Mollusc fauna of the Early Cambrian Bastion Formation of North-East Greenland

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A diverse mollusc fauna from the Bastion Formation (Early Cambrian, middle Dyeran Stage) of North-East Greenland includes fifteen species (thirteen helcionelloids and two bivalves), adding considerable detail to the known fossil record of Early Cambrian molluscs from Laurentia. The occurrence of secondarily phosphatized shell surfaces together with phosphatic internal moulds in acid resistant residues allows new morphological details to be observed in several taxa. The fauna shows affinity to contemporaneous faunas from the Taconic allochthon of the eastern United States, but also to mollusc faunas of South Australia, China and Europe. The following new helcionelloid taxa are described: *Capitoconus inclinatus* n. gen. and n. sp. *Capitoconus artus* n. sp., *Figurina groenlandica* n. sp. and *Latouchella ostenfeldense* n. sp.

Key words: Mollusca, Helcionelloida, Bivalvia, Biostratigraphy, Dyeran, Botoman, Early Cambrian, Greenland.

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Mollusc faunas from Lower Cambrian successions around the world have been intensively studied during the last 35 years, and faunas from Siberia (Rozanov *et al.* 1969; Missarzhevsky 1989), Kazakhstan (Missarzhevsky & Mambetov 1981), Mongolia (Esakova & Zhegallo 1996), China (Yu 1987; Qian & Bengtson 1989), Europe (Kerber 1988; Elicki 1994, 1996; Gubanov *et al.* 2004) and Australia (Bengtson *et al.* 1990, Gravestock *et al.* 2001) are relatively well known. In contrast, our knowledge of Early Cambrian molluscs from Laurentia is limited. Modern techniques of acid maceration of limestone samples to retrieve molluscs and other small shelly fossils, complementing earlier studies of hand specimens (e.g. Billings 1871; Walcott 1886; Shaler & Foerste 1888; Lochman 1956), have not yet been widely applied in Laurentia and only a few studies of this type of material have been published. Voronova *et al.* (1987) described a fauna including molluscs from the Mackenzie mountains in north-west Canada while Landing & Bartowski (1996) and Landing *et al.* (2002) described faunas from the Taconic Allochthon of New York State and Quebec respectively. Reports concerning occurrences of single species have also been published (Runnegar & Pojeta 1980; Peel 1979, 1980, 1988a, 1989; Gubanov *et al. in press*), as well as studies of Middle Cambrian forms (Peel 1988b; Geyer 1994). This report concerns a well preserved and diverse mollusc fauna from the late Early Cambrian Bastion Formation (middle Dyeran Stage, Botoman equivalent) discovered during an ongoing investigation of the Early Cambrian shelly faunas of North-East Greenland. More than 1800 specimens belonging to 15 mollusc species were studied. Two bivalve species were found, but the fauna is dominated by 13 helcionelloid molluscs.

Material and methods

The specimens described herein were mainly derived from carbonate rock samples collected in 1988 by J.S. Peel and M.P. Smith during fieldwork by the Geological Survey of Greenland (GGU) in northern Hudson Land (Fig. 1A). The samples were collected from a reference section described by Cowie & Adams (1957), in the south-western part of the Albert Heim Bjerge region (Fig. 1B), and from two previously undescribed sections at the northern tip of C.H. Ostenfeld Nunatak, within Wordie Gletscher, 35 km to the north (Fig. 1B). Parts of the latter sections are badly exposed and detailed stratigraphical correlation between the two areas is difficult.

Acid resistant residues of two rock samples collected during Christian Poulsen's (1932) investigation of the Early Cambrian faunas of North-East Greenland, deposited in the Geological Museum in Copenhagen, also yielded molluscs. Sample 879 was collected from the west coast of Ella Ø, and sample 842 from Hyolithus Creek in Andrée Land, both areas lying south of Hudson Land. No detailed stratigraphical information is available for this material. Mollusc specimens described by Poulsen (1932) were also examined (ten specimens of the bivalve *Fordilla troyensis* Barrande, 1881 and a single specimen of *Helcionella cingulata* Cobbold, 1921). The latter specimen has apparently been damaged and only fragments remain. It may represent *Capitoconus inclinatus* n. gen. and n. sp. described below.

All rock samples from the upper Bastion Formation were treated with buffered 10% acetic acid to retrieve acid-resistant microfossils. The resulting residues were sieved and the heavy mineral fraction separated using sodium polytungstate (procedure described by Schiøler 1989). Selected acid-isolated specimens were gold-coated and examined using a Phillips Scanning Electron Microscope.

Geological setting

The fossiliferous Cambrian rocks of the Bastion Formation form part of a thick succession of shallow marine Proterozoic to Ordovician sediments deposited on the Laurentian shelf prior to the Caledonian orogeny. The uppermost Vendian sediments of North-East Greenland are truncated by an erosional unconformity (Stouge *et al.* 2001) and are overlain by the coarse siliciclastic Kløftelv Formation containing Cambrian trace fossils (Hambrey & Spencer 1987). The Kløftelv Formation is overlain by the fossiliferous Bastion Formation of late Early Cambrian age. The Bastion Formation (total thickness 150 m at the Albert Heim Bjerge locality, Cowie & Adams 1957) is dominated by glauconite-rich sands and silt in the lower part and by shale with minor carbonate rocks in the upper part. The sequence varies slightly between the Albert Heim Bjerge area and C.H. Ostenfeld Nunatak, where the shales contain less carbonate material (J.S. Peel personal communication, 2003). Body fossils have only been found in the upper part of the Bastion Formation. The overlying Ella Island Formation is dominated by limestone and carbonate sedimentation continued in the area throughout the remaining Cambrian and into the Late Ordovician (Stouge *et al.* 2001).

Molluscs in the Bastion Formation are associated with a rich fauna of Early Cambrian fossils. The brachiopods *Eoobolus priscus* (Poulsen, 1932), *Botsfordia caelata* (Hall, 1847), *Obolella crassa* (Hall, 1847), craniopsid sp. and *Mickwitzia* cf. *occidens* Walcott, 1908 have been recently redescribed (Holmer *et al.* 2002; Skovsted & Holmer 2003; Skovsted & Holmer *in press*), but trilobites, bradoriids, and hyoliths are also known (Poulsen 1932; Cowie & Adams 1957). Problematic fossil groups are represented by *Mongolitubulus* Missarzhevsky, 1977 (Skovsted & Peel 2001), *Discinella* Hall, 1872 (Skovsted 2003), coeloscleritophorans and lapworthellids.
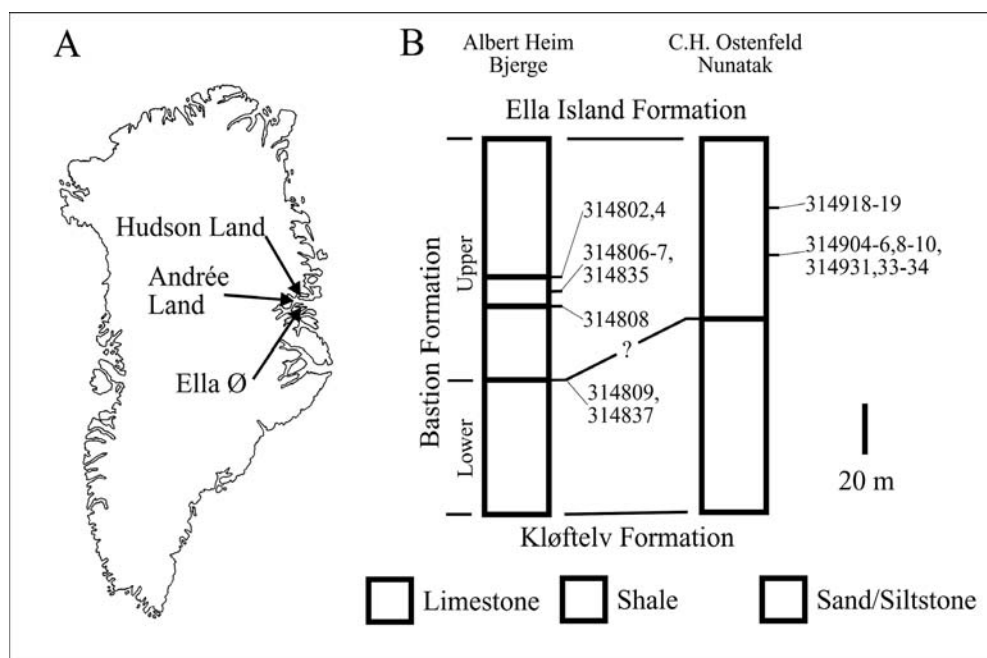

Fig. 1. – A, Map of Greenland with sampled areas indicated. B, Simplified stratigraphical column for the Bastion Formation of the Albert Heim Bjerge region and C.H. Ostenfeld Nunatak respectively, with position of samples indicated.

