

## Mollusks from the upper Shackleton Limestone (Cambrian Series 2), Central Transantarctic Mountains, East Antarctica

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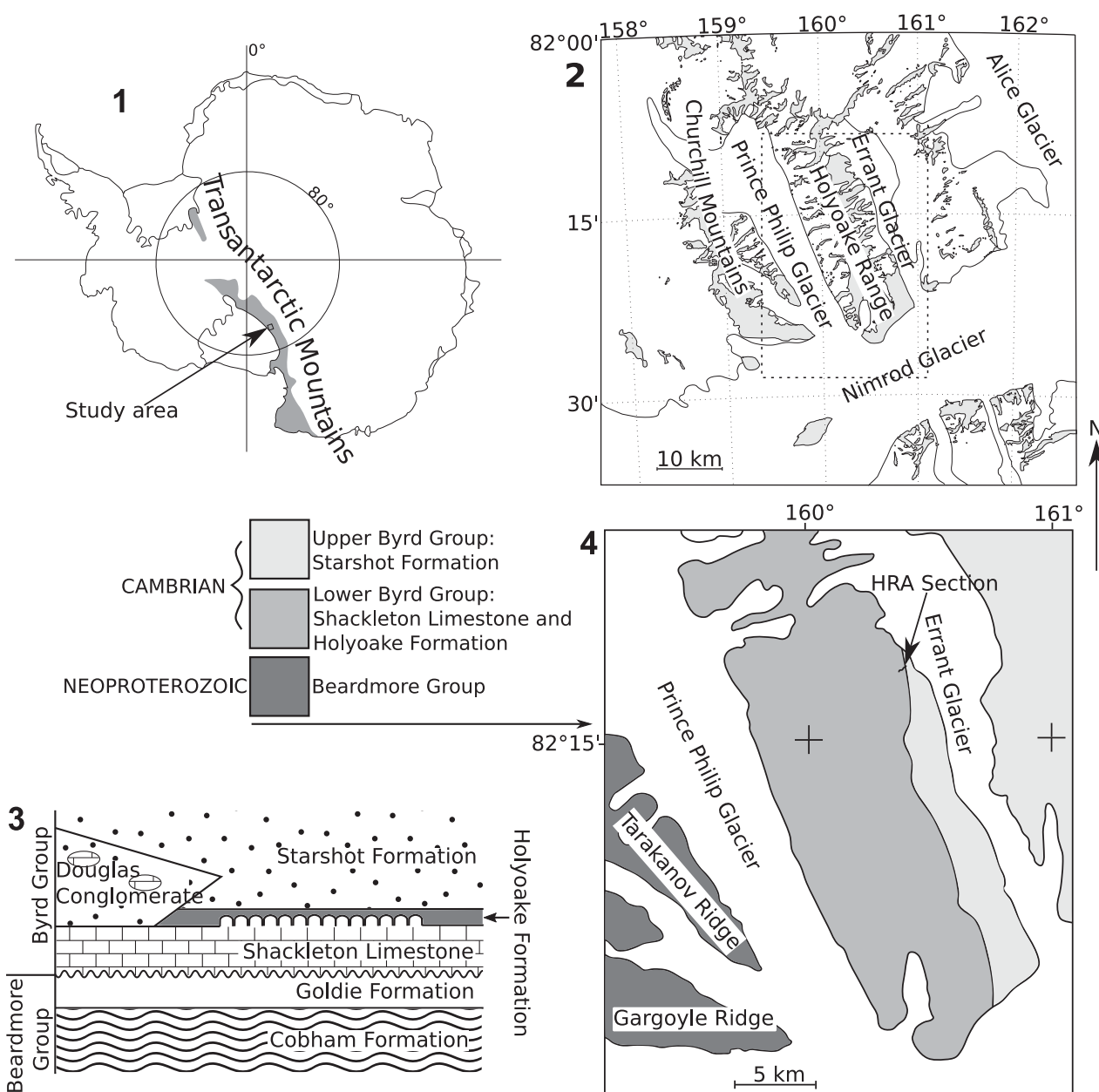
**Abstract.**—An assemblage of Cambrian Series 2, Stages 3–4, conchiferan mollusks from the Shackleton Limestone, Transantarctic Mountains, East Antarctica, is formally described and illustrated. The fauna includes one bivalve, one macromollusk, and 10 micromollusks, including the first description of the species *Xinjispira simplex* Zhou and Xiao, 1984 outside North China. The new fauna shows some similarity to previously described micromollusks from lower Cambrian glacial erratics from the Antarctic Peninsula. The fauna, mainly composed of steinkerns, is relatively low diversity, but the presence of diagnostic taxa, including helcionelloid *Davidonia rostrata* (Zhou and Xiao, 1984), bivalve *Pojetaia runnegari* Jell, 1980, cambroclavid *Cambroclavus absonus* Conway Morris in Bengtson et al., 1990, and bradoriid *Spinospitella coronata* Skovsted et al., 2006, as well as the botsfordiid brachiopod *Schizopholis yorkensis* (Ushatinskaya and Holmer in Gravestock et al., 2001), in the overlying Holyoake Formation correlates the succession to the *Dalysia odyseae* Zone (Cambrian Stages 3–4) in South Australia.

### Introduction

During the early Cambrian, East Antarctica was sutured between the now southern coast of Australia, Southeast Africa, and India and located at tropical latitudes (Brock et al., 2000; Torsvik and Cocks, 2013a, b). The Shackleton Limestone crops out meridionally and episodically along the Central Transantarctic Mountains (Fig. 1). While the true thickness of this carbonate unit remains uncertain (Myrow et al., 2002), it is estimated to be up to 2,000 m thick in places (Laird et al., 1971; Burgess and Lammerink, 1979). The unit consists of many lithofacies including sandy carbonates, pure limestones, and archaeocyath-microbialite bioherms (Rees et al., 1989; Myrow et al., 2002). The newly recovered fauna from measured stratigraphic sections through autochthonous exposures of the Byrd Group, central Transantarctic Mountains, includes archaeocyaths, brachiopods, bradoriid arthropods, cambroclavids, chancelloriids, hyoliths, sponge spicules, and tommotiids. This paper focusses on descriptions and biostratigraphy of eight helcionelloids, two pelagiellids, one scenellid, and the bivalve *Pojetaia runnegari* Jell, 1980. Helcionelloids are typical components of ‘small shelly fossil’ (SSF) assemblages in lower Cambrian (Terreneuvian, Cambrian Series 2) strata around the world (Bengtson, 2004; Kouchinsky et al., 2012). Widespread phosphatized steinkerns of micromorphic univalved helcionelloids appear in the

pre-trilobitic Terreneuvian (Khomentovsky et al., 1990; Kouchinsky et al., 2012) and range through to the Early Ordovician (Gubanov and Peel, 2001; Peel and Horný, 2004).

The taxonomic position of helcionelloids remains unresolved, with numerous authors suggesting different affinities and phylogenetic relationships (Parkhaev 2008, table 3.1). Early efforts placed some asymmetrically coiled helcionelloids in the late Paleozoic macluritid gastropods and bilaterally symmetrical forms with the monoplacophoran tryblidiids—then considered a ‘primitive’ gastropod taxon (Knight, 1952). Helcionelloids have also been suggested by some authors to be basal to the rest of the Gastropoda (e.g., Golikov and Starobogatov, 1975; Runnegar and Jell, 1976; Parkhaev, 2017a); a polyphyletic approach was proposed by other authors, with some helcionelloids considered ancestral to the major groups of mollusks (Runnegar and Jell, 1976, fig. 4; Runnegar, 1983, fig. 1) while others (the superfamily Helcionellacea Wenz, 1938) were referred to the monoplacophorans. Problems with these classification schemes are apparent, as a diagnostic criterion of the gastropods is torsion (Salvini-Plawen, 1980; Ponder and Lindberg, 1997), a characteristic obvious only in soft anatomy and never convincingly demonstrated in any helcionelloid taxon (but see Runnegar, 1981). A monoplacophoran affinity is also difficult to demonstrate as helcionelloids invariably lack the serially repeated muscles scars on the shell interior



**Figure 1.** (1) Map of Antarctica showing approximate extent of the Transantarctic Mountains and area shown in (2). (2) Map of Nimrod Glacier, Holyoake Range, and Churchill Mountains. (3) Generalized relationship of Cambrian (Byrd Group) and Neoproterozoic (Beardmore Group) rock units of the Holyoake Range, adapted from Myrow et al. (2002). (4) Simplified geological map of the Holyoake Range, adapted from Myrow et al. (2002).

reflecting the muscle attachment common to all extant monoplacophorans (Lindberg, 2009). Lindsey and Kier (1984) hypothesized a separate paraphyletic class for some asymmetrical helcionelloid mollusks (the Paragastropoda) on the basis that they lacked evidence of both torsion and serially repeated muscle scars, which included the pelagiellids. However, the asymmetrically coiled pelagiellids are perhaps the best candidates for inclusion in the gastropods. Preserved features such as muscle scars similar to those found in torted gastropods (Landing et al., 2002, fig. 9), a large mantle cavity, and potential anal notch have been inferred by some authors as indirect evidence of torsion (Landing et al., 2002). The class Helcionelloida Peel, 1991a was erected to include bilaterally symmetrical forms, excluding asymmetrical forms of the Paragastropoda.

Recognized sinistral and dextral asymmetrical deviations from typically symmetric forms remain within Helcionelloida (Gubarov and Peel, 2000). Recent systematic treatment of pelagiellids has them assigned to the helcionelloids (e.g., Skovsted and Peel, 2007; Topper et al., 2009; Wotte and Sundberg, 2017) or to the gastropods (e.g., Landing et al. 2002; Parkhaev, 2007a, 2017a).

While many authors have worked on the paleobiology of the helcionelloids (e.g., Peel, 1991a; Brock, 1998; Parkhaev, 2000, 2001), these and other SSFs can also be utilized in biostratigraphy, with certain caveats. Parkhaev in Gravestock et al. (2001) created loosely defined molluscan assemblage ‘zones’ for their work on the biostratigraphy of the lower Cambrian succession in the Stansbury Basin, South Australia. These were defined according to the presence of certain key taxa, and four

'zones' were recognized (oldest to youngest): *Pelagiella subangulata*, *Bemella communis*, *Stenotheca drepanoida*, and *Pelagiella madianensis* 'zones.' Jacquet et al. (2017) criticized these molluscan biozones noting they have very poorly defined boundaries and are based on poorly preserved, long-ranging taxa with considerable overlapping ranges. Close inspection of the data provided by Gravestock et al. (2001) reveals clear temporal discrepancies between the sections on Yorke and Fleurieu peninsulas (see Jacquet et al., 2017, p. 1093–1094 for details; Betts et al., 2016a).

Broad biostratigraphic correlations of lower Cambrian rocks have proven difficult due to strong provincialism and facies dependence in faunas (Landing, 1992; Mount and Signor, 1992; Steiner et al., 2004, 2007; Landing et al., 2013; Jacquet et al., 2016a; Yun et al., 2016). Betts et al. (2016a, 2017) created regional SSF biozones for the early Cambrian of South Australia and used mollusks as key accessory taxa. The choice of the primarily phosphatic tommotiid taxa *Kulparina rostrata* Conway Morris and Bengtson in Bengtson et al., 1990, *Micrina etheridgei* (Tate, 1892), and *Dailyatia odyssei* Evans and Rowell, 1990 to define these zones avoided some of the taxonomic and taphonomic problems associated with facies dependence and incomplete steinkern preservation in lower Cambrian carbonates (Mount and Signor, 1992; Jacquet et al. 2016a). Molluscan steinkerns are also often difficult to identify accurately to species level due to lack of information on the shell exterior, especially micro-ornament and other surficial features, an important criterion for species differentiation (Skovsted, 2006a; Betts et al., 2016b; Jacquet and Brock, 2016). The base of Cambrian Series 2, Stage 3, remains unresolved, although the first appearance datum of trilobites occurs around this boundary (see Babcock et al., 2017 and Zhang et al., 2017 for recent reviews). The use of SSFs, including mollusks, for establishing regional bases of Series 2 and Stage 3 has been put forward by some authors, for example, the *Pelagiella subangulata* taxon-range zone for South China (Steiner et al., 2007, 2011).

