et al. 1994) and Antarctica (Claybourn et al. 2019). The only known species, Xinjispira simplex, is almost identical to the co-occurring Protowenella flemingi in gross appearance, particularly in the fact that both species develop a pair of prominent channels along the circumumbilical shoulders.

2016 Xinjispira simplex Zhou & Xiao; Yun et al., p. 59, fig. 5L.
2019 Xinjispira simplex Zhou & Xiao; Claybourn et al., figs 5.17–5.26.
The principal distinguishing feature relates to the chirality of the shells, with sinistral and planispiral coiling in *Xinjispira* and *Protowenella*, respectively. Interestingly, in the Shackleton Formation of Antarctica, the only known fauna from outside North China where *Xinjispira* occurs, *Protowenella* (described as *Protowenella?* sp.) is also present (Claybourn et al. 2019), perhaps indicating a close phylogenetic relationship between these taxa.

**Occurrence.** Xinji Formation in Shaanxi, Henan and Anhui provinces, North China; Shackleton Limestone, Antarctica, Cambrian Series 2, Stages 3–4.

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**FIG. 27.** *Pojetaia runnegari* Jell, 1980 from the Cambrian Series 2 Xinji Formation of North China. A, LC0606-07, internal mould with delicate replicas of external shell microstructures, lateral view. B–D, LC0633-04, foliated aragonite microstructure with crystallite of aragonite in distinct imbricated pattern. E, LC0630-22, internal mould, view of hinge margin with interlocking teeth. Scale bars represent: 100 μm (A, B, E); 50 μm (C, D).
Class BIVALVIA Linnaeus, 1758
Order & Family UNCERTAIN
Genus POJETAIA Jell, 1980
Pojetaia runnegari Jell, 1980

Figure 27A–E

Holotype. NMV P59669 (Jell 1980, fig. 2A–B).

Material. LC0606-07, LC0630-22, LC0633-04, and more than 400 additional specimens from the Cambrian Stages 3–4 Xinji Formation of Chajiajia section in Shaanxi Province, 12 specimens from the Shangzhangwan section in Shaanxi Province, 12 specimens from the Sanjianfang section in Henan Province, North China.

Description and synonyms. See review by Elicki & Gürsu (2009).

Remarks. Internal moulds of bivalved molluscs are relatively common in our collections from the Xinji Formation of North China. The specimens often show impressions of one or two interlocking teeth and a short ligament (Fig. 26B, D, E) and are indistinguishable from Pojetaia runnegari, which is known to have a worldwide distribution in Cambrian Stages 3 and 4. Specimens of P. runnegari in our collections often preserve delicate replicas of shell microstructures (Fig. 27A, C). The lamellar layer is composed of lath or blade-shaped crystallites that develop straight growth fronts, a typical crystal shape of aragonite. These lath or blade-shaped crystallites of aragonite are assembled into a distinct imbricated pattern with straight growth fronts overlapping each other, and perpendicular to shell margin. This type of shell microstructure, i.e. foliated aragonite, has also been found among other Cambrian molluscs (Vendrasco et al. 2011; Li et al. 2017), which might represent a common and primitive shell microstructural fabric among Cambrian molluscs.

Occurrence. This species is known to have a worldwide distribution in Cambrian Stages 3–4, see review by Elicki & Gürsu (2009).

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