Middle Cambrian (Miaolingian Series, Wuliuan Stage) molluscs and mollusc-like microfossils from North Greenland (Laurentia)

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Diverse assemblages of helcionelloid molluscs and mollusc-like microfossils are described from the upper Henson Gletscher Formation (Cambrian, Miaolingian Series, Wuliuan Stage) of Lauge Koch Land and western Peary Land, North Greenland (Laurentia). The fauna compares closely to an assemblage of similar age from the Coonigan Formation of Australia, although the latter is preserved as silica replicas while the North Greenland fossils are dominantly preserved as phosphatized internal moulds. These internal moulds often retain a detailed impression of the inner surface of the shell, with a fine pitted texture typically present. Prominent deep grooves on the sub-apical surface in the erect helcionellids *Dorispira* and *Erugoconus*, corresponding to ridges on the shell interior, seem to be associated with control of water flow through the mantle cavity. Well-developed shell pores, preserved as tubercles on the internal mould, are common in species of the laterally compressed *Mellopegma*. New taxa: *Dorispira avannga* sp. nov., *Dorispira septentrionalis* sp. nov., *Dorispira tavsenensis* sp. nov., *Dorispira tippik* sp. nov., *Erugoconus acuminatus* gen. et sp. nov., *Scenella*? *siku* sp. nov., *Sermeqiconus* gen. nov., *Tavseniconus erectus* gen. et sp. nov., *Vendrascospira troelseni* gen. et sp. nov., *Vendrascospira frykmani* gen. et sp. nov.

Keywords: Molluscs, Henson Gletscher Formation, Miaolingian Series (Wuliuan Stage), North Greenland, Laurentia.

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It was a surprise when the middle Cambrian microfossil *Protowenella* was reported from Denmark (Berg-Madsen & Peel 1978) and northernmost Greenland (Peel 1979) shortly after its original description by Runnegar & Jell (1976) from the Coonigan Formation and Currant Bush Limestone (Gowers Formation) in Australia, half a world away. However, since that time, *Protowenella* and various mollusc-like fossils from the Queensland and New South Wales assemblages described by Runnegar & Jell (1976, 1980) have been widely reported (MacKinnon 1985; Peel 1986, 2021a, b; Brock 1998; Gubanov *et al.* 2004; Vendrasco 2010, 2011; Kouchinsky *et al.* 2011). Their distribution demonstrates that the diversity of molluscs in assemblages of small shelly fossils described from the early Cambrian, originally mainly by Russian and Chinese

workers (summaries of extensive literature by Geyer 1986; Bengtson *et al.* 1990; Skovsted 2004; Parkhaev & Demidenko 2010; Parkhaev 2019; Li *et al.* 2021), was maintained into the middle Cambrian (Miaolingian Series).

The present paper describes molluscs and mollusc-like fossils (Miaolingian Series, Wuliuan Stage; *Ptychagnostus gibbus* Zone) from the Henson Gletscher Formation of Lauge Koch Land and western Peary Land, North Greenland (Figs 1, 2). The diverse assemblages (Figs 3–16) are compared with the fauna of the Coonigan Formation of similar age. The Greenland fossils are mainly preserved as phosphatized internal moulds in contrast to the silica replicas of the Coonigan Formation, although phosphatized material has been described from the slightly younger Gowers

Formation (Drumian Stage; Runnegar & Jell 1976; Vendrasco *et al.* 2010, 2011). Numerous macromolluscs ('knock-out' specimens) have been described from the Miaolingian in North America (Geyer 1994 for references), but the present material represents the first substantial small shelly molluscan fauna of this age described from Laurentia.

The affinities of two conspicuous members of the Henson Gletscher Formation assemblage were reinterpreted recently and they are no longer considered to be molluscs, although their morphologies are mollusc-like (Fig. 3). Ironically, the isostrophically coiled *Protowenella* was transferred to Hyolitha by Peel (2021a) following the description of an inplace operculum of orthothecid type. The bivalved stenothecoids, which Yochelson (1968, 1969) established as a new class of molluscs, are now accepted as being more closely related to brachiopods on account of their inferred pedicle attachment (Rozov 1984; Johnston 2019; Peel 2021c; Johnston & Streng 2021a).

Anisostrophically coiled shells of pelagiellids are also prominent in the Henson Gletscher Formation assemblage. Pelagiellids are perhaps the most com-monly reported and widely distributed mollusc-like small shelly fossils from the Cambrian, with Parkhaev (2001a) noting 30 named species. They have been assigned to various non-molluscan and torted or un-torted molluscan groups, as summarized by Thomas *et al.* (2020) and Landing *et al.* (2021), although most modern workers have favoured placement within the molluscs (Kouchinsky *et al.* 2011; Li *et al.* 2017, 2021; Parkhaev 2019).

The remarkable description of bristles (setae) pro-truding from the aperture in specimens of *Pelagiella exigua* Resser & Howell, 1938 from the Kinzers Formation (Cambrian Series 2, Stage 4) of Pennsylvania prompted Thomas *et al.* (2020) to interpret *Pelagiella* as a mollusc and a member of Total group Gastropoda Cuvier, 1797. However, Landing *et al.* (2021) restricted *Pelagiella* Matthew, 1893 to the type species, *Pelagiella atlantoides* Matthew, 1893 from the Hanford Brook Formation (Cambrian Series 2, Stage 4) of New Brunswick, which they considered to be a mollusc. In a controversial action, Landing *et al.* (2021) interpreted other members of the *Pelagiella* morphological group as annelids. This opinion is not followed here, largely

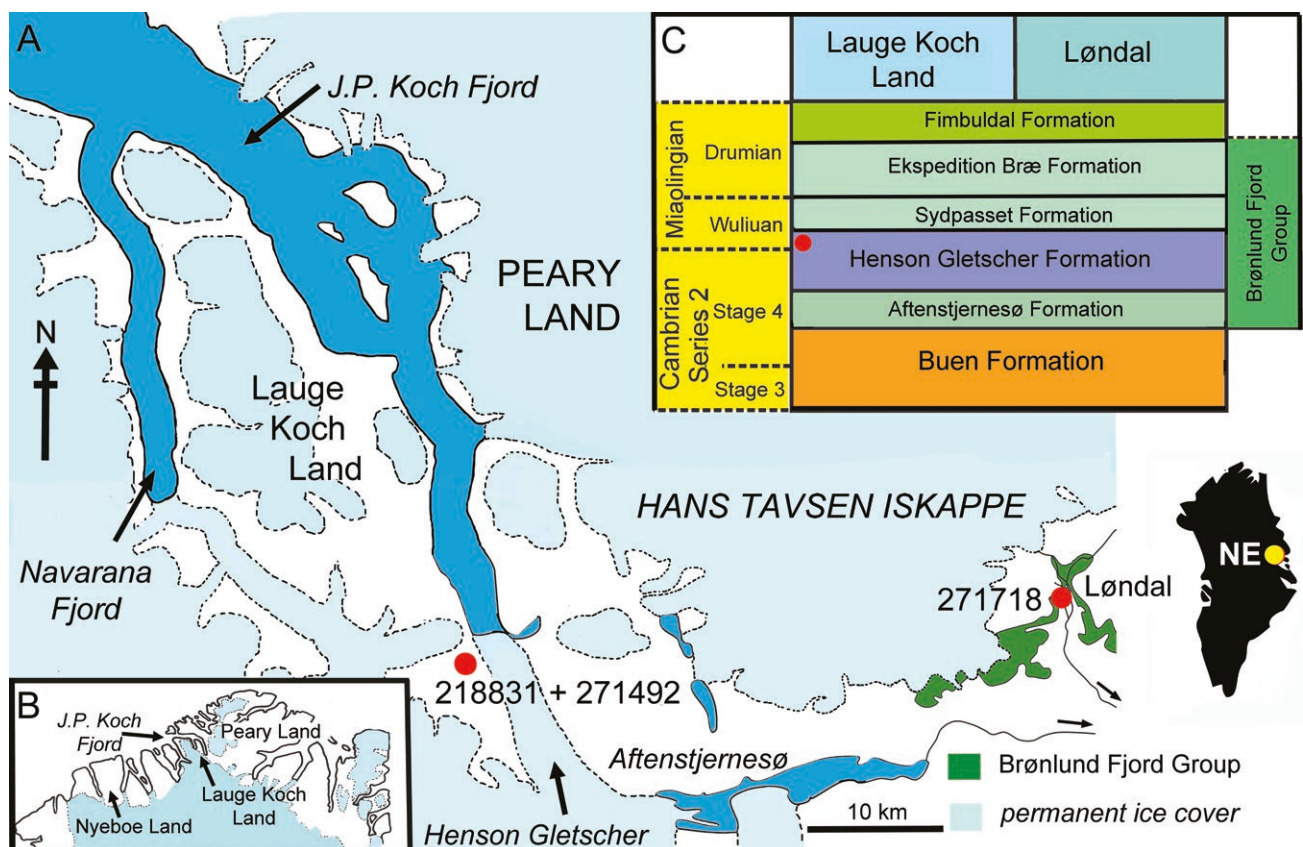**Fig. 1.** Locality maps for GGU samples. **A,** southern Lauge Koch Land and Løndal region of southern Peary Land showing sample localities (filled circles), with inset of Greenland indicating North-East Greenland. **B,** overview of northern Greenland. **C,** Cambrian stratigraphy in Lauge Koch Land and Løndal, indicating derivation of GGU samples from the Henson Gletscher Formation (filled circle).

on account of descriptions of shell structure in pelagiellids by Kouchinsky (2000a), Vendrasco *et al.* (2010) and Li *et al.* (2017, 2021).

Geological background

The Henson Gletscher Formation in the Peary Land–Lauge Koch Land region of North Greenland (Fig. 1) is a highly fossiliferous unit within a prograding complex of shelf carbonates and siliciclastic sediments, referred to the Brønlund Fjord Group (Higgins *et al.* 1991; Ineson & Peel 1997; Geyer & Peel 2011; Peel *et al.* 2016). The formation is composed mainly of dark, recessive, bituminous and cherty limestones, dolostones and mudstones, with a middle member of pale fine-grained sandstones (Fig. 2). Thin carbonate debris flows occur sporadically. At its type locality in southern Lauge Koch Land, from which GGU samples 218831 and 271492 were collected, the Henson Gletscher Formation is 62 m thick (Figs 1A, 2A), but it

Fig. 2. Stratigraphic sections through the Henson Gletscher Formation at its type section in southern Lauge Koch Land (A) and in Løndal (B) showing derivation of GGU samples (after Jon R. Ineson).

GGU samples	218831	271492	271718
Phylum uncertain Class Hyolitha Order Orthothecida			
Protowenella flemingi	●	●	●
Phylum uncertain Class Stenothecoida			
Stenothecoides cf. *elongata*		●	
Stenothecoides terraglaciei		●	●
Stenothecella cf. *sibirica*		●	●
Phylum Mollusca Class uncertain Order Pelagiellida			
Costipelagiella cf. *nevadense*		●	●
Class Helcionelloida			
Dorispira accordionata		●	●
Dorispira cf. *arguta*			●
Dorispira avannga			●
Dorispira septentrionalis			●
Dorispira tavsenensis			●
Dorispira tippik		?	●
Dorispira? cf. *penecyrano*			●
Erugoconus acuminatus			●
Helcionella? sp.	●		
Helcionellid spp. indet.		●	●
Mellopegma chelata			●
Mellopegma cf. *georginense*			●
Mellopegma schizocheras		●	
Mellopegma sp.		●	
'Obtusoconus' sp.			●
Parailsanella sp.		●	
Scenella? siku			●
Sermeqiconus polaris	●		●
Tavseniconus erectus			●
Vendrascospira troelseni		●	
Vendrascospira frykmani		●	

Fig. 3. Faunal list of molluscs and mollusc-like species from the Henson Gletscher Formation, North Greenland, Cambrian, Miaolingian Series, Wuliuan Stage.

thins to 47 m in Løndal in south-western Peary Land, to the east (Figs 1A, 2B).

Fossil assemblages from the Henson Gletscher Formation in southern Lauge Koch Land and Løndal range in age from Cambrian Series 2 (Stage 4) to the Miaolingian Series (Wuliuan Stage; *Ptychagnostus gibbus* Biozone), but Drumian Stage strata occur in Nyeboe Land along the northern coast of North Greenland (Higgins *et al.* 1991; Robison 1994; Blaker & Peel 1997; Ineson & Peel 1997; Geyer & Peel 2011; Fig. 1B). Trilobite faunas from the Henson Gletscher Formation have a dominantly Laurentian character but the assemblages include agnostoids and taxa that are important for international correlation with Siberia, the Altai Sayan foldbelt and South China (Blaker & Peel 1997; Geyer & Peel 2011). Elements of the diverse associated fauna were described by Clausen & Peel (2012), Peel *et al.* (2016) and Peel (2017, 2019, 2021c).

Derivation of samples. GGU samples 218831 and 271492 were collected at 56.5 m above the base of the Henson Gletscher Formation (thickness 62 m) at its type locality in Lauge Koch Land, in scours on the top of a 1 m thick mass flow deposit (82°10′N, 40°24′W; Ineson & Peel 1997, fig. 31; Geyer & Peel 2011, fig. 3; Figs 1A, 2A). GGU sample 218831 was collected by Peter Frykman on 24th June 1979; processed weight about 200 g. GGU sample 271492 was collected by J.S. Peel on 25th June 1978; processed weight about 2 kg.

GGU sample 271718 was collected by J.S. Peel on 15th July 1978 from a thin-bedded, phosphatized, dark dolomitic limestone occurring about 1 m below the top of the formation on the west side of Løndal (82°18′N, 37°03′W; Clausen & Peel 2012, fig. 1; Figs 1C, 2B), where the formation has thinned to 47 m. About 5 kg of limestone were processed.

Material. Specimens were hand-picked from wet sieved residues of limestone dissolved in 10% acetic acid prior to examination and imaging of selected specimens by scanning electron microscopy. The initial images were assembled in Adobe Photoshop CS4.

Preservation. Almost all examined specimens recovered from the acid residues are phosphatic internal moulds that display details of the inner surface of the original shell with great fidelity (Fig. 4A–C,E,G). The apertural margin is rarely preserved, indicating that phosphatization was usually confined to the earlier growth stages of the shell. The moulds have thin walls, with a granular or spherulitic inner surface, and the inner cavity is generally filled with phosphatized sediment (Fig. 4A). Exceptionally, encrustation on the shell exterior, in conjunction with the internal mould, provides an indication of the thickness of the

dissolved calcareous shell (Figs 4H, 5D). However, the shell itself is not preserved and phosphatized details of its internal structure, as described by Kouchinsky (2000a, b) and Vendrasco *et al.* (2010, 2011), generally are not known. Rare specimens retain patches of phosphatized shell attached to the internal mould that show details of the ornamentation of the shell exterior such as fine spiral ribs and comarginal growth lines not usually visible on the internal moulds (Figs 4F,H,I, 5G). Transverse rugae are more acutely presented on the shell exterior than in corresponding internal moulds (Fig. 4F,H,I). As noted by Runnegar (1985, fig. 1) and Skovsted (2004, figs 3M,N,5R), rugae on internal moulds are not always expressed on the shell exterior in helcionelloids, as is also the case with the circumbilical channels on internal moulds of *Protowenella* (Fig. 5A–D).

Internal structures

Features of the surface of internal moulds include muscle scars (Fig. 6A,B,E,F) and a complex of spiral grooves and associated transverse segments deeply impressed into the subapical surface of several helcionelloids (Fig. 4A–C,E–H). Tubercles representing pores in the shell are characteristic of *Mellopegma* Runnegar & Jell, 1976 (Fig. 14), while development of a finely pitted surface is widespread (Figs 10L, 16D).

Spiral ridge and groove complex
Grooves on the sub-apical surface of internal moulds, corresponding to ridges on the internal surface of the helcionelloid shell, were described by Runnegar & Jell (1976) and Peel (1991a, fig. 23) in silicified specimens of *Dorispira merino* (Runnegar & Jell, 1976) from the Coonigan Formation of New South Wales. Similar structures were reported in Miaolingian material from Utah by Robison (1964) and by Hu *et al.* (2021) from China. Two deep grooves on the internal mould are usually present, but some specimens show four grooves that may even be flanked by a third, discontinuous pair (Fig. 4A,C). Peel (1991a) noted that the grooves appear suddenly on the sub-apical surface of the internal mould (Fig. 4A), were often L- or T-shaped in cross-section (Fig. 4E) and terminated just within the apertural margin (Fig. 4I). Runnegar & Jell (1976) and Peel (1991a) concluded that the ridges reflected folding in the mantle that probably helped control water currents to the mantle cavity. This function may parallel, or be partially equivalent to, the development of a snorkel on the subapical surface in yochelcionellid helcionelloids (Peel 1991a, 2006). However, the surface of the internal mould in the area between the

innermost pair of grooves often carries numerous transverse grooves representing ridges on the shell interior that intuitively are difficult to reconcile with the notion of control of longitudinal folding attributed to the larger spiral ridges (Fig. 4A,C, 9C–E). Large pits set into the finely pitted texture of the internal mould of some specimens, on the lateral surfaces of the shell adjacent to the ridges, appear to represent diagenetic crystal growth on the shell interior (Figs 4F,G).

Parkhaev (2000) rejected the mantle control function and suggested that the ridges and separating channels served to steer and support muscle threads that were attached to the shell in the sub-apical region, drawing comparison with the columellar folds of many gastropods. Such a function implies substantial extension of the soft parts beyond the shell margin in the subapical region since there would be little need for extensive muscle control if soft parts were restricted to the inner part of the shell without extension and withdrawal. Extension and withdrawal of the head-foot complex into the shell is a general adaptation against predation in heliciform gastropods but in cap-shaped forms, such as patelliform gastropods, tryblidiids and probably most helcionelloids, the soft parts do not extend substantially beyond the apertural margin and defence is achieved by clamping the shell down against the substrate. Restriction of the supposed muscle channels to the sub-apical surface does not suggest effective clamping at the supra-apical margin, but this would not be required in a model where soft parts were withdrawn into the shell. However, withdrawal would require that the principal muscle scars were attached deep within the shell, as in most heliciform gastropods and the morphologically similar isostrophic bellerophontoids (Peel 1976, 1982, 1991a, 1993, 2004), whereas the ridges on the shell interior in the present material terminate almost at the apertural margin (Figs 4H, 9E).