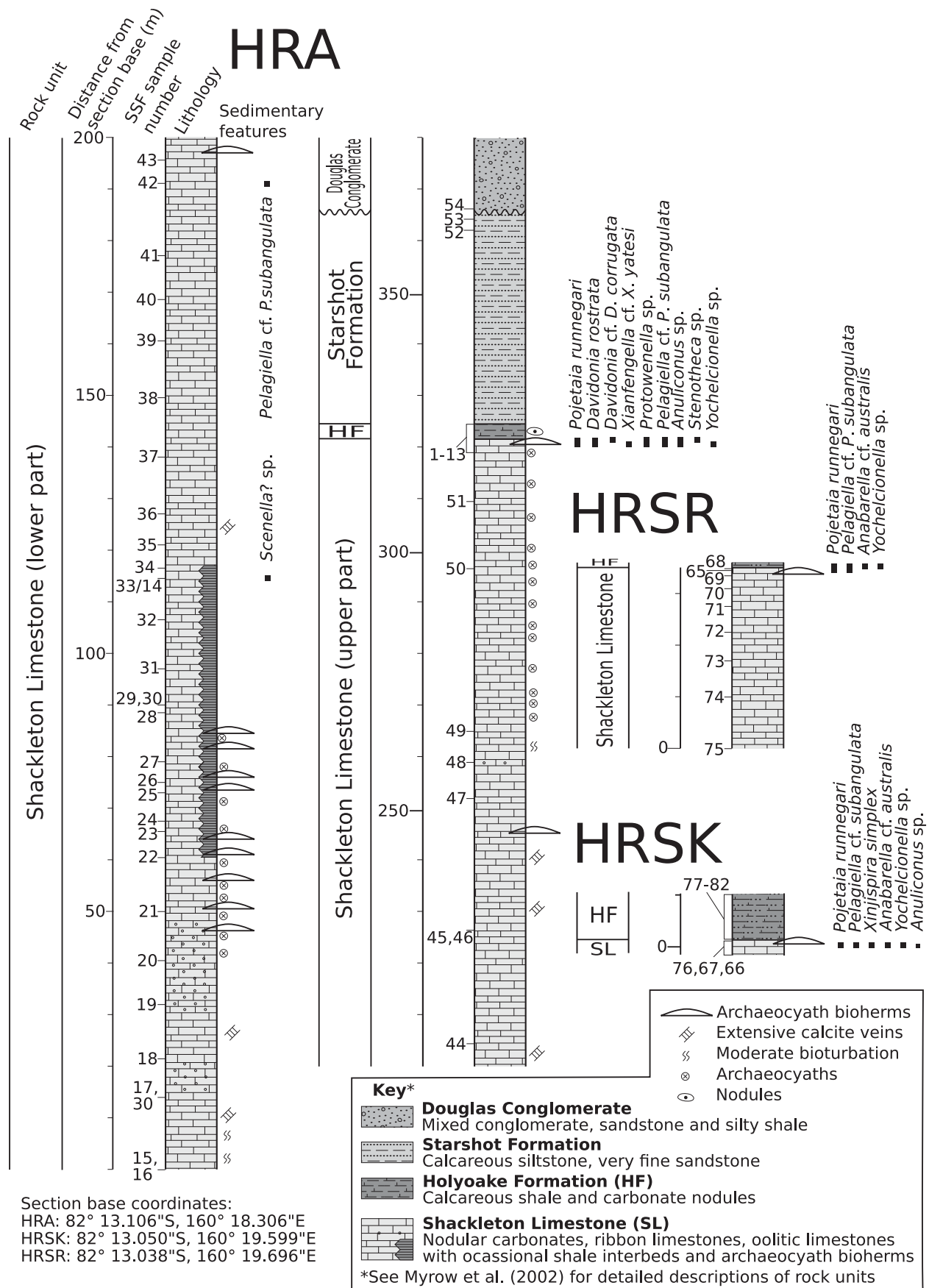
The fossils described herein are almost exclusively steinkerns of calcium phosphate, with occasional external molds. Primary mineralized or secondarily replaced shells are not present, but mineral imprints are present on the exterior of some steinkerns, which correspond to a variety of calcitic or aragonitic crystal morphologies. Examples of this, among others, include polygonal imprints that are interpreted as calcitic semi-nacre (Kouchinsky, 2000; Vendrasco et al., 2010; Vendrasco and Checa, 2015) and elongated crystal laths that are interpreted to be aragonitic (Landing and Bartowski, 1996; Kouchinsky, 2000; Landing et al., 2002; Vendrasco et al., 2010; Li et al., 2017). The chemical formation of phosphatic steinkerns is biased toward micromorphic forms (Creveling et al., 2014), suggesting some helcionelloid fossils might represent the juvenile shells (protoconchs) of macroscopic univalved mollusks (see Martí-Mus et al., 2008; Jacquet and Brock, 2016; Jacquet et al., 2016b). One of the first quantitative analyses of the fidelity of steinkern representation of the original shell identified the size of the umbilicus of anisostrophically coiled Ordovician mollusks as an indicator of the size of the original organism (Dattilo et al., 2016). This indicated the size of the steinkerns of the micromolluscan fauna studied was taphonomically, not ecologically, controlled. The basic size of the steinkern therefore cannot be

used to indicate ontogeny, and morphological differences between two steinkerns of the same size may not indicate taxonomically meaningful differences. The term 'teilsteinkern' was introduced to describe incomplete internal molds (Dattilo et al., 2016).

Some evidence suggests that the preservation of phosphatic steinkerns is tied to particular lithologies and depositional processes. Phosphate replacement and coating of originally calcareous fossils was related to phosphate precipitation and intense denitrification within sediments or above an oxygen minimum zone (Landing 1992; Landing et al., 2002). Subsequently, Jacquet et al. (2016a) noted the occurrence of abundant micromolluscan residues was linked to facies characterized by sediment reworking (i.e., tempestites) or low sedimentation rates (i.e., firmgrounds and true hardgrounds).

*Geological setting and previous work.*—The bulk of fossil material recovered is derived from an archaeocyath-rich biohermal unit near the top of a stratigraphic section (HRA) measured through the Shackleton Limestone and the overlying dark nodular carbonates and interbedded calc-siltstones of the Holyoake Formation. These rock units make up part of the Byrd Group (Figs. 1, 2), which crops out along the Central Transantarctic Mountains (Myrow et al., 2002). The deposition of the Shackleton Limestone was interrupted by the Ross Orogenic events, involving a change in the East Antarctic plate margin from passive to orogenic subduction regime (Boger and Miller, 2004). Subsidence resulted in a brief marine transgression across the continental shelf and deposition of the deeper-water argillaceous Holyoake Formation (Goodge et al., 1993, 2004; Myrow et al., 2002) at approximately 515–510 Ma (Paulsen et al., 2007). This was followed by a shallowing succession and ?syn-orogenic deposition of fine to medium calcareous sandstones of the Starshot Formation and overlying boulder conglomerates of the Douglas Conglomerate (Rowell et al., 1988a; Myrow et al., 2002; Goodge et al., 2004; Paulsen et al., 2007). Stratigraphic sections through the Shackleton Limestone have proven difficult to interpret into a coherent in situ stratigraphy due to pervasive folding and faulting (including fault repetition) of the carbonate-dominated succession, the result of tectonism associated with the Ross Orogeny (Paulsen et al., 2007).

Paleontological studies on parautochthonous lower Cambrian rocks from the Shackleton Limestone have largely focused on trilobites (Palmer and Gatehouse, 1972; Palmer and Rowell, 1995) and archaeocyaths (Debrenne and Kruse, 1986, 1989). In terms of other clades, only tommotiids (Evans and Rowell, 1990), the helcionelloid mollusk *Marocella mira* Evans, 1992, and a single bradoriid arthropod species, *Bicarinellata evansi* Rode et al., 2003, have been formally described systematically. Rowell et al., (1988b, figs. G, L, P, Q) also illustrated some taxa, including an elkaniid-like lingulid, *Lingulella* sp. and the mollusk *Latouchella* sp., as well as an unnamed 'euomphalid mollusk' but without formal description. Brachiopods, mollusks, tommotiids, and other SSFs derived from allochthonous clasts redeposited in a Miocene glacial-marine succession on King George Island, near the tip of the Antarctic Peninsula, were probably originally deposited within sediments equivalent to the Shackleton Limestone (Wrona, 1989, 2003, 2004; Holmer



**Figure 2.** Sedimentary columns with micromollusk occurrences of measured sections of the Holyoake Range. HF = Holyoake Formation; SL = Shackleton Limestone.



et al., 1996). These discoveries have formed the bulk of knowledge of lower Cambrian faunas from Antarctica and confirm strong biostratigraphic and paleobiogeographic links with South Australia (Brock et al., 2000; Betts et al., 2016a, 2017), Northeast Greenland (Skovsted, 2004, 2006b), and North China (Yang et al., 2015) during Cambrian Series 2, Stages 3–4.

### Stratigraphic correlation

**Antarctica.**—Lower Cambrian limestone erratics have been recovered within early Miocene glaciomarine deposits of King George Island, north of the Antarctic Peninsula (Gaździcki and Wrona, 1986; Wrona, 1989); these contain a diverse fauna of poriferan spicules and cancellorid, sactitiid, and tommotiid sclerites (Wrona, 2004), organophosphatic brachiopods (Holmer et al., 1996), bradoriids and phosphatocopids (Wrona, 2009), and mollusks (Wrona, 2003). The molluscan fauna from the erratics is similar to the Shackleton Limestone samples recovered from the Holyoake Range, including the genera *Yochelcionella* Runnegar and Pojeta 1974, *Anabarella* Vostokova, 1962, and *Pelagiella* (Matthew, 1895) (Wrona, 2003). The erratics most likely belong to the Shackleton Limestone and host the age-diagnostic tommotiid *Dailyatia odyseii* (Evans and Rowell, 1990; Wrona, 2004; Skovsted et al., 2015).

**South Australia.**—Previous studies suggesting a link between the Shackleton Limestone and South Australia were based on relatively few in situ samples from Antarctica, particularly of SSFs (see Brock et al., 2000; Topper et al., 2011; Yang et al., 2015). Biostratigraphic correlation has previously been based on trilobites (Palmer and Gatehouse, 1972; Palmer and Rowell, 1995). Palmer and Rowell (1995) tentatively assigned their six assemblages of trilobites to be from Atdabanian to Toyonian in age, and their assemblage 4 was correlated to the *Pararaia janae* zone of South Australia on the basis of co-occurrence of *Balcoracania* (Jell in Bengtson et al., 1990). Paterson and Brock (2007) described *Yunnanoccephalus macromelos* from the Mernmerna Formation, indicating a link between Palmer and Rowell's (1995) Assemblage 1 (which contains members of the genus) and the *Pararaia bunyenroensis* Zone. Caution was suggested in these ages due to few easily compared species (Palmer and Rowell, 1995, p. 4). Debrenne and Kruse (1986, 1989) indicated an Atdabanian–Botoman age for Antarctic archaeocyaths and considered most species to be found in common with the Wilkawillina and Ajax Limestones (Debrenne and Kruse, 1989, p. 24). Accurately correlating the Shackleton Limestone on the basis of the molluscan fauna alone is problematic due to issues already discussed with steinkern formation (Creveling et al., 2014; Jacquet et al., 2016a) and long stratigraphic ranges of helcionelloids (Landing, 1988; Geyer and Shergold, 2000; Jacquet et al., 2017; Zhang et al., 2017). This problem was discussed by Betts et al. (2017, p. 202) and Jacquet et al. (2017) in reference to the informal molluscan assemblage biozonations in Gravestock et al. (2001). A close correlation to the *Dailyatia odyseii* Zone in South Australia is strengthened by the shared presence of the accessory taxa

*Cambroclavus absonus* Conway Morris in Bengtson et al., 1990 (Skovsted et al., 2006, fig. 2) in the biohermal facies at the top of the Shackleton Limestone and *Spinospitella coronata* in the overlying Holyoake Formation, both of which co-occur in the *D. odyseii* Zone with accessory taxon *Schizopholis* (=Karathele) *yorkensis* (Ushatinskaya and Holmer in Gravestock et al., 2001). The presence of these taxa exclude the biohermal unit from correlation with the underlying *Micrina etheridgei* Zone, in which the steinkerns of the mollusks *Pojetaia runnegari*, *Pelagiella*, *Anabarella*, and *Davidonia* Parkhaev, 2017b also occur (Betts et al., 2017, figs. 3, 4, 7, 8, 12). *Xianfengella*, *Yochelcionella*, and *Stenotheca* are all restricted to the *D. odyseii* Zone in South Australia, allowing for stronger correlation (Betts et al., 2017, figs. 5, 10, 12). *Protowenella* Runnegar and Jell, 1976 is also known from the Cambrian Series 3 in Australia (Runnegar and Jell, 1976; Brock, 1998; Vendrasco et al., 2010), as well as Cambrian Series 2, Stage 4 (Smith et al., 2015), but the utility of this taxon in correlation with South Australia is doubtful due to problems with consistent identification.

The Shackleton Limestone fauna has most similarity with the Mernmerna Formation in the Arrowie Basin, which shares the micromollusks *Pojetaia runnegari*, *Davidonia*, *Pelagiella*, *Anabarella*, *Stenotheca* Hicks, 1872, and *Xianfengella* He and Yang, 1982 (Topper et al., 2009). The macromollusk *Marocella mira* not reported in this study is also present in the upper Mernmerna Formation (Topper et al., 2009; Jacquet and Brock, 2016) and the Shackleton Limestone that outcrops in the Churchill Mountains (Evans, 1992). The Ajax Limestone in the Arrowie Basin also contains *Davidonia* and *Anabarella* steinkerns as well as *Pelagiella subangulata* (Tate, 1892) (Betts et al., 2016a, fig. 2). *Pojetaia runnegari* has also been reported from the Ajax Limestone (Bengtson et al., 1990, fig. 6) although the range extends down into the underlying *M. etheridgei* Zone. The Shackleton Limestone thus strongly correlates with the *D. odyseii* zone in the upper Ajax Limestone (Betts et al., 2016a, fig. 2). *Yochelcionella chinensis* Pei, 1985 has also been reported from the younger Orparinna Shale (Runnegar in Bengtson et al., 1990) of the *Pararaia janae* Zone (Jago et al., 2012).

Highly diverse assemblages of micromollusks have been reported from the lower Cambrian Stansbury Basin (Bengtson et al., 1990; Gravestock et al., 2001), many of which also occur in the Shackleton Limestone. *Davidonia rostrata* (Zhou and Xiao, 1984), *Pojetaia runnegari*, as well as the genera *Anuliconus* Parkhaev in Gravestock et al., 2001, *Anabarella*, *Pelagiella*, and *Stenotheca* occur in the uppermost Kulpara Formation and disconformably overlying Parara Limestone in the western Stansbury Basin (Bengtson et al., 1990; Parkhaev in Gravestock et al., 2001), indicating long stratigraphic ranges of limited correlation potential. *Xianfengella yatesi* Parkhaev in Gravestock et al., 2001 has a more restricted occurrence, in the Parara Limestone at Yorke Peninsula (Parkhaev in Gravestock et al., 2001). Betts et al. (2017, fig. 22) identified the *D. odyseii* Zone in the Parara Limestone at Horse Gully on Yorke Peninsula. A condensed *Kulparina rostrata* Zone and overlying *Micrina etheridgei* Zone occur in the disconformably underlying Kulpara Formation (Betts et al., 2017, p. 202).

**North China.**—Cambrian Series 2 strata from North China are divided into three biozones: the informal *Stenotheca drepanoida*-*Pelagiella madianensis* Biozone (Feng et al., 1994), considered equivalent to the *Pararaia janeae* trilobite zone of South Australia (Yun et al., 2016), and the overlying *Redlichia* and *Redlichia chinensis* informal trilobite zones (Yun et al., 2016). Mollusks from the Cambrian Series 2, Stages 3–4, Xinji Formation in Shaanxi Province, Henan Province, and Anhui Province on the southwestern, southern, and southeastern margins of the North China Platform, respectively, can be closely correlated to the Shackleton Limestone based on shared genera *Stenotheca*, *Pelagiella*, *Yochelcionella*, Yu and Rong, 1991, and *Anabarella* and species *Xinjispira simplex*, *Pojetaia runnegari*, and *Davidonia rostrata* (He et al., 1984; Zhou and Xiao, 1984; He and Pei, 1985; Pei, 1985; Li and Zhou, 1986; Yu and Rong, 1991; Feng et al., 1994; Yun et al., 2016). The presence of *Xinjispira simplex* in the Shackleton Limestone represents the first discovery of the species outside North China and helps strengthen this correlation. Putative *Protowenella* steinkerns are also known from the Xinji Formation (Zhou and Xiao, 1984). However, it should be noted that diagnostic muscle scars are not preserved on specimens from the Xinji Formation or Shackleton Limestone (and other putative pre-Series 3 specimens), making taxonomic assignment to this genus tentative at this stage (Berg-Madsen and Peel, 1978; Brock, 1998).