Species:	N	%	CHO	AHB
Pelagiella primaeva	755	40,9%	70,5%	29,5%
Mackinnonia taconica	599	32,5%	0,8%	99,2%
Latouchella ostenfeldense	113	6,1%	95,6%	4,4%
Mackinnonia rostrata	40	2,2%	5,3%	94,7%
Figurina greenlandica	34	1,8%	0%	100%
Capitoconus artus	28	1,5%	0%	100%
Anabarella australis	22	1,2%	27,3%	72,7%
Oelandia sp.	21	1,1%	0%	100%
Capitoconus inclinatus	21	1,1%	14,7%	85,7%
Helcionelloid ind.	9	0,5%	0%	100%
Asperconella troyensis	2	0,1%	0%	100%
Stenotheca sp.	1	0,1%	100%	0%
Yochelcionella sp.	1	0,1%	0%	100%
Pojetaia runnegari	188	10,2%	42,9%	57,1%
Fordilla troyensis	11	0,6%	100%	0%
Sum:	1845	100,0%	-	-

Table 1. Number of specimens (N) and proportion of the total fauna for all mollusc species. The proportion of specimens found in samples from C.H. Ostenfeld Nunatak (CHO) and Albert Heim Bjerge (AHB) is also indicated.
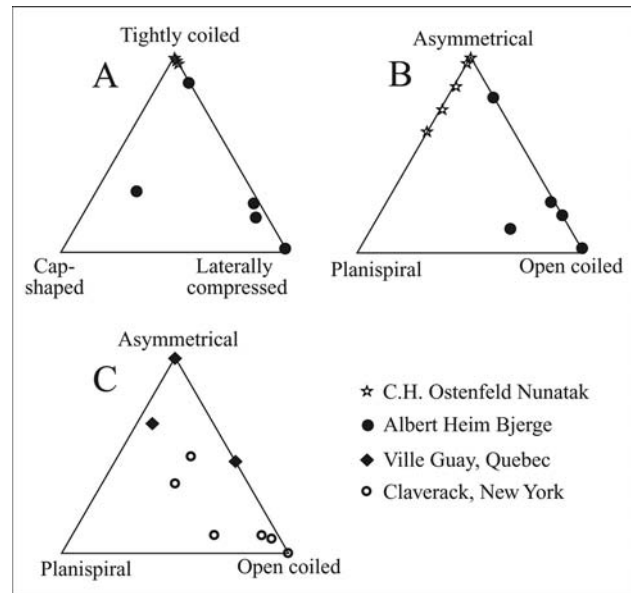

Fig. 2. Triangular diagrams illustrating the morphological composition of individual samples (helcionelloids only). A, division of helcionelloids into (1) cap-shaped, (2) tightly coiled and (3) laterally compressed forms. B and C, division into (1) tightly coiled and planispiral, (2) tightly coiled and asymmetrical and (3) open coiled forms. Diagram C is based on tables 1 and 2 of Landing et al (2002).

Discussion
Composition of fauna

In acid-resistant residues from the Bastion Formation, 1845 mollusc specimens belonging to 15 different species were found (Table 1). In addition three problematic species of possible molluscan affinity, the bivalved *Apistoconcha* sp. (six specimens) and cap-shaped fossils comparable to *Xianfengella* He & Yang, 1982 (13 specimens) and *Ocruranus* Liu, 1979 (24 specimens) were found. The latter species are not dealt with further in this paper. The four most common molluscs comprise 89.7% of all specimens (Table 1), while none of the remaining taxa are represented by more than 40 specimens (0.1–2.2% of the total fauna).

Samples from the Albert Heim Bjerge area and C.H. Ostenfeld Nunatak are markedly different in the composition of their helcionelloid faunas, although the most common species are found in both areas. The bivalve *Pojetaia runnegari* occur in similar numbers in samples from both localities. The greatest diversity of helcionelloids is found in samples from Albert Heim Bjerge, and ten out of 13 species are mainly or exclusively known from this area. The samples from C.H. Ostenfeld Nunatak contain fewer taxa and only four molluscs are found primarily in this area (Table 1 lists the proportion of specimens found at both localities). However, the main difference between the two subfaunas appear to be the abundance of species with certain morphologies. To illustrate this difference in morphological composition, samples from Greenland with 15 or more helcionelloid specimens were plotted in triangular diagrams (Fig. 2). Similar methods have been employed to illustrate ecological differences between samples of Silurian gastropods (Peel 1977) and Jurassic bivalves (Duff 1975).

Figure 2A is based on a division of Early Cambrian univalved molluscs into three morphological groups: 1, broad, cap-shaped forms (e.g. *Figurina*, helcionelloid indet.); 2, broad and tightly coiled forms (>1 whorl, whorls in contact; e.g. *Latouchella*, *Pelagiella*, *Asperconella*); 3, laterally compressed forms (e.g. *Mackinnonia*, *Capitoconus*, *Oelandia*, *Anabarella*, *Stenotheca*). This division is not unequivocal, as certain forms could be placed in more than one group (e.g. *Anabarella*, a tightly coiled and laterally compressed form, here placed in group number 3), but nevertheless probably represents a division of molluscs exploiting different ecological niches (cf. Gubanov 1998). Very few cap-shaped helcionelloids were found in the Bastion Formation and in Fig. 2B the same set of samples are plotted based on a division of helcionelloids into: 1, asymmetrical, tightly coiled (e.g. *Pelagiella*); 2, planispiral, tightly coiled (e.g. *Latouchella*, *Asperconella*, *Anabarella*); 3, erect or open coiled forms (e.g. *Mackinnonia*, *Capitoconus*, *Oelandia* etc.).

The samples from C.H. Ostenfeld Nunatak are completely dominated by tightly coiled specimens (96–

100%) and the majority of these are asymmetrically coiled (*Pelagiella*). Very few open coiled specimens are present (Fig. 2B). Samples from Albert Heim Bjerge are dominated by laterally compressed (Fig. 2A) and open coiled specimens (Fig. 2B). Tightly coiled specimens form only a small component. Two samples with aberrant compositions contain only a few specimens (N=16), but both still have higher proportions of open coiled and laterally compressed specimens than any sample from C.H. Ostenfeld Nunatak. Although no detailed sedimentological study exists, the upper Bastion Formation of C.H. Ostenfeld Nunatak contains less carbonate than in the Albert Heim Bjerge area, possibly reflecting deposition in deeper water (J.S. Peel personal communication, 2003). Although all carbonate matter in the Bastion Formation (and hence the fossils investigated here) has probably been transported prior to deposition, the differences in the helcionelloid faunas of the two areas possibly reflects real environmental differences. The majority of forms in both sub-faunas are soft bottom dwellers, but the abundance of tightly coiled forms (e.g. *Pelagiella*, *Latouchella*) in C.H. Ostenfeld Nunatak, could indicate that these molluscs were dominant in deeper water environments. The sub-fauna of Albert Heim Bjerge is instead dominated by two species of *Mackinnonia*. Mollusc faunas of the Bastion Formation from other parts of North-East Greenland (e.g. Ella Ø, Andrée Land) are not known in any detail.

Analogous patterns of morphological distribution can be observed (Fig. 2C), although less clearly, when information on roughly coeval mollusc faunas from the Taconic Allochthon is presented. Data for three samples from 'Anse Maranda' Formation of Ville Guay, Québec, and six samples from the Browns Pond Formation of Claverack, New York was derived from tables 1 and 2 of Landing *et al*. (2002). With few exceptions the sample sizes are smaller than the 15 specimens limit deployed for the Greenland material. Samples from Claverack contain, like the Bastion Formation of Albert Heim Bjerge, a relatively high proportion of open coiled and laterally flattened helcionelloids, mainly of the genus *Mackinnonia*. In contrast, samples from Ville Guay are dominated by asymmetrical and tightly coiled forms (e.g. *Pelagiella*), and thus compare best to the Bastion Formation of C.H. Ostenfeld Nunatak. Although all samples from the Taconic Allochthon were derived from debris-flow deposists (Landing & Bartowski 1996; Landing *et al*. 2002), this result seems to confirm that two types of mollusc communities (dominated by *Pelagiella* and *Mackinnonia* respectively) existed on the Early Cambrian shelf of eastern Laurentia.