Circumbilical channels on the internal mould are a diagnostic character of *Protowenella* (Berg-Madsen & Peel 1978). The broad, rounded thickenings of the internal shell wall are distinct from the acute ridges
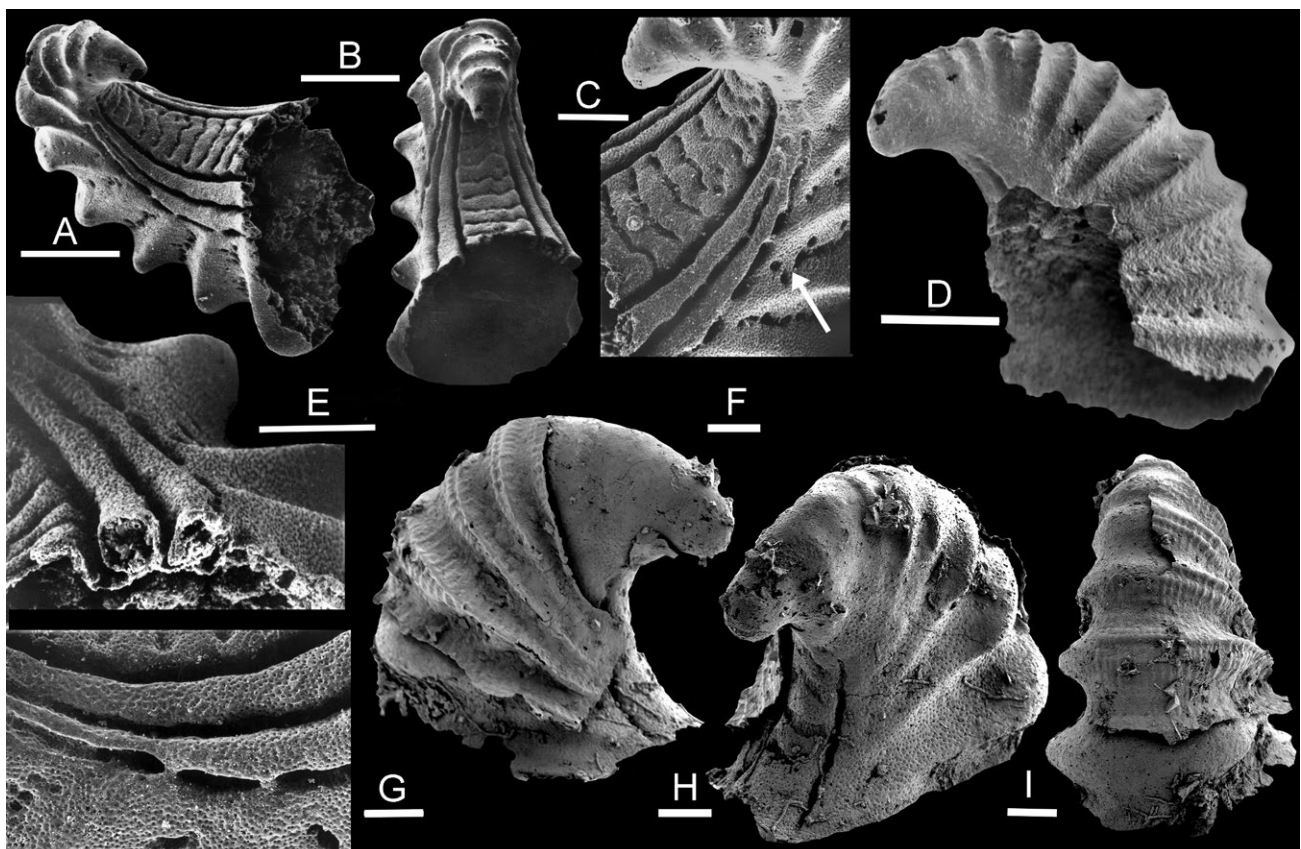
Fig. 4. Preservation of helcionelloids from the upper Henson Gletscher Formation, Miaolingian Series, Wuliuan Stage. **A–E, G:** *Dorispira tippik* sp. nov., MGUH 19561 from GGU sample 271718, Løndal, internal mould with details of groove complex on sub-apical surface. Arrow (C) indicates diagenetic crystal growth on shell interior. **D:** *Dorispira accordionata* (Runnegar & Jell, 1976), PMU 39172 from GGU sample 271492, Lauge Koch Land, phosphatic composite replica with trace of apical termination of spiral groove. **F, H, I:** PMU 39173 from GGU sample 271718, Løndal, internal mould with patches of thin phosphate encrustation formed on the outer surface preserving ornamentation. Scale bars: 500 μm (A, B), 400 μm (D), 200 μm (C, E), 100 μm (F–I).

seen in *Dorispira*. The channels in *Protowenella* were interpreted as possible sinuses in the apertural margin that might be related to inhalant currents entering the mantle cavity (Berg-Madsen & Peel 1978). Peel (2021a) noted that the channels did not result in sinuses on the outer shell surface and discounted a relationship to mantle currents. He suggested that the broad circumbilical thickenings may have acted as a support for the internal margin of the operculum, which also may have hinged against the termination of the ridges on opening. Peel (2021a) compared the channels on the internal mould of *Protowenella* to longitudinal furrows developed on the dorsal surface of some hyoliths (Malinky 2002; Marek et al. 1997).

There are only few published descriptions of muscle scars in helcionelloids. Parkhaev (2002) described muscle attachment scars on the supra-apical surface of *Bemella* Missarzhevsky *in* Rozanov & Missarzhevsky, 1966 and on the sub-apical surface of *Anhuiconus microtuberus* Zhou & Xiao, 1984, but these are low shells that expand rapidly in the direction of growth without sub-apical ridges. Li *et al.* (2021) described well preserved muscle scars in *Figurina figurina* Parkhaev, 2001a, which also has a low shell. Vendrasco *et al.* (2010) described a pair of muscle scars near the apex on the supra-apical surface of *Yochelcionella snorkorum* Vendrasco, Porter, Kouchinsky, Li & Fernandez, 2010 from the Miaolingian Gowers Formation of Australia, which is a tall shell but also lacks the ridges on the sub-apical surface.

Columellar folds in marine gastropods are often associated with burrowing high-spired forms at the present day (Signor & Kat 1984), but not exclusively so (Vermeij 2017). While some helcionelloids develop strong lateral compression that suggests a semi-infaunal mode of life (Gubanov *et al.* 1999; Peel 1991a), the wider aperture in most forms, including the present material, and often slightly flared margins are inconsistent with burrowing. A study of columellar muscle attachment in neogastropods by Price (2004) suggested that columellar folds did not guide the muscles as the snail extended or withdrew its soft parts.

Terrestrial snails often develop apertural barriers of teeth to resist predation and desiccation (Gittenberger 1994; Sulikowska-Drozd *et al.* 2014). The restriction of the ridges in the present marine material just to a small segment of the sub-apical apertural margin clearly refutes an effective defensive function in terms of the apertrure as a whole. Predation on helcionelloids was present in Cambrian seas, as documented by injuries described by Skovsted (2004) and Vendrasco *et al.* (2011), and illustrated here (Figs 7D,G, 14F).

The presence of the sub-apical ridges in such morphologically diverse taxa as the various species of the strongly rugose *Dorispira* (Figs 4, 7–9) and the smooth *Erugoconus* gen. nov. (Fig. 16F–K) may suggest that these forms comprise a distinct phylogenetic group of Miaolingian helcionelloids. However, it is considered premature to formalize such a step, with reference to the conclusions of Price (2004) that columellar folds in neogastropods evolved convergently on several occasions and that their function is not understood. The nature of the adaptation in helcionelloids remains problematic.

Pits, pores and polygons
A large proportion of the examined internal moulds displays a surface pattern of closely spaced fine pits with a diameter of 2–3 μm (Figs 4G, 9D, 10L). Occasionally, the pits are seen to be oriented in rows separated by low ridges (Fig. 14L) or lie centrally within a network of low ridges (Fig. 10D). Often, the apical area of specimens is smooth while the pitted texture is developed on the flanks (Fig. 10E). Bengtson *et al.* (1990) suggested that similar pits may reflect boring by endoliths, and traces of such activity may be widespread in Cambrian fossils (Runnegar 1985; Stockfors & Peel 2005), but not with the density, fineness and wide distribution seen here.

Vendrasco *et al.* (2010) described a similar pitted structure on internal moulds of molluscs and mollusc-like fossils from the Gowers Formation (Drumian) of Australia, which they considered to result from replacement of organic matrix associated with the prismatic microstructure of the shell, or as moulds of the crystal prisms after degradation of the organic meshwork. Li *et al.* (2021) illustrated similar pitting on internal moulds from the Xinji Formation (Cambrian Series 2) of North China. However, the pitting in some of the illustrated Australian specimens does not appear to show a high degree of correlation with prism boundaries and passes through several foliations (Vendrasco *et al.* 2010, pl. 4, figs 6–8, pl. 5, fig. 8). Furthermore, the pits are usually circular in cross-section in contrast to the polygonal form of the prisms. Peel (2021c) interpreted somewhat coarser pits in the apical area of juvenile stenothecoids to be the attachment sites of pedicle fibres, but such an interpretation is clearly not applicable to the widely distributed pits of the present context.

Internal moulds of *Tavseniconus erectus* gen. et sp. nov. (Fig. 16A–D) preserve a zone of larger pits (transverse diameter 5 μm) near the apertural margin that is set against a background of the fine pits on the flanks of the shell; the apical area is smooth (Fig. 16D). These larger pits slope down and inwards towards the apertural plane, giving them an elliptical shape on the mould surface, whereas the finer background pits penetrate perpendicular to the surface (Fig. 16D).

Internal moulds of *Mellopegma* show conical to sub-

cylindrical tubercles 5–8 μm in diameter, often with a blunt termination, that represent pores in the shell surface (Fig. 14D,E,I,K). The structures were described in detail by Vendrasco *et al.* (2011). They may be distributed randomly or follow a comarginal pattern associated with rugae (Fig. 14H). Vendrasco *et al.* (2011) considered that the pores extended through much or all of the shell wall and noted that similar structures had been described by Kouchinsky (2000a), Parkhaev (2006) and Feng & Sun (2006) in a variety of Cambrian helcionelloids. While some pores opened to the shell exterior, others appear to have been connected with the organic components of the shell structure and periostracum. Vendrasco *et al.* (2011) noted that the pores in *Mellopegma* were most similar to those developed in bivalves (Taylor *et al.* 1969) and suggested that shell pores might be a primitive character of the Phylum Mollusca.

Polygonal structures are widespread on phosphatized internal moulds of Cambrian helcionelloids (Parkhaev 2001; Skovsted 2004) and some may result from diagenesis. Ushatinskaya & Parkhaev (2005) suggested that they may represent imprints of the outer ephithelium of the mantle, and described similar structures in brachiopods, but a detailed review by Vendrasco *et al.* (2010, p. 125) concluded that the polygonal pattern of raised ridges or shallow grooves in Cambrian molluscs was a reflection of the organic framework of prismatic shell structure. Polygonal structures associated with muscle attachment areas in helcionelloids have been described by Parkhaev (2002), Vendrasco *et al.* (2010), Vendrasco *et al.* (2010) and Li *et al.* (2021).

Polygonal structures are not widely represented in the material from the Henson Gletscher Formation, but a weak pattern of polygonal grooves surrounding convex surfaces 8–10 μm in diameter is visible in some specimens of *Dorispira* and *Vendrascospira* gen. nov. (Figs 8E, H, 12D), comparable to that illustrated by Ushatinskaya & Parkhaev (2005, fig. 3) in *Oelandiella korobkovi* Vostokova, 1962 from the Tommotian of the Siberian Platform.

Age and faunal comparisons

Robison (1984) determined agnostoids from GGU sample 271492, including *Onymagnostus seminula* (Whitehouse, 1939), *Ptychagnostus gibbus* (Linnarsson, 1869) and specimens of *Ptychagnostus intermedius* (Tullberg, 1880) transitional to *P. atavus* (Tullberg, 1880), which were considered to be indicative of the *Ptychagnostus gibbus* Biozone (Wuliuan Stage). Subsequently, the last-named species was re-identified as *Ptychagnostus sinicus* Lu, 1957 (Ahlberg *et al.* 2007, p. 713). Poorly preserved agnostoids are present in GGU sample 271718 but this sample is considered to be a correlative of GGU sample 271492 on the basis of its lithostratigraphic position.

Strata of the upper Henson Gletscher Formation deposited during the Wuliuan Stage in Løndal and southern Lauge Koch Land yield diverse assemblages of molluscs and mollusc-like fossils (Figs 3–16). The main difference between the two areas concerns the abundance and diversity of *Dorispira* Parkhaev *in* Parkhaev & Demidenko, 2010 in GGU sample 271718 from Løndal relative to the samples from southern Lauge Koch Land. The mollusc faunas from the two areas are not closely similar, but this may result from the rarity of many individual taxa. Mollusc-like taxa such as *Protowenella* and stenothecoids occur in both areas.

Molluscs are less conspicuous in a fauna from the *Ovatoryctocara granulata* assemblage (Cambrian Series 2, uppermost Stage 4) of the Henson Gletscher Formation in Løndal that was described by Geyer & Peel (2011) and Peel *et al.* (2016) from about 13 m below GGU sample 271718 (Fig. 2B). The assemblage lacks the abundant specimens of *Dorispira* that characterize GGU sample 271718. Helical shells of pelagiellids are conspicuous in both faunas. *Yochelcionella* Runnegar & Pojeta, 1974 is well represented in the lower assemblage, where it occurs together with *Capitoconus* Skovsted, 2004 and *Mellopegma simesi* (MacKinnon, 1985), but all three are absent from the Wuliuan assemblage. Rare specimens of *Mellopegma* sp. (Peel *et al.* 2016, fig. 13N) may be referred tentatively to *Mellopegma georginense* Runnegar & Jell, 1976, which is also present in GGU sample 271718. *Coreospira* sp. of Peel *et al.* (2016, fig. 14N, O), a rare constituent of the *Ovatoryctocara granulata* assemblage, was considered to more closely resemble *Igorella* Missarzhevsky *in* Rozanov *et al.*, 1969 by Oh *et al.* (2021).

As in GGU sample 271718, an abundance of *Dorispira* is characteristic of the silicified fauna of the First Discovery Limestone (Coonigan Formation) of New South Wales (Runnegar & Jell 1976) of probable Ordian age, considered to be earliest middle Cambrian by Runnegar & Jell (1976), but late Cambrian Stage 4 by Geyer (2019). Percival *et al.* (2011) suggested that the formation was of slightly younger age (Templetonian Stage) but the age was regarded as uncertain, possibly Cambrian Series 2, Stage 4, by Smith *et al.* (2015, p. 44). The Coonigan Formation has also yielded three species of *Yochelcionella* but this genus is not known from the current Greenland material. However, *Yochelcionella gracilis* Atkins & Peel, 2004 occurs in Løndal within the *Ovatoryctocara granulata* assemblage (Cambrian Series 2, uppermost Stage 4) of the Henson Gletscher Forma-

tion and may be compared closely with *Yochelcionella ostentata* Runnegar & Jell, 1976 from the Coonigan Formation. The orthothecid hyolith *Protowenella* occurs in the Coonigan Formation and the current material from the Henson Gletscher Formation (Peel 2021a).

Mellopegma georginense Runnegar & Jell, 1976, from the Currant Bush Limestone (Gowers Formation) of the Georgina Basin, Australia (Runnegar & Jell 1976; Vendrasco *et al.* 2010) is tentatively identified from GGU sample 271718. In both areas, it occurs together with *Mellopegma schizocheras* Vendrasco, Kouchinsky, Porter & Fernandez, 2010, although the Australian occurrences are of Drumian age, compared to the Wuliuan material from the Henson Gletscher Formation in North Greenland. *Protowenella flemingi* Runnegar & Jell, 1976 and *Pseudomyona queenslandica* (Runnegar & Jell, 1976) also occur in the Currant Bush Limestone (Runnegar & Jell 1976). The former is present in the Wuliuan part of the Henson Gletscher Formation in North Greenland (Figs 3, 5A–D; Peel 2021b), whereas *Pseudomyona* Runnegar, 1983 occurs in the Ekspedition Bræ and Fimbuldal formations (Drumian) of North Greenland (Peel 2021b; Fig. 1C). *Yochelcionella* and *Eotebenna* Runnegar & Jell, 1976 occur in the Coonigan and Gowers formations (Runnegar & Jell 1976; Vendrasaco *et al.* 2010). While both genera occur in Cambrian Stage 4 strata of the Henson Gletscher Formation (Atkins & Peel 2004, 2008; Peel 1989; Peel *et al.* 2016), they are not recorded from the Wuliuan part of the Henson Gletscher Formation.

Brock (1998) described *Dorispira accordionata* (Runnegar & Jell, 1976) from Miaolingian limestone blocks within the Murrawong Creek Formation of New South Wales, associated with *Protowenella* and pelagiellids. A species assigned to *Mellopegma* is similar to *Mellopegma chelata* (Skovsted, 2006b) from GGU sample 271718. *Yochelcionella* described by Brock (1998) is not recorded from the present material but occurs in older and younger strata in North Greenland (Peel *et al.* 2016).

A diverse fauna of helcionelloids from Morocco and Spain was described by Geyer (1986). Moroccan material derived from the *Morocconus notabilis* and *Ornamentaspis frequens* biozones, corresponding to Cambrian Series 2, latest Stage 4 and the earliest Wuliuan Stage, respectively, contains *Marocella* Geyer, 1986, *Eotebenna* Runnegar & Jell, 1976 and *Yochelcionella* that are not represented in the current material from Greenland. *Protowenella*, pelagiellids and *Tavseniconus erectus* gen. et sp. nov. are present in both faunas. Strongly rugose helcionellids are common in both, although lower-shelled forms are more conspicuous in Morocco.

A silicified fauna derived from the Kuonamka Formation (upper Cambrian Stage 4–lower Drumian Stage) of northern Siberia shares *Costipelagiella* Horný,

1964 and *Protowenella* with the Henson Gletscher Formation (Gubanov *et al.* 2004; Kouchinsky *et al.* 2011), as well as *Pseudomyona queenslandica* (Runnegar & Jell, 1976) that occurs in Greenland in the Ekspedition Bræ Formation of Drumian age (Peel 2021b; Fig. 1C).

Systematic palaeontology

Institutional abbreviations and repositories. GGU prefix indicates a sample collected by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. Specimen repositories: Natural History Museum of Denmark, Copenhagen (MGUH prefix); Museum of Evolution, Uppsala University, Sweden (PMU prefix).

Unless otherwise stated, all figured specimens are derived from the upper Henson Gletscher, Cambrian, Miaolingian Series, Wuliuan Stage, *Ptychagnostus gibbus* Biozone in Lauge Koch Land (GGU samples 218831 and 271492) or Løndal (GGU sample 271718) and located in Figs 1–3.

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Phylum uncertain

Class Hyolitha Marek, 1963

Order Orthothecida Marek, 1966

Family Protowenellidae Peel, 2021a

Genus *Protowenella* Runnegar & Jell, 1976

Type species. *Protowenella flemingi* Runnegar & Jell, 1976, Currant Bush Limestone (Gowers Formation), Queensland, Australia, Miaolingian Series, Drumian Stage.

***Protowenella flemingi* Runnegar & Jell, 1976**
Fig. 5A–D

1976   *Protowenella flemingi* Runnegar & Jell, p. 133, fig. 6B–K.
1978   *Protowenella flemingi*; Berg-Madsen & Peel, p. 119, figs 4C–E, 6.
2021   *Protowenella flemingi*; Li *et al.*, p. 556, fig. 25a–j.
2021a *Protowenella flemingi*; Peel, figs 3, 4 (includes additional citations).

Figured material. PMU 39329 from GGU sample 218831 and PMU 39333 from GGU sample 271492, southern Lauge Koch Land; PMU 38330, PMU 38331 from GGU sample 271718, Løndal.