**South China.**—Palmer and Rowell (1995) correlated their Trilobite Assemblage 1 (tentatively ‘Atdabanian’) to the *Eoredlichia*-*Wutingaspis* Zone of South China, which has significant overlap with the *Dailyatia odyseii* Zone of South Australia (Betts et al., 2017). The *Eoredlichia*-*Wutingaspis* Zone is equivalent to the *Pelagiella subangulata* Zone of East Yunnan and central Sichuan in South China (Steiner et al., 2007). The uppermost Shiyantou, Yuanshan (Yunnan Province) and upper Jiulaodong (Sichuan Province) formations of this zone have no shared helcionelloids for correlation to the Shackleton Limestone. The Yuanshan Formation of East Yunnan is predominantly siliciclastic and preserves phosphatic SSFs only in the lowermost phosphatic conglomerate unit, which contains SSFs of the *Sinosachites flabelliformis*-*Tannuolina zhangwengtangii* Zone (Steiner et al., 2001), immediately below the *Pelagiella subangulata* Zone (Steiner et al., 2007). This zone shares the taxon *Xianfengella* with the Shackleton Limestone only, in the Terreneuvian Yanjiahe Formation of Hubei (Guo et al., 2014) and Zhujianqing Formation of Yunnan (*Anabarites trusulcatus*-*Protohertzina anabarica* to *Watsonella crosbyi* zones) (Parkhaev and Demidenko, 2010).

**Laurentia.**—The SSF composition of eastern Laurentia suggests a continuous shelf margin during the early Cambrian (Skovsted, 2006b; Skovsted and Peel, 2010). Landing and Bartowski (1996) and Landing et al. (2002) reported diverse assemblages of SSFs from the Browns Pond Formation of the Taconic Allochthon of New York (Landing and Bartowski, 1996) and the ‘Anse Maranda Formation’ of Quebec (Landing et al., 2002), which contain a similar molluscan component of

*Davidonia rostrata*, *Yochelcionella*, and *Pelagiella*. The material from the Browns Pond Formation was collected from the *Elliptocephala asaphoides* assemblage, recognized as part of the *Bonnina-Olenellus* Zone by Siveter and Williams (1997). Also from Eastern Laurentia, the Forteau Formation of Newfoundland contains an abundant micromolluscan fauna (Skovsted and Peel, 2007), which shares *Pojetaia runnegari*, *Davidonia*, *Stenotheca*, and *Pelagiella* with the Shackleton Limestone. The formation also belongs to the *Bonnina-Olenellus* Zone as both trilobite genera occur there (Schuchert and Dunbar, 1934; Knight et al., 2017). Betts et al. (2017) recognized an overlap between the younger *Olenellus* Zone (the base of which is the same as the *Bonnina-Olenellus* Zone; Landing et al., 2013) and the uppermost part of the *Dailyatia odyseii* Zone of South Australia. The Kinzers Formation of Pennsylvania, of upper Cambrian Series 2 age, also contains steinkerns of *Yochelcionella* and *Pelagiella* (Atkins and Peel, 2008; Skovsted and Peel, 2010).

Northeast Greenland has lower Cambrian SSFs recognized as similar to those in South Australia and from the glacial erratics recovered from King George Island, Antarctica (Malinky and Skovsted, 2004; Skovsted, 2004; Skovsted and Holmer, 2005; Skovsted, 2006b). Skovsted (2004) reported a micromolluscan fauna from the Bastion Formation for Northeast Greenland, also correlated to the *Bonnina-Olenellus* Zone (Skovsted, 2006b, fig. 5.1–5.3), placing them as Dyeran in age of Laurentian regional scheme (Landing et al., 2013). The micromollusk fauna of the Bastion Formation is very similar to that found in the Shackleton Limestone and shared taxa include *Davidonia rostrata*, *Pojetaia runnegari*, *Anabarella*, *Stenotheca*, and *Yochelcionella*, (Skovsted, 2004) of which the latter four can be more loosely correlated at the generic level.

For western Laurentia, Skovsted (2006a) and Wotte and Sundberg (2017) provided systematic descriptions of lower Cambrian micromollusks from the Great Basins area. *Pelagiella* and *Anabarella* appear widespread across the province, with *Pelagiella* aff. *P. subangulata* occurring in the Emigrant Formation, Montenegro Member of the Campito Formation and the Combined Metals Member of the Pioche Formation, in rocks of upper Montezuman to Dyeran Stages (Wotte and Sundberg, 2017) given Cambrian Series 2, Stage 3 (Montezuman) and Stages 3–4 (Dyeran) (Peng et al., 2012).

## Materials and methods

Fossils were collected in the Austral summer during five weeks of fieldwork in October–November, 2011 (by LEH, CBS, GAB) from measured stratigraphic sections (HRA, HRSK, and HRSR) in the Holyoake Range, Central Transantarctic Mountains (Figs. 1, 2). The sections intersect the upper carbonate-dominated successions of the Shackleton Limestone, including inner shelf, shoal, and archaeocyath-microbialite bioherm facies, and the overlying and nonlapping dark silty carbonates and argillites from the Holyoake Formation. The most diverse and abundant fossil materials are derived from well-exposed biohermal facies at the top of the Shackleton Limestone (Fig. 2). Stratigraphically, the sections are an extension of the section originally sampled and illustrated by Myrow et al. (2002). Phosphatic residues were extracted from the carbonate matrix with dilute 10% acetic

acid solution following standard acid-leaching protocols (see Jeppsson et al., 1999). Images were taken with a Zeiss Supra 35 SEM at Uppsala University, a Hitachi S-4300 SEM at the Natural History Museum, Stockholm, and a PHENOM XL Benchtop SEM at Macquarie University.

**Repository and institutional abbreviation.**—All specimens are deposited at the Swedish Museum of Natural History (SMNH), Stockholm, Sweden.

### Systematic paleontology

The phylogenetic relationships of the likely polyphyletic class Helcionelloida Peel, 1991a is still unresolved. Many simple, poorly preserved and minute cap-shaped steinkerns recovered from the Shackleton Limestone during this study are not dealt with here due to a lack of taxonomically informative features.

Phylum Mollusca Cuvier, 1797

Class Bivalvia Linnaeus, 1758

Order and family uncertain

Genus *Pojetaia* Jell, 1980

**Type species.**—*Pojetaia runnegari* Jell, 1980, ‘*Salterella* Limestone,’ near Ardrossan, South Australia, by original designation. This likely corresponds to the Parara Limestone at Horse Gully, near Ardrossan, South Australia (cf. Jell, 1980, p. 234; Bengtson et al., 1990, fig. 4).

*Pojetaia runnegari* Jell, 1980

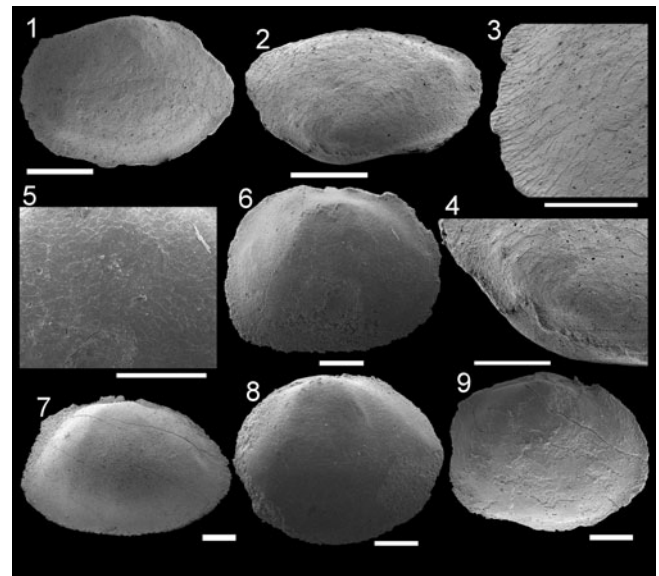
Figure 3

See Elicki and Gürsu (2009, p. 281–282) for a detailed synonymy.

- 1980 *Pojetaia runnegari* Jell, p. 235, figs. 1–3.
- 2004a *Pojetaia runnegari*; Parkhaev, p. 600, pl. 2, figs. 15–18.
- 2007 *Pojetaia runnegari*; Skovsted and Peel, p. 737, fig. 4 K, L.
- 2008 *Pojetaia runnegari*; Parkhaev, p. 38, fig. 3.4.
- 2009 *Pojetaia runnegari*; Elicki and Gürsu, p. 281, pl. 1, pl. 2, E–H.
- 2009 *Pojetaia runnegari*; Topper et al., p. 238, fig. 12 K–M.
- 2010 *Pojetaia runnegari*; Heuse et al., p. 107, fig. 2.14.
- 2011 *Pojetaia runnegari*; Vendrasco et al., pl. 1–4.
- 2015 *Pojetaia runnegari*; Vinther, fig. 2H.
- 2016 *Pojetaia runnegari*; Yun et al., fig. 5M.
- 2017 *Pojetaia runnegari*; Betts et al., fig. 170.

**Holotype.**—P59669, Paleontological collections, National Museum of Victoria, Melbourne, Australia. Internal mold of articulated valves, ‘*Salterella* limestone,’ lower Cambrian, South Australia.

**Occurrence.**—See Elicki and Gürsu (2009, p. 273) for a full review of global stratigraphic distribution. Distribution now includes Cambrian unnamed Series 2, Stages 3–4, of Newfoundland, Canada (Skovsted and Peel, 2007), and East Antarctica.



**Figure 3.** *Pojetaia runnegari* Jell, 1980 from the Shackleton Limestone. (1–4) Specimen SMNH Mo185039 in (1) lateral view, (2) dorsal view, (3) magnification of the central margin, showing laminar crystalline imprints, (4) magnification of the cardinal teeth shown in (2). (5, 6) Specimen SMNH Mo185040, (5) lateral view, (6) magnification of lateral surface, showing laminar crystalline imprints. (7) Specimen SMNH Mo185041 in lateral view. (8) Specimen SMNH Mo185042 in lateral view. (9) Specimen SMNH Mo185043. (5, 6, 8) imaged under low vacuum settings. (1, 2, 6–9) Scale bars = 200  $\mu$ m; (3–5) scale bars = 100  $\mu$ m.

**Description.**—Small equivalved steinkerns, suboval or subcircular in outline to slightly extended caudally, range from 0.8–1.5 mm in length, 0.4–1.1 mm in height. Umbo central to subcentral and prosogyral. Shells 0.8–1.5 mm in length, 0.4–1.1 mm in height. One to two cardinal teeth on straight dorsal hinge but sometimes not preserved. Small, projecting auricle present on posterior part of the hinge. Ventral margin slightly convex, transition to anterior and posterior margins variable from distinct bend to gentle curve. Ligament or muscle scars not preserved. Prismatic imprints present on the internal mold, covering the majority of the steinkern, becoming smaller but clearer at the ventral margin.

**Materials.**—Thirty-six steinkerns from localities HRSR 65, 68, HRSK 66, and HRA 2, 4, and 6 (Fig. 2)

**Remarks.**—Antarctic specimens are exclusively steinkerns, which hinders comparison to specimens preserved as external molds that are used to diagnose the species (e.g., Jell, 1980; Runnegar and Bentley, 1983; Runnegar in Bengtson et al., 1990; Skovsted, 2004; Elicki and Gürsu, 2009). The specimens fit within the known size and morphological range for *P. runnegari* (see Runnegar in Bengtson et al., 1990, figs. 165, 166; Parkhaev in Gravestock et al., 2001, p. 201–203, pl. 49, figs. 1–13, pl. 50, figs. 1–9; Elicki and Gürsu, 2009) and have a similar distribution of foliated aragonite imprints on the steinkern surface (Fig. 3.3, 3.5; cf. Runnegar and Bentley, 1983, fig. 6A, B, E, I; Bengtson et al., 1990, fig. 165E–G; Vendrasco et al., 2011, pl. 3, 4). Compared to measured specimens, height-to-length ratios and overall size of the Antarctic specimens cover the range of values for *Pojetaia*



and *Fordilla* (Parkhaev in Gravestock et al., 2001, p. 202; Elicki and Gürsu, 2009, p. 275), although measurements given are few. The specimens are assigned to *P. runnegari* due to lack of visible muscle scars, typical for *P. runnegari* (Runnegar and Bentley, 1983) and shorter caudal extension than in *Fordilla*, a taxon not reported from East Gondwana.

Antarctic specimens are typically missing the anterior auricle, which appears to be broken off, although the posterior auricle is occasionally present (Fig. 3.7). Judging by the variation in caudal extension, the Antarctic specimens appear to conform to Jell's (1980) observation that the size of the posterior auricle is variable.

'Class Helcionelloida' Peel, 1991a  
Order Helcionellida Geyer, 1994  
Family Helcionellidae Wenz, 1938  
Genus *Davidonia* Parkhaev, 2017b

*Type species.*—*Davidonia davidi* (Runnegar in Bengtson et al., 1990), by original designation (= *Mellopegma rostratum* Zhou and Xiao, 1984) from the lower Cambrian Parara Limestone, Stansbury Basin, South Australia, *Dailyatia odyseii* Zone.

*Remarks.*—Steinkerns of *Davidonia* exhibit a range of characteristics (Parkhaev in Gravestock et al., 2001, p.175) such as bilateral symmetry and presence of rugae (Parkhaev in Gravestock et al., 2001, p. 175–176) but typically preserve microstructural polygonal imprints of tabular aragonite on their surface (Vendrasco and Checa, 2015). Cyrtconic *Davidonia rostrata* is typically more recurved than others (Fig. 4.6, 4.8, 4.6, 4.12; e.g., Parkhaev in Gravestock et al., 2001, pl. 40, figs. 1–3, 5, 8, pl. 41, figs. 1, 2, 7, 8, 9). At the other end of the spectrum lies the erect, almost orthoconic *Davidonia taconica* (e.g., Landing and Bartowski, 1996, fig. 5.5, 5.7–5.9; Skovsted, 2004, fig. 3I, L). *Davidonia taconica* was originally included in the genus *Stenotheca* (Landing and Bartowski, 1996) but later removed and placed in a new genus '*Aequiconus*' (Parkhaev in Gravestock et al., 2001). Skovsted (2004) later placed the species in *Davidonia* due to the prominent lateral rugae with polygonal aragonite imprints. This reassignment leaves *M. taconica* and another species, *M. puppis* Høyberget et al., 2015, from the Cambrian Stage 4 Evjevik Member of the Ringstrand Formation Norway (Høyberget et al., 2015), as outliers within the genus, as they lack a parietal train.