Faunal comparisons

The Bastion Formation can be broadly correlated with the middle Dyeran Stage (*Bonnia-Olenellus* Zone, see Palmer 1998) of the Laurentian Lower Cambrian by the presence of *Wanneria* Walcott, 1910 and other olenellid trilobites (Palmer & Repina 1993). The closest comparison of the fauna is to the *Elliptocephala asaphoides* assemblage from the Browns Pond Formation of the Taconic Allochthon of New York State (Walcott 1886; Lochman 1956; Landing & Bartowski 1996). *Mackinnonia taconica*, *M. rostrata*, *Asperconella troyensis* (Resser, 1938) and *Fordilla troyensis* are common to both faunas. Further evidence comes from brachiopods (Skovsted & Holmer *in press*) and small shelly fossils (unpublished data). The mollusc fauna of the Bastion Formation can also be compared to undescribed faunas from the lowermost Aftenstjernesø Formation of North Greenland. *Mackinnonia taconica*, *M. rostrata*, *Asperconella troyensis* and *Pojetaia runnegari* are common to both areas (C. Atkins, personal communication 200×).

In terms of intercontinental correlation, the fauna of the Bastion Formation is probably best compared to late Early Cambrian (Botoman–Toyonian equivalent) faunas of South Australia. *Mackinnonia rostrata*, *Anabarella australis*, *Pojetaia runnegari*, *Pelagiella subangulata* and possibly *Capitoconus inclinatus* n. gen. et n. sp. are found in both areas, as are morphologically similar species of the genera *Figurina* Parkhaev in: Gravestock *et al*., 2001, *Stenotheca* Salter in: Hicks, 1872 and *Xianfengella* (Bengtson *et al*. 1990; Brock & Cooper 1993; Parkhaev in: Gravestock *et al*. 2001). This pattern is further corroborated by the presence of the brachiopod *Eoobolus priscus*, the arthropod spine *Mongolitubulus henrikseni* Skovsted & Peel, 2001, the hyolith *Microcornus petilus* Bengtson in: Bengtson *et al*., 1990 and possibly other small shelly fossils (Skovsted & Peel 2001; Skovsted & Holmer *in press*). The Bastion Formation further shares *Mackinnonia rostrata*, *Pojetaia runnegari* and possibly related species of *Figurina* with the late Early Cambrian Yutaishan Formation of Anhui Province, North China (Zhou & Xiao 1984; Li & Zhou 1986). *Mackinnonia rostrata*, *Fordilla troyensis* and the brachiopod *Botsfordia caelata* facilitate comparison to the Botoman Stage of Siberia (Pelman 1977; Jermak 1988; Kouchinsky 2000). The presence of *Capitoconus artus* n. sp., *Pojetaia runnegari* and *Anabarella australis* in eastern Germany (Elicki 1994, 1996; Parkhaev in: Gravestock *et al*. 2001), as well as species of *Latouchella* Cobbold, 1921 in England and Spain (Cobbold 1921; Gubanov *et al*. a), suggests correlation of the North-East Greenland fauna to the Early Cambrian of west Gondwana. The relatively large number of species in the Bastion Formation

fauna known from other palaeocontinents could be interpreted as support for recent suggestions of a close jutaxposition of continents in the Early Cambrian (Dalziel 1997; Brock *et al.* 2000; Gubanov 2002; Gubanov *et al.* 2004 *in press* a, b).

Systematic Palaeontology

Phylum Mollusca Cuvier, 1797

Class Helcionelloida Peel, 1991

Discussion. The majority of Early and Middle Cambrian molluscs are univalved and rapidly expanding, and can not be readily placed in any of the extant molluscan classes. The fossils are relatively small, coiled to various degrees and have usually been referred to informally as 'helcionellids'. The simple morphology, small size and often poor preservation has resulted in a number of quite different reconstructions of the animals, and hence their taxonomic affinity. Helcionelloids have been placed in the Classes Monoplacophora (Runnegar & Jell 1976; Missarzhevsky 1989; Runnegar 1996), Gastropoda (Starobogatov 1970; Golikov & Starobogatov 1988; Parkhaev 2001a, 2002) or in the extinct Helcionelloida (Peel 1991; Geyer 1994). Although probably a paraphyletic grouping (Budd & Jensen 2000), the Class Helcionelloida is supported here because of its usefulness in view of the presently unresolved nature of the Early and Middle Cambrian stem lineages of the extant mollusc groups.

Taxonomic division of the helcionelloids is controversial and a number of orders, superfamilies, families etc. has been suggested. The most recent division was put forward by Parkhaev (2002) who recognised two superfamilies and six families of the order Helcionelliformes (within the gastropod subclass Archaeobranchia). In addition Parkhaev recognised the orders Khairkhaniiformes and Pelagielliformes as closely related to and derived from the Helcionelliformes. The helcionellid superfamilies and families recognised by Parkhaev are usually defined by simple modifications of the shell. For example, the family Igarkiellidae is defined by the presence of a supra-apical 'peripheral buttress', and the superfamily Yochelcionelloidea is defined by the presence of a sub-apical 'siphonal groove'. It is recognised here that such simple modifications of the shell as a sub-apical flexure of the aperture directed towards the apex (siphonal groove or parietal train of Parkhaev 2002), or a supra-apical buttress, could very well evolve independently in different lineages living under simi-

lar conditions. Indeed, the type species of the genera *Figurina* Parkhaev in: Gravestock *et al.*, 2001 and *Mackinnonia* Runnegar in: Bengtson *et al.*, 1990 both possess a prominent sinus beneath the apex, but in specimens referred to these genera herein (*Figurina groenlandica* n. sp. and *Mackinnonia taconica*) the structure is completely, or almost completely absent. We know little about most helcionelloids, especially the forms known from internal moulds only, and until we have more information about the morphology, microstructure and variability of these molluscs, any detailed supragenetic classification is likely to be arbitrary.

Order Helcionellida Geyer, 1994

Family Helcionellidae Wenz, 1938

Genus *Mackinnonia* Runnegar in: Bengtson *et al.*, 1990

Type species. *Mackinnonia rostrata* (Zhou & Xiao, 1984) (junior synonym: *Mackinnonia davidi* Runnegar in: Bengtson *et al*, 1990).

Composition. Type species, *Mackinnonia corrugata* (Runnegar in: Bengtson *et al.*, 1990) and *M. taconica* (Landing & Bartowski, 1996).

1990   *Mackinnonia* n.gen.Runnegar in: Bengtson *et al.*, p. 233.
2001   *Mackinnonia* Runnegar in: Bengtson *et al.*, 1990 – Parkhaev in: Gravestock *et al.*, p. 175.

Discussion. Species of *Mackinnonia* combine an externally smooth or almost smooth shell with internal furrows, and internal moulds usually possess corresponding characteristic rugae with alternating furrows (Runnegar in: Bengtson *et al.* 1990). Well preserved internal moulds show a micro-ornamentation of polygonal depressions, supposedly imprints of aragonitic prisms in the original shell material (Runnegar in: Bengtson *et al.* 1990; Kouchinsky 2000). *Mackinnonia* was expanded by Parkhaev (in: Gravestock *et al.* 2001) to include *Leptostega*? *corrugata* Runnegar in: Bengtson *et al.*, 1990. For reasons that are unclear Parkhaev synonymised *L.*? *corrugata* with *Isitella plicata* Missarzhevsky, 1989 from the Botoman of Siberia. The holotype of *I. plicata* (Missarzhevsky 1989, pl. 10, fig. 7) is an internal mould of a relatively strongly coiled helcionellid mollusc without obvious similarities to *Leptostega*? *corrugata*. Consequently, *L.*? *corrugata* is here referred to as *Mackinnonia corrugata* (Runnegar in: Bengtson *et al.*, 1990).

Mackinnonia rostrata (Zhou & Xiao, 1984)
Fig. 3A–H

1984 *Mellopegma rostratum* n.sp. Zhou & Xiao, p. 132, pl. 3, figs 7–10.
1984 *Bemella costata* n.sp. Zhou & Xiao, p. 128, pl. 1, figs 7–8.
1984 *Bemella anhuiensis* n.sp. Zhou & Xiao, p. 129, pl. 1, fig. 10.
1990 *Mackinnonia davidi* n.sp. Runnegar in: Bengtson *et al.*, p. 234, fig. 159.
1994 *Mellopegma rostratum* Zhou & Xiao – Feng, Qian & Rong, p. 7, pl. 2, figs 5–9.
1996 *Mackinnonia obliqua* n.sp. Landing & Bartowski, p. 754, figs 5.10–5.16.
2000 *Mackinnonia* sp. Kouchinsky, p. 131, fig. 10.
2001 *Mackinnonia rostrata* (Zhou & Xiao) – Parkhaev in: Gravestock *et al.*, p. 176, pl. 40, figs 1–11, pl. 41, figs 1–11.
?2002 *Mackinnonia obliqua* Landing & Bartowski – Landing *et al.*, fig. 8.3.