Other material. More than 100 additional specimens from GGU samples 271492 and 271718.

Discussion. Following its original description from Drumian strata in Queensland by Runnegar & Jell (1976), *Protowenella* was redefined by Berg-Madsen & Peel (1978) on the basis of a specimen from Bornholm
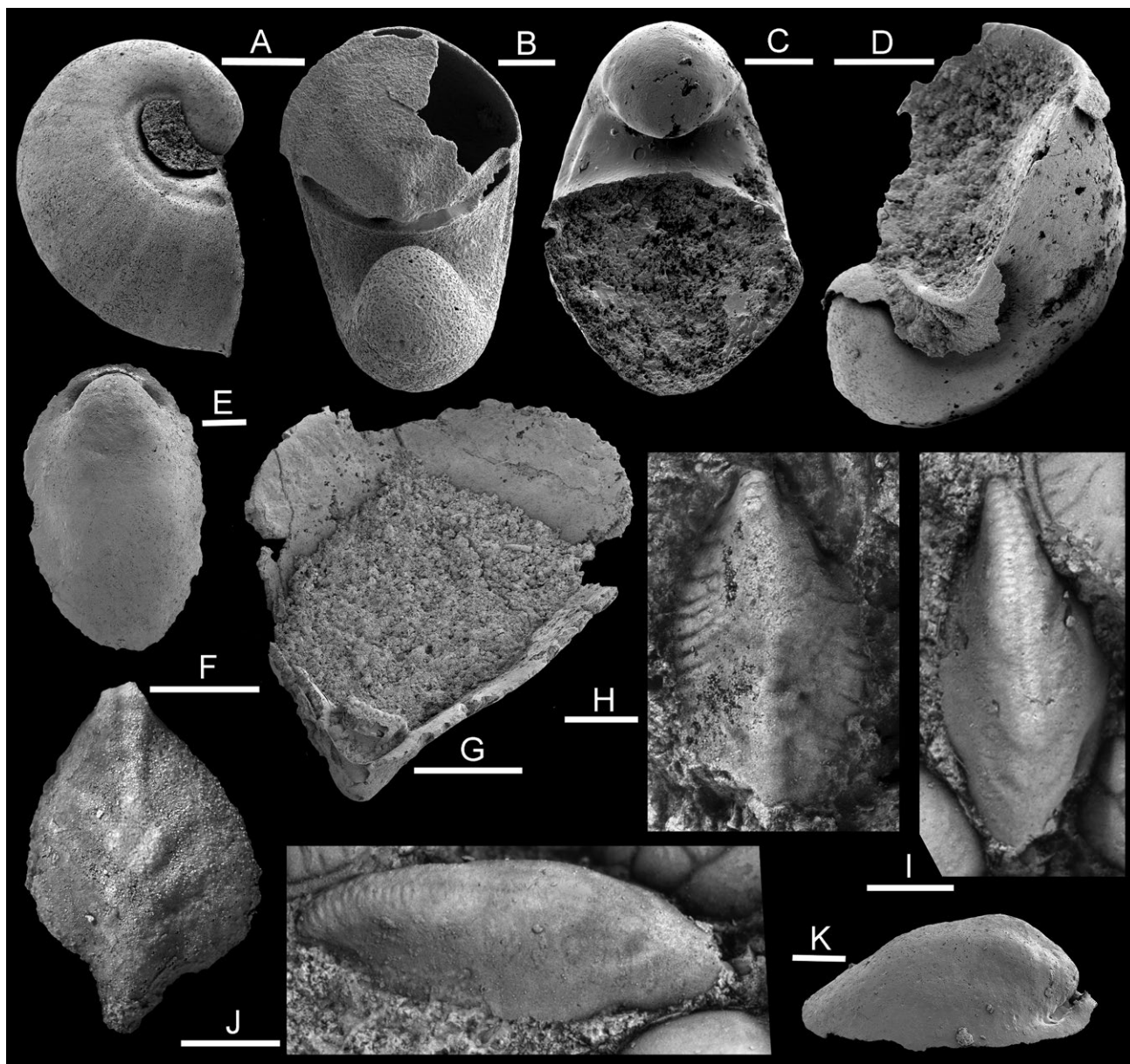
Fig. 5. Mollusc-like fossils, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage; internal moulds from GGU sample 271718 unless stated. **A–D:** *Protowenella flemingi* Runnegar & Jell, 1976. **A:** PMU 38330, lateral view. **B:** PMU 39329, apertural view with operculum in place from GGU sample 218331. **C:** PMU 38331 , apertural view. **D:** PMU 38333 from GGU sample 271492, oblique view of internal mould with phosphatization of external surface at apertural margin. **E–G, K:** *Stenothecoides terraglaciei* Peel, 2021b. **E:** PMU 38317 from GGU sample 271492, juvenile in plan view showing transverse sub-apical groove. **F:** PMU 38310. **G:** PMU 38322, holotype, internal view of ventral valve. **K:** PMU 38320 from GGU sample 271492, juvenile in lateral view showing sub-apical groove. **H:** *Stenothecoides* cf. *elongata* (Walcott, 1884), MGUH 33948 from GGU sample 271492 with lateral grooves on surface of internal mould. **I, J:** *Stenothecella* cf. *sibirica* Aksarina in Aksarina & Pelman, 1978, MGUH 33949 from GGU sample 271492, in plan (I) and oblique lateral (J) views. Scale bars: 1 mm (G), 100 μm (A, C–E, K), 50 μm (B).

to include the diagnostic circumbilical channels on the internal mould (Fig. 5A–C). It was reported from the Henson Gletscher Formation (GGU sample 271718) by Peel (1979). The history of research and phylogenetic placement of the genus were reviewed by Peel (2021a) who transferred *Protowenella* to Class Hyolitha on account of the presence of an in-place operculum of orthothecid type. *Protowenella* is widely distributed in Cambrian Series 2 and the Miaolingian Series (Wuliuan and Drumian stages).

Phylum uncertain

Class Stenothecoida Yochelson, 1968

Discussion. The bivalved stenothecoids were established as a new class of molluscs by Yochelson (1968, 1969) but their inferred pedicle attachment to the substrate promotes a closer relationship to brachiopods (Rozov 1984; Johnston 2019; Peel 2021c; Johnston & Streng 2021a). Rozov (1984) proposed a Phylum Stenothecata.

Genus *Stenothecoides* Resser, 1938

Type species. *Stenotheca elongata* Walcott, 1884, Eureka District, Nevada, Miaolingian Series, late Wuliuan Stage.

Stenothecoides cf. elongata (Walcott, 1884)
Fig. 5H

1954   *Stenothecoides* cf. *S. elongata*; Rasetti, p. 63, pl. 11, figs 6–10, pl. 12 figs 1–4.
1957   *Stenothecoides* cf. *S. elongata*; Rasetti, p. 972, pl. 12, figs 1, 2.
1969   *Stenothecoides* cf. *elongata*; Yochelson, p. 55, fig. 4A–C.
2021c   *Stenothecoides* cf. *elongata*; Peel, p. 390, fig. 7.

Figured material. MGUH 33948 from GGU sample 271492, internal mould, Lauge Koch Land.

Discussion. *Stenothecoides* cf. *S. elongata* is rare in GGU sample 271492, but the distinctive grooves on the internal mould, corresponding to ridges on the interior surface of the shell, perpendicular to the margin (Fig. 5H) compare well with material from the Mount Whyte Formation of British Columbia (Rasetti 1954; Yochelson 1969; Peel 2021c).

Stenothecoides terraglaciei Peel, 2021c
Fig. 5E–G, K

2021c   *Stenothecoides terraglaciei* Peel, p. 388, figs 4–6.

Figured material. PMU 38317 and PMU 38320 from GGU sample 271492, Lauge Koch Land; PMU 38310 and PMU 38322 (holotype) from GGU sample 271718, Løndal.

Discussion. *Stenothecoides terraglaciei* is common in GGU sample 271718. Internal moulds of numerous juveniles in GGU sample 271492, associated with rare specimens of *Stenothecoides* cf. *S. elongata*, cannot be distinguished from similarly preserved specimens in GGU sample 271718 and are therefore referred collectively to *Stenothecoides terraglaciei* (Peel 2021c).

Genus *Stenothecella* Aksarina in Aksarina & Pelman, 1978

Type species. *Stenothecella sibirica* Aksarina in Aksarina & Pelman, 1978, Kuznetsk Alatau, Altai–Sayan foldbelt, Siberia; Cambrian Series 2, Stage 4.

Stenothecella cf. sibirica Aksarina in Aksarina & Pelman, 1978
Fig. 5I, J

2021c   *Stenothecella* cf. *sibirica*; Peel, p. 391, fig. 8.

Figured material. MGUH 33949 from GGU sample 271492, Lauge Koch Land.

Discussion. The series of small muscle scars along the supra-apical surface of a well-preserved internal mould from GGU sample 271492 (Fig. 5I,J) compares well with the species described by Aksarina & Pelman (1978) from Cambrian Series 2, Stage 4, in Siberia (Peel 2021c). Several incomplete phosphatized internal moulds are also known from GGU sample 271718.

Phylum Mollusca Cuvier, 1797

Class uncertain

Order Pelagiellida MacKinnon, 1985

Genus *Costipelagiella* Horný, 1964

Type species. *Costipelagiella zazvorkai* Horný, 1964, Skryje Formation, Czech Republic; Cambrian, Miaolingian Series.

Costipelagiella cf. nevadense Skovsted, 2006b
Fig. 6

Figured material. PMU 39174 – PMU 39178, PMU 39180

from GGU sample 271718, Løndal. PMU 39179 from GGU sample 271492, Lauge Koch Land.

Discussion. *Costipelagiella* cf. *nevadense* is common in GGU sample 271718, but rare in GGU sample 271492. The material from the Henson Gletscher Formation resembles material from the upper Emigrant Formation (Cambrian Series 2, Stage 4) of Nevada described by Skovsted (2006b) in the presence of well-developed comarginal ribs on the upper whorl surface (Fig. 6C,D,I), whereas such ribs are limited to the whorl periphery and base in the type species illustrated by Horný (1964, pl. 2, figs 1–3). Specimens assigned to *Costipelagiella* by MacKinnon (1985) from the Tasman Formation of New Zealand are lower spired and have more numerous comarginal ribs.

Internal moulds of pelagiellids are widespread in samples from Cambrian Series 2 and the Miaolingian Series in North Greenland but only rarely preserve traces of external ornamentation. *Costipelagiella kochi* Peel, 1988 from the Holm Dal Formation (Cambrian, Miaolingian Series, Guzhangian Stage) of western Peary Land, North Greenland, has a shell with a less inflated base and a more rounded whorl periphery (Peel 1988, fig. 20). In contrast, most specimens of *Costipelagiella* from the Henson Gletscher Formation have a flattened upper whorl surface and more angular periphery, although both features are variable. Peel *et al.* (2016) reported pelagiellids with a fine reticulate ornamentation from the Henson Gletscher Formation in Løndal (Cambrian Series 2, Stage 4) about 12 m below GGU sample 271718. Skovsted (2004) described well preserved specimens from Cambrian Series 2, Stage 4, in North-East Greenland with sub-spiral ribs forming a deep V-shaped pattern at the whorl periphery, unlike the simple comarginal ribs of *Costipelagiella* (Fig. 6C,D).

A pelagiellid from the Kuonamka Formation of Siberia, which Kouchinsky *et al.* (2011) compared to *Costipelagiella zazvorkai* Horný, 1964, shows comarginal corrugation seen in the illustrated Henson Gletscher Formation specimens (Fig. 6) but it differs in the greater height of the aperture.

Internal moulds from GGU sample 271718 often preserve a muscle scar at the suture with the previous whorl (Fig. 6A(arrow),B(arrow),E,J). Traces of euendolithic borings within the original calcareous shell are often visible as cord-like ridges on the internal mould (Fig. 6J, arrows).

Class Helcionelloida Peel, 1991b

Diagnosis. Emended by Geyer *et al.* (2019, p. 212): 'Generally bilaterally symmetrical univalves in which the calcareous shell is usually coiled through up to several whorls; the whorls may be in contact or open coiled and are often laterally compressed. The aperture is
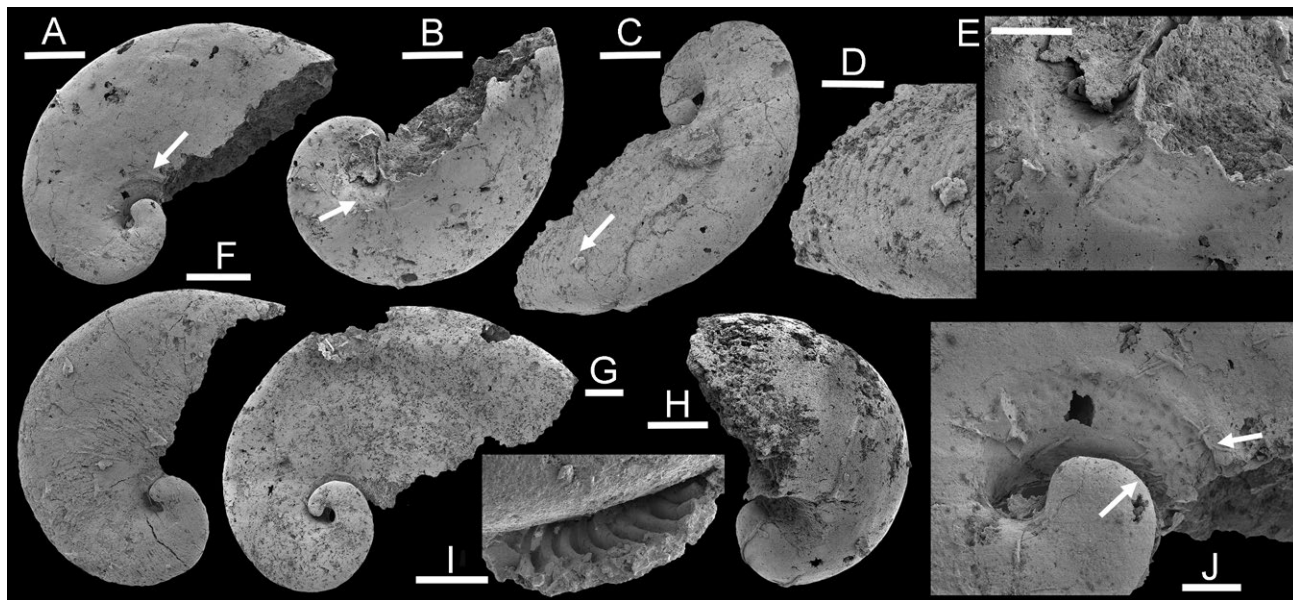
Fig. 6. *Costipelagiella* cf. *nevadense* Skovsted, 2006b, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage; internal moulds from GGU sample 271718 in Løndal unless stated. **A, J:** PMU 39174, apical view with arrow in A showing location of muscle scar (J); arrows in J show infilling of euendolithic borings. **B, E:** PMU 39175, umbilical surface showing detail of muscle scar (E). **C, D:** PMU 39176, oblique apical view with arrow in C locating detail of comarginal ribs (D). **F:** PMU 39177, apical view with traces of transverse ornamentation. **G:** PMU 39178, apical view. **H:** PMU 39179 from GGU sample 271492 from Lauge Koch Land, umbilical view. **I:** PMU 39180, showing impression of comarginal ribs from external surface. Scale bars: 200 μm (A–C, F, G), 100 μm (D, E, H), 50 μm (I, J).

oval, without re-entrant, but the sub-apical surface may develop a median sinus which in some taxa is deep and slit-like or trematose, with a single perforation at the end of an elongate tube termed the snorkel. In some forms, the lateral areas of the aperture may become prosocyrt, extended into weak lateral fields and producing broad emarginations in both the supra-apical and sub-apical surfaces astride the plane of symmetry. Ornamentation may include both comarginal and spiral elements; prominent comarginal rugae are common (modified from Peel 1991)'.

Discussion. There is no general agreement concerning the placement of helcionelloids in molluscan systematics. A series of papers by Parkhaev (2001a, b, 2002, 2017, 2019), Parkhaev & Demidenko 2010 and Parkhaev *in* Bouchet *et al.* (2017) has proposed that they should be placed as a separate Order Helcionelliformes Golikov & Starobogatov, 1989 (= Order Helcionelloida *sensu* Golikov & Starobogatov 1975) within the gastropod Subclass Archaeobranchia Parkhaev, 2001a, despite their interpreted untorted anatomy. Bellerophonts, a group of isostrophically coiled molluscs (Peel 1991a, b; Frýda 1999; Harper & Rollins 2000; Frýda *et al.* 2008; Ponder *et al.* 2020) often considered to be gastropods or untorted relatives of helcionelloids (or a polyphyletic grouping of both) were placed in a separate gastropod subclass by Parkhaev in Bouchet *et al.* (2017). Geyer *et al.* (2019) did not accept Parkhaev's archaeobranchian thesis and instead supported an opposing view that helcionelloids formed a Class Helcionelloida Peel, 1991b of untorted molluscs (Peel 1991a, 1991b; Jacquet & Brock 2016; Li *et al.* 2021), which is followed here. Discussion of other proposals and a historical review were given by Peel (1991a) and Ponder *et al.* (2020).

Missarzhevsky (1989, p. 171) proposed a new Order Eomonoplacophora for exogastric monoplacophorans without the muscle scars characteristic of *Tryblidium* Lindström, 1880, *Pilina* Koken & Perner, 1925 and their relatives. However, muscle scars are now known in several helcionelloid or helcionelloid-like genera (Rasetti 1954; Geyer 1994; Parkhaev 2002; Vendrasco *et al.* 2011; Li *et al.* 2021). Peel (1991a) generally accepted the content of Eomonoplacophora as helcionelloids but rejected the interpretation as exogastric and maintained the concept of Class Helcionelloida Peel, 1991b as endogastric molluscs. Eomonoplacophora has not gained widespread acceptance. However, Parkhaev in Bouchet *et al.* (2017) elevated Eomonoplacophora to a subclass of Class Monoplacophora Knight, 1952 but retained within it only one family (Maikhanellidae Missarzhevsky, 1989) of the eight families originally placed there by Missarzhevsky (1989, table 2). Most of the other seven families were considered to be gastropods of Subclass Archaeobranchia Parkhaev,

2001a (Parkhaev 2001a, 2002; Bouchet *et al.* 2017, p. 368, footnote 6) and placed within Order Helcionelliformes.

Parkhaev (2002) gave a detailed and valuable overview of the families and their included genera that he placed within Order Helcionelliformes (gastropod Class Archaeobranchia). Later versions were given by Bouchet *et al.* (2017) and Parkhaev (2019). Despite differences in the naming, content and placement of constituent families, most core genera are common to Eomonoplacophora *sensu* Missarzhevsky (1989), Helcionelloida (Peel, 1991a, b) and Helcionelliformes *sensu* Parkhaev (2001a, 2002).