*Davidonia rostrata* (Zhou and Xiao, 1984)  
Figure 4.6–4.14

1984 *Mellopegma rostratum* n. sp. Zhou and Xiao, p. 132, pl. 3, figs. 7–10.

?1984 *Bemella anhuiensis* n. sp. Zhou and Xiao, p. 129, pl. 1, figs. 8, 9.  
?1984 *Bemella costa* n. sp. Zhou and Xiao, p. 128, pl. 1, fig. 10.  
1990 *Mackinnonia davidi* n. sp. Runnegar in Bengtson et al., p. 234, figs. 159, 160 J.  
1994 *Mellopegma rostratum*; Feng et al., p. 7, pl. 2, figs. 5–9.  
1996 *Mackinnonia obliqua* n. sp. Landing and Bartowski, p. 754, figs. 5.10–5.16.  
2001 *Mackinnonia rostrata*; Parkhaev in Gravestock et al., p. 176, pl. 40, 41.  
?2002 *Mackinnonia obliqua*; Landing et al., p. 296, fig. 8.3.  
2004 *Mackinnonia rostrata*; Skovsted, p. 16, fig. 3A–H.  
?2006 *Mackinnonia* cf. *M. rostrata*; Wotte, p. 151, fig. 5 g–k.  
2014 *Mackinnonia rostrata*; Parkhaev, p. 374, pl. 3, figs. 2, 3.  
2016 *Mackinnonia* sp.; Jacquet and Brock, p. 340, fig. 5 H, J.  
2016a *Mackinnonia rostrata*; Betts et al., p. 196, fig. 18N–U.

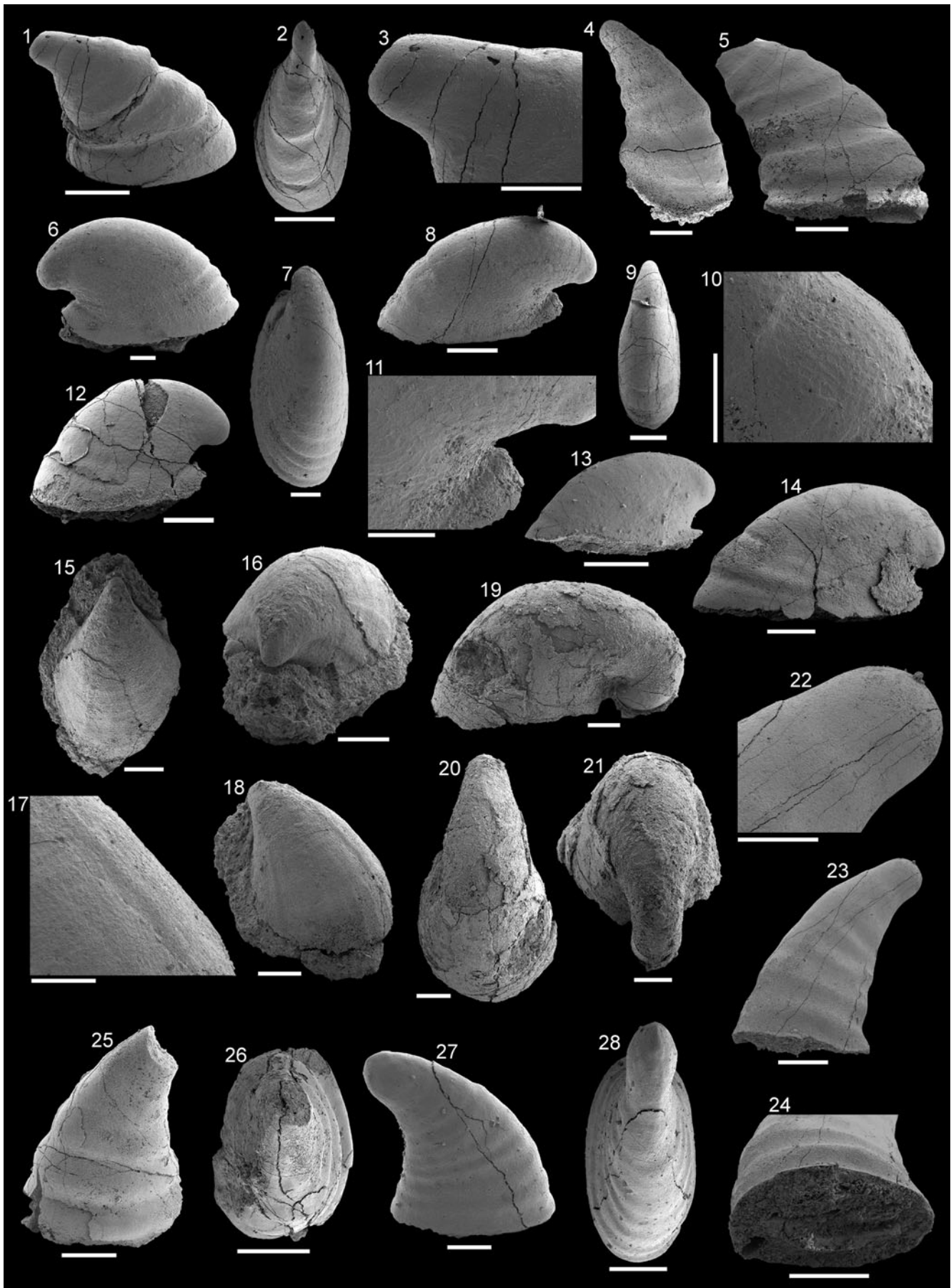
*Holotype.*—No. 800059, Geological Institute, Anhui Province, People's Republic of China. Internal mold from the Xinji (=Yutaishan) Formation of the lower Cambrian of Anhui Province, China.

*Occurrence.*—Cambrian, Stage 2 and Series 2, Stages 3–4 *Dailyatia odyseii* Zone of South Australia, Cambrian Series 2 Stages 3–4 of North China, Northeast Greenland, Taconic Allochthon of New York, USA, Quebec, Canada, and East Antarctica. Potentially Cambrian Stage 5 of northwestern Spain.

*Description.*—Moderately high, cyrtconic steinkerns, coiled through one-third of a whorl and moderately laterally compressed. Range 0.5–1.3 mm in length, 0.2–0.8 mm in height (see Table 1), and approximately 1.5 times longer than high. Protoconch reclined, rounded, rapidly expanding, and distinct from the teleoconch by change in microstructural imprints from smooth to polygonal. Strongly hooked apex directly above the parietal train or displaced up to one-quarter the length of the steinkern beyond the parietal train. Supra-apical field evenly convex, subapical field short and concave; moderate rate of expansion. Apertural outline elongated elliptical, sometimes with short rounded parietal train separated by a distinct indent from the subapical field. Rounded parietal train tilts upward at an angle. In lateral view the aperture exhibits a convex profile. Transverse rugae subdued, not present on all Antarctic material but terminate before subapical field when present. Some small juvenile specimens lack rugae. Polygonal microstructural imprints (9–12 µm wide) are exhibited on the surface of the co-marginal rugae, with

**Figure 4.** Helcionellids from the Shackleton Limestone. (1–5) *Davidonia* cf. *D. corrugata* Runnegar in Bengtson et al., 1990. (1–3) Specimen SMNH Mo185044 in (1) oblique lateral view, (2) apical view, (3) magnification of apical region in lateral view, showing protoconch and transition to teleoconch; (4) specimen SMNH Mo185045, oblique view of supra-apical field; (5) specimen SMNH Mo185046 lateral view. (6–14) *Davidonia rostrata* (Zhou and Xiao, 1984), (6, 7) specimen SMNH Mo185047, (6) lateral view, (7) dorsal view of supra-apical field; (8–11) specimen SMNH Mo185048, (8) magnification of lateral view of parietal train, showing polygonal crystalline imprints on the side surface, (9) dorsal view of supra-apical field, (10) lateral view, (11) magnification of oblique lateral view of supra-apical field, showing polygonal crystalline imprints; (12) specimen SMNH Mo182501 in lateral view; (13) specimen SMNH Mo182502 in lateral view; (14) specimen SMNH Mo182503 in lateral view. (15–18) *Xianfengella* cf. *X. yatesi* Parkhaev in Gravestock et al., 2001, specimen SMNH Mo185049, (15) dorsal view, (16) oblique apical view, (17) magnified view of supra-apical field showing crystalline imprints, (18) oblique lateral view. (19–21) *Protowenella*? sp. Runnegar and Jell, 1976 specimen SMNH Mo185050, (19) lateral view, (20) dorsal view, (21) apical view. (22–28) *Anuliconus* sp. Parkhaev in Gravestock et al. (2001), (22–24) specimen SMNH Mo185051, (23) lateral view, (22) magnification of apex in lateral view, (24) apertural view; (25, 26) specimen SMNH Mo185052, (25) lateral view, (26) apical view; (27, 28) specimen SMNH Mo185053, (27) lateral view, (28) apical view. (3, 10, 11, 17, 22, 24) Scale bars = 100 µm; all others, scale bars = 200 µm.





**Table 1.** Height and length measurements of selected specimens of *Davidonia rostrata* (Zhou and Xiao, 1984).

Specimen ref.	Length (μm)	Height (μm)	L/H ratio
HRA2-POSt01-Sa02	745	428	1.740654
HRA2-POSt01-Sa05	1,053	596	1.766779
HRA2-POSt01-Sa06	658	381	1.727034
HRA4-POSt01-Sa03	1,083	869	1.24626
HRA4-POSt01-Sa04	576	359	1.604457
HRA6-POSt01-Sa02	827	488	1.694672
HRA6-POSt01-Sa04	788	497	1.585513
HRA6-POSt01-Sa08	748	472	1.584746
HRA6-POSt01-Sa14	581	367	1.583106
HRA6-POSt01-Sa15	699	494	1.41498
HRA6-POSt01-Sa17	513	245	2.093878
HRA6-POSt02-Sa02	650	338	1.923077
HRA6-POSt02-Sa05	623	349	1.7851
HRA6-POSt02-Sa07	928	586	1.583618
HRA6-POSt02-Sa08	703	515	1.365049
HRA6-POSt02-Sa09	582	382	1.52356
HRA6-POSt02-Sa12	963	558	1.725806
HRA6-POSt02-Sa13	726	419	1.732697
HRA6-POSt02-Sa15	777	515	1.508738
HRA6-POSt02-Sa18	550	320	1.71875
HRA6-POSt02-Sa19	1,328	843	1.575326

smooth furrows. The parietal train has pitted depressions on the steinkern surface (3–5 μm wide), and the protoconchs are smooth.

**Materials.**—ca. 100 steinkerns of varying size and quality of preservation from HRA 2, 4–6.

**Remarks.**—Specimens identified as *Davidonia rostrata* from the Shackleton Limestone range in size and shape (see Table 1), lending support to the concept that this is a morphologically variable species (Parkhaev in Gravestock et al., 2001). This morphological variation is interpreted to reflect ontogenetic, taphonomic, and potential intraspecific variation in this taxon group. Significant variation in the shape of the protoconch between biogeographically distinct assemblages of this species indicate they were morphologically distinct from an early ontogenetic stage, although qualitatively identical at later stages (Jackson and Claybourn, 2018). Smaller specimens (e.g., Fig. 4.13: ~0.6 mm in length, 0.3 mm in height) resemble a similarly recurved helcionellid, *Figurina nana* (Zhou and Xiao, 1984), which can otherwise be readily distinguished from *D. rostrata* by the lack of distinct rugae, a transverse depression above the aperture, and circular protoconch. Some of the specimens (e.g., Fig. 4.13) from the Shackleton Limestone where the rugae are absent are considered juveniles of *D. rostrata* due to their smaller size compared to figured specimens of *F. nana* (Zhou and Xiao, 1984, pl. 3, fig. 11a; Parkhaev in Gravestock et al., 2001, pl. 35, figs. 4–8) and shared microstructure with other *D. rostrata* specimens from the Shackleton Limestone (Fig. 4.10, 4.11). A similar pattern was recognized among Australian specimens by Parkhaev in Gravestock et al. (2001, pl. 41, fig. 11).

Figured specimens of *Davidonia rostrata* from the Xinji Formation of the North China platform (Zhou and Xiao, 1984, pl. 1, figs. 8–10, pl. 2, figs. 1–10; Feng et al., 1994 pl. 2, figs. 5–8) are typically tall, strongly recurved examples of *Davidonia rostrata* with prominent rugae and with weakly developed parietal trains. Exceptions are two specimens figured by Zhou and Xiao (1984, pl. 1, figs. 8, 9), which are longer than high,

are more recurved, and lack parietal trains. The loss of the train is probably due to an incomplete formation of the steinkern, as the rugae are truncated at the base. This morphological variability in height is also reflected in Antarctic specimens, with moderate (Fig. 4.6, 4.12) and low specimens (Fig. 4.8, 4.14) occurring together, but with identical rugae, microstructural imprints, and parietal train.

A wide range of morphologies is figured in Gravestock et al. (2001, pl. 40, 41) from the Parara Limestone (Stansbury Basin, Cambrian Series 2, Stages 3–4), Sellick Hill Formation (Stansbury Basin, Terreneuvian, Stage 2), and the Mernmerna Formation (Arrowie Basin, Cambrian Series 2, Stages 3–4), South Australia. Larger specimens have more prominent rugae than those from the Shackleton Limestone (Gravestock et al., 2001, pl. 40, figs. 1–3, 5a, 8, pl. 40, figs. 1–7, 9), and smaller specimens tend to lack (Gravestock et al., 2001, pl. 41, fig. 11) or have subdued rugae (Gravestock et al., 2001, pl. 41, figs. 6, 10). This probably reflects the ontogeny of *Davidonia rostrata*, with shell thickenings (preserved as rugae observed on steinkerns) only developing later in their ontogeny. This distribution is comparable to some smaller *D. rostrata* specimens (Fig. 4.13). Another feature that only appears to occur on larger specimens is the development of a sinus on the parietal train (Gravestock et al., 2001, pl. 40, figs. 4, 6). Compared to specimens from the Shackleton Limestone, Australian specimens generally have a larger maximum size, with more prominent rugae, but share the same strong recurvature and microstructure. Runnegar in Bengtson et al. (1990) figured specimens (fig. 159 A–H) from the Parara Limestone and the upper part of the Ajax Limestone (Cambrian Series 2, Stages 3–4), also in South Australia. These share a common morphology with other specimens figured in Gravestock et al. (2001), as well as having a transverse thickening on the subapical field (Runnegar in Bengtson et al., 1990, fig. 159A, B), a feature that is lacking in Antarctic specimens.