Holotype. No. 800059, Geological Institute, Anhui Province, Peoples Republic of China. Internal mould from the Lower Cambrian Yutaishan Formation, Anhui Province, North China.

Material. MGUH 26962–26965 from GGU sample 314807. 34 additional internal moulds from the same sample and two questionable specimens from GGU samples 314931 and 314933.

Discussion. *Mackinnonia davidi* Runnegar in: Bengtson *et al.*, 1990 from South Australia and *M. obliqua* Landing & Bartowski, 1996 from the Taconic Allochthon of New York State were recognised by Parkhaev (in: Gravestock *et al.* 2001) as junior synonyms of. *M. rostrata* (Zhou & Xiao, 1984) from the Early Cambrian of China (originally *Mellopegma rostratum* Zhou & Xiao, 1984). Internal moulds of *Mackinnonia* sp. from the Early Cambrian (Botoman) of Siberia are ornamented by knob-like protrusions (mainly along the crests of rugae, Kouchinsky 2000, fig. 10A–F) in addition to the familiar polygonal pattern of depressions, but otherwise appear identical to the chinese type material of the species. A fragmentary specimen from Québec could also belong to this species (Landing *et al*. 2002). The Greenland material of *M. rostrata* (Fig. 3A–H) is closely comparable to the material from North China and New York State. The gently ornamented specimens from Greenland and more strongly rugose specimens from Australia (Runnegar in: Bengtson *et al.* 1990, fig. 159; Parkhaev in: Gravestock *et al.* 2001, pls 40–41) are interpreted as end members of a morphological continuum in a very variable spe-

cies. *M. rostrata* differ from *M. corrugata* and *M. taconica* by the more strongly coiled and laterally compressed shell.

The polygonal pattern of depressions typical of internal moulds of *Mackinnonia* is present in the Greenland material of *M. rostrata*, but the depressions sometimes degenerate into circular rather than polygonal units (Fig. 3H).

Occurrence. Late Early Cambrian of North China, South Australia, Siberia, eastern USA and North-East Greenland

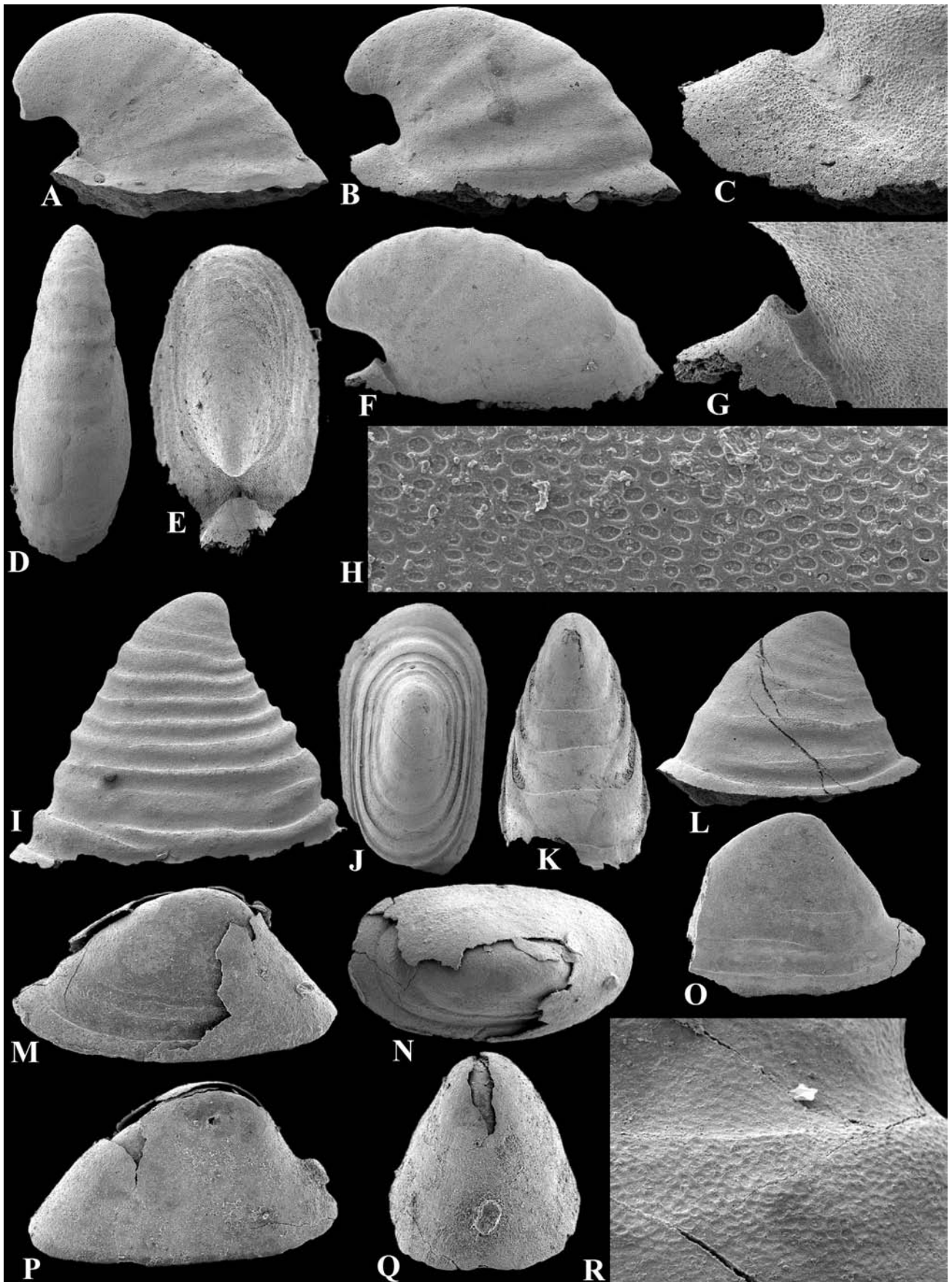*Mackinnonia taconica* (Landing & Bartowski, 1996)
Figs 3I–R, 4A–C

1996 *Stenotheca taconica* n.sp. Landing & Bartowski, p. 753, Figs 5.5,5.7–9, 10.2–3.
2001 *Aequiconus taconica* (Landing & Bartowski) – Parkhaev in: Gravestock *et al.*, p. 138.
2002 *Stenotheca taconica* Landing & Bartowski – Landing *et al.*, fig. 8.4.

Holotype. New York State Museum 15529. Internal mould from the late Lower Cambrian uppermost Browns Pond Formation, Claverack, New York State, USA.

Material. Figured material: MGUH 26966-26974 from GGU sample 314835 and MGUH 26975 from GGU sample 314804. 588 additional specimens from GGU samples 314802, 314804, 314806, 314807, 314809, 314835, 314905 and 314934. One specimen from sample 842.

Fig. 3. Helcionelloid molluscs from Albert Heim Bjerge, North-East Greenland. A–H, *Mackinnonia rostrata* (Zhou & Xiao, 1984). All specimens from GGU sample 314807. A, internal mould MGUH 26962, lateral view, ×37. B–C, internal mould MGUH 26963; B, lateral view, ×37; C, close-up of sub-apical apertural margin, ×115. D–G, internal mould MGUH 26964; D, dorsal view, ×37; E, oblique apical view, ×55; F, lateral view, ×37; G, close-up of sub-apical apertural margin, ×115. H, internal mould MGUH 26965, detail of surface ornamentation, ×460. I–R, *Mackinnonia taconica* (Landing & Bartowski, 1996). All specimens from GGU sample 314835. I, internal mould MGUH 26966, lateral view, ×35. J, internal mould MGUH 26967, apical view, ×45. K, internal mould MGUH 26968, view of sub-apical surface, ×45. L, internal mould MGUH 26969, lateral view, ×35. M-N, internal mould with partly preserved shell coating MGUH 26970; M, lateral view, ×70; N, apical view, ×65. O, internal mould MGUH 26971, lateral view, ×45. P–Q, internal mould with almost complete shell coating MGUH 26972; P, lateral view, ×75; Q, view of sub-apical surface, ×85. R, internal mould MGUH 26973, detail of surface ornamentation, ×230.