Note on terminology. At numerous places in their text, Parkhaev & Demidenko (2010, pp. 1051, 1053, 1054) referred to the described helcionelloid genera as not having a 'planospiral' shell. The term is used also by Parkhaev (2017). Their meaning of planospiral is indicated by Parkhaev & Demidenko (2010, p. 1029) as "… shell does not form a complete whorl, so that the shell is not planospiral", which appears to indicate that planospiral reflects the degree of coiling (through at least one complete whorl) of a shell coiled in a single plane. 'Planospiral' is thus not synonymous in the usage of Parkhaev & Demidenko (2010) with the widely used 'planispiral' that means a shell coiled within a single plane, irrespective of the number of whorls (Knight *et al.* 1960, p. *I*132, see also Parkhaev 2000, 2001a). Such planispiral shells are not necessarily bilaterally symmetrical about that plane, but if so, they are described as isostrophic. Neither planospiral nor planispiral were used in Parkhaev (2019). Planospiral is sometimes used mainly in older literature as a synonym of planispiral in molluscs and foraminiferans, e.g. Cushman (1910). Planospiral is not used herein, where the degree of coiling is given as fractions of a shell whorl. This is less than a full revolution in most helcionelloids, but in a few forms such as *Coreospira* Saito, 1936 more than a full whorl may be present (Oh *et al.* 2021).

Family Helcionellidae Wenz, 1938

Genus *Dorispira* Parkhaev *in* Parkhaev & Demidenko, 2010

Type species. Helcionella terraustralis Runnegar & Jell, 1976 from the Coonigan Formation of New South Wales, Australia; Cambrian, Miaolingian Series, Wuliuan Stage.

Dorispira accordionata (Runnegar & Jell, 1976)
Figs 4D, 7A, E, F, J, N

1976   *Latouchella accordionata* Runnegar & Jell, p. 126, fig. 10C.1–C.18.

1998   *Latouchella accordionata*; Brock, p. 576, fig. 3.4–3.6.
2010   *Dorispira accordionata*; Parkhaev *in* Parkhaev & Demidenko, 2010, p. 1060.

Figured material. PMU 39172 from GGU sample 271492, Lauge Koch Land. PMU 339181 – PMU 39184 from GGU sample 271718, Løndal.

Description. Tall, laterally compressed, isostrophic shell coiled through half to two thirds of a whorl with a rectangular aperture, numerous prominent angular comarginal rugae and fine spiral threads. The shell exterior is preserved in a single specimen from GGU sample 271492 (Fig. 4D) but all other specimens are internal moulds in which the comarginal rugae are more rounded in crosssection (Fig. 7A,E,F,J,N). Specimens vary in curvature from tightly coiled, in which the apex substantially overhangs the sub-apical margin, as preserved (Fig. 7F), to tall, relatively slender forms (Fig. 7J). In the internal mould, the rounded apex is delimited by a shallow constriction from later growth stages (Fig. 7J). Two deep spiral grooves representing sharp ridges on the shell interior are present on the sub-apical surface in the latest half whorl, as preserved (Fig. 7A,F).

Discussion. *Dorispira accordionata* is abundant in GGU sample 271718. Specimens similar in shape to the slender form (Fig. 7J) were described by Brock (1998) from the Murrawong Creek Formation (Drumian Stage) of New South Wales. The sub-apical margin is extended in the larger silicified specimens illustrated by Runnegar & Jell (1976, fig. 10C) from the Coonigan Formation such that the apex does not extend beyond it. *Dorispira pearylandica* (Peel, 1988) from the Holm Dal Formation (Guzhangian Stage) of western Peary Land has a lower rate of whorl expansion.

Specimens from the Top Springs Limestone and Gum River Formation (Ordian Stage; Cambrian Stage 4–Wuliuan Stage) of Northern Territory, Australia, illustrated by Kruse (1991, 1998) often show a greater degree of coiling and more widely spaced comarginal rugae than material from North Greenland here referred to *Dorispira accordionata* (Fig. 7E,F,J,N). In this respect they more closely resemble *Dorispira tippik* sp. nov. (Fig. 7M,O,R). Kruse (1998) noted that the comarginal rugae often did not cross over the mid-dorsum in specimens from the Gum River Formation, a feature he attributed to erosion or exfoliation. Gubanov & Peel (1998) noted that restriction of prominent rugae to the lateral areas was the diagnostic feature of *Latouchella* Cobbold, 1921 from the Comley Limestone (Cambrian Stage 2) of Shropshire, England, although the name has been extensively applied to rugose Cambrian helcionelloids.

Tall specimens identified as *Oelandiella* cf. *accordionata* were described from the Tsinghsutung Formation (Cambrian Stage 4) of Guizhou, South China by Yang *et al.* (2012) and from the Miaolingian of Henan Province, North China by Hu *et al.* (2021) without reference to the establishment of *Dorispira* by Parkhaev & Demidenko (2010). The coarse rugae and the form of the aperture suggest placement in *Dorispira tippik* sp. nov., described below.

Dorispira cf. *arguta* (Resser, 1939)
Fig. 8A–H

Figured material. PMU 39192 – PMU 39194 from GGU sample 271718, Løndal.

Description. Slowly expanding isostrophic cone coiled through half to two thirds of a whorl, with the uniformly curved supra-apical surface traversed by two broad, shallow constrictions (in available material) on the internal mould prior to the latest growth stage. Aperture subcircular, shell length about twice shell width, with shallow sub-apical fold along the median line. A pair of prominent spiral grooves extends from the first constriction to the aperture on the sub-apical surface of the internal mould, equivalent to sharp ridges on the shell interior. The apex of the internal mould is blunt, rounded, with slightly swollen apex. External ornamentation is not known, but the surface of the internal mould may show a pattern of low, meandering ridges (Fig. 8G,H).

Discussion. The few internal moulds placed here show the same pattern of broad comarginal rugae separated by narrow channels that is characteristic of *Dorispira arguta* (Resser, 1939) from the Miaolingian of Idaho (Geyer 1994, fig. 4). Type material of *Dorispira arguta* displays a fine reticulation of growth lines and spiral ridges on the shell exterior, whereas external ornamentation is not known in the Greenland specimens. In contrast, the spiral grooves on the sub-apical surface of the Greenland internal moulds have not been observed in material from Idaho.

The specimens from the Henson Gletscher Formation can be compared to the early growth stages of some specimens of *Dorispira merino* (Runnegar & Jell, 1976) from the Coonigan Formation of New South Wales (Runnegar & Jell 1976). Most illustrated specimens from the Coonigan Formation are silicified specimens that attain a length of about 6 mm, with the shell coiled through a full whorl. The dorsal and lateral areas of the shell surface are ornamented by prominent, pouch-like, transverse rugae, separated by deep channels. However, in the earliest half whorl of a partly exfoliated specimen illustrated by Runnegar
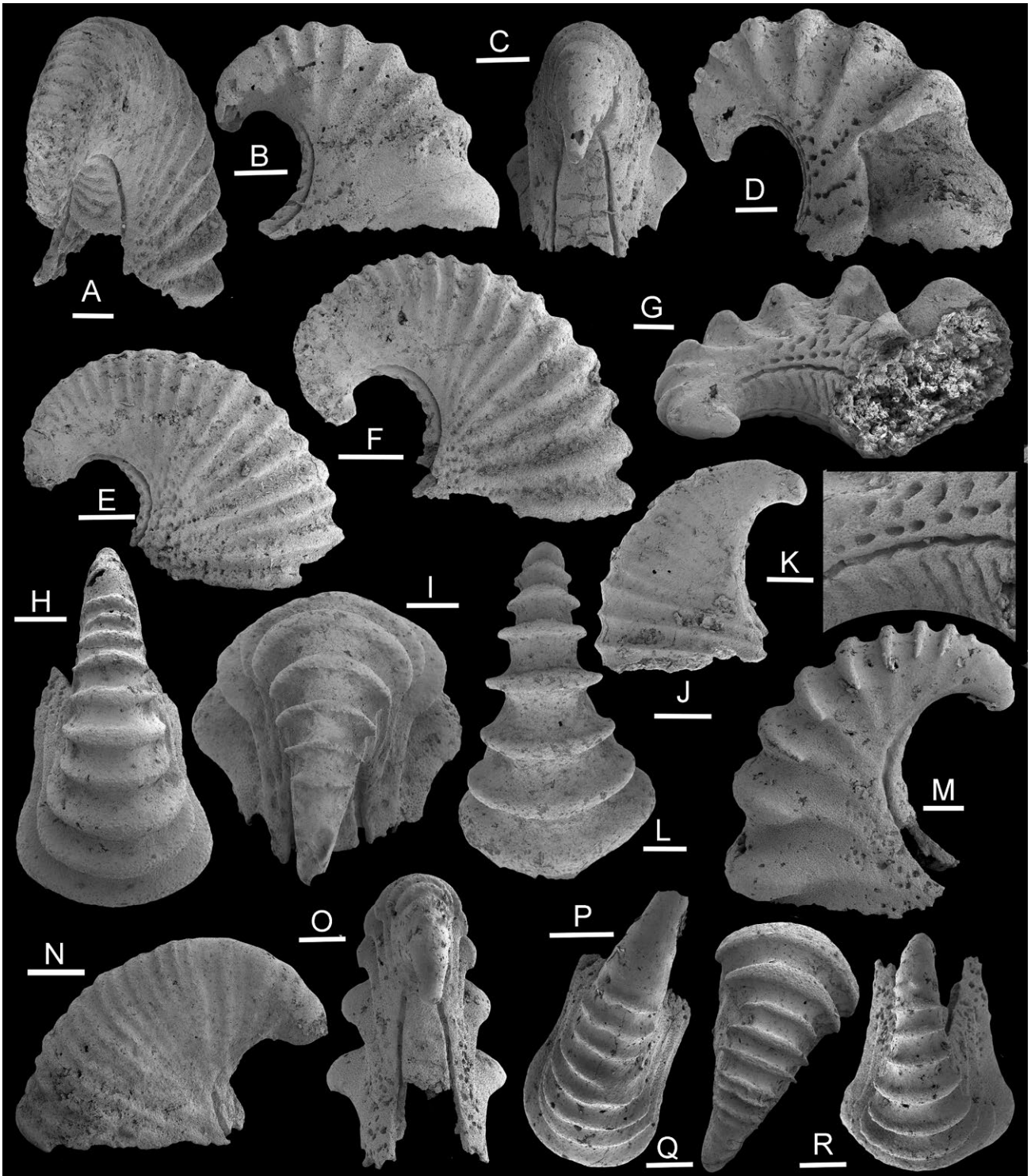
Fig. 7. *Dorispira*, upper Henson Gletscher Formation, Løndal, Peary Land, Miaolingian Series, Wuliuan Stage; internal moulds from GGU sample 271718. **A, E, F, J, N:** *Dorispira accordionata* (Runnegar & Jell, 1976). **A, F:** PMU 39181, oblique view of sub-apical surface. **E:** PMU 39182, lateral view. **J:** PMU 39183, lateral view. **N:** PMU 39184, lateral view. **B, C, D, G–I, K, L, M, O–R:** *Dorispira tippik* sp. nov. **B, C;** PMU 39185, lateral view (B) and sub-apical view with spiral grooves (C). **D, G, K:** PMU 39186, lateral view with repaired injury (D), oblique sub-apical view (G) with enlarged detail (K). **H:** PMU 39187, dorsal view. **I, L:** PMU 39188, dorsal (I) and supra-apical (L) views. **M, O, R:** PMU 39189, holotype in lateral (M), sub-apical (O) and dorsal (R) views. **P:** PMU 39190, dorsal view with concave lateral apertural margins. **Q:** PMU 39191, dorsal view. Scale bars: 400 μm (E, F, L), 200 μm (A–D, G–J, M–R), 100 μm (K).

& Jell (1976, fig. 9D.3), deep transverse channels on the internal mould are separated by broad transverse lobes that are lower in relief than the prominent lobes of the shell exterior at later growth stages This early stage closely resembles the small specimens (length about 1.3 mm) from the Henson Gletscher Formation (Fig. 8A–G).

Dorispira avannga sp. nov.
Fig. 8K–N

Holotype. PMU 39197 from GGU sample 271718, Henson Gletscher Formation, Løndal, western Peary Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Figured material. PMU 39196 from GGU sample 271718.

Diagnosis. Species of *Dorispira* with a circular aperture and numerous, closely spaced, angular comarginal rugae.

Derivation of name. From the Greenlandic 'avannga' meaning from the north.
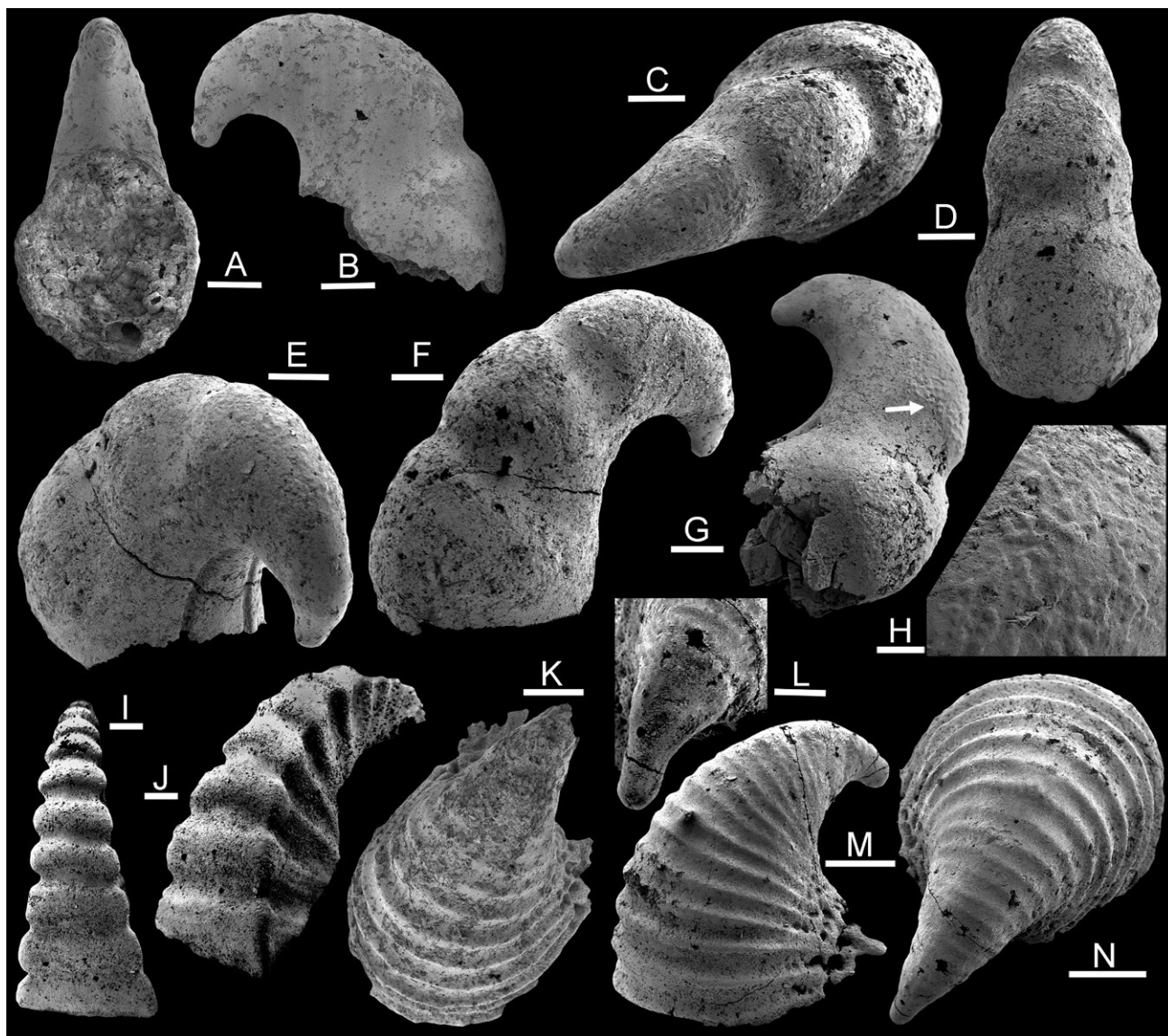
Fig. 8. *Dorispira*, upper Henson Gletscher Formation, Løndal, Peary Land, Miaolingian Series, Wuliuan Stage; internal moulds from GGU sample 271718. **A–H:** *Dorispira* cf. *arguta* (Resser, 1939). **A, B:** PMU 39192, apertural and lateral views. **C–F:** PMU 39193, dorsal (C, D) and oblique lateral (E, F) views. **G, H:** PMU 39194, lateral view, with detail of surface of internal mould (H, located by arrow in G). **I, J:** *Dorispira tavsenensis* sp. nov., PMU 39195, holotype, in dorsal (I) and dorso-lateral (J) views. **K–N:** *Dorispira avannga* sp. nov. **K:** PMU 39196. **L–N:** PMU 39197, holotype in oblique lateral (M) and dorsal (N) views with detail of early growth stage (L). Scale bars: 200 μm (A–G, I–K, M, N), 100 μm (L), 30 μm (H).

Description. Tall, isostrophic shell, coiled through half to two thirds of a whorl, in which the inflated shell has a circular apertural periphery (Fig. 8N). Supra-apical and lateral areas of the internal mould with numerous closely spaced, uniform, comarginal rugae, which become obscure on the subapical surface; traces of fine spiral ribs in the intervening concave channels. Apex strongly overhanging the sub-apical margin, with earliest growth stage smooth in the internal mould, sub-cylindrical and slightly constricted prior to transition to the rugose later growth stages (Fig. 8L). Two deep spiral grooves representing sharp ridges on the shell interior are present on the sub-apical surface of the internal mould in the latest half whorl, as preserved.

Discussion. *Dorispira avannga* sp. nov. is a rare species known only from internal moulds in GGU sample 271718. In terms of the shape and abundance of its comarginal rugae, *Dorispira avannga* closely resembles *Dorispira accordionata*. It is distinguished by the more inflated shell, with a circular aperture in plan view (Fig. 8N), when compared to the rectangular aperture of *Dorispira accordionata*. *Dorispira pearylandica* from the Holm Dal Formation (Guzhangian) of western Peary Land is more laterally compressed, with a lower rate of whorl expansion (Peel 1988).

Dorispira septentrionalis sp. nov.
Figs 4F, H, I, 9A–E

Holotype. PMU 39173 from GGU sample 271718, Henson Gletscher Formation, Løndal, western Peary Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. PMU 39198 and PMU 39199 from GGU sample 271718.

Derivation of name. From the Latin 'septentrionalis' meaning northern.

Diagnosis. Tall, laterally compressed species of *Dorispira* in which the aperture narrows towards the sub-apical margin. Ornamentation of coarser comarginal rugae, cords and ribs crossed by spiral ridges.

Description. The aperture in the tall, laterally compressed, isostrophic shell narrows towards the sub-apical margin. The earliest growth stage is smooth with a round termination, and may be delimited from the later shell by a shallow constriction on the internal mould (Fig. 9B). Comarginal rugae are prominent on the supra-apical and lateral areas of the internal mould but much reduced or absent immediately below the apex. Ornamentation of comarginal cords and ribs

crossed by spiral ridges to form a reticulate pattern. Internal mould with two deep spiral grooves on the sub-apical surface, its surface covered with fine pits (Fig. 9D).