Skovsted (2004, fig. 3A, B, F) described *Davidonia rostrata* from the Bastion Formation (unnamed Cambrian Series 2, Stages 3–4) of northeast Greenland, which consists of specimens with lower profiles, more subdued rugae, and parietal trains that lack sinuses (Skovsted, 2004, fig. 3G, C). Both characteristics are more similar to specimens from the Shackleton limestone (e.g., Fig. 4.6, 4.8, 4.14). Included in Skovsted's (2004) synonymy of *Davidonia rostrata* was '*Mackinnonia* sp.' (Kouchinsky, 2000, fig. 10) from Siberia, which was reassigned to *Davidonia anabarica* Parkhaev, 2005. Although similar to *D. rostrata* in its overall morphology, the steinkerns of *D. anabarica* show prominent transverse tubercles, clearly distinguishing it from *D. rostrata* (Kouchinsky, 2000, fig. 10 E; Parkhaev, 2005, pl. 2, fig. 2E).

'*Mackinnonia* cf. *M. rostrata*' from the Leonian (Cambrian Stage 5) Láncara Formation of northern Spain (Wotte, 2006) is only tentatively included in the synonymy list, due to the poor preservation and younger stratigraphic age compared to *D. rostrata* sensu stricto. The synonymization by Parkhaev (in Gravestock et al., 2001) of *Bemella anhuiensis* Zhou and Xiao 1984 and *B. costa* with *Davidonia rostrata* have been followed here, but with some uncertainty due to the low clarity of the images available from the original descriptions by Zhou and Xiao (1984). Kouchinsky et al. (2015, p. 430) expressed

doubt in the synonymy of *Davidonia davidi* with *D. rostrata* due to *D. davidi* having a higher profile, greater degree of coiling, and more prominent rugae on the steinkerns. Material from the Shackleton Limestone have examples that have both moderate profiles and subdued rugae (Fig. 4.6, 4.12), indicating these characteristics alone are not sufficient to distinguish the two species. This leaves the prominence of rugae alone to distinguish the two, which might be ontogenetic, ecophenotypic, or influenced by taphonomic processes of replication of the shell and shell interior of micromollusks by calcium phosphate (Creveling et al., 2014).

*Davidonia* cf. *D. corrugata* (Runnegar in Bengtson et al., 1990)  
Figure 4.1–4.5

See Supplementary file 1 for taxa assigned to *Davidonia corrugata*

**Holotype.**—‘*Lepostega? corrugata*’ Runnegar in Bengtson et al., 1990, SAMP29006, Cambrian Stage 3 Parara Limestone, Carramulka, South Australia.

**Occurrences.**—*Davidonia corrugata* occurs in the Cambrian Stages 3–4 *Dailyatia odysssei* Zone in South Australia.

**Description.**—High cyrtconic, erect steinkerns with hooked apex, moderately laterally compressed, apex displaced beyond subapical margin. Steinkerns 0.5–0.6 mm in length and 0.5–0.6 mm in height. Protoconch smooth, small, and pinched, distinct from teleoconch, which expands more rapidly. Supra-apical field convex, subapical field gently concave, moderate rate of expansion. Aperture elliptical to subquadrate. Transverse rugae broad, flat, and subrectangular in profile with reduced width of furrows. Rugae encircle the teleoconch and preserve surficial polygonal imprints, which extend to the uppermost parts of the furrows. Lower parts of the furrows and protoconch are smooth. Parietal train not present in any recovered specimens.

**Materials.**—Five steinkerns from locality HRA6.

**Remarks.**—*Davidonia corrugata* was synonymized with *Davidonia plicata* (= *Isitella plicata* Missarzhevsky, 1989) without detailed explanation (Parkhaev in Gravestock et al., 2001, p. 178) and only a brief discussion in a later publication (Parkhaev 2005, p. 618). We follow Skovsted (2004, p. 15) and refer the specimens to *Davidonia* cf. *D. corrugata* (Runnegar in Bengtson et al., 1990).

Compared to specimens of *Davidonia rostrata* from the Shackleton Limestone, these specimens are far less recurved and have more prominent rugae. The lack of a parietal train and less recurved form are similar to *D. taconica* from Northeast Greenland (Skovsted, 2004, p. 17–18, figs. 3I–R, 4), but the greater recurvature and more prominent rugae are sufficient to distinguish the two. *Davidonia puppis* Høyberget et al., 2015 is similar to *Davidonia* cf. *D. corrugata* but is much larger in size, up to 6.5 mm in length (Høyberget et al., 2015, p. 49), and has a less recurved apex (Høyberget et al., 2015, fig. 16, A–J).

Specimens from South Australia show different rates of expansion from the apex: from rapidly expanding with a short protoconch (Runnegar in Bengtson, 1990, p. 237, fig. 160A–G; Parkhaev in Gravestock et al., 2001, p. 296, pl. 39, figs. 6–12) to morphologies with a narrow, elongate protoconch (Topper et al., 2009, p. 226, fig. 9A–H). The specimens are referred to *Davidonia* cf. *D. corrugata* due to their broad, prominent rugae (Fig. 4.5) and upright suborthoconic profile (Fig. 4.1, 4.4, 4.5), which are most similar to those figured by Topper et al. (2009, fig. 9A–H). A more certain assignment to a species is precluded by lack of information on the aperture and low number of specimens. The broad rugae, narrow furrows, and high profile also differentiate the specimens from *Davidonia rostrata*, which is characterized by narrower and less prominent rugae and a protoconch that is broader and more rounded. *Davidonia taconica* can also be readily distinguished from *D.* cf. *D. corrugata* by having a more upright form, broader protoconch, and reduced bilateral compression (cf. Skovsted, 2004, fig. 3I–R). The specimens of *D. corrugata* from the Mermerna Formation, South Australia, have the same pinched protoconch as the Shackleton Limestone specimens (cf. Fig. 4.1–4.3 with Topper et al., 2009, pl. 9, fig. H), while specimens from the Parara Limestone (Stansbury Basin) and Orparinna Shale (Arrowie Basin) have broad, more spoon-shaped protoconchs in outline, leading to a more regular rate of whorl expansion (Runnegar in Bengtson et al., 1990, fig. 160A–F; Gravestock et al., 2001, pl. 39, figs. 4, 6b). The Shackleton Limestone specimens also lack a parietal train, unlike specimens from South Australia (Gravestock et al., 2001, pl. 38, fig. 7, pl. 39, figs. 2, 3, 7), although this is likely taphonomic due to incomplete steinkern formation.

Genus *Xianfengella* He and Yang, 1982

**Type species.**—*Xianfengella prima* He and Yang, 1982 by original designation, from the lower Cambrian Zhongyicun Member of the Meishucun Formation, Yunnan Province, China.

*Xianfengella* cf. *X. yatesi* Parkhaev in Gravestock et al., 2001  
Figure 4.15–4.18

See Supplementary file 1 for taxa assigned to *Xianfengella yatesi*.

**Holotype.**—PIN 4664/1506, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia. Steinkern from the Parara Limestone, Horse Gully, Yorke Peninsula, South Australia, *Dailyatia odysssei* Zone.

**Occurrence.**—*Xianfengella yatesi* is known from Cambrian Stages 3–4 *Dailyatia odysssei* Zone of South Australia. Possibly known from Northeast Greenland and East Antarctica.

**Description.**—Low, cap-shaped steinkern, recurved to approximately one-third of a whorl, apex recurved, displaced beyond the aperture. Single specimen approximately 0.6 mm wide, 0.6 mm high, and 0.9 mm long: two-thirds as wide as it is long. Apex narrow, expands rapidly after first 200 µm, with no distinction between protoconch and teleoconch. Lateral fields and supra-apical field strongly convex. Subapical field



short and concave with pegma-like brim at base. Ovoid apertural outline, tapered to the apex, rounded to the base of the supra-apical field. Radial rugae extend from near the apex to the aperture. Polygonal imprints present on entire steinkern surface 13–18  $\mu\text{m}$  wide.

**Materials.**—Single well-preserved steinkern from HRA 4.

**Remarks.**—*Xianfengella* has been included within the helcionelloids despite previous comparisons to the cap-like terminations in halkieriids as well as *Ocruranus*-like fossils (Peel and Skovsted, 2005). The polygonal imprints on the steinkern of this specimen (Fig. 4.17) resemble the polygonal aragonite imprints found on other helcionelloids (e.g., Vendrasco et al., 2010, p. 1, figs. 4, 5; Vendrasco and Checa, 2015, figs. 2A–D) rather than the layered fibrous bundles that characterize *Ocruranus* (Vendrasco et al., 2009, pl. 1). The Antarctic specimens differ from those figured from South Australia (Gravestock et al., 2001, pl. 34). Diamond-shaped depressions and smooth ridges were reported, but not clearly figured, on the surfaces of the South Australian steinkerns (Parkhaev in Gravestock et al., 2001), which may correspond to the polygonal imprints and longitudinal ridges on the Antarctic specimen. Other features are more easily compared, such as a notch at the subapical margin of the aperture (compare Fig. 4.16 with Gravestock et al., 2001, pl. 34, figs. 6b, 8a, 8b; Topper et al., 2009, fig. 10J) and strongly recurved and posteriorly displaced apex (Fig. 4.16, 4.18; Gravestock et al., 2001, pl. 34, figs. 1, 6a, 8b; Topper et al., 2009, fig. 10J). Unfortunately, the aperture and some of the subapical field are both obscured by clastic material in this specimen, making this feature difficult to decipher for closer comparison to *X. yatesi* from South Australia.

The specimen appears most similar to *Xianfengella*? cf. *X. yatesi* from the Bastion Formation, Northeast Greenland (Peel and Skovsted, 2005) in terms of the polygonal microstructure on the steinkern exterior (Peel and Skovsted, 2005, fig. 5P) and radial ridges (fig. 5F). Both the Antarctic and Northeast Greenland specimens preserve a brim at the subapical part of the aperture (Fig. 4.16; Peel and Skovsted, 2005, fig. 5A–G, J), which is not present on South Australian specimens (cf. short parietal train of Parkhaev in Gravestock et al., 2001, pl. 34, figs. 1, 2, 8a). For this reason and the fact that only a single specimen has been recovered from the Shackleton Limestone, a cautious taxonomic approach is taken, and we refer this specimen to *Xianfengella* cf. *X. yatesi*.

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

**Type species.**—*Anuliconus magnificus*, Parkhaev in Gravestock et al., 2001 by original designation from Kulpura Formation (Cambrian Stages 2–3) and Parara Limestone (Cambrian Stages 3–4) in the Stansbury Basin and Mernmerna Formation (Cambrian Stages 3–4) in the Arrowie Basin, South Australia.

*Anuliconus* sp.  
Figure 4.22–4.28

**Description.**—High cyrtconic and moderately bilaterally compressed steinkerns with lateral fields concave at the apex

transitioning to flat on the teleoconch. Apex gently recurved over subapical field. Specimens approximately 0.4–0.5 mm wide, 0.5–0.7 mm long, and 0.7–0.9 mm high. Protoconch elongated to knob-like, separated from the teleoconch by a distinct pinching. Supra-apical surface gently convex, subapical surface moderately concave, low to moderate rate of expansion. Apertural outline varies from elliptical to subcircular. Regular, rounded, concentric rugae encircle teleoconch.

**Materials.**—Thirty-three steinkerns from HRSK 66, HRA 2, 6.

**Remarks.**—The Antarctic specimens generally fall within the documented intraspecific variation of the genus based on the original description of *Anuliconus* (Parkhaev in Gravestock et al., 2001, p. 142, pl. 25, figs. 8–17). The steinkerns are moderately bilaterally compressed, gently recurved with a concave subapical field and a convex supra-apical field, with a displacement of the apex over the subapical field and concentric rugae. It is possible the specimens from the Shackleton Limestone represent more than one species due to variations in these features, such as having more subdued (Fig. 4.27) to more prominent (Fig. 4.23, 4.24) rugae and a more (Fig. 4.27) or less (Fig. 4.23) concave subapical field, but these differences alone are insufficient for species distinction. Most of the collection have irregular apertural outlines (Fig. 4.26) or rugae truncated at the aperture (Fig. 4.23, 4.24, 4.25), indicating incomplete steinkerns ('teilsteinkerns' sensu Dattilo et al., 2016). *Anuliconus* sp. are easily distinguished from the similarly shaped *Obtusoconus* Yu, 1979 by having a protoconch overcurving over the subapical field.

Parkhaev in Gravestock et al., (2001) named three new species from Cambrian Series 2 sediments of South Australia, of which *Anuliconus magnificus* Parkhaev in Gravestock et al., (2001, p. 141) and *Anuliconus truncatus* Parkhaev in Gravestock et al. (2001, p. 144) bear some similarities to specimens from the Shackleton Limestone. *Anuliconus magnificus* shares a similar profile to taller Antarctic specimens (compare Fig. 4.23 with Gravestock et al., 2001, pl. 24, figs. 8–17) and rounded triangular ribs (Fig. 4.25), and the more irregular, subdued ribs on some specimens (Fig. 4.27, Gravestock et al., 2001, pl. 25, figs. 8–15) are similar to *A. truncatus* (Gravestock et al., 2001, pl. 26, fig. 1–4).

Genus *Protowenella* Runnegar and Jell, 1976

**Type species.**—*Protowenella flemingi* Runnegar and Jell, 1976 by original designation from the Cambrian Series 5 Currant Bush Limestone, Locality L128, Queensland, Australia.

*Protowenella*? sp.  
Figure 4.19–4.21

**Description.**—Planispiral, open-coiled steinkern coiling through three-quarters of a whorl, apex displaced beyond subcircular apertural margin. Height ~0.9 mm and total length ~1.5 mm. Protoconch slender and elongate with no clear distinction from the teleoconch. Supra-apical field strongly convex; shell exhibits gradual expansion to half a whorl, followed by more rapid expansion of the rest of the

teleoconch. Aperture outline subcircular to ovoid, tapering toward apex. Sinus or umbilicus absent.

*Materials*.—Four poorly preserved steinkerns from HRA 2, 5, 6.