Discussion. Internal moulds of this species were described in detail by Landing & Bartowski (1996) from the Taconic Allochthon of New York State, but the abundant and well preserved material from Greenland exhibits a number of new details. In most aspects the material from Greenland is identical to the New York type material, but the apical angle is somewhat smaller (70–110 degrees in lateral view). The majority of specimens are represented by internal moulds only, but thin phosphatic coatings replicating the external shell morphology are preserved in a small number of specimens. When present, phosphatic coatings appear to be perfectly smooth without any traces of growth lines or other ornamentation on the shell exterior, and the prominent rugae of the internal moulds are not reflected externally (Fig. 3M–N, P–Q). The Greenland collections includes larger specimens (up to 1.9 mm high and 1.5 mm long) than the material available to Landing & Bartowski and up to ten rugae are present on internal moulds (Fig. 3I). The rugae and corresponding furrows are developed to different degrees in different specimens and are usually more strongly developed towards the aperture in large specimens (Figs 3I, L). A few internal moulds appear almost smooth with only vestiges of rugae (Fig. 3O). Well preserved surfaces of internal moulds are ornamented with a roughly hexagonal pattern of shallow depressions. This pattern is sometimes present on all surfaces, but usually more strongly developed on the rugae (Fig. 3R).

Without referring specifically to any illustrated material, Landing & Bartowski (1996, p. 753) claimed that the prominent furrows and rugae were present, although subdued, on the external surface of the shell. This claim can not be supported as all external surfaces in the well preserved material from Greenland appear to be perfectly smooth. *Protoconchoides varians* (Walcott, 1886) from Vermont and Quebec exhibits a similar, but slightly wider external shell (Walcott, 1886, pl. 12, fig. 2), and could possibly represent the same, or a related species.

Stenotheca taconica Landing & Bartowski, 1996 was designated type species of *Aequiconus* Parkhaev in: Gravestock *et al*., 2001 (Parkhaev in: Gravestock *et al*., 2001, p. 138, although on p. 182 of the same publication, the author simply state that the species should be referred to a "new genus of the Helcionellidae"). A second species of *Aequiconus*, *A. zigzac* Parkhaev in: Gravestock *et al*., 2001 from the Botoman of Australia lacks the prominent rugae and the polygonal pattern of depressions on internal moulds. Nothing is known about its external appearance. The Laurentian species is here referred to *Mackinnonia* on the basis of the new material from Greenland. *M. taconica* differs from species of *Stenotheca* Salter in: Hicks 1872
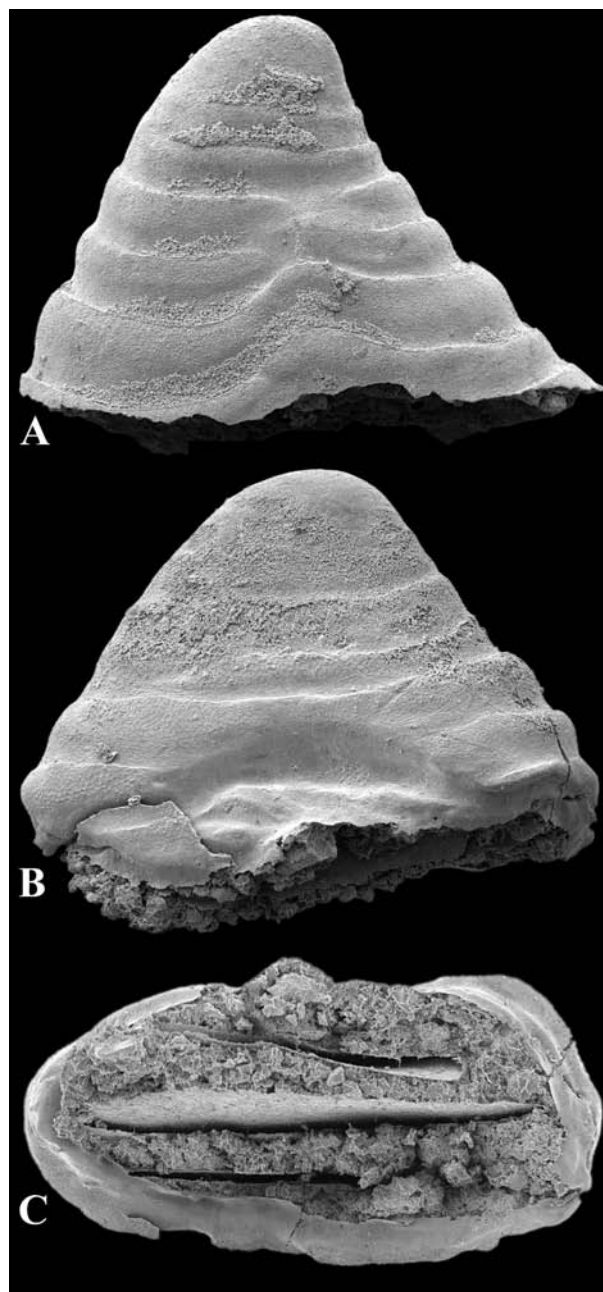

Fig. 4. A–C, *Mackinnonia taconica* (Landing & Bartowski, 1996) from Albert Heim Bjerge, North-East Greenland. A, internal mould with possible repaired shell damage MGUH 26974, lateral view, ×45. Sample 314835. B-C, internal mould with possible repaired shell damage MGUH 26975; B, lateral view, ×70; C, apertural view, ×70. Sample 314804.

by its spoon-shaped protoconch and in the combination of a smooth exterior shell with prominent internal rugae. *Mackinnonia taconica* differs from *M. corrugata* in being less compressed laterally, in the more centrally placed apex and in the less well developed sub-apical flexure of the aperture. It differs from *M. rostrata* by the sub-central rather than strongly overhanging apex.

Two specimens of *Mackinnonia taconica* from GGU samples 314804 and 314835 respectively exhibit evidence of repair after breakage of the shell (Fig. 4). In one specimen the third rugae on one of the lateral sides is interrupted by a smooth area, and subsequent rugae are bent conspicuously towards the apex below this feature, presumably to compensate for a lost piece of shell (Fig. 4A). In a second specimen an embayment cutting across the fourth and parts of the third rugae is present on one lateral surface (Fig. 4B), although the opposite lateral side also appears to have been affected (not illustrated). After growth was resumed this presumed damage caused a constriction (14% in length and 15% in width) of the aperture of the shell (Fig. 4C). Shell repair after failed predatory attacks has been described in Palaeozoic gastropods (e.g. Lindström & Peel 2003 and references therein), as well as in the Ordovician helcionelloid *Chuiliella* Gubanov & Peel, 2001 (Gubanov & Peel 2001, pl. 1, figs 10–15). However, the mode of preservation and the limited number of damaged shells of *Mackinnonia taconica* preclude meaningful comparison.

Occurrence. Late Early Cambrian of New York State, Quebec and North-East Greenland.

Genus *Capitoconus* n. gen.

Type species. *Capitoconus inclinatus* n. gen. et n. sp.

Composition. Type species, *C. artus* n. sp. and possibly *Helcionella* sp. of MacKinnon (1985) from the Middle Cambrian of New Zealand.

Etymology. Latin, *Capitos* (large head), relating to the large and well defined, head-like, protoconch.

Diagnosis. Shell narrow, moderately high, coiled through about one quarter of a whorl; apex almost reaching the margin in lateral view. Supra-apical surface evenly convex; sub-apical surface concave, in lateral perspective aperture elongated elliptical with a slightly constricted, shallow, sub-apical sinus. External ornamentation of co-marginal ribs; internal moulds with co-marginal rugae, not always corre-

sponding closely to the exterior ribs. Protoconch large, hemispherical and laterally compressed; on internal moulds delineated from teleoconch by prominent constriction.

Discussion. *Capitoconus* n. gen. can be distinguished from other helcionelloids by the strong lateral compression, prominent internal rugae and bulbous protoconch. Internal moulds of *Capitoconus* are similar to several laterally compressed helcionelloid genera, most notably to *Stenotheca* Salter in: Hicks, 1872, *Parailsanella* Zhegallo in: Voronova *et al.*, 1987 and *Mellopegma* Runnegar & Jell, 1976. *Capitoconus* is distinguished from *Stenotheca* as currently defined (Runnegar in: Bengtson *et al.* 1990, p. 243) by the larger protoconch. However, the type species, *S. cornucopia* Salter in: Hicks, 1872 appears to have a larger protoconch than other species of the genus (Cobbold 1934, pl. 23, fig. 1). Unfortunately the lectotype of *S. cornucopia* seems to have been lost (Runnegar in: Bengtson *et al.* 1990, p. 243). *Capitoconus* is distinguished from *Parailsanella* and *Mellopegma* by the larger and more elongated protoconch. *Capitoconus* further differs from *Ilsanella* Missarzhevsky, 1981 by being more compressed laterally, by the posterior flexure of the aperture and the larger protoconch. The genus is distinguished from *Bemella* by the large protoconch and the more laterally compressed shell, and from *Mackinnonia* by the exterior ridges and larger protoconch. Specimens from the Middle Cambrian of New Zealand assigned to *Helcionella* sp. by MacKinnon (1985) have a well defined protoconch of a morphology similar to that of *Capitoconus* from Greenland, and may possibly belong to the same genus.