Discussion. *Dorispira septentrionalis* sp. nov. differs from co-occurring species of *Dorispira* in terms of its greater lateral compression, with the aperture narrowing towards its sub-apical margin. *Dorispira accordionata* is distinguished by its more numerous, evenly developed and acute comarginal rugae (Fig. 4D). In silicified specimens of *Dorispira merino* illustrated from the Coonigan Formation by Runnegar & Jell (1976, fig. 9D), the shell is coiled through a full whorl and the comarginal rugae are more strongly developed, often pouch-like, with shallow emarginations on the lateral areas.

Dorispira tavsenensis sp. nov.
Fig. 8I, J

Holotype. PMU 39195, partial internal mould from GGU sample 271718, Henson Gletscher Formation, Løndal, western Peary Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Derivation of name. From Hans Tavsen (Tausen) Iskappe, western Peary Land (Fig. 1A).

Diagnosis. Species of *Dorispira* in which the flattened dorsal surface is perpendicular to the flat or shallowly concave lateral areas. Ornamentation of prominent transverse channels and rugae of similar width, the latter slightly nodose as they cross from the lateral areas to the dorsum.

Description. Isostrophic, laterally compressed, with the flattened dorsal (supra-apical) surface perpendicular to the flat to shallowly concave lateral areas (Fig. 8J). Surface with prominent comarginal rugae separated by deep U-shaped channels, with greatest width at nodes at the junction between the dorsal and lateral surfaces. The nodes create the impression of a spiral ridge on each whorl shoulder emphasised by the intervening channels being deepest close to the transition from the dorsum to the lateral areas. Rugae with fine comarginal cords and obscure spiral lines.

Discussion. *Dorispira tavsenensis* sp. nov. is known only from rare internal moulds in GGU sample 271718, amongst which the holotype, although broken, most clearly displays the quadratic transverse whorl profile (Fig. 8I, J). *Wakayella kandiingi* Kruse, 1998 from the Ranken Limestone (Ordian Stage; Cambrian Stage 4–Wuliuan Stage) of Northern Territory, Australia, dis-

plays a similar quadratic dorsal profile, with nodes at the transition from the dorsum to the lateral areas, but differs in its cap-shaped, rapidly expanding, strongly laterally compressed shell (Kruse 1998, fig. 40B).

Coreospira Saito, 1936, originally described from the middle Cambrian of Korea, has a similar quadratic whorl profile but the angulation between the dorsum and lateral areas is marked by a continuous prominent spiral cord (Oh *et al.* 2021).

Dorispira tippik sp. nov.
Figs 4A–C, E, G, 7B, C, D, G–I, K, L. M, O–R

Holotype. PMU 39189 from GGU sample 271718, Henson Gletscher Formation, Løndal, western Peary Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. MGUH 19561 and PMU 39185 – PMU 39188, PMU 39190 and PMU 39191 from GGU sample 271718, Løndal.

Diagnosis. Species of *Dorispira* with the tall, laterally compressed shell coiled through about half a whorl and strongly defined comarginal rugae that are raised into turbercles at the transition from the supra-apical surface to the lateral areas.

Derivation of name. From the Greenlandic 'tippik' meaning the transverse supporting ribs of a boat, alluding to the prominent comarginal rugae.

Description. Tall, isostrophic, lateral compressed shell in which the aperture in later growth stages is key-shaped in plan view (Fig. 7H,P,R), with concave lateral areas. Apex of internal mould smooth, sometimes delimited from the later growth stages by a shallow constriction (Fig. 7O). Prominent, but narrow comarginal rugae originate at the junction between the sub-apical and lateral surfaces and increase in relief and become tuberculate as they cross the supra-apical (dorsal) surface (Fig. 7M). Sub-apical surface with one to three pairs of deep, continuous or slightly interrupted grooves (Fig. 4A) formed by ridges on the shell interior that may be L- or T-shaped in cross-section (Fig. 4E). Median area between the innermost pair of spiral grooves with comarginal grooves on the internal mould (Figs 4B, 7G). Surface of internal mould often covered with fine pits (Fig. 4G).

Discussion. Specimens of *Dorispira tippik* sp. nov. are abundant as internal moulds in GGU sample 271718 and rare specimens are identified tentatively on limestone surfaces from GGU sample 271492. Many specimens (Fig. 7L,M) have a similar erect shell with

prominent comarginal rugae to *Dorispira iacobinica* (Geyer, 1986) from the *Morocconus notabilis* zone (Cambrian Series 2, upper Stage 4; Agzdian regional stage) of Morocco (Geyer 1986, pl. 3, figs 29, 30), while other Greenland specimens show a greater rate of whorl expansion in lateral perspective (Fig. 7B,D). *Dorispira iacobinica* differs in that the comarginal rugae are uniformly developed all around the shell whereas the rugae are much more prominent across the supra-apical surface of *Dorispira tippik* than on the sub-apical surface. However, the Moroccan holotype illustrated by Geyer (1986, pl. 3, fig. 29) preserves the shell exterior, with fine details of spiral ornamentation and transverse growth lines, in contrast to the internal moulds from Greenland.

Yang *et al.* (2012) described *Oelandiella* cf. *accordionata* from the Tsinghsutung Formation (Cambrian Stage 4) of Guizhou, South China, without reference to *Dorispira*. The erect shell and protruding sub-apical surface clearly distinguish the illustrated specimens from *Oelandiella* from the early Cambrian of the Siberian Platform (Vostokova 1962; Rozanov *et al.* 2010), as discussed by Parkhaev & Demidenko (2010). The coarse rugae suggest placement in *Dorispira tippik* sp. nov. An accompanying specimen in the Chinese fauna (Yang *et al.* 2012, pl. 2, figs 7, 8) is only slightly coiled and resembles the species described as *Helcionella callahani* Resser, 1938 from Cambrian Series 2, Stage 4 in the southern Appalachians, USA (Resser 1938), a shell form not known from the present North Greenland collections.

Hu *et al.* (2021) assigned Miaolingian (Drumian–Guzhangian) fossils from Henan Province, North China, to *Oelandiella accordionata* also without reference to *Dorispira*. The erect shell clearly distinguishes the illustrated specimens from *Oelandiella*, as discussed by Parkhaev & Demidenko (2010), and illustrated by Rozanov *et al.* (2010) and the coarse rugae and form of the aperture suggest placement in *Dorispira tippik* sp. nov.

Dorispira? cf. *penecyrano* (Runnegar & Jell, 1976)
Fig. 9F, G

Figured material. PMU 39200 from GGU sample 271718.

Discussion. This rare member of the assemblage from GGU sample 271718 is known from laterally compressed internal moulds that display subdued comarginal transverse corrugation and an overhanging apex. The arched sinus in the apertural margin on the sub-apical surface characteristic of the silicified material from the Coonigan Formation is not seen, but its absence may reflect the much greater size (length up to 3 mm) of the Australian specimens. The

external ornamentation of fine spiral lirae illustrated by Runnegar & Jell (1976, fig. 10A) is not preserved on the internal moulds, which display the fine pits seen in many other specimens from the Henson Gletscher Formation material. The initial growth stage in the latter is blunt and delimited from the later parts of the internal mould by a shallow constriction (Fig. 9G).

Runnegar & Jell (1976) considered that the arched sinus in the apertural margin beneath the apex indicated a relationship to *Yochelcionella* Runnegar & Jell, 1974; it is not typically well developed in *Dorispira*. For this reason, and on account of the lack of spiral grooves on the sub-apical surface of the internal mould (Fig. 9F), the species is only tentatively assigned to *Dorispira*, where it was placed by Parkhaev (2019). Specimens from the Holm Dal Formation (Guzhangian Stage) of Peary Land described by Peel (1988) as *Latouchella holmdalense* Peel, 1988 are morphologically close to the Australian material described by Runnegar & Jell (1976). They differ from the specimens in GGU sample 271718 in having a prominent sub-apical arched sinus, coarser comarginal corrugation and a more overhanging apex, although these features may be in part be due to their greater size and preservation with retained shell. Robison (1964, pl. 92, fig. 14) illustrated a similar silicified specimen with a proportionately longer shell from the Drumian Stage of Utah.

Genus *Scenella* Billings, 1872

Type species. *Scenella reticulata* Billings, 1872, Cambrian Series 2, Conception Bay, Avalonian southeastern Newfoundland, Canada.

Scenella? *siku* sp. nov.
Fig. 10G, K, M–O

Holotype. PMU 39207, internal mould from GGU sample 271718, Henson Gletscher Formation, Løndal, western Peary Land, North Greenland, Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. PMU 39205 and PMU 39206, internal moulds from GGU sample 271718.

*Derivation of name.* From 'siku', one of many Greenlandic words for ice.
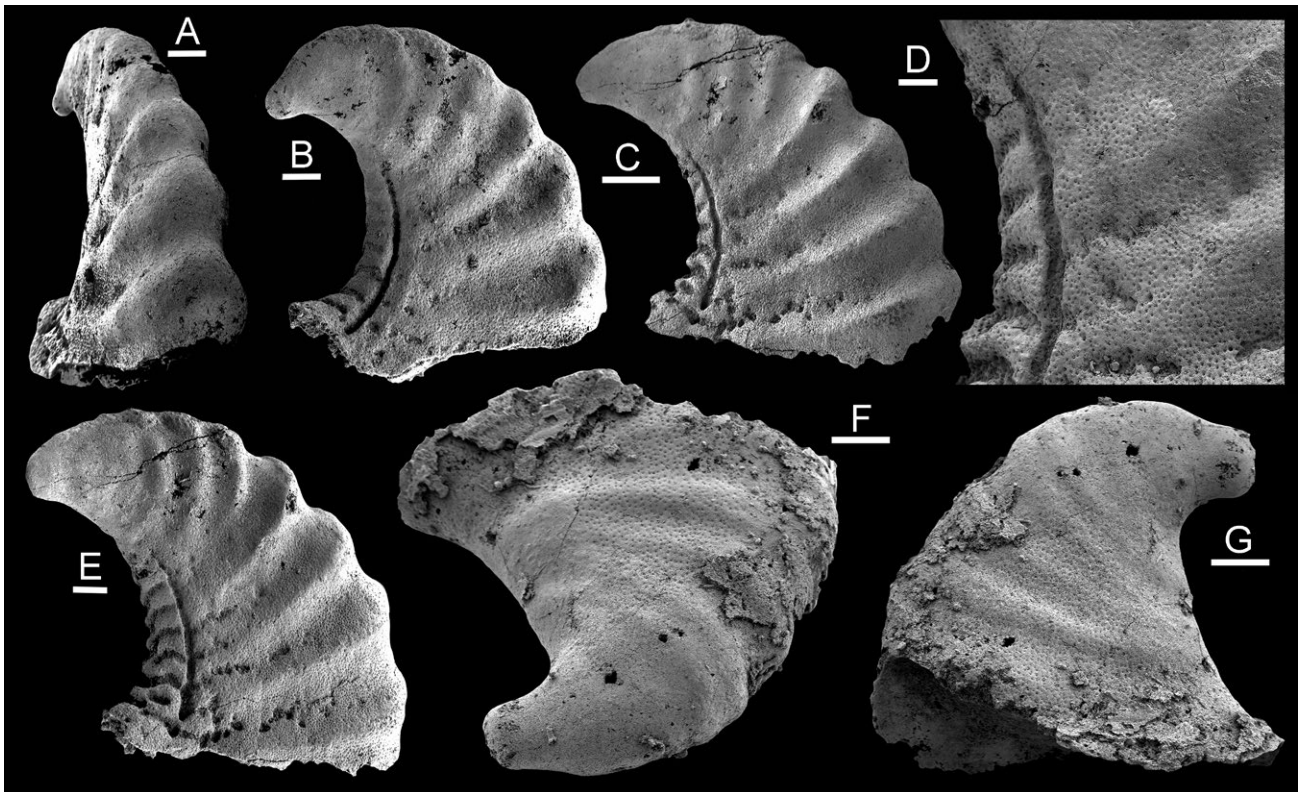
Fig. 9. *Dorispira*, upper Henson Gletscher Formation, Løndal, Peary Land, Miaolingian Series, Wuliuan Stage; internal moulds from GGU sample 271718. **A–E:** *Dorispira septentrionalis* sp. nov. **A, B:** PMU 39198, oblique lateral views. **C–E:** PMU 39199, oblique lateral (E) and lateral (C) views, with detail of pitted surface (D). **F, G:** *Dorispira*? *penecyrano* (Runnegar & Jell, 1976). PMU 39200, in lateral (G) and dorso-lateral (F) views. Scale bars: 200 *μ*m (C), 100 *μ*m (A, B, E–G), 50 *μ*m (D).

Diagnosis. Tentatively a species of *Scenella* with an elongate form and the slightly overhanging apex lying close to the sub-apical margin.

Description. Isostrophic, low, limpet-like, in which the width of the elongate shell is about two thirds of its length. Apex lying close to the sub-apical margin, slightly overhanging the sub-apical wall. Supra-apical surface shallowly convex in lateral profile (Fig. 10G) with the point of greatest height above the apertural plane lying at about one fifth of the distance from the sub-apical margin to the supra-apical margin. Surface of internal mould may retain low, widely spaced rugae (Fig. 10K). External ornamentation not known.

Discussion. The question of the relationship between *Scenella* and *Protoconchioides* Shaw, 1962 has been discussed in detail by Geyer (1994). In *Protoconchioides douli* Geyer, 1994, from the Miaolingian of Idaho, the apex of the oval shell is located almost centrally, in
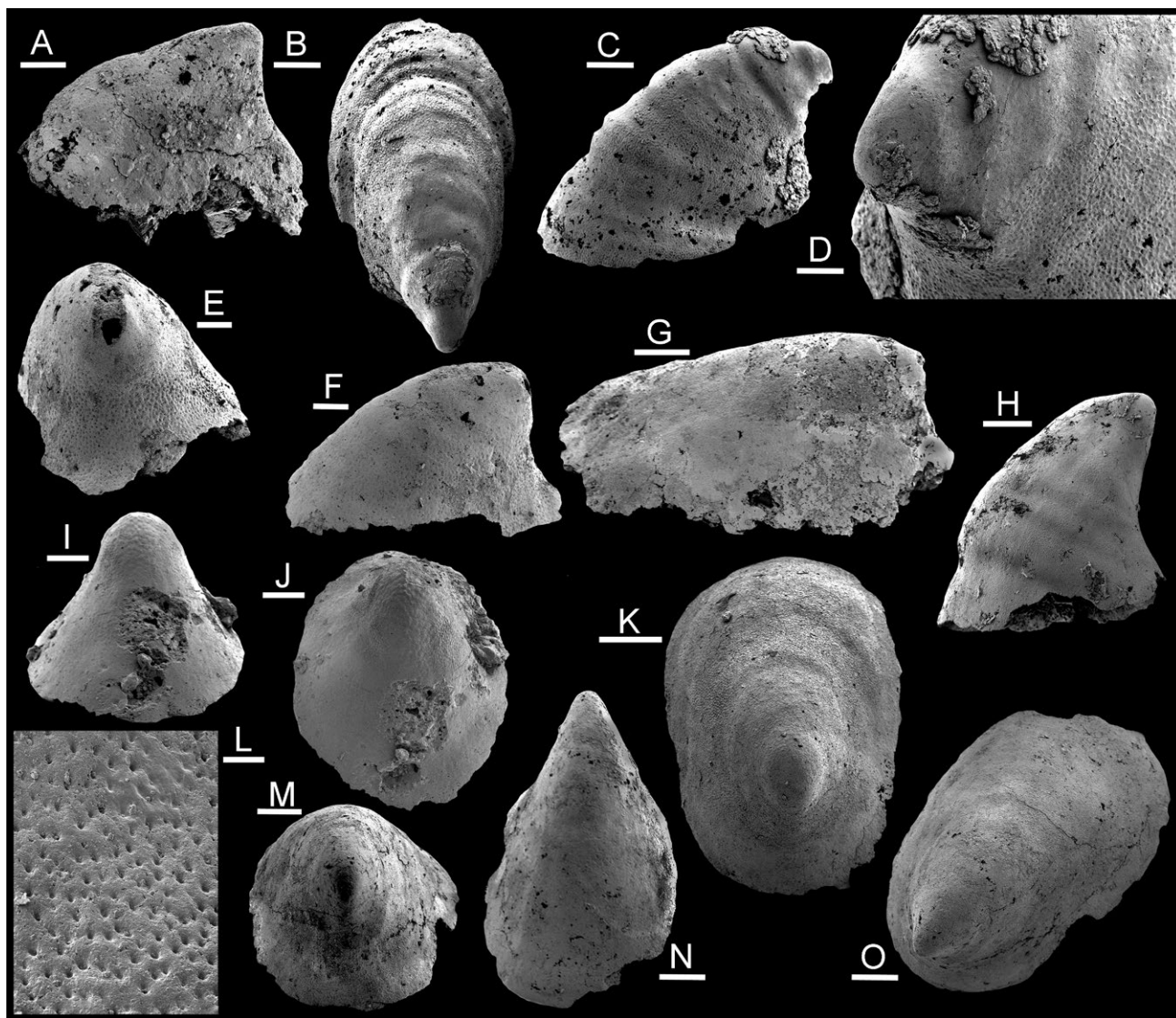
Fig. 10. Helcionellids, internal moulds from the Henson Gletscher Formation, Miaolingian Series, Wuliuan Stage, of Lauge Koch Land (GGU sample 271492) and Løndal (GGU sample 271718). **A, E, F, H,** Helcionellids spp. indet. **A:** PMU 39201 from GGU sample 271718, lateral view. **E, F,** PMU 39202 from GGU sample 271492, lateral view (F) and oblique view of sub-apical surface showing smooth surface around apex and pitted flanks (E). **H:** PMU 39203 from GGU sample 271718, lateral view. **B–D:** *Parailsanella* sp., PMU 39204 from GGU sample 271492, dorsal (B) and lateral (C) views with detail of early growth stage (D). **G, K, M–O:** *Scenella*? *siku* sp. nov. from GGU sample 271718. **G:** PMU 39205, lateral view. **K:** PMU 39206, apico-dorsal view. **M–O:** PMU 39207, holotype, in oblique apical (M), oblique dorsal (N) and oblique dorso-lateral (O) views. **I, J, L:** *Vendrascospira frykmani* gen. et sp. nov., PMU 39208 from GGU sample 271492, holotype, profile from supra-apical margin (I), dorsal view (J), detail of pitted surface (L). Scale bars: 200 µm (A–C, G, H, M–O), 100 µm (D–F, I–K), 20 µm (L).

contrast to its marginal position in *Scenella*? *siku*. This is also the case in *Protoconchioides*? *rasettii* Geyer, 1994, from the Mount Whyte Formation of British Columbia, originally described as *Scenella* sp. by Rasetti (1954). Described specimens of *Scenella*, including the type species (Knight 1941, pl. 2, fig. 5), also differ from *Scenella*? *siku* in having the apex placed more centrally and an oval to sub-circular dorsal plan. Comarginal rugae are only weakly developed, if present, and the shell exterior is ornamented with a fine reticulation of growth lines and radial ribs not known from *Scenella*? *siku*. *Scenella amii* (Matthew, 1902), abundant in the Burgess Shale of British Columbia, differs from *Scenella*? *siku* in the sub-circular dorsal plan and central location of the apex on the cap-shaped shell (Conway Morris & Peel 2013, fig. 1.6).