*Remarks*.—These globose planispiral steinkerns recovered from the Shackleton Limestone are included in the genus *Protowenella*, but only tentatively due to their poor preservation and low number. The specimens from the Shackleton Limestone have the general morphological features of the genus, such as planispiral, involute profile (Fig. 4.19–4.21), overall globose appearance, and they lack an apertural sinus (Runnegar and Jell, 1976, p. 133). The specimens do not have the important circumbilical channels figured but not included in the original diagnosis (Runnegar and Jell, 1976, fig. 6E; see also Brock, 1998) and described in the revised diagnosis (Berg-Madsen and Peel, 1978, p. 118). The Antarctic specimens are more tightly coiled (Fig. 4.19) than *Protowenella cobbensis* Mackinnon, 1985 (fig. 9G), so they can be more closely compared to the more openly coiled type species *Protowenella flemingi* Runnegar and Jell, 1976 (fig. 6). The only other Cambrian Series 2 species that have been described are from the Xinji Formation of South China: *Protowenella primaria* Zhou and Xiao, 1984 and *Protowenella huainanensis* Zhou and Xiao, 1984. *P. primaria* figured from the Xinji Formation is typically planispiral, but some specimens might demonstrate slight asymmetry (e.g., Zhou and Xiao, 1984, pl. 3, fig. 19a, b, pl. 4, figs. 4b, 5b). They also do not coil as tightly as the Shackleton Limestone specimens, and they have a broad umbilicus. This asymmetry seems to be more pronounced in *P. huainanensis* (Zhou and Xiao, 1984, pl. 3, figs. 18b, 19b). These specimens also appear to lack circumbilical channels (Zhou and Xiao, pl. 3, figs. 18–20, pl. 4, figs. 1–5). The lack of circumbilical channels in specimens described as *Protowenella* indicate they may not have the necessary features to be included in the genus (Berg-Madsen and Peel, 1978), an issue discussed by Brock (1998), who pointed out another species, *P. plena* Missarzhevsky and Mambetov, 1981, may also be excluded on the same basis. The only specimen of *Protowenella* that can be confidently assigned to the genus from Cambrian Series 2 rocks is *Protowenella* sp. from the Cambrian Series 2, Stage 4, Tempe Formation from the Northern Territory, Australia, on the basis of well-preserved muscle scars (Smith et al., 2015, fig. 6H).

With these factors in mind, the specimens from the Shackleton Limestone have only been tentatively included in *Protowenella*, with the caveat that if better-preserved specimens are discovered that entirely lack circumbilical channels, they should be removed from the genus (Brock, 1998). A full re-description of all *Protowenella* specimens is necessary to resolve these problems. The degree of expansion and elongation of the apex is similar to figured specimens of *Protowenella* sp. from the middle Cambrian of Siberia (Gubanov et al., 2004, fig. 10). Another planispiral, *Protowenella*-like univalved mollusk from Shackleton Limestone has been figured but not described (Rowell et al., 1988b, pl. 1, figs. O, P) and is referred to only as a ‘euomphalid mollusk.’

Family Yochelcionellidae Runnegar and Jell, 1976  
Genus *Yochelcionella* Runnegar and Pojeta, 1974

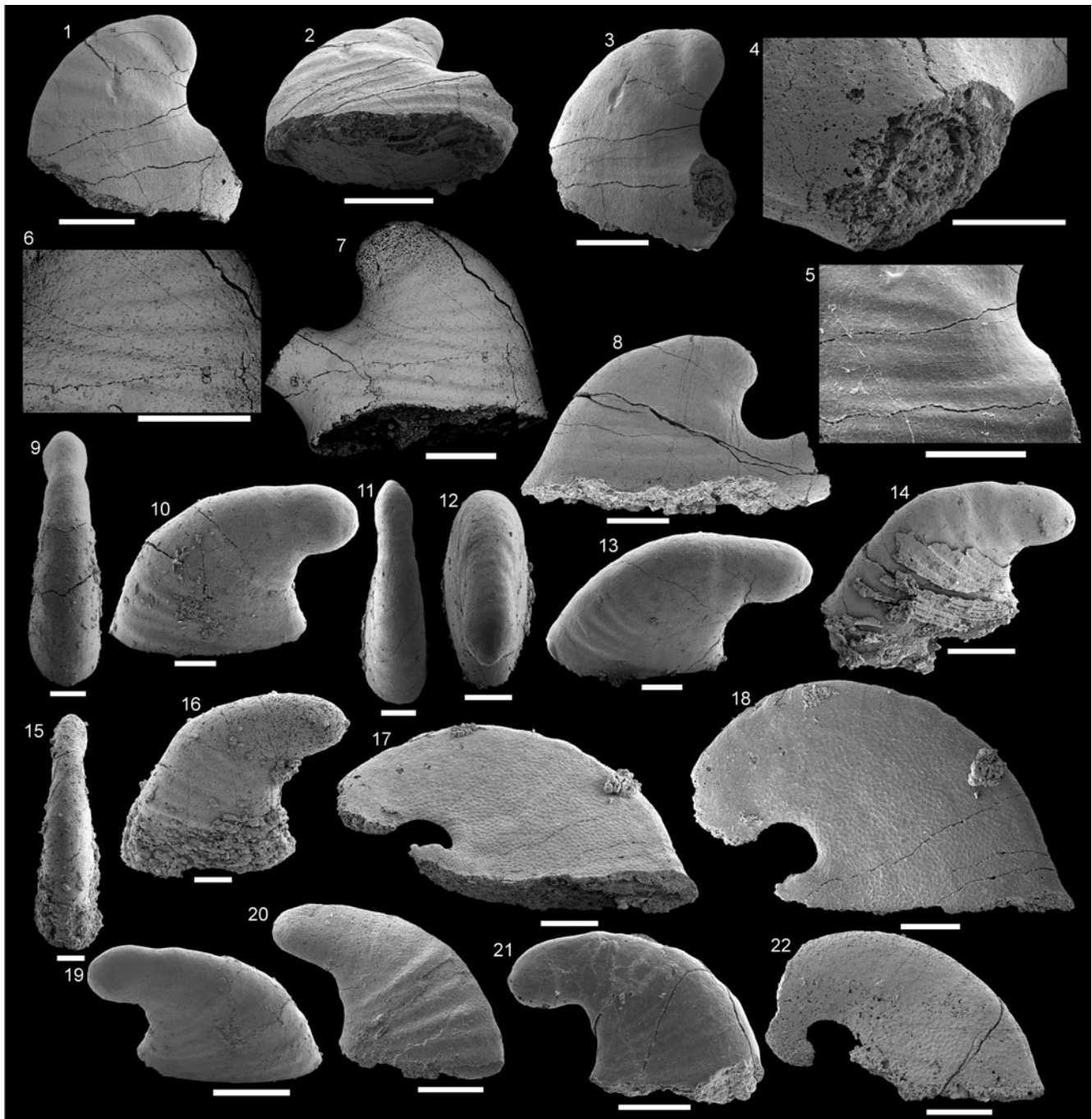
*Type species*.—*Yochelcionella cyrano* Runnegar and Pojeta, 1974 by original designation, Cambrian Series 3, ‘first discovery limestone’ Member of the Coonigan Formation, New South Wales, Australia.

*Yochelcionella* sp.  
Figure 6.1–6.8

*Description*.—Cyrtconic, moderately bilaterally compressed steinkerns with cylindrical subapical extension or cross section of shell forming a snorkel. Apex positioned above commencement of snorkel in lateral view. Protoconch rounded with distinctive pinching marking transition between protoconch and teleoconch; one specimen with faint polygonal imprints (Fig. 2). Subapical field short and concave, supra-apical field evenly convex. Elongate oval aperture broken in both specimens. Faint transverse rugae present between protoconch and snorkel. Irregular pitted microstructural imprints in surface of the teleoconch steinkern, 2–5 µm wide.

*Materials*.—Five steinkerns from HRSK 66, HRSR 68, and HRA 2.

*Remarks*.—Although the specimens are damaged, they appear most similar to *Yochelcionella chinensis* Pei, 1985 as both specimens show displacement of the apical part of the shell above the snorkel away from the subapical field (Pei, 1985, fig. 1a). Specimens from the Shackleton Limestone have rounded, rapidly expanding protoconchs with a distinctive pinch at the transition to the teleoconch (Fig. 6.1, 6.2). The specimens can be distinguished from *Y. gracilis* Atkins and Peel, 2004 from the Henson Gletscher Formation (Cambrian Stages 2–3) of North Greenland by their convex supra-apical field, where *Y. gracilis* has a concave supra-apical field (Atkins and Peel, 2004, fig. 3A, F). *Yochelcionella greenlandica* Atkins and Peel, 2004 from the Aftenstjernesø Formation (Cambrian Stage 2) of North Greenland has a similar displacement in the subapical field below the snorkel (Atkins and Peel, 2004, fig. 2B, D, L, N) but has well-developed rugae, which are fewer in number and much larger than *Yochelcionella* sp. from the Shackleton Limestone (Fig. 6.2, 6.5–6.8; see Atkins and Peel, 2004, fig. 2A, F, J). Specimens of *Y. crassa* Esakova and Zhegallo, 1996 from the Bystraya Formation (Siberian Botoman Stage), Eastern Transbaikalia, figured by Parkhaev (2014, pl. 1, figs. 15–18), show a similar strongly concave subapical field and highly reduced rugae, but the Shackleton Limestone specimens are not well preserved enough to draw closer comparisons. The rounded protoconch, pinching, fine rugae, and displacement are also present in *Yochelcionella* cf. *Y. chinensis* from the Forteau Formation (Cambrian Series 2, Stages 3–4), Newfoundland (Skovsted and Peel, 2007, fig. 4D). Specimens preserve a pitted microstructure on the steinkern exteriors of the teleoconchs (Fig. 6.5, 6.6). Microstructure preserved on



**Figure 5.** *Yochelcionella* sp., *Stenotheca* sp., and *Anabarella* cf. *A. australis* Runnegar in Bengtson et al., 1990 from the Shackleton Limestone. (1–8) *Yochelcionella* sp., (1–5) specimen SMNH Mo185063, (1) lateral view, (2) apertural view, (3) apical view of subapical field and broken snorkel, (4) magnified view of concentric structures within snorkel, (5) magnified view of pitted microstructure; (6, 7) specimen SMNH Mo185064, (6) magnification of lateral view, (7) lateral view; (8) specimen SMNH Mo185065, lateral view. (9–16, 19–21) *Stenotheca* sp. (9, 10) specimen SMNH Mo185066, (9) oblique lateral view, (10) dorsal view; (11–13) specimen SMNH Mo185067, (11) oblique lateral view, (12) dorsal view of subapical field, (13) apical view; (14) specimen SMNH Mo185068, lateral view; (15, 16) specimen SMNH Mo185069, (15) oblique lateral view, (16) dorsal view; (19) specimen SMNH Mo185071 in lateral view; (20) specimen SMNH Mo185072 lateral view; (21) specimen SMNH Mo185073 lateral view; (17, 18, 22) *Anabarella* cf. *A. australis* (17, 18) specimen SMNH Mo185070 in (18) lateral view, (17) apertural view (22) specimen SMNH Mo185074 in lateral view. Scale bars 100 µm (5, 6) all others 200 µm. All images taken using secondary electrons except (5) taken in low vacuum mode and (6, 7) taken using backscattered electrons.

steinkerns of *Yochelcionella* has been reported previously. Vendrasco et al. (2010) described laminar and polygonal microstructures (pl. 6) on *Y. saginata* Vendrasco et al., 2010 and *Y. snorkorum* Vendrasco et al., 2010, inverted relative to those seen on other micromollusks (i.e., the polygon is raised

and the walls between them are depressed) from the Drumian Gowers Formation from the Geogina Basin in Queensland, Australia. Kouchinsky (2000) described *Yochelcionella* sp. from the lower Cambrian of Siberia that preserved both polygons (with normal relief) and tubercles at the apex



(Kouchinsky, 2000, fig. 9). These five microstructural types, laminar, inverted polygons, normal polygons, tubercles, and now pits, on a single genus of helcionelloid represents a wide range of strategies for biomineralization.

Wrona (2003) reported a single specimen of *Yochelcionella?* sp. from glacial erratics of King George Island, West Antarctica. The specimen is poorly preserved, with no information on the teleoconch below the snorkel (Wrona, 2003, fig. 13A<sub>1</sub>). The apex has a similar rounded shape to the Shackleton Limestone specimens (Fig. 6.1, 6.7, 6.8; Wrona, 2003, fig. 13A<sub>1</sub>).

Family Stenothecidae Runnegar and Jell, 1980

Genus *Stenotheca* Hicks, 1872

*Type species.*—*Stenotheca cornucopia* Salter in Hicks, 1872 by original designation, lower Cambrian, Pembrokeshire, Wales. The type specimen was reported lost while on loan from the Sedgwick Museum, Cambridge (Runnegar in Bengtson et al., 1990).

*Stenotheca* sp.

Figure 6.9–6.16, 6.19–6.21

*Description.*—Bilaterally compressed steinkern, coiled to one-quarter of a whorl. Hooked apex, with entire protoconch displaced beyond subapical margin. Apertural length 0.3–0.5 mm, total height 0.35–0.55 mm. Distinct pinching at termination of protoconch, which is knob-like, elongated, and straight. Supra-apical field convex and almost flat from apex to mid-shell length. Subapical field short and concave. Lateral fields almost flat. Apertural outline elliptical in outline. Smooth regular transverse rugae present encircling teleoconch. Partial preservation of pseudomorphic phosphatic coating shows transverse ribs with more relief, closely packed nearer to the aperture (furrows 6–9 µm wide) and more widely spaced toward the apex (furrows 13–23 µm wide) (Fig. 6.14).

*Materials.*—Approximately 12 steinkerns from HRA 6.

*Remarks.*—These specimens are assigned to *Stenotheca* due to their strong bilateral compression and recurvature (Fig. 6.9–6.16, 6.19–6.21). Most specimens retain transverse rugae on the exterior of the steinkern teleoconch (Fig. 6.8, 6.9) and, in one specimen, part of the external mold with lirae (Fig. 6.14). These features are present on *Stenotheca* cf. *S. drepanoida* from the Parara and Ajax limestones from South Australia (Runnegar in Bengtson et al., 1990, fig. 163B–E). The recurved morphology and bilateral compression are similar to other figured specimens of *Stenotheca drepanoida* (He and Ting in He et al., 1984) from the Xinji Formation (He et al., 1984, pl. 2, figs. 1–5; Feng et al., 1994, pl. 3, figs. 3, 6) of North China. The morphology of *Stenotheca* sp. is similar to the apical parts of *S. drepanoida* in having strong bilateral symmetry and recurvature (Gravestock et al., 2001, pl. 43, figs. 1–6) and an egg-shaped protoconch, with a pinch at the transition to the teleoconch (Runnegar in Bengtson et al., 1990, fig. 163G; Gravestock et al., 2001, pl. 43, figs. 8, 9). This feature is not present on all specimens assigned to *S. drepanoida*; specimens from the Mernmerna Formation of

South Australia have a slender, slowly expanding apex without a clear transition to the teleoconch (Topper et al., 2009, fig. 10B–D). *Stenotheca transbaikalia* Parkhaev, 2004a also has a similar apical part of the shell, with a straightened, more elongate protoconch at an angle to the teleoconch on the subapical field (Parkhaev, 2004a, pl. 2, fig. 3).