Capitoconus inclinatus n. sp.
Fig. 5M–S

?1993 *Latouchella* sp. aff. *iacobinica* Geyer, 1986 – Brock & Cooper, p. 778, fig. 13.6–7.

Holotype. MGUH 26982 (Fig. 5M-O). Internal mould from GGU sample 314835, Bastion Formation, Albert Heim Bjerge, North-East Greenland.

Etymology. Latin, *Inclinare* (inclined), for the humbly bowing, head-like protoconch.

Diagnosis. Shell narrow, moderately high, coiled through about one quarter of a whorl; apex almost reaching the margin in lateral view. Protoconch large, hemispherical and laterally compressed; in internal moulds delineated from teleoconch by prominent constriction. Supra-apical surface evenly convex; sub-

apical surface gently concave. Aperture elongated elliptical; with a slightly constricted, shallow, sub-apical sinus. External ornamentation of gentle co-marginal ribs; internal moulds with strong co-marginal rugae that do not correspond closely to the exterior ribs.

Material. Figured material: MGUH 26982, 26984, 26985 from GGU sample 314835, MGUH 26983 from GGU sample 314804. 17 additional specimens from GGU samples 314802, 314835, 314908, 314933.

Description. Shell relatively high (2/3 of shell length), moderately compressed laterally. Apex displaced from the centre, just about reaching the margin in apical view. Supra-apical surface gently convex; sub-apical surface gently concave. Aperture elongate oval, with gently convex or flattened lateral margins and rounded anterior margin. Sub-apical margin narrower and slightly flexed towards the apex. Internal moulds ornamented by four to five prominent rugae separated by shallow furrows. Rugae sometimes wider than the furrows, but in other specimens the opposite situation is apparent. Shell ornamented by gentle ribs and fine growth lines. Protoconch elongated globose (on average 0.35 mm long and 0.25 mm wide), clearly delineated by constriction of the shell.

Discussion. *Capitoconus inclinatus* n. sp. is conspicuous in the Greenland material, and even specimens represented by the protoconch alone can sometimes be distinguished. The shell exterior is poorly known, but a fragmentary internal mould is partly covered with a phosphatic coating of the shell exterior and a single small specimen has a coarsely preserved phosphatic coating covering one of the lateral sides. No specific micro-ornamentation is known from the internal moulds, but the prominent rugae of the internal moulds appear to be reduced on the exterior surface. Although too fragmentary for evaluation, a single specimen from Andrée Land questionably referred to *Helcionella cingulata* Cobbold, 1921 by Poulsen (1932, pl. 2, fig. 9) could possibly belong to this species.

The prominent protoconch of *Capitoconus inclinatus* is reminiscent of internal moulds of *Latouchella iacobinica* Geyer, 1986 and *L.* cf. *iacobinica* from the Middle Cambrian of Morocco (Geyer 1986). In the latter species the bulbous protoconch is effectively stalked by a severe constriction of the shell, and Geyer speculated whether the protoconch eventually became separated from the teleoconch by the formation of a septum. *Capitoconus inclinatus* is distinguished from *Latouchella iacobinica* by the absence of strong co-marginal ribs on the shell exterior and from *L.* cf. *iacobi-*

nica by being less strongly curved. Brock & Cooper (1993) described specimens of *L.* sp. aff. *iacobinica* from the late Early Cambrian (Toyonian) of South Australia. This Australian form is not well preserved, but seems to be closely comparable to *Capitoconus inclinatus*. *Helcionella* sp. from the Middle Cambrian of New Zealand (MacKinnon 1985) is lower and has a wider shell, but could represent a related species. A form described by Brasier (1984) from the Early Cambrian of England as *Bemella pauper* (Billings, 1872) is more questionably related to the present material. *Capitoconus inclinatus* differs from *Ilsanella aksarinae* Zhegallo in: Esakova & Zhegallo, 1996 from the Early Cambrian of Mongolia by the larger protoconch and the sub-apical sinus.

Occurrence. Late Early Cambrian of North-East Greenland and possibly South Australia.

Capitoconus artus n. sp.
Fig. 5A–L

?1994 *Bemella* sp. Elicki, fig. 4/16.
?1996 *Bemella* sp. Elicki, p. 153, pl. 6, fig. 7.

Holotype. MGUH 26976 (Fig. 5A–B, F). Phosphatized shell from GGU sample 314835, Albert Heim Bjerge, North-East Greenland.

Etymology. Latin *artus* (narrow), for the laterally compressed shell interior.

Diagnosis. Shell narrow, moderately high, coiled

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Fig. 5. Helcionelloid molluscs from Albert Heim Bjerge, North-East Greenland. A–L, *Capitoconus artus* n. gen. et n. sp. All specimens from GGU sample 314835. A–B, F, phosphatized shell MGUH 26976; A, apical view, ×65; B, view of sub-apical surface, ×75; F, lateral view, ×65. C–D, internal mould with partly preserved shell coating MGUH 26977; C, apical view, ×70; D, view of supra-apical surface, ×70. E, H, internal mould with remnants of shell coating MGUH 26978; E, view of supra-apical surface, ×25; H, lateral view, ×25. G, internal mould with partly preserved shell coating MGUH 26979, lateral view, ×50. I–J, L, internal mould MGUH 26980; I, dorsal view, ×7; J, apical view, ×55; L, detail of shell micro structure, ×270. K, internal mould MGUH 26981, lateral view, ×47.
M–S, *Capitoconus inclinatus* n. gen. et n. sp. All specimens except P from GGU sample 314835. M-O, internal mould MGUH 26982; M, dorsal view, ×30; N, view of sub-apical surface, ×45; O, oblique lateral view, ×45. P, internal mould MGUH 26983, lateral view, ×45. GGU sample 314804. Q-R, internal mould with partly preserved shell coating MGUH 26984; Q, apical view, ×60; R, lateral view, ×55. S, fragmentary internal mould with partly preserved shell coating MGUH 26985, lateral view, ×50.
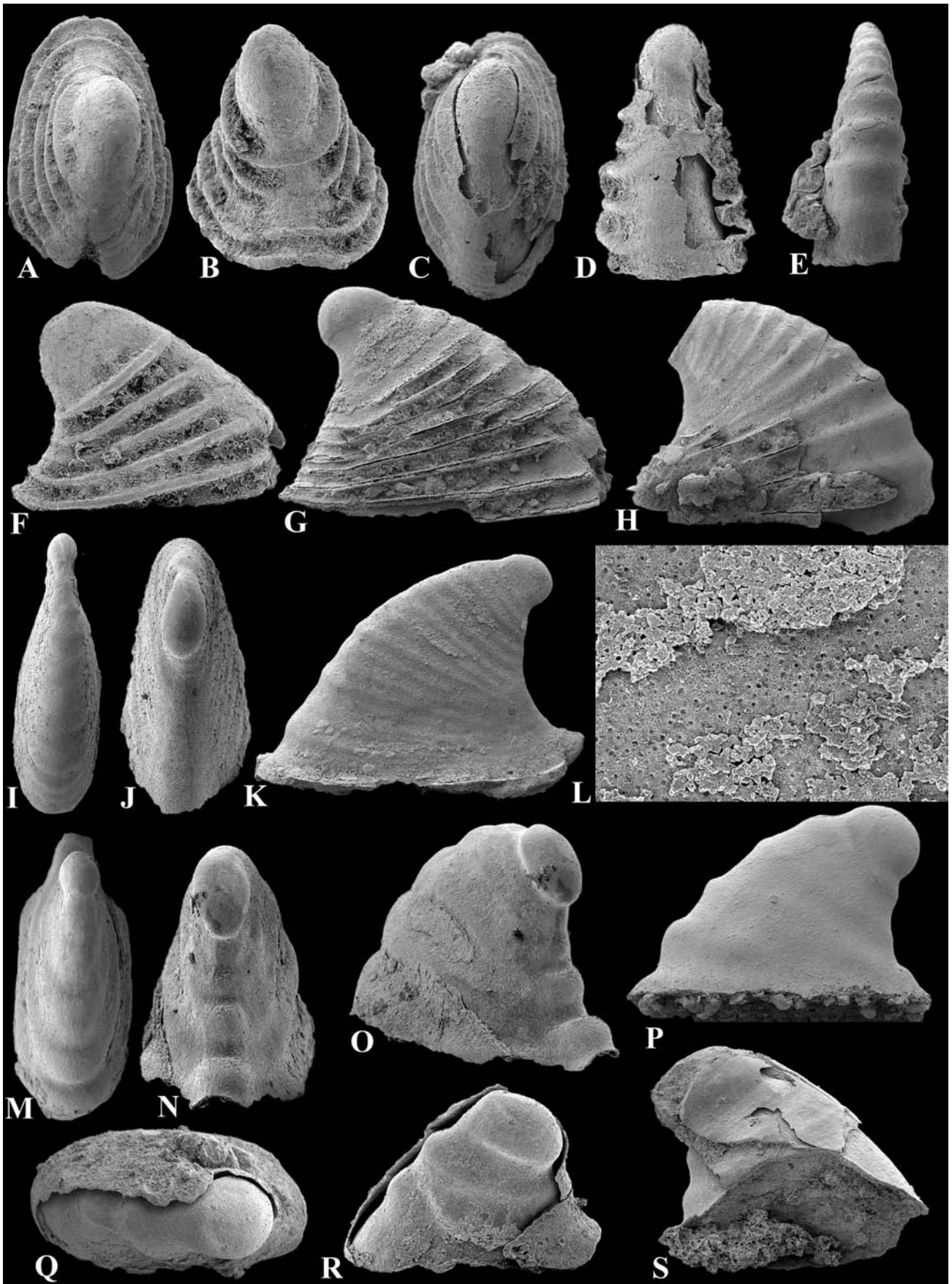
through about one quarter of a whorl; apex almost reaching the margin in lateral view. Protoconch large, laterally compressed teardrop-shaped. Supra-apical surface evenly convex; sub-apical surface concave. Aperture elongated elliptical; slightly constricted below the apex; with a shallow sub-apical sinus. External ornamentation of greatly extended co-marginal ribs formed by periodical flaring of the aperture; internal moulds with gentle co-marginal rugae ornamented by rows of fine pits.