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

Type species. *Parailsanella acris* Zhegallo in Voronova *et al.*, 1987 from Cambrian Series 2, Stage 3 (Montezuman Regional Stage) of Northwest Territories, Canada.

Discussion. *Helcionella* Grabau & Shimer, 1909 and *Bemella* Missarzhevsky *in* Rozanov & Missarzhevsky, 1966 are frequently cited helcionelloids with low cap-shaped shells and prominent comarginal rugae. Their relationship was recently discussed by Geyer *et al.* (2019) who discounted the significance of the globose apex overhanging the sub-apical margin that Missarzhevsky (in Rozanov *et al.* 1969) and Parkhaev (2001a, b) considered a diagnostic feature of *Bemella*. Instead, Geyer *et al.* (2019) placed emphasis on the differentiation of the early part of the shell from the later more strongly rugose teleoconch in *Bemella jacutica* Missarzhevsky in Rozanov & Missarzhevsky, 1966, as illustrated by Rozanov *et al.* (1969, pl. 4, fig. 3). The laterally compressed, early Cambrian genus *Parailsanella* Zhegallo in Voronova *et al.*, 1987 also has a rugose shell but differs in that the apex is elevated above the plane of the aperture, such that a shallowly concave subapical wall is well developed (Kouchinsky *et al.* 2015, fig. 5). It is morphologically close to *Capitoconus* Skovsted, 2004, originally described from the Bastion Formation (Cambrian Series 2, Stage 4) of North-East Greenland, but the latter differs in terms of its strongly inflated protoconch (Skovsted 2004).

Parailsanella **sp.**
Fig. 10B–D

Figured material. PMU 39204 from GGU sample 271492, Lauge Koch Land.

Discussion. This single internal mould lacks the apertural margin. It is laterally compressed (Fig. 10B) and coiled through about one quarter of a whorl, with the apex overhanging the sub-apical surface (Fig. 10C). Irregular comarginal rugae are most strongly developed on the supra-apical and lateral areas. The early growth stage preserves two prominent comarginal channels on the internal mould that seem to delimit the early growth stage which Geyer *et al.* (2019) considered to be diagnostic of *Bemella*. This interpretation is supported by the surface pattern developed on the internal mould in ontogenetic stages approximately adapertural of the second comarginal constriction, but absent from the apical area (Fig. 10C,D), although this is also a feature of the internal moulds of other North Greenland species (Figs 10E,13B). Initially this pattern is a fine reticulation of ridges, but it gradually transforms to a structure of fine pits as the aperture is approached. However, the sub-apical wall is well developed, such that the apex in lateral perspective is raised high above the plane of the aperture, motivating assignment to *Parailsanella*. The lateral profile is thus closely similar to internal moulds illustrated by Kouchinsky *et al.* (2015, fig. 15) from the Emyaksin Formation (Atdabanian Stage) of northern Siberia, although these have broader, more regular comarginal rugae than the North Greenland specimen.

Capitoconus borealis Peel, Streng, Geyer, Kouchinsky & Skovsted, 2016, from the the lower beds of the Henson Gletscher Formation in Løndal (Cambrian Series 2, Stage 4, *Ovatoryctocara granulata* beds), has a similar shell form to *Parailsanella* sp. from GGU sample 271492, but its protoconch is more prominent and comarginal rugae are lacking. Growth lines are crossed by fine spiral threads that have not been observed in *Parailsanella* sp.

A specimen from the Coonigan Formation described by Runnegar & Jell (1976, fig. 8A, 1-2) as *Anabarella* sp. was transferred to *Bemella* by Parkhaev (2019). The specimen is more than five times larger than *Parailsanella* sp. from North Greenland, more laterally compressed, with a well-developed sub-apical surface and flanks with coarser and more widely spaced rugae. Runnegar & Jell (1976, fig. 9A.1–9A.5) described as *Vallototheca* [sic] sp. a silicified, strongly rugose specimen from the Coonigan Formation that exhibits a similar lateral profile and elongate form to *Parailsanella* sp. from the Henson Gletscher Formation. The latter specimen lacks the prominent rugation of the Australian example, although in part this may reflect the preservation of *Parailsanella* sp. as an internal mould. *Vallatotheca* Foerste, 1914, originally described from the Late Ordovician of Manitoulin Island, Canada, has a globose shell more than ten times larger than *Parailsanella* sp., and was considered by Knight (1941) to be closely

related to the tergomyan *Tryblidium* Lindström, 1880.

A fragment from the Top Springs Limestone (Ordian Stage; Cambrian Stage 4–Wuliuan Stage) in the Georgina Basin of Northern Territory, Australia, illustrated by Kruse (1991, fig. 10K, L) as ?scenellid indet., has a similar shell form to *Parailsanella* sp. from North Greenland, but with coarser comarginal rugae. Both taxa have a prominent comarginal channel delimiting the earliest growth stage. *Bemella wiri* Kruse, 1998 from the Montejinni and Gum Ridge formations of similar age, also in Northern Territory, Australia, is based on larger, more strongly coiled specimens (length 1 cm) in which the apex is curved down close to the plane of the aperture (Kruse 1998). The sub-apical surface of *Bemella wiri* is therefore strongly concave in lateral profile when compared to the almost straight subapical surface below the elevated apex of *Parailsanella* sp. (Fig. 10C).

Parailsanella sp. is distinguished from *Scenella*? *siku* by its more tightly coiled shell with a lower rate of whorl expansion, in lateral view, protruding apex and strong rugae.

Genus *Helcionella* Grabau & Shimer 1909

Type species. *Metoptoma*? *rugosa* Hall, 1847 from the Browns Pond Formation, New York State, Cambrian Series 2, Stage 4.

***Helcionella*? sp.**
Fig. 11A, B

Figured material. PMU 39209 from GGU sample 218831, Lauge Koch Land.

Discussion. As preserved, width and length are about equal in this low internal mould, although the subapical surface is incomplete (Fig. 11B). The dorsal and lateral areas carry prominent, flared rugae and finer interspersed comarginal cords, the latter most prominent near the apex. Both are crossed by fine radial ribs (Fig. 11B, arrow). A similar low shell, but with more frequent rugae, was illustrated from the Currant Bush Limestone (Gowers Formation) by Runnegar & Jell (1976, fig. 9B.1–B.3) as *Vallatotheca*? sp.

Helcionellids spp. indet.
Figs 10A, E, F, H, 13A–C, E–H

Figured material. PMU 39202 and PMU 39216 from GGU sample 271492, Lauge Koch Land. PMU 39201, PMU 39203, PMU 39213 – 39215, PMU 39217 from GGU sample 271718, Løndal.

Discussion. Smooth internal moulds are common in GGU sample 271718 from Løndal but are difficult to assign due to their variation and lack of distinguishing characters. The apex forms the highest part of the shell in a single internal mould from GGU sample 271718 in which a shallow comarginal constriction is preserved near the broken apertural margin (Fig. 10A). Rare internal moulds with an oval cross-section from GGU sample 271492 have the blunt apex located close to the sub-apical margin, above a vertical sub-apical wall (Figs 10F, 13G). The supra-apical wall is uniformly convex but more strongly curved than in *Scenella*? *siku*. The internal mould is smooth close to the apex, but otherwise covered with fine pits (Fig. 10E). Internal moulds with a similar profile were described by Kruse (1998) from the Ordian Stage (Cambrian Stage 4–Wuliuan Stage) of Northern Territory, Australia. The internal mould of *Parailsanella* sp. has a similar lateral profile, but the apex is overhanging and the surface is traversed by prominent comarginal rugae (Fig. 10C).

The lateral profile of a single internal mould from GGU sample 271718 (Fig. 10H) is similar to that of an upright internal mould illustrated by Runnegar & Jell (1976, fig. 10B.4, B.5) from the Coonigan Formation, although comarginal rugae in the latter specimen are more strongly expressed. The aperture is oval, but its margins are not preserved. The apical area is smooth, but the surface of the rest of the specimen is covered by fine pits.

The apex strongly overhangs the sub-apical margin in several laterally compressed internal moulds from GGU sample 271718 (Fig. 13A,B,C,F), as in *Erugoconus acuminatus* gen. et sp. nov. (Fig. 16F,H), but the rate of expansion in lateral view is greater. Rare internal moulds with a strongly overhanging apex show a conical early growth stage (Fig. 13E). A more tightly coiled internal mould (Fig. 13H) is similar to *Erugoconus acuminatus* (Fig. 16F,H) but the apex overhangs the elongate aperture by a proportionately shorter distance (Fig. 13H).

Genus *Sermeqiconus* gen. nov.

Type species. *Figurina*? *polaris* Peel, 2021d, Aftenstjernesø Formation, Navarana Fjord, northern Lauge Koch Land, North Greenland; Cambrian Series 2, Stage 4 (Peel 2021d).

Derivation of name. From the Greenlandic 'sermeq' meaning an active glacier, referring to the position of the collection locality immediately west of Henson Gletscher (Fig. 1A).

Diagnosis. Isostrophic, low, with oval plan, and swollen apex lying close to the sub-apical margin. Ornamentation of a few widely spaced ribs and finer striations,

the former most prominent on the supra-apical surface, crossed by slightly lamellose comarginal growth lines.

Discussion. Internal moulds from the Parara Formation (Cambrian Series 2) in South Australia, assigned to *Figurina* Parkhaev, 2001a by Parkhaev (2001a), are more laterally compressed, with a narrower, more strongly overhanging apex, and lack the prominent widely spaced radial ribs characteristic of *Sermeqiconus*. *Calyptroconus* Parkhaev, 2001a, also from the Parara Formation (Cambrian Series 2) in South Australia, has broad radial folds distributed all around the low, oval shell and a sub-central apex in contrast to the overhanging apex of *Sermeqiconus*. In North Greenland, *Sermeqiconus* ranges from Cambrian Series 2, Stage 4 (Aftenstjernesø Formation; Peel 2021d) to the Miaolingian Series, Wuliuan Stage (Henson Gletscher Formation).

Sermeqiconus polaris (Peel, 2021d)
Figure 11C, D

2021d *Figurina*? *polaris* Peel, p. 29, fig. 4.7, 4.8.

Figured material. PMU 39210 from GGU sample 218831, Lauge Koch Land.

Diagnosis. As for genus.

Description. The internal mould is isostrophic, low, oval, with width about two-thirds of length; the swollen apex lies above, but just within the sub-apical margin. Supra-apical surface shallowly convex in lateral view, flattening as the supra-apical margin is approached; sub-apical surface concave and steeply inclined (Fig. 11C). Initial growth stage forming one third of the preserved length; smooth, with a shallowly impressed pegma on the sub-apical surface at the junction with the ornamented later shell growth stage. Ornamentation consists of widely spaced, prominent radial ribs with rounded upper surfaces and intervening fine striations, which are crossed by slightly lamellose comarginal growth lines. Fine pits are prominent on the sub-apical surface and lateral margins.
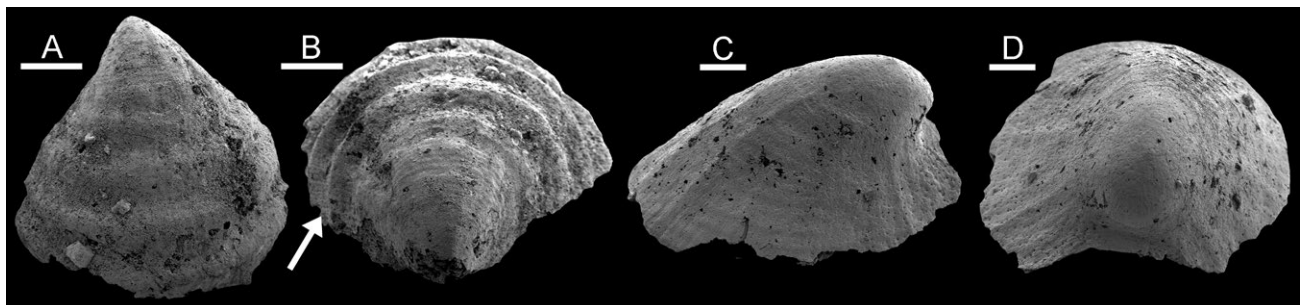
Discussion. *Sermeqiconus polaris* (Peel, 2021d) from the basal Aftenstjernesø Formation, northern Navarana Fjord, northern Lauge Koch Land, North Greenland (Fig. 1A; Cambrian Series 2, Stage 4) was referred tentatively to *Figurina* by Peel (2021d). The distinctive widely spaced radial ribs located mainly on the dorsal area of the holotype of *Sermeqiconus polaris* (Peel, 2021d, fig. 4.7, 4.8) are clearly preserved in the specimen from the Henson Gletscher Formation (Fig. 11C,D). *Sermeqiconus polaris* has a wider shell than the laterally compressed *Figurina figurina* Parkhaev, 2001a, and its broader apex less strongly overhangs the sub-apical surface.

Figurina? *groenlandica* Skovsted, 2004 from the Bastion Formation (Cambrian Series 2, Stage 4) of North-East Greenland has a narrower shell than *Sermeqiconus polaris* in which the supra-apical surface of the internal mould is more strongly curved in lateral view (Skovsted 2004). In lateral view, prominent grooves and ridges present on the half of the internal mould closest to the sub-apical margin slope obliquely, sub-parallel to the supra-apical surface. Similar ridges on the sub-apical surface of *Sermeqiconus polaris* are confined to the sub-apico-lateral areas and run parallel to the sub-apical surface (Fig. 11C). Partial phosphate coating of the outer surface of the shell near the supra-apical margin in some specimens from the Bastion Formation shows weak traces of radial ribs reminiscent of *Sermeqiconus* (Skovsted 2004, fig. 6G).

Genus *Vendrascospira* gen. nov.

Type species. *Vendrascospira troelseni* gen. et sp. nov.

Derivation of name. For Michael J. Vendrasco in recognition of his studies of Cambrian molluscs.

Fig. 11. Helcionelloids from GGU sample 218831, Henson Gletscher Formation, southern Lauge Koch Land, Miaolingian Series, Wuliuan Stage. **A, B:** *Helcionella*? sp., PMU 39209, dorsal (A) and apico-dorsal (B) views. **C, D:** *Sermeqiconus polaris* (Peel, 2021d), PMU 39210, internal mould in oblique lateral (C) and apico-dorsal (D) views. Scale bars: 300 μm (A, B), 100 μm (C, D).

Diagnosis. Isostrophic, laterally compressed to oval, erect, coiled through about one quarter of a whorl, with the blunt apex lying close to the sub-apical margin, slightly overhanging the concave (in lateral view) sub-apical wall of the internal mould. Apertural margin shallowly convex in lateral view, forming a shallow median fold and emargination below the apex. Internal mould surface may develop weakly expressed comarginal rugae and constrictions.

Discussion. Vendrasco *et al.* (2010) assigned this form to *Figurina*, originally described from the Parara Formation of the Stansbury Basin of South Australia (Cambrian Series 2, Stage 4), on the basis of material from the Gowers Formation (Drumian) of the Georgina Basin. *Figurina* differs in its lower shell in which the pointed apex of the internal mould is hooked, overhanging the sub-apical margin. In *Vendrascospira* the crest of the bluntly rounded apex lies at about one quarter of the distance from the sub-apical margin to the supra-apical margin, lying within the shell periphery in dorsal view (Fig. 11A,K).

In terms of its erect and compressed shell form, *Vendrascospira* resembles some species of *Davidonia* Parkhaev, 2017, proposed as a replacement name for the pre-occupied *Mackinnonia* Runnegar in Bengtson *et al.*, 1990 (see discussion in Peel 2021d, p. 26). While the outer surface of *Davidonia* is smooth, the internal surface is marked by prominent comarginal ridges that produce corresponding channels on the internal mould (Bengtson *et al.* 1990, fig. 159; Skovsted 2004, fig. 3). Such channels are not present in *Vendrascospira*, although the holotype of the type species, *Vendrascospira troelseni* gen. and sp. nov., preserves a low comarginal ruga near the apex (Fig. 11C). *Capitoconus* Skovsted, 2004, originally described from the Bastion Formation (Cambrian Series 2, Stage 4) of North-East Greenland, differs in possessing a swollen early growth stage delimited from the rest of the internal mould by a broad, shallow, constriction. Additionally, while the outer surface of *Capitoconus* varies from ribbed to smooth, the internal mould is ornamented by comarginal rugae.

Vendrascospira troelseni gen. et sp. nov.
Fig. 12A–C, E, F
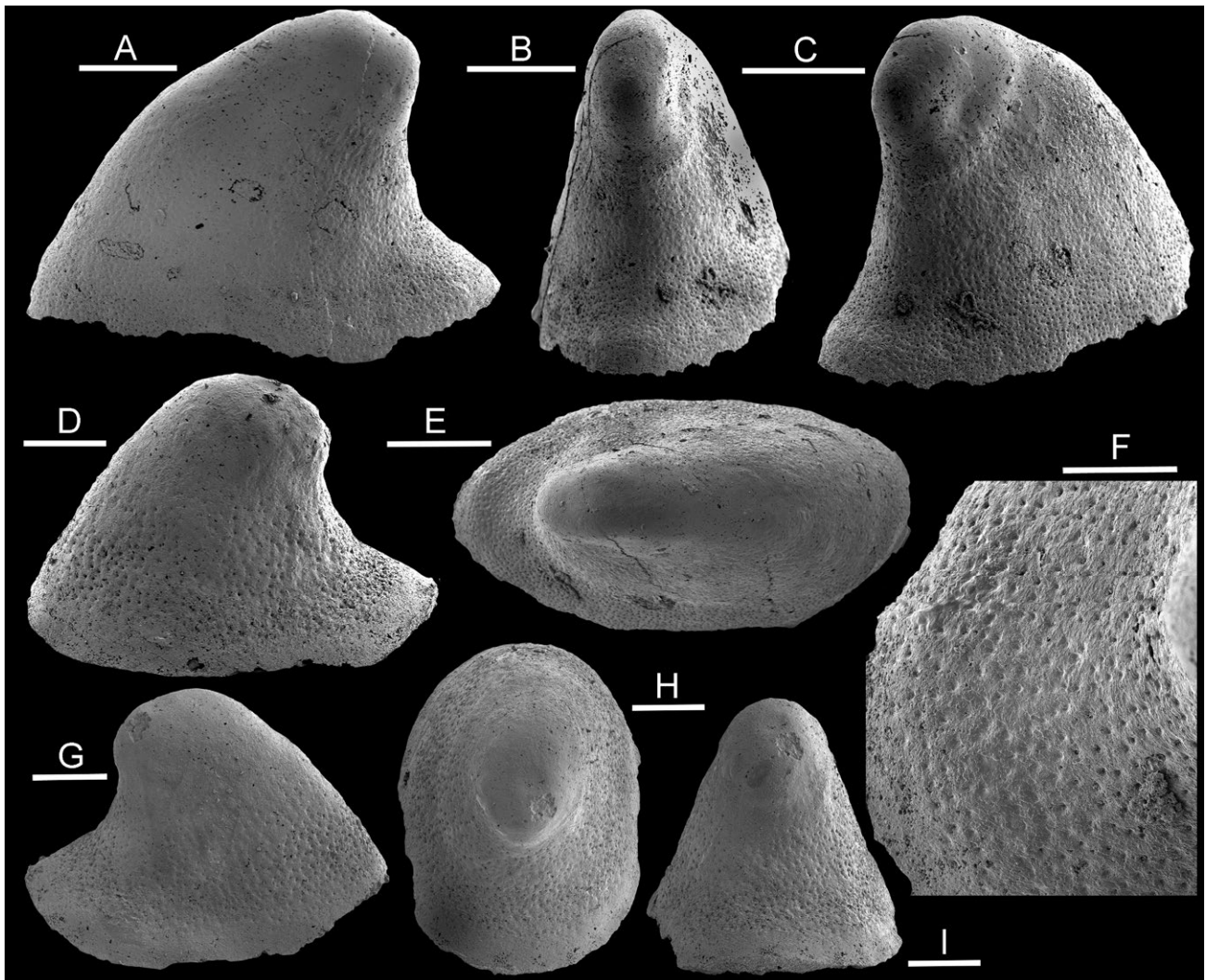
Holotype. PMU 39211 from GGU sample 271492, internal mould, Lauge Koch Land, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. PMU 39212 from GGU sample 271492, paratype.