Missing from the Shackleton Limestone specimens is information on the aperture. For this reason, *Stenotheca* sp. has been left in open nomenclature. This may be a taphonomic loss of information potentially due to steinkern-type preservation partially forming molds within quickly dissolving aragonitic shells (i.e., teilsteinkerns). Evidence for this can be seen in the truncation of the rugae at the apertural margin of the specimens (Fig. 6.10, 6.19–6.21) and the relatively small size when compared to specimens from other regions (cf. Parkhaev in Gravestock et al., 2001, p. 183).

Genus *Anabarella* Vostokova, 1962

*Type species.*—*Anabarella plana* Vostokova 1962 by original designation, Nemakit-Daldynian–Tommotian Stages, Siberia, Russia.

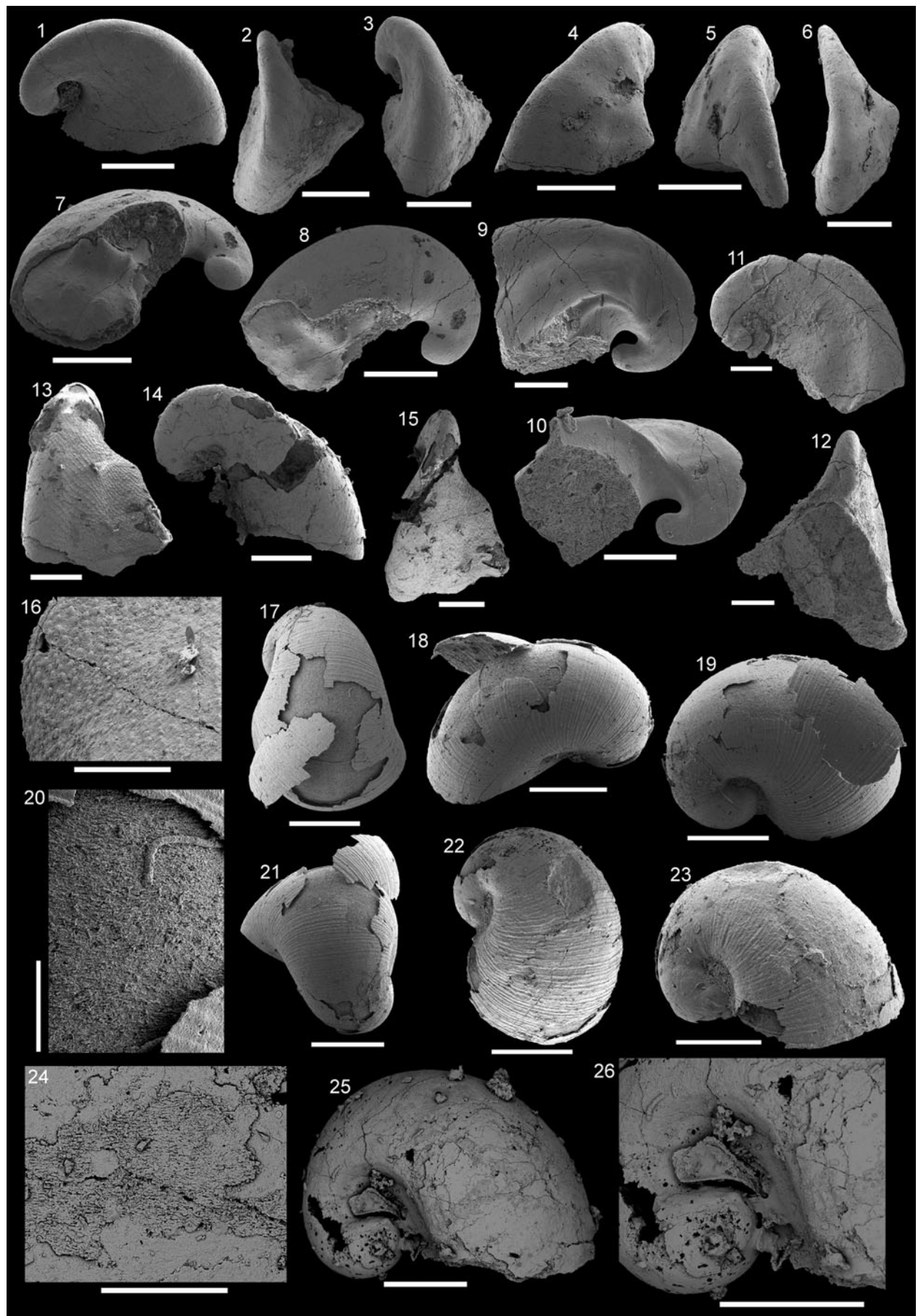
*Anabarella* cf. *A. australis* Runnegar in Bengtson et al., 1990  
Figure 6.17, 6.18, 6.22

See Supplementary file 1 for taxa assigned to *Anabarella australis*.

*Description.*—Strongly bilaterally compressed steinkerns, rapidly expanding and coiled to less than half a whorl. Apex strongly recurved, with subapical field almost circular in profile, subapical margin extended by short parietal train (Fig. 6.17, 6.18). Supra-apical field evenly convex; lateral fields flat. Aperture narrow ellipsis, slightly tapering toward subapical margin. External ornament evident by faint rugae. Extensive polygonal microstructures on younger parts of steinkern but smooth at apex.

*Materials.*—Three steinkerns from HRSR 66 and HRSK 68.

*Remarks.*—The specimens are assigned to *Anabarella* rather than another stenothecid genus due to the greater shell recurvature, subcircular subapical field, and coiling through more than half a whorl (Gubanov and Peel, 2003). In profile, these specimens are most comparable to *Anabarella australis*, with recurvature and a subapical field similar to *A. australis* (Runnegar in Bengtson et al., 1990). The polygonal imprints on the surface of the steinkern (Fig. 6.17, 6.18, 6.22) have been observed on the aperture below the apex on some specimens of *A. australis* (Runnegar in Bengtson et al., 1990, fig. 164N; Parkhaev 2004b, pl. 2, figs. 3, 4), but it lacks the prismatic and fibrous imprints also found on *Anabarella plana* Vostokova, 1962 (Kouchinsky, 1999). The profile of the specimens from the Shackleton Limestone are most similar to *A. australis*, but the low number of specimens and polygonal microstructure (typically not present on *A. australis*) covering the surface of the steinkern prohibit a definitive assignment.



Total group Gastropoda Cuvier, 1797  
 Order unknown  
 Family Pelagiellidae Knight, 1956

**Remarks.**—The asymmetrically coiled pelagiellids are one of the better candidates to be considered stem-group gastropods known from the lower Cambrian fossil record. As mentioned previously, authors have indicated an affinity for the gastropods (the Paragastropoda of Lindsey and Kier, 1984 included pelagiellids) or placement within a gastropod order (e.g., ‘Archaeogastropoda’ Thiele, 1925; see Landing et al., 2002; Parkhaev, 2017a). Their exact placement on the poorly understood stem of the gastropods remains contentious, however, and an ordinal designation to taxa in the gastropod crown-group will not be made here.

Genus *Pelagiella* Matthew, 1895

**Type species.**—*Cyrtolites atlantoides* Matthew, 1894 by original designation, from the Cambrian Series 2–3 Hanford Brook Formation, St. John Group of New Brunswick, Canada.

*Pelagiella* cf. *P. subangulata* (Tate, 1892)  
 Figure 5.1–5.16

See Supplementary file 1 for taxa assigned to *Pelagiella subangulata*.

**Lectotype.**—SAMP1234a, South Australian Museum, Palaeontological Collections, Adelaide, Australia, designated by Runnegar in Bengtson et al. (1990) from the Cambrian Stage 4 Parara Limestone, near Ardrossan, South Australia, *Dailyatia odyssei* Zone.

**Occurrence.**—*Pelagiella subangulata* is known from Cambrian Series 2, Stages 3–4 of South Australia, Laurentia, and South China. Possible specimens known from Cambrian Series 2, Stages 3–4 of East Antarctica, the Great Basins area of the United States, and the middle Cambrian of Germany.

**Description.**—Anisometrical, dextrally coiled shells with a little over three-quarters of a whorl. Shells rapidly expanding, with slender apex and no clear distinction between teleoconch and protoconch. Total length of steinkerns 0.58 mm–0.64 mm, height 0.38 mm–0.48 mm. In well-preserved specimens, aperture flares outward from lateral margin of umbilical side, forming subtriangular apertural outline, 0.4 mm long and 0.2–0.3 mm wide. Spiral side slightly concave; one specimen preserves distinct narrow ridge (~70 µm high) commencing

from near subapical surface and extending to aperture (Fig. 5.9, 5.10). One specimen preserves phosphatic (pseudomorphic) shell material with clear rows of pustulose ornament on the flank of the umbilical side (Fig. 5.13–5.16) converging along shell dorsum. Faint concentric growth lines visible on the concave spiral side of same specimen.

**Materials.**—Approximately 30 steinkerns, from HRSR 65, 68, HRSK 66, and HRA 2, 4–6, and 42.

**Remarks.**—Gradational forms between different species of *Pelagiella* have been identified by numerous authors. Runnegar in Bengtson et al. (1990, p. 253–254) recognized *Pelagiella subangulata* from South Australia to be variable in size and shape and grade into *Pelagiella adunca* (He and Pei in He et al., 1984). Parkhaev in Gravestock et al. (2001, p. 194) described a gradation in forms between *P. subangulata* and *Pelagiella madianensis* (Zhou and Xiao, 1984), but the majority of forms have the general morphologies of one species or the other, and Parkhaev in Gravestock et al., (2001) synonymized *P. adunca* with *P. subangulata*.

Such difficulties in the discrimination of species of *Pelagiella* have often been overlooked in systematic work. Parkhaev in Gravestock et al. (2001, p. 193) included *P. emeishanensis* He in Xing et al., 1984 and *P. lorenzi* Kobayashi, 1939 from ‘lower Cambrian’ Ludwigsdorf Member, Charlottenhof Formation, Saxony (Elicki 1994, 1996) in *P. subangulata* without explanation. Wotte and Sundberg (2017) provided an extensive synonymy list with their description of *Pelagiella* aff. *P. subangulata*. None of the new synonymies were given with an explanation, and they followed Parkhaev in Gravestock et al. (2001). Many of those included appear to be based on general similarities to *P. subangulata* in overall shape, with no information on microstructure, apertural morphology, or ornamentation. The same broad concept is applied by Wotte and Sundberg (2017) to *P. subangulata* specimens from the ‘lower to middle Cambrian’ Campo Pisano Formation, Sardinia (Elicki, 2002; Elicki et al., 2003), the ‘middle Cambrian’ Láncarna Formation, Spain (Wotte, 2006), and the Marianian (Cambrian ?Stages 3–4) Upper Ludwigsdorf Member, Charlottenshof Formation, Saxony (Elicki, 2003). These should be only tentatively assigned to *P. subangulata* (Supplementary file 1), as the specimens are unornamented steinkerns, lacking microstructural details and often poorly preserved (Elicki, 2002, pl. 1; Elicki, 2003, pl. 2, fig. 1; Elicki et al., 2003, pl. 5, figs. 3–5; Wotte, 2006, fig. 5n–p).

Specimens from the Shackleton Limestone are tentatively assigned to *Pelagiella* cf. *P. subangulata* based only on general morphological features. These include rapidly expanding whorls (Fig. 5.1, 5.9, 5.14), an initially concave then convex apical side

**Figure 6.** Pelagiellids from the Shackleton Limestone. (1–16) *Pelagiella* cf. *P. subangulata* Tate, 1892, (1–3) specimen SMNH Mo185054, (1) view of spiral side, (2) dorsal view, (3) dorsal view of supra-apical field; (4–6) specimen SMNH Mo185055, (4) apical view, (5) apical view, (6) dorsal view; (7, 8) specimen SMNH Mo185056, with possible hyolith operculum embedded in aperture, (7) oblique apertural view, (8) umbilical side; (9, 10) specimen SMNH Mo185057, (9) lateral view of abapical side, (10) oblique apertural view, showing curved groove passing through the umbilicus; (11, 12) specimen SMNH Mo185058, (11) apical view, (12) apertural view; (13–16) specimen SMNH Mo185059, (13) view of supra-apical field, (14) apical view, (15) dorsal view, (16) magnified dorsal view of part of the abapical side on the projecting wing, showing pustulose ornamentation. (17–26) *Xinjispira simplex* Zhou and Xiao, 1984, (17–21) specimen SMNH Mo185060, (17) oblique dorsal view of supra-apical field, (18) lateral view of abapical side, (19) lateral view of apical side, (20) magnification of internal mold with transverse fibrillar crystalline imprints, (21) view of supra-apical field; (22, 23) specimen SMNH Mo185061, (22) dorsal view, (23) lateral view of apical side; (24–26) specimen SMNH Mo185062, (24) apical view, (25) magnification of circumbibical channel on apical side, (26) magnification of transverse fibers on supra-apical surface of the steinkern. (16, 20, 24) Scale bars = 100 µm; all others, scale bars = 200 µm. All images taken using secondary electrons except (24–26) taken using backscattered electrons.



(Fig. 5.2, 5.6), and a projecting wing on the abapical side (Fig. 5.2, 5.12, 5.15; see also Runnegar in Bengtson et al., 1990, p. 254). The variation displayed in specimens from the Shackleton Limestone are both morphological and taphonomic. Specimens range from having a broader aperture (Fig. 5.2, 5.7, 5.12) to a narrower aperture (Fig. 5.5, 5.6). The low number of *P. cf. P. subangulata* steinkerns from the Shackleton Limestone (27 steinkerns), with only one similar to the *P. madianensis* morphology, does not allow a detailed comparison of aperture size and shape and degree of coiling. Two figured specimens (Fig. 5.7–5.10) show clear taphonomic artifacts common to steinkern-type preservation. One specimen preserves a possible hyolith operculum in its aperture (Fig. 5.7, 5.8) and one material introduced then lost during formation, represented by a groove across the umbilicus of the steinkern in Figure 5.9–5.10.

A detailed study of *Pelagiella madianensis* from the Xinji Formation (Cambrian Series 2), North China, has recently shown the shell microstructure to be a complex of four hierarchical types, signifying complex and differentiated controls on biomineralization in early mollusks (Li et al., 2017). Unfortunately, steinkerns from the Shackleton Limestone have smooth surfaces lacking any remnant microstructure. One specimen has a pustulose ornamentation, running obliquely toward the aperture (Fig. 5.13, 5.15). This is similar to the ornament figured by Runnegar in Bengtson et al. (1990, fig. 167A–E) but lacks the clear chevron pattern of their specimen.