Material. Figured material: MGUH 26976–26981 from GGU sample 314835. 22 additional specimens from the same sample.

Description. Shell moderately high (about ¾ of shell length), strongly compressed laterally, coiled through about ¼ of a whorl, the apex almost reaching the margin in apical view. Aperture elongated, oval, with gently convex lateral margins; supra-apical margin rounded, with the sub-apical margin slightly flexed towards the apex. Shell exterior ornamented by up to ten horizontally protruding (representing up to 35% of shell width), but very narrow (30 µm mm in cross-section) co-marginal ribs. Ribs separated by deep furrows, in available specimens partly filled with matrix. Ribs sometimes partly subdued on the dorsum and on the sub-apical surface, with spacing of ribs changing through ontogeny from approximately ten ribs per mm (measured on the dorsum) in juveniles to about three ribs per mm in larger specimens. Internal moulds ornamented by much less conspicuous and gently rounded rugae, apparently corresponding to the prominent external ribs. Well preserved internal moulds with ornamentation of fine pits (2–3.5 µm in diameter) irregularly arranged along the crests of the ribs. Protoconch cap-shaped, high, narrow, separated from the teleoconch by the first rib, in internal moulds teardrop-shaped (0.28 mm long, 0.14 mm wide) and defined by a shallow constriction.

Discussion. *Capitoconus artus* n. sp. is distinguished from *C. inclinatus* by its greater latteral compression, the teardrop-shaped protoconch and the horizontally extended co-marginal ribs on the shell exterior. Prominent and densely spaced exterior ribs are present in *Miroconulus parvulus* Parkhaev in: Gravestock *et al.*, 2001 and *Salanyella costulata* Missarzhevsky, 1981, but *Capitoconus artus* differs from both these forms by the greater horizontal extension of the ribs, the pronounced lateral compression of the shell and by the development of a shallow sub-apical sinus. Internal moulds of *C. artus* are indistinguishable from an east German specimen assigned to *Bemella* sp. by Elicki (1994, 1996). However, the Greenland material is dis-

tinguished from other species of *Bemella* Missarzhevsky in: Rozanov *et al.*, 1969 by the strong lateral compression and by the posterior sinus. *Capitoconus artus* is further distinguished from *Stenotheca cornucopia* Salter in: Hicks, 1872 from the Early Cambrian of Wales by the external shell ornamentation and the shorter, wider aperture, from *Parailsanella murenica* Zhegallo in: Esakova & Zhegallo, 1996 from Mongolia by the larger protoconch and the less strongly marked ribs and furrows on internal moulds and from *Mellopegma georginensis* Runnegar & Jell, 1976 from the Middle Cambrian of Australia, by the taller shell, the shorter aperture and the larger and more clearly defined protoconch.

The flange-like ribs of *Capitoconus* represent a periodic flaring of the aperture, a feature that could hardly be anticipated from the gentle ribs on internal moulds. This illustrates the importance of combining internal moulds and shell exterior for full appreciation of the morphology of helcionelloids.

*Occurrence*. Late Early Cambrian of North-East Greenland and eastern Germany.

Genus *Figurina* Parkhaev in: Gravestock *et al.*, 2001

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

Composition. Type species, *F. capitata* Parkhaev in: Gravestock *et al.*, 2001 from South Australia, *F. groenlandica* n. sp. from Greenland and possibly *Mellopegma nana* Zhou & Xiao, 1984 from North China.

2001 *Figurina* Parkhaev in: Gravestock *et al.*, p. 167.