Derivation of name. For Johannes C. Troelsen, who first collected Cambrian fossils from southern Peary Land during the 1940s (Peel *et al.* 1974).

Diagnosis. As for genus, but laterally compressed, with aperture almost twice width (Fig. 12E).

Description. The isostrophically coiled shell is laterally compressed, erect, and coiled through about one quarter of a whorl. The apex of the internal mould is bluntly rounded and lies closer to the sub-apical margin, slightly overhanging the concave (in lateral view) sub-apical wall (Fig. 12A). In lateral view, the apertural margin is shallowly convex forming a shallow median fold and emargination below the apex (Fig. 12D,G). Weakly expressed comarginal rugae and constrictions may be present near the apex of the internal mould (Fig. 12C), the surface of which is covered, except for the apical area, with fine pits (Fig. 12D,F). Characters of the external surface are not known.

Discussion. *Vendrascospira troelseni* occurs only rarely in GGU sample 271492. MacKinnon (1985) grouped several similarly coiled shells from the Tasman Formation (Guzhangian Stage) of New Zealand into *Helcionella* sp. Three smooth specimens (MacKinnon 1985, fig. E–L) are similar to *Vendrascospira* in terms of height and the bluntly rounded apex, but MacKinnon (1985) stated that larger specimens developed transverse rugae. Such rugae are have not been seen in the North Greenland material. MacKinnon (1985) commented that the surface of his material was finely tuberculate but the North Greenland material (excluding the smooth initial growth stage) of the holotype and all the marginal areas of the paratype (Fig 11D, G–I) is finely pitted.

The apex in internal moulds of *Davidonia taconica* (Landing & Bartowski, 1996), as illustrated by Peel (2021d) from the Aftenstjernesø Formation (Cambrian Series 2, Stage 4) of northern Lauge Koch Land, barely protrudes beyond the line of the straight sub-apical wall, in contrast to *Vendrascospira troelseni*. Additionally, comarginal channels are well-developed distally, although typically absent in *Vendrascospira troelseni*. Specimens of *Davidonia taconica* illustrated by Skovsted (2004) from the Bastion Formation of North-East Greenland, and by Landing & Bartowski (1996) from the Browns Pond Formation of New York State, have a more steeply inclined supra-apical surface and more strongly developed channeling of the surface of the internal mould than the specimens from northern Lauge Koch Land (Peel 2021c).

Vendrascospira troelseni resembles *Parailsanella sayutinae* Parkhaev, 2004 from the Bystraya Formation (Botoman Stage; Cambrian Series 2, Stage 4) of the Transbaikal region (Parkhaev 2004), but has a more

rounded apex and lacks comarginal rugae. Specimens referred to *Mellopegma uslonica* Parkaev, 2004 from the Botoman part of the Emyaksin Formation have a pointed apex and greater lateral compression (Kouchinsky *et al.* 2015). The latter specimens, and specimens illustrated by Vendrasco *et al.* (2011) are taller and with a more overhanging apex than the elongate specimens described by Parkhaev (2004) from the Bystraya Formation.

Vendrascospira frykmani gen. et sp. nov.
Fig. 10I–L

Holotype. PMU 39208 from GGU sample 271492, internal mould, Lauge Koch Land, Henson Gletscher Formation, Cambrian, Miaolingian Series, Wuliuan Stage.

Derivation of name. For Peter Frykman, with thanks for his companionship in the field and help in the collection of material.

Diagnosis. Species of *Vendrascospira* with width of oval aperture about four fifths of length.

Description. The isostrophical shell is oval in plan view, with width about four fifths of length, and coiled through about a quarter of a whorl. The apex of the internal mould is bluntly rounded and lies close to the sub-apical margin (Fig. 10J). The surface of internal mould lacks comarginal rugae and is finely pitted (Fig. 10L). The apex displays an irregular pattern of closely spaced, low tubercles. Characters of the shell exterior are not known.

Fig. 12. *Vendrascospira troelseni* gen. et sp. nov., from GGU sample 271492, internal moulds, upper Henson Gletscher Formation, southern Lauge Koch Land, Miaolingian Series, Wuliuan Stage. **A–C, E, F:** PMU 39211, holotype in lateral (A), sub-apical (B), oblique lateral (C) and dorsal (E) views, with detail of sub-apical margin (F). **D, G–I:** PMU 39212, paratype in lateral (D, G) and sub-apical (H, I) views. Scale bars: 200μm (A–C, E), 100 μm (D, G–I), 50 μm (F).

Discussion. The apertural margin is not preserved in the single specimen of *Vendrascospira frykmani* from GGU sample 271492. It is distinguished from *Vendrascospira troelseni* by its less laterally compressed form and oval aperture in plan view (compare Fig. 10J with Fig. 12E). The conspicuous pattern of low tubercles on the apical area of *Vendrascospira frykmani* (Fig. 10I,J) is very weakly developed in the paratype of *Vendrascospira troelseni* (Fig. 12D).

Family Stenothecidae Runnegar & Jell, 1976

Genus *Mellopegma* Runnegar & Jell, 1976

Type species. Mellopegma georginense (= *georginensis*) Runnegar & Jell, 1976, Currant Bush Limestone (reassigned in part to the Gowers Formation (Miaolingian Series, Drumian Stage) of Queensland; see discussion in Vendrasco *et al.* 2010).

Discussion. Mellopegma was first noted from North Greenland by Peel (1986) from the Ekspedition Bræ Formation (Drumian Stage; Fig. 1C) and subsequently described from the Henson Gletscher Formation (Cambrian Series 2, Stage 4) by Peel *et al.* (2016). A detailed review of the systematics, shell structure and ecology of *Mellopgema* species was given by Vendrasco *et al.* (2011).

Mellopegma schizocheras Vendrasco, Kouchinsky, Porter & Fernandez, 2011
Fig. 14A–F, H–J, M–O

2010 *Mellopegma schizocheras* Vendrasco, Kouchinsky, Porter & Fernandez, 2011, p. 9, figs 7.1–7.2, 8–9.

Figured material. PMU 39219 – PMU 39225 from GGU sample 271492, southern Lauge Koch Land.

Other material. More than 100 specimens from GGU sample 271492; uncommon in GGU sample 271718.

Description. Isostrophic, elongate, laterally compressed, with faint, variable, comarginal rugae on the internal mould that are obscure near the sub-apical and supra-apical margins and across the dorsum. Apex of internal mould bluntly rounded in lateral view (Fig. 14M), slightly bulbous in dorsal view (Fig. 14A,D), although it may seem sharp due to an apical tubercle (Fig. 14E,I). Supra-apical surface uniformly convex in lateral view with the concave sub-apical surface extended distally, becoming almost parallel with the dorsum (Fig. 14C,H). The convex apertural margin, in lateral view, may account for half of the total height (Fig. 14H,J,M). In apertural view, the aperture narrows medially (Fig. 14N) such that lateral areas of the shell may be slightly concave (Fig. 14J).

Tubercles are variably distributed over much of the surface of internal moulds, sometimes in comarginal bands (Fig. 14H), but typically they are most common along the sub-apical and supra-apical margins, including the apex (Fig. 14D), and along the rugae. Between tubercles, the internal mould surface is usually smooth, but it may be locally pitted (Fig. 14J) or with very fine papillae or ridges (Fig. 14C).
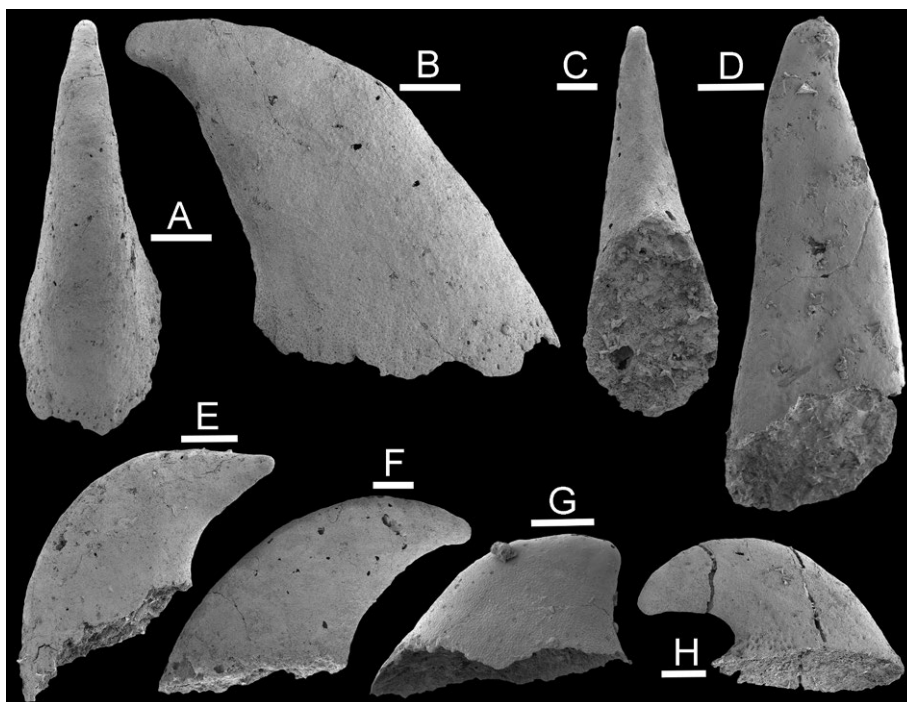
Fig. 13. Helcionellids, internal moulds from the Henson Gletscher Formation, Miaolingian Series, Wuliuan Stage. GGU sample 271718 (Løndal) unless stated. **A–C, E–H:** helcionellids spp. indet. **A, B:** PMU 39213, dorsal (A) and lateral (B) views. **C, F:** PMU 39214, sub-apical (C) and lateral views. **E:** PMU 39215, lateral view. **G:** PMU 39216 from GGU sample 271492, southern Lauge Koch Land, lateral view. **H:** PMU 39217, lateral view. **D:** '*Obtusoconus*' sp., PMU 39218, lateral view showing sigmoidal form. Scale bars: 200 *μ*m except G (300 *μ*m).

Discussion. Vendrasco *et al.* (2011) noted that *Mellopegma schizocheras* and the type species *Mellopegma georginense* Runnegar & Jell, 1976 occurred together in the Gowers Formation but ruled out that they were ontogenetic variants of the same species or sexual dimorphs. Evidence of lamellar shell structures rep-
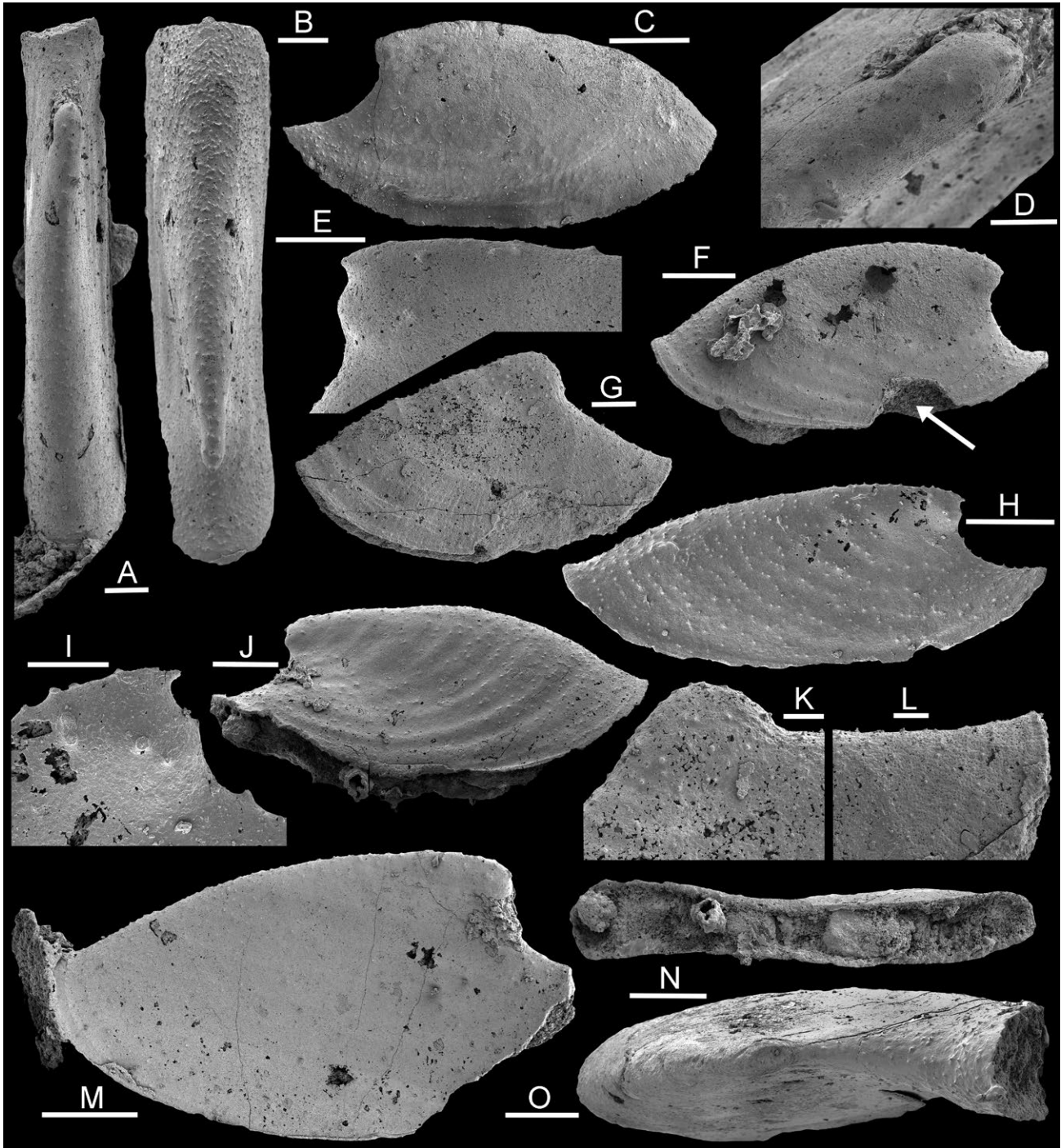
Fig. 14. *Mellopegma*, internal moulds from GGU sample 271492, southern Lauge Koch Land, upper Henson Gletscher Formation, Miaolingian Series, Wuliuan Stage. **A–F, H–J, M–O:** *Mellopegma schizocheras* Vendrasco, Kouchinsky, Porter & Fernandez, 2011. **A, D, M:** PMU 39219, dorsal (A) and lateral (M) views, with detail of apex (D). **B:** PMU 39220, dorsal view. **C, O:** PMU 39221, lateral (C) and oblique dorsal (O) views. **E:** PMU 39222, apex in lateral view. **F:** PMU 39223, lateral view with pre-fossilization fracture in apertural margin (arrow). **H, I:** PMU 39224, lateral view (H) with detail of apex (I). **J, N:** PMU 39225, lateral (J) and apertural view (N). **G, K, L:** *Mellopegma* sp., PMU 39226, lateral view (G) with details of apex (K) and sub-apical margin (L). Scale bars: 200 μm (C, F, H, J, M, N), 100 μm (A, B, G, O), 50 μm (D, E, I, K, L).

licated in the surface of internal moulds is generally absent, although a rudimentary pattern may occur locally (Fig. 14I). Vendrasco *et al.* (2011) described a polygonal network reflecting the imprint of prismatic shell structure in the sub-apical and distal supra-apical areas of internal moulds of *Mellopegma schizocheras*. Such structures are rarely visible in available material, where the surface is often very finely papillate.

Vendrasco *et al.* (2011) summarized observations by Kouchinsky (2000a), Parkhaev (2006) and Feng & Sun (2006) concerning tubercles rising perpendicular from the surface of the internal moulds in helcionelloids that were interpreted as pores entering into, or passing through, the shell. Comparable tubercles are widely and variably distributed in specimens of *Mellopegma schizocheras* from GGU sample 271492. They are often prominent on the apical area (Fig. 14B,E,I) and the sub-apical and supra-apical margins (Fig. 14J,O), but some specimens show tubercles in comarginal rows (Fig. 14H). Individual tubercles are usually conical in shape, with rounded apices, but some are truncated suggesting termination at a shell surface (Fig. 14I).

Mellopegma cf. *georginense* **Runnegar & Jell, 1976**
Figs 15A

Figured specimens. PMU 39227 from GGU sample 271718, Løndal.

Discussion. Mellopegma georginense was originally described by Runnegar & Jell (1976) from the Currant Bush Limestone of Queensland (reassigned in part to the Gowers Formation, Drumian Stage, by Vendrasco *et al.* 2010). It is distinguished from *Mellopegma schiz-* *ocheras*, with which it occurs in the Gowers Formation (Vendrasco *et al.* 2010), by its more prominent comarginal rugae that are continuous around the shell margins and across the dorsum (Fig. 15A), as is the case in an apical fragment illustrated by Peel *et al.* (2016, fig. 13N) from older strata of the Henson Gletscher Formation in Løndal (Cambrian Series 2, Stage 4, *Ovatoryctocara granulata* beds). The single large specimen from GGU sample 271718 placed here preserves fine radial ridges on the supra-apical surface close to the apex (Fig. 15A, arrow) and a coarse, tuberculate, prismatic pattern in more distal areas.

Specimens from late Cambrian Stage 4 strata at Ville Guay, Québec, assigned to *Mellopegma georginense* by Landing *et al.* (2002, fig. 8.1, 8.2), are closely similar to the earliest growth stage of the Henson Gletscher Formation specimen (Fig. 15A). The much greater length and curved ventral profile of the latter specimen reflects its later ontogenetic stage. Caron *et al.* (2014, supplementary fig. 6r) illustrated a single specimen from the Burgess Shale Formation of Canada that is also comparable in shape to the early growth stages of the specimen from the Henson Gletscher Formation (Fig. 15A), although the comarginal rugae are less strongly expressed in the latter internal mould.