Family Pelagiellidae? Knight, 1956  
Genus *Xinjispira* Yu and Rong, 1991

*Type species.*—*Xinjispira simplex* Zhou and Xiao, 1984 from the lower Cambrian Xinji Formation (=Yutaishan Formation), Anhui Province, China.

*Xinjispira simplex* Zhou and Xiao, 1984  
Figure 5.17–5.26

- 1984 *Barskovia simplex* Zhou and Xiao, p. 135, pl. 4, figs. 6–12.
- 1987a *Xinjispira simplex*; Yu, p. 54, pl. 4, figs. 14–16.
- 1987b *Xinjispira simplex*; Yu, p. 210, pl. 68, figs. 1–6.
- 1990 *Xinjispira simplex*; Yu, p. 146, fig. 4.
- 1991 *Xinjispira simplex*; Yu and Rong, p. 341, pl. 1, figs. 10–13.
- 1994 *Xinjispira simplex*; Feng et al., p. 13, pl. 1, figs. 14–18.
- 2016 *Xinjispira simplex*; Yun et al., p. 59, fig. 5L.

*Holotype.*—No. 800096, Geological Institute, Anhui Province, People's Republic of China. Internal mold from the Xinji Formation (=Yutaishan Formation) of the lower Cambrian (Series 2) of the North China Platform of Anhui Province, China.

*Occurrence.*—*Xinjispira simplex* is known from the Cambrian Series 2, Stages 3–4, of the southern margin of the North China Platform and from the Cambrian Series 2, Stages 3–4, of East Antarctica.

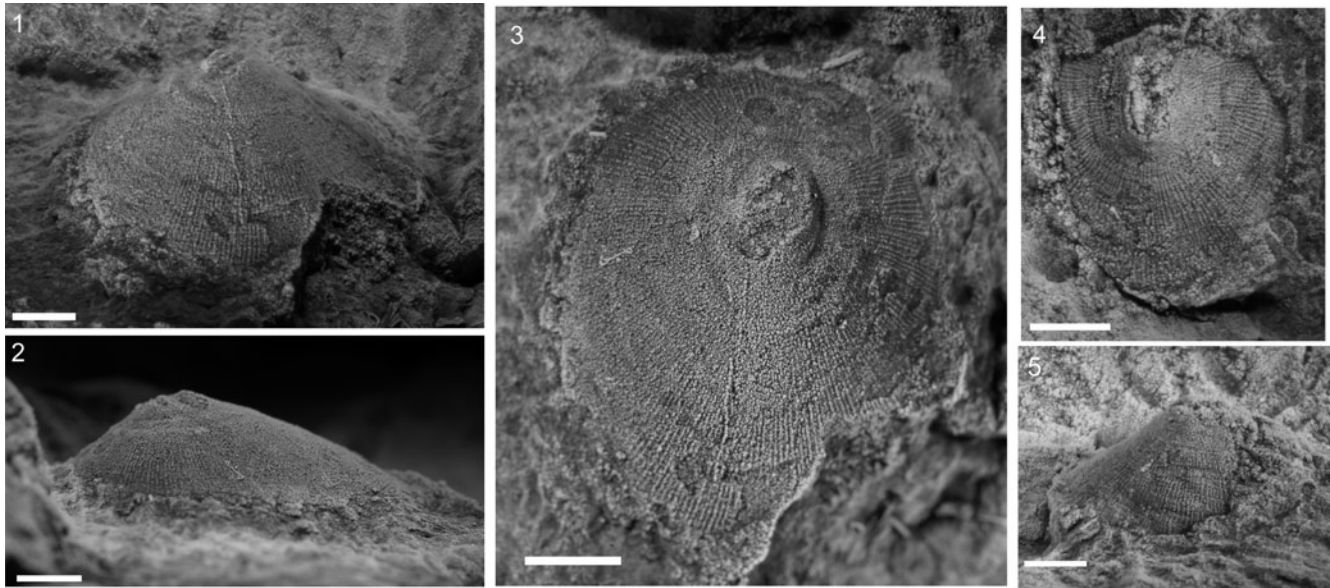
*Description.*—Turbospiral, globose, coiled through almost one whorl. Slight projection of apex on apical side, but no spire

present. Aperture rounded, with small projecting wing on abapical side of the shell. Aperture approximately 0.3 mm long and 0.4 mm wide. Total length 0.5–0.6 mm and height 0.4 mm. No clear distinction between protoconch and teleoconch, but may be marked by beginning of lirae. Pseudomorphic phosphatic shell coating with regular transverse lirae, 10 µm in width. Internal mold preserved imprints of comarginal fibrous bundles parallel to the ribs; some evidence of endolithic bacteria in form of phosphatized strands (Fig. 5.20). Umbilicus present on one specimen, with circumbilical channel (Fig. 5.25, 5.26).

*Materials.*—Approximately 10 steinkerns from HRSK 66, HRA 4, 5; with two steinkerns from HRSK 66 with external ornament preserved.

*Remarks.*—*Xinjispira* was assigned to the pelagiellids by Zhou and Xiao (1984), but later authors assigned them to the macluritids (Yu and Rong, 1991; Feng et al., 1994), in both cases considered gastropods. Yu and Rong (1991, p. 344) go so far as to say their specimens are missing their operculae. Parkhaev in Gravestock et al. (2001) and Parkhaev (2002, 2007a) placed *Xinjispira* with the family Khairkaniidae Missarzhevsky, 1989. The use of the family Khairkaniidae as defined in Parkhaev in Gravestock et al. (2001) and Parkhaev (2002) is not used here due to issues regarding the inclusion of symmetric (*Protowenella*) and asymmetric (e.g., *Xinjispira*, *Barskovia* Golubev, 1976) forms, under the assumption that they form a phylogenetic series. As no formal phylogenetic analysis has been performed to support this hypothesis, *Xinjispira* is tentatively included here with the pelagiellids. The inclusion in the pelagiellids is supported by their lack of spire on the concave apical side (Fig. 5.19, 5.23, 5.25), small projecting wing on the abapical side of the shell (Fig. 5.17, 5.21), and transverse fibrous microstructure preserved on the steinkern (Fig. 5.20, 5.24; cf. Li et al., 2017, fig. 3), which indicate an affinity with this family. Although microstructural imprints do not always preserve and similar patterns can appear in different lineages of early shelled molluscs, this microstructure, lack of spire, and noncircular aperture lead to a stronger argument for their inclusion in the pelagiellids.

Specimens figured by Zhou and Xiao (1984), Feng et al. (1994), Yu (1990), Yu and Rong (1991), and Yun et al. (2016) from the Xinji Formation are all 'sinistrally' coiled (when viewed from the apical, older end of the shell), whereas under the same scheme, *Xinjispira simplex* specimens from the Shackleton Limestone would be considered 'dextrally' coiled. In a review of shell chirality in the Cambrian asymmetrically coiled univalved mollusk *Aldanella* Vostokova 1962, Parkhaev (2007b) agreed with earlier conclusions of Landing (1988) and Landing et al. (1989) that chiral members of the same species are 'aberrations' or exceptions, that is, those that coil in the opposite direction to most members of a species. From the Tommotian Stage of Siberia, sinistral forms of *Aldanella* from a single stratigraphic horizon were reported and speculated to be members of a new species, rather than aberrations (Parkhaev, 2007b; but see Jacquet et al., 2017 for comments on Australian sinistral *Aldanella*). In their diagnosis of Pelagiellidae, Lindsey and Kier (1984, p. 250) included only



**Figure 7.** *Scenella?* sp. from the Shackleton Limestone. (1–3) Specimen SMNH Mo185075, (1) oblique view along supra-apical field, (2) lateral view, (3) apical view. (4, 5) Specimen SMNH Mo185076, (4) apical view, (5) lateral view, angled obliquely toward subapical field. Scale bars = 2 mm.

dextral forms, indicating the sinistral forms of *Xinjispira simplex* could not be included in the family. Whether *X. simplex* from the Shackleton Limestone can be considered ‘aberrant’ or of a new species is uncertain due to their low abundance. A comprehensive review of sinistrally coiled forms of Cambrian helcionelloids is probably necessary to resolve the paleobiological relevance of chirality and resolve taxonomic questions.

Only Yu and Rong (1991, p. 344) report ‘growth lines’ ornamenting the surface, but this is not defined, or clear in their figures, whereas Antarctic specimens retain both transverse fibrous microstructure (Fig. 5.20, 5.24) on the steinkern and transverse costae (Fig. 5.17–5.19, 5.21–5.23) on phosphatized exteriors. Of the two Shackleton Limestone specimens, one has a well-developed but small projecting wing (Fig. 5.17, 5.21) similar to that figured in Zhou and Xiao (1984, pl. 4, fig. 7c) and Feng et al. (1994, pl. 2, fig. 18), which is apparently not always well preserved or developed. Yu (1987b, p. 210) described two umbilical channels on the apical and abapical sides of *Xinjispira*, similar to those preserved on steinkerns of *Protowenella*. Circumbilical channels are exposed on a specimen of *X. simplex* from the Shackleton Limestone that is lacking an external phosphatic coating (Fig. 5.25, 5.26).

Class, Order, and Family unknown

**Remarks.**—The placement of *Scenella* in the chondrophorine (or porpitiid) hydrozoans has been reviewed in detail by Landing et al. (2018, p. 113–114), who concluded *Scenella* is a mollusk and the “chondrophorine paradigm” of incorrectly identified Cambrian macromollusks is unwarranted. This better resolved placement in the mollusks is unlikely to resolve its taxonomic position. The genus has, for example, been considered a member of the helcionellaceans, within the monoplacophora (Runnegar and Jell, 1976) and as a helcionelloid (Peel, 1991a; see Isakar and Peel, 2007, p. 255–256 for a review of the taxonomic history of *Scenella* as a mollusk). Due to the low number of specimens

described here and the uncertainty surrounding the taxonomy of *Scenella*, an attempt to rectify its higher taxonomic relationships shall not be made.

Genus *Scenella* Billings, 1872

**Type species.**—*Scenella reticulata* Billings, 1872 by original designation, from the Branchian Stage (Series 2) Brigus Formation of Newfoundland, Canada.

*Scenella?* sp.

Figure 7

**Description.**—Patelliform, univalved, low, blunt shells and very rapidly expanding. Single unbroken specimen has apertural length 9.8 mm and width 8.5 mm; elliptical in outline. Height 3.1 mm; specimen three times as long as it is high. Apex offset from center; subapical field less than half the length of the supra-apical field, creating an angle of ca. 110°. Both fields gently convex; supra-apical field concave nearer to apex. Protoconch poorly preserved; apical parts of both specimens damaged. External ornamentation consists of fine radial ribs. No concentric growth lines or ribs present. No muscle scars visible.

**Materials.**—Two silicified shells from HRA 14 and HRS 59.

**Remarks.**—Placement of the specimens of *Scenella?* sp. from the Shackleton Limestone in a group of similar, simple, patelliform mollusks is problematic. As noted in Jacquet and Brock (2016), *Scenella* is a wastebasket taxon of dubious taxonomic validity. Its problematic history once led to its inclusion in the derived group of chondrophorine hydrozoans (e.g., Yochelson and Gil Cid, 1984; Babcock and Robison, 1988; Narbonne et al., 1991). It is herein considered a mollusk, following its reidentification by a number of authors (e.g., Conway Morris and Peel, 2013; Peel, 1991b, 2003;

Landing and Narbonne, 1992; Geyer, 1994; Landing et al., 2018). In lieu of a much-needed systematic revision of the genus, the specimens from the Shackleton Limestone are referred to *Scenella?* sp. due to the broadly encompassing description of the genus as having a low patelliform profile (Fig. 7.2, 7.5), subcentral apex, elliptical outline (Fig. 7.3), and subdued concentric rugae and lirae (Billings, 1872, p. 479; Knight, 1941, p. 309–310, pl. 2, fig. 5a–e). The specimens from the Shackleton Limestone fit all criteria except the presence of either concentric comarginal rugae or growth lines, only bearing fine radial ribs (Fig. 7). *Scenella?* sp. from the Shackleton Limestone shares this lack of concentric features with *Scenella amii* (Matthew, 1902) from the middle Cambrian Stephen Formation of British Columbia, Canada, and *Scenella radians* Babcock and Robison, 1988 from the Drumian (Series 3) Spence Shale and Chisholm Formation of Utah, USA, but compares more closely to the latter. Figured specimens of *S. radians* also share the offset apex and concave part of the supra-apical field just below the apex (Babcock and Robison, 1988, fig. 4.1–4.5). The lack of concentric features prevents a more certain inclusion of the Shackleton Limestone specimens in the genus *Scenella* and indicates that species such as *S. amii* and *S. radians* may also be incorrectly placed in this genus. The diagnosis for *S. radians* is also written under the assumption it is a chondrophonrine hydrozoan, hindering a better comparison to other Cambrian univalved mollusks (Babcock and Robison, 1988, p. 10). *Scenella?* sp. differs from the similarly ornamented and shaped *Scenella barrandei* (Linnarsson, 1879) in having an elliptical, rather than subrectangular, apertural outline (Berg-Madsen and Peel, 1986, fig. 2d) and lack of comarginal rugae (Berg-Madsen and Peel, 1986, figs. 2c, 3e). The type species, *S. reticulata*, has a distinct reticulate ornamentation formed by radial and concentric ribs. Figures in Knight (1941, pl. 2, fig. 5a–e) and Landing (1988, fig. 12.1, 12.2) show *S. reticulata* has a higher shell and apex offset further over the subapical field, giving the subapical field an almost vertical profile.

*Scenella?* sp. from the Shackleton Limestone can be excluded from the similar monospecific genus *Estoniadiscus* Peel 2003 from the lower Cambrian Tiskre Formation of Estonia, as *Estoniadiscus* has ‘wrinkled’ periodic ribs and a more circular, less elliptical outline. The apex is also offset toward the supra-apical field. These features are figured by Peel (2003) for the species *Estoniadiscus discinoides* (Schmidt, 1888). From the monospecific *Galeaclavus* Jacquet and Brock, 2016 from the Third Plains Creek Member of the Mernmerna Formation (Cambrian Series 2, Stage 3) of South Australia, *Scenella?* sp. can be excluded due to a lack of faint comarginal growth lines present on *Galeaclavus coronarius* (Jacquet and Brock, 2016, fig. 12 A, D) and *G. coronarius* having a more inclined apex. *Scenella?* sp. also has a much lower profile, with height-to-length ratio of 0.31, just below the lowest measured height-to-length ratio of 0.33 for *G. coronarius*.

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## Accessibility of supplemental data

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3bb462v>.

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