Mellopegma chelata **(Skovsted, 2006b)**
Fig. 15B–D

2006b *Anabarella chelata* Skovsted, p. 489, fig. 2A–E.

Figured material. PMU 39228 from GGU sample 271718, Løndal.
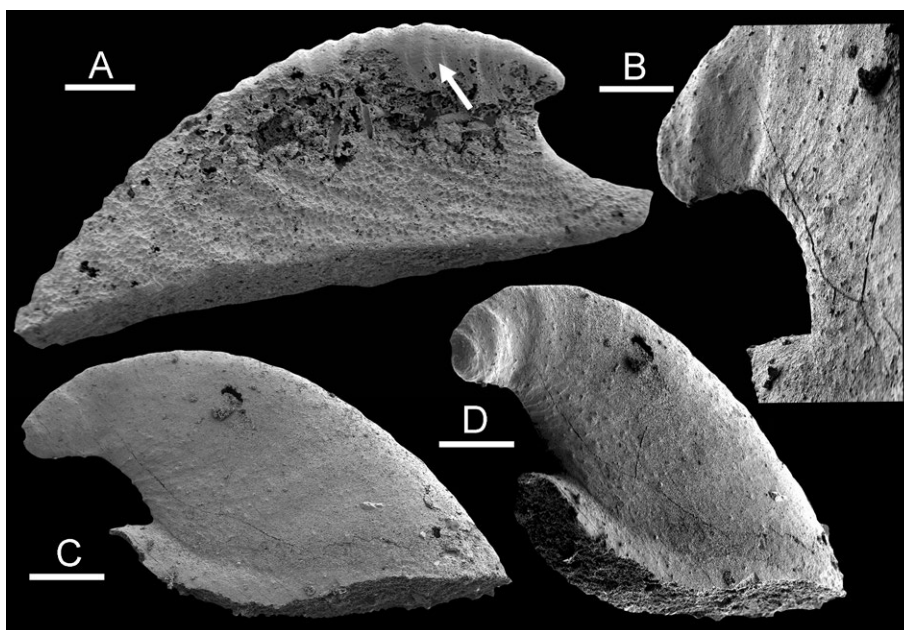
Fig. 15. *Mellopegma*, internal moulds from GGU sample 271718, Løndal, upper Henson Gletscher Formation, Miaolingian Series, Wuliuan Stage. **A:** *Mellopegma* cf. *georginense* Runnegar & Jell, 1976, PMU 39227, lateral view. **B–D:** *Mellopegma chelata* (Skovsted, 2006b), PMU 39228 from GGU sample 271718, in lateral (C) and apico-lateral (D) views, with detail of sub-apical surface (B). Scale bars: 300 *μ*m (A), 100 *μ*m (C, D), 50 *μ*m (B).

Discussion. Mellopegma chelata from the basal Emigrant Formation of Nevada (Cambrian Series 2, Stage 4; upper Dyeran) resembles *Mellopegma simesi* (MacKinnon, 1985), originally described from the Tasman Formation (Guzhangian Stage) of New Zealand (MacKinnon 1985), but has a much lower shell in lateral aspect (Fig. 15C). Specimens of *Mellopegma simesi* illustrated from New Zealand by MacKinnon (1985), from Queensland by Vendrasco *et al.* (2011) and by Peel *et al.* (2016), the latter from the Henson Gletscher Formation (Cambrian Series, Stage 4) in Løndal, show greater convexity of the supra-apical surface in lateral view and have a hooked apex.

The single internal mould from GGU sample 271718 displays an incipient pegma at the angular junction between the sub-apical surface and the protruding sinuate marginal field (Fig. 15C, D). A shallow comarginal channel, representing a thickening of the shell interior, extends from the deepest point of this pegma towards the distal supra-apical margin. Constrictions and rugae on the apical area suggest periodic flaring of the aperture in the juvenile shell. Fine tubercles and traces of comarginal growth lines are present on the subapical surface.

Mellopegma sp.
Fig. 14G, K, L

Figured material. PMU 39226 from GGU sample 271492, Lauge Koch Land.

Discussion. The rounded apex of several specimens from GGU sample 271492 forms the highest point on the dorsal surface (Fig. 14G), unlike the dominant, co-occurring specimens of *Mellopegma schizocheras* (Fig. 14C,H,J), and may suggest comparison to *Stenotheca* Salter *in* Hicks, 1872, although the type species of that genus is poorly known (Vendrasco *et al.* 2011). However, the tubercles and fine pits on the internal mould favour assignment to *Mellopegma*. The supra-apical and sub-apical slopes are flattened, and almost equal in inclination when viewed in lateral aspect (Fig. 14G). In addition to tubercles and the finely pitted intervening surface (Fig. 14G,K,L), these specimens show radial ridges and traces of acute, but wrinkled, comarginal growth lines that may reflect the periostracum. Similar radial ridges and growth lines were illustrated by Vendrasco *et al.* (2011, fig. 5.15, 5.18).

Family uncertain

Genus *Erugoconus* gen. nov.

Type species. Erugoconus acuminatus gen. et sp. nov., from the Henson Gletscher Formation of North Green-

land. Cambrian, Miaolingian Series, Wuliuan Stage.

Derivation of name. From the Latin 'erugo' meaning without wrinkles, relating to the smooth shell.

Diagnosis. Isostrophic, slowly expanding cone coiled through slightly more than one quarter of a whorl. Laterally compressed, with width of the oval aperture about two thirds of its length. Protoconch small on internal mould, bulbous. Early growth stages slender and only slightly coiled, considerably overhanging the sub-apical margin. External surface seemingly smooth. Internal surface smooth, without comarginal rugae. Internal mould with a pair of deep channels on the sub-apical surface in late growth stages.

Discussion. The low rate of whorl expansion and rapid divergence of the logarithmic spiral of the shell in *Erugoconus* produce a widely open-coiled shell in which the apex strongly overhangs the subapical margin. Early growth stages have a tall, almost conical form but curvature increases with passage into the latest growth stage. In this respect, *Erugoconus* is clearly distinct from the tightly coiled hyolith *Protowenella* with which it occurs (Peel 2021a; Fig. 5A–D).

In lateral view, *Erugoconus* is similar in curvature to specimens from the Tommotian regional stage (Cambrian Stage 2) of the Siberian Platform assigned to *Ceratoconus* Chen & Zhang, 1980 by Missarzhevsky (1989), Rozanov *et al.* (2010) and Kouchinsky *et al.* (2017), but these are more strongly curved than the tall Chinese specimens illustrated by Chen & Zhang (1980, pl. 1, figs 29–32). However, the shell of *Ceratoconus* is more slowly expanding and less laterally compressed than *Erugoconus*. *Ceratoconus* Chen & Zhang, 1980 is a junior homonym of *Ceratoconus* Borgmeier, 1928, a parasitic dipteran from South America (Borgmeier 1928; Brown *et al.* 2017). *Masculuconus* Feng, Sun & Qian, 2000 from the Meishucunian (Cambrian Stage 2) of Yunnan, China, has similar curvature to Chinese specimens of *Ceratoconus* but differs by its greater rate of shell expansion and transversely elliptical aperture; it is much less strongly coiled than *Erugoconus*.

Mellopegma simesi (MacKinnon, 1985), as illustrated by Peel *et al.* (2016, fig. 14D–G) from the Henson Gletscher Formation (Cambrian Stage 4) in Løndal, has an extended and slender early growth stage overhanging the sub-apical margin, as in *Erugoconus acuminatus*, but differs in the proportionally longer and narrower aperture and incipient pegma.

Genus incertum et species incerta B of Geyer (1986, pl. 3, fig. 45) from Morocco displays similar curvature to *Erugoconus*, with a strongly overhanging apex, but the exterior is ornamented with rugae that are also present in a subdued form on the internal mould.

***Erugoconus acuminatus* gen. et sp. nov.**
Fig. 16E–N

Derivation of name. From the Latin 'acuminatus' refer-ring to the pointed apex.

Holotype. PMU 39232 from GGU sample 271718, Hen-son Gletscher Formation, Løndal, western Peary Land,

North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. PMU 39230, PMU 39231, PMU 39233 – PMU 39235, paratypes, from GGU sample 271718.

Diagnosis. As for genus.
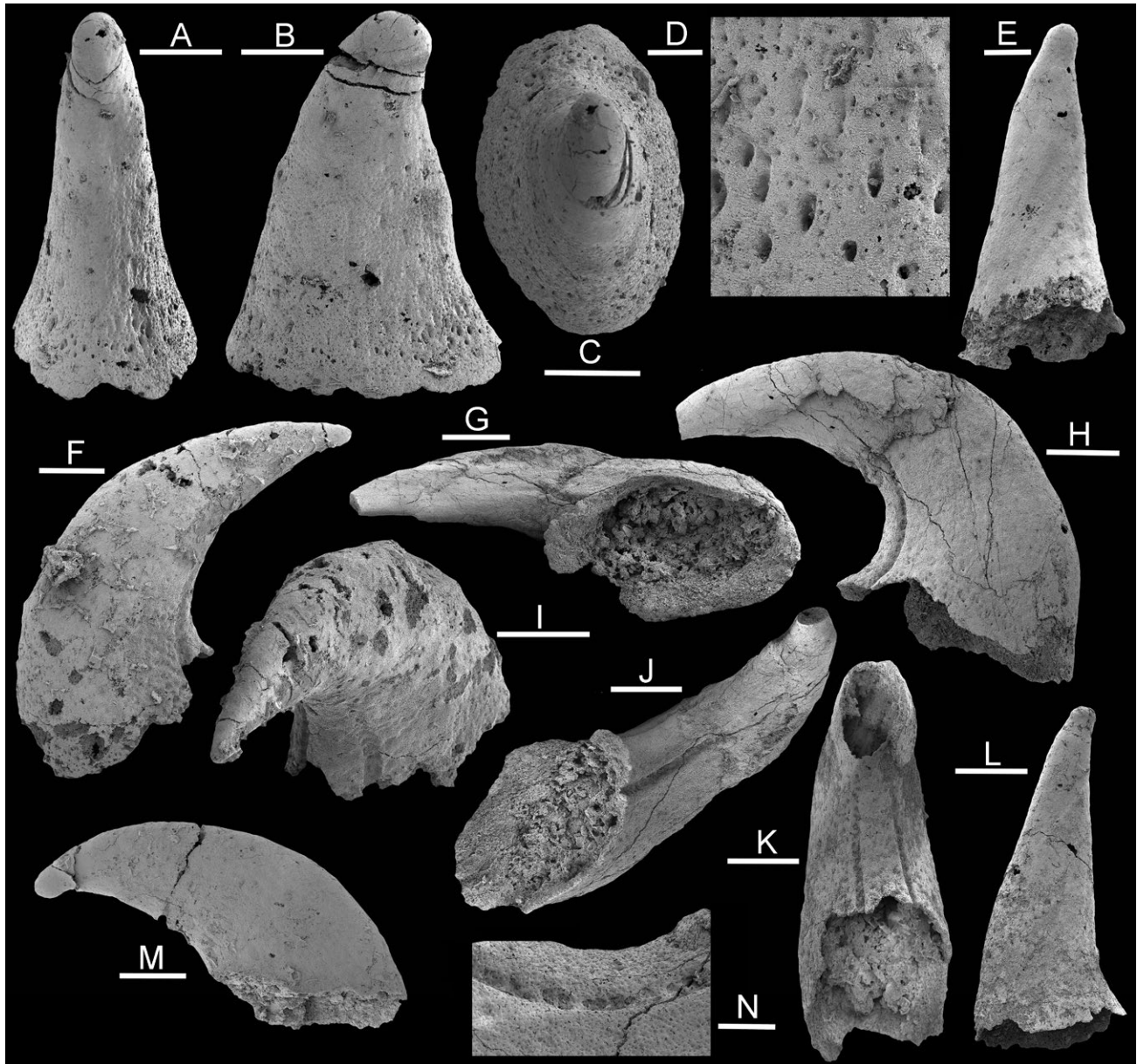
Fig. 16. Helcionellids, internal moulds from the Henson Gletscher Formation, Miaolingian Series, Wuliuan Stage. GGU sample 271718, Løndal. **A–D:** *Tavseniconus erectus* gen. et sp. nov., PMU 39229, holotype, in sub-apical (A), lateral (B) and apical (C) views, with detail of pitted surface (D). **E–N:** *Erugoconus acuminatus* gen. et sp. nov. **E:** PMU 39230, lateral view of early growth stage. **F, I:** PMU 39231, lateral (F) and oblique lateral view with sub-apical grooves (I). **G, H, J, N:** PMU 39232, holotype, in apertural (G), lateral (H) and oblique sub-apical (J) views, with detail of sub-apical groove (N). **K:** PMU 39233, sub-apical view showing grooves. **L:** PMU 39234, lateral view of early growth stage. **M:** PMU 39235, lateral view. Scale bars: 400 *μ*m (F–M), 200 *μ*m (A–C, E), 100 *μ*m (N), 20 *μ*m (D).

Description. Isostrophic, with the slowly expanding cone coiled through slightly more than one quarter of a whorl. Laterally compressed, with width of the oval aperture about two thirds of its length. The protoconch as preserved on internal mould is small and slightly inflated, with a shallow constriction separating it from the following growth stage (Fig. 16E). Early growth stage is slender and with only slight curvature, but the early part of the shell considerably overhangs the sub-apical margin by a distance exceeding the length of the aperture in available material (Fig. 16F,H,M). The external surface is seemingly smooth, as is the internal mould, without comarginal rugae. A pair of deep channels is present on the sub-apical surface of the internal mould in late growth stages. Surface of internal mould with abundant closely spaced fine pits in later growth stages. Larger pits close to the apertural margin on the internal mould, are directed obliquely in and towards the aperture (Fig. 16H).

Discussion. *Erugoconus acuminatus* is very common in GGU sample 271718. The slender early growth stage may develop a slight angulation on the sub-apical surface as it passes into the later shell (Fig. 16L). In its form it is reminiscent of tall specimens described as *Obtusoconus foliaceus* MacKinnon, 1985 from the Tasman Formation (Guzhangian Stage) of New Zealand, which Parkhaev (2001b) referred to *Anuliconus* Parkhaev, 2001b, although these show substantial variation in the rate of expansion and curvature of the shell cone when compared to the early stages of the holotype of *Erugoconus acuminatus*. Most of MacKinnon's (1985) specimens have a lamellose external ornamentation or pronounced comarginal rugae (MacKinnon 1985, fig. 2) not known in available material from Greenland.

Genus novum et species nova? G of Geyer (1986, pl. 2, fig. 27) from the Wuliuan part of the Jbel Wawrmast Formation of the Lemdad Syncline of Morocco, has a longer shell in lateral aspect than the early growth stage of *Erugoconus acuminatus*. It is here assigned to *Tavseniconus* gen. nov. *Tavseniconus erectus* gen. et sp. nov., from GGU sample 271718 differs from the early stages of *Erugoconus acuminatus* in its greater length in lateral view and more rounded apical termination (Fig. 16A–D).

Genus *Tavseniconus* gen. nov.

Type species. *Tavseniconus erectus* gen. et sp. nov., from the Henson Gletscher Formation of North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Derivation of name. From Hans Tavsen Iskappe, the prominent ice field lying north-west of the type locality in Løndal (Fig. 1A).

Diagnosis. Isostrophic, tall, laterally compressed helcionelloid with a sub-conical shell; the rounded apex slightly overhanging the sub-apical surface.

Discussion. Genus novum et species nova? G of Geyer (1986, pl. 2, fig. 27), a mainly exfoliated internal mould about 3 mm tall from the lower part (of Wuliuan age) of the Lemdad Syncline) of the High Atlas, Morocco, has a closely similar shell form and can be assigned to *Tavseniconus*.

Tavseniconus erectus gen. et sp. nov.
Fig. 16A–D

Holotype. PMU 39229 from GGU sample 271718, internal mould, Løndal, Henson Gletscher Formation, western Peary Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Derivation of name. With reference to the upright form.

Diagnosis. As for genus.

Description. The upright, tall, slowly expanding isostrophic shell is slightly curved, such that the rounded apex of the internal mould slightly overhangs the sub-apical surface, but not the sub-apical margin. Length is about two thirds of height in lateral view (Fig. 16B). In plan view, apertural width is about two thirds of length (Fig. 16C). The surface of the internal mould is covered by fine pits except around the smooth apex. Larger, deeper pits close to the apertural margin slope obliquely inwards and down towards the aperture. External ornamentation not known.

Discussion. As with many other internal moulds from GGU sample 271718, the holotype internal mould of *Tavseniconus erectus* has a smooth apical area while the flanks are covered by closely spaced fine pits (Fig. 16A–D). Scattered, larger pits located close to the preserved apertural margin slope obliquely in and down towards the apertural plane (Fig. 16D), a pattern also seen in *Erugoconus acuminatus* gen. et sp. nov. (Fig. 16H).

The specimen illustrated by Geyer (1986, pl. 2, fig. 27) as Genus novum et species nova? G, from the Lemdad Syncline of Morocco, is here referred to *Tavseniconus*. In lateral perspective, it has a longer shell (height:length ratio of 1.2) than the holotype of *Tavseniconus erectus* (1.4).

Genus *Obtusoconus* Yu, 1979

Type species. *Obtusoconus paucicistatus* Yu, 1979 from the early Cambrian of Hubei, China.

‘*Obtusoconus*’ sp.
Fig. 13D

Figured material. PMU 39218 from GGU sample 271718, Løndal.

Discussion. In addition to the type species and other species illustrated by Yu (1979), several early Cambrian species were referred to *Obtusoconus* by Esakova & Zhegallo (1996) and Vasileva (1990). The single slender internal mould with an oval cross-section from GGU sample 271718 retains the slightly sigmoidal form characteristic of *Obtusoconus*, but no trace of the prominent comarginal ornamentation is seen in most described species. The swollen protoconch overlies a shallowly convex sub-apical surface, while the supra-apical surface is initially convex before becoming shallowly concave (Fig. 13D). However, assignment of the Greenland specimen to ‘*Obtusoconus*’ is just a matter of convenience. It is not inconceivable that it represents the early growth stage of a species of *Erugoconus* gen. nov., although the sigmoidal form is not seen in *Erugoconus acuminatus*.

Tavseniconus erectus has a similar overall shape to ‘*Obtusoconus*’ sp. but its shell has a greater rate of whorl expansion in lateral perspective (Fig. 16B). The pits in the surface of the internal mould of *Tavseniconus erectus* (Fig. 16D) have not been observed in ‘*Obtusoconus*’ sp. (Fig. 13D).

Obtusoconus foliaceus MacKinnon, 1985 from the Tasman Formation (Guzhangian Stage) of New Zealand, shows substantial variation in the rate of expansion and curvature of the shell. Parkhaev (2001b) referred *Obtusoconus foliaceus* to *Anuliconus* but this assignment is rejected. Most of MacKinnon's (1986, fig. 2) illustrated specimens resemble *Tavseniconus*, but one shows a slightly sigmoidal, but more rapidly expanding shell than ‘*Obtusoconus*’ sp. (MacKinnon 1985, fig. 2B).

Acknowledgements

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