Fig.6. Helcionelloid molluscs from the Bastion Formation of Albert Heim Bjerge, North-East Greenland. A–I, *Figurina groenlandica* n. sp. All specimens from GGU sample 314835. A–B, internal mould MGUH 26986; A, lateral view, ×65; B, dorsal view, ×50. C, internal mould with partly preserved shell coating MGUH 26987, apical view, ×70. D, I, internal mould MGUH 26988; D, lateral view, ×40; I, oblique lateral view, ×60. E, H, partial internal mould MGUH 26989; E, lateral view, ×50; H, detail of surface ornamentation, ×480. F–G, internal mould with partly preserved shell coating MGUH 26990; F, view of sub-apical surface, ×60; G, dorsal view, ×40. J–O, *Oelandia* sp. All specimens from GGU sample 314835. J–K, internal mould with almost complete shell coating MGUH 26991; J, dorsal view, ×50; K, lateral view, ×50. L–M, internal mould MGUH 26992; L, dorsal view, ×31; M, view of supra-apical surface, arrows indicate alternating lateral plications, ×45. N–O, internal mould MGUH 26993; N, lateral view, ×43; O, dorsal view, ×43.
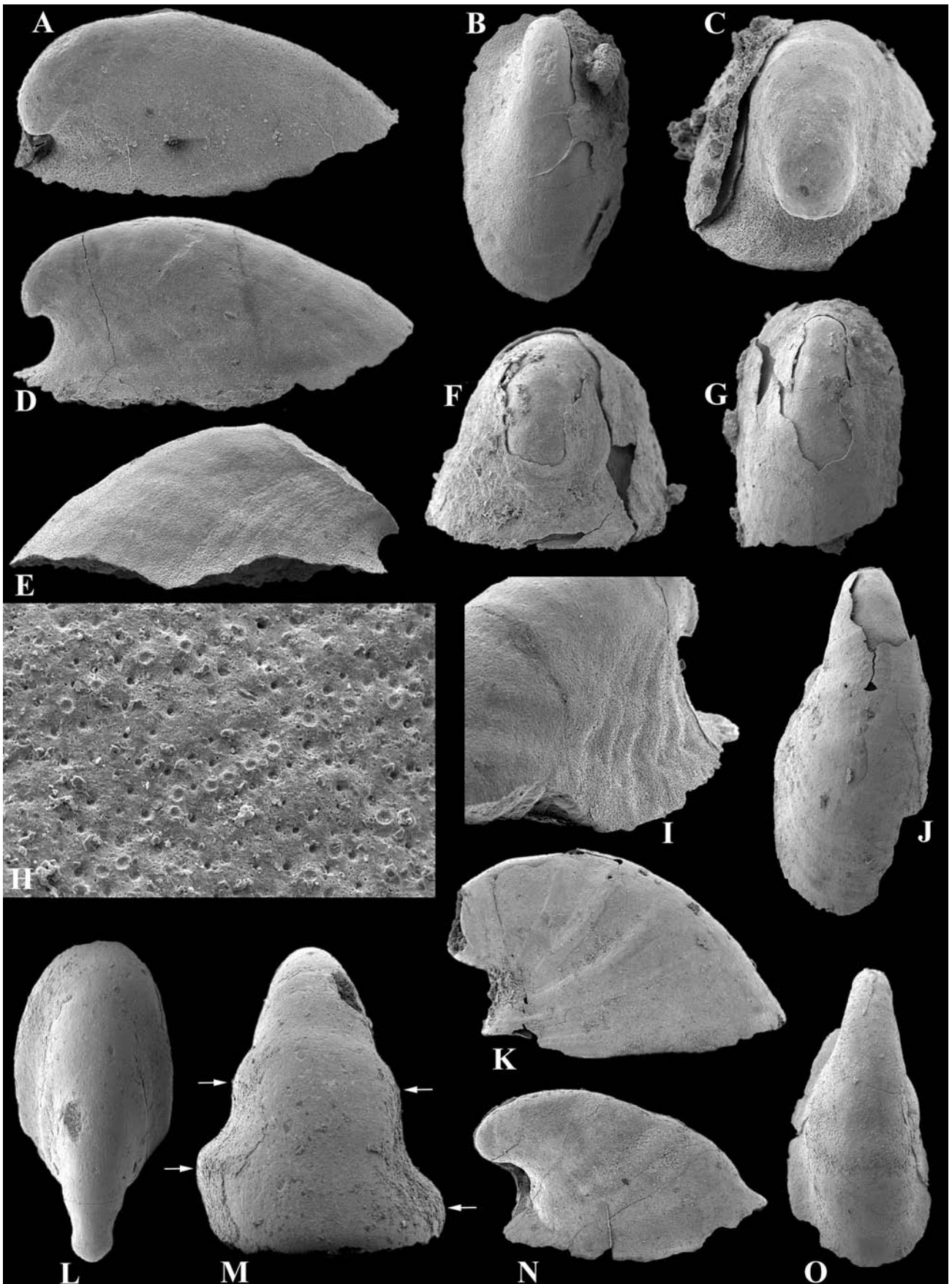
Discussion. *Figurina figurina* and *F. capitata* from the Lower Cambrian of South Australia (Parkhaev in: Gravestock *et al*. 2001) are low helcionelloids with a characteristic pitted micro-ornamentation on internal moulds (presumably corresponding to an internal shell surface covered with minute tubercles or spine-like protrusions). Similar structures have been reported in Early and Middle Cambrian species of *Obtusoconus*, *Helcionella*, *Latouchella* and *Ilsanella* (Runnegar & Jell 1976; MacKinnon 1985; Peel 1991; Kouchinsky 2000). Parkhaev (in: Gravestock *et al*. 2001) transferred *Mellopegma nana* Zhou & Xiao, 1984 from the Lower Cambrian of Anhui Province, North China to *Figurina* and figured supposedly conspecific material from South Australia. The only figured specimen of *Mellopegma nana* (Zhou & Xiao 1984, pl. 3, fig 11) from China could possibly belong to *Figurina*, but differs from the Australian material in the extension of the apex beyond the posterior apertural margin. The Australian material instead appears similar to *Figurina capitata*.

Figurina groenlandica n. sp.
Fig. 6A–I

Holotype. MGUH 26988 (Fig 5D, I). Phosphatic internal mould from GGU sample 314835, Bastion Formation, Albert Heim Bjerge, North-East Greenland.

Etymology. From the occurrence of the species in Greenland.

Diagnosis. Species of *Figurina* with low, cap-shaped shell, moderately compressed laterally. Aperture elongated oval; lacking a sub-apical sinus. External shell with faint radial ribs.

Material. Figured material: MGUH 26986–26990 from GGU sample 314835. 28 additional specimens from GGU samples 314804 and 314835, one specimen from sample 879.

Description. Shell low (height ½ the length of the shell), cap-shaped, with the apex displaced towards the margin, moderately compressed laterally; lateral fields straight to slightly convex. Shell exterior ornamented by faint concentric and radial ribs on the dorsal and lateral fields. Aperture elongated oval, sometimes slightly wider towards the sub-apical margin. Apertural margin simple without invaginations or other modifications. Where secondarily formed replicas of the shell exterior are preserved, the sub-apical surface of the shell is almost vertical and the apex is not clearly delineated. Internal moulds with apex hooked over the sub-apical wall, with spoon-shaped protoconch (0.35 mm long, 0.2 mm wide) delineated by a faint furrow. Sub-apical surface of internal moulds strongly concave; dorsum convex, more or less smooth. Faint concentric ribs give the profile a slightly uneven outline. Lateral sides ornamented by curved radial ridges, alternating furrows running from the apical region to the lateral margins of the aperture. Internal moulds further exhibit a micro-ornamentation of apparently evenly distributed pits (diameter 2.5–3 µm). The pits can be observed on all surfaces except on the apical region. The shallow furrows on the lateral fields are ornamented by larger, crater-like pits (diameter 4–6 µm) arranged in slightly uneven rows.

Discussion. *Figurina groenlandica* n. sp. is closely comparable to *F. figurina* Parkhaev in: Gravestock *et al*., 2001 from the late Early Cambrian of South Australia. The most noticeable difference is the absence in the Greenland species of a deep sinus on the sub-apical margin of the aperture. Specimens of a similar morphology were described from Australia by Parkhaev as *Bemella communis* Parkhaev in: Gravestock *et al*., 2001, but these differ from the type specimen of that species by the absence of strong concentric ribs, by the pitted microstructure and by curved radial ridges on the lateral sides. The illustrated specimens (Gravestock *et al*. 2001, pl. 26, figs 6, 8 and pl. 29, figs 3, 5) do not appear identical to *Figurina groenlandica*, but affinity to *Figurina* seems plausible. *Helcionella*? n. sp. from the Middle Cambrian of Spain and Morocco (Geyer 1986) has internal moulds similar to *Figurina groenlandica* in general morphology, but appear to have a more strongly hooked apex. Nothing is known about external morphology or microstructure of this form.

The external shell morphology is partly preserved in *Figurina groenlandica* n. sp. The shell is (at least superficially) similar to almost featureless simple oval shells with low or depressed apices described from the Early Cambrian of China as *Actinoconus pyriformis* Yu, 1987 and *Bemella simplex*, Yu, 1987. As *Figurina* is mainly defined on features known only from internal moulds, detailed comparison is extremely difficult, highlighting the general problem of comparing differentially preserved mollusc shells. A similar example, *Trenella bifrons* Parkhaev, 2001 from the Early Cambrian of South Australia with widely different external and internal shell morphology, was illustrated by Parkhaev (2001b).

Occurrence. Late Early Cambrian of North-East Greenland.

Genus *Oelandia* Westergård, 1936

Type species. *Oelandia pauciplicata* Westergård, 1936.

Composition. Type species, *Oelandia comma* (Geyer, 1986), and possibly *Latouchella jingheensis* Yu & Ning, 1985.

1936   *Oelandia* n.sp. Westergård, p. 25.
1986   *Latouchella* Cobbold, 1921 – Geyer, p. 77 (*pars*).
1987   *Oelandia* Westergård, 1936 – Peel & Yochelson, p. 264.

Discussion. Planispirally coiled helcionelloids characterised by an asymmetrical alternation of ribs on the two sides of the shell have been described from the Middle Cambrian of Sweden (Westergård 1936; Peel & Yochelson 1987), China (Yu & Ning 1985) and Morocco (Geyer 1986). Undescribed material is also known from Bohemia (Gubanov & Peel 1998). *Oelandia pauciplicata* and *O. comma* from Sweden and Morocco respectively are laterally flattened, open coiled species with broad lateral ribs interfingering on the dorsum. The possibly related *Latouchella jingheensis* from north-west China has a rapidly expanding limpet-like shell with a similar arrangement of ribs.

Oelandia sp.
Fig. 6J–O

Material. Figured material: MGUH 26991–26993 from GGU sample 314835. 18 additional specimens from the same sample.

Description. Shell planispirally coiled, with the apex overhanging the margin of the aperture. Shell height about 3/5 of shell length. Dorsum gently convex; sub-apical surface strongly concave but straightened out towards the aperture. Aperture elongated oval, with a slight sub-apical constriction. Exterior smooth, with faint growth lines and rounded co-marginal ribs not crossing the dorsum. Plications also observable on internal moulds, and at least in larger specimens, asymmetrically developed on the lateral sides. Sub-apical part of the aperture not well preserved in available larger specimens, but in small internal moulds a fold or shallow furrow reminiscent of the pegma-like structure in *Mackinnonia rostrata* developed below the apex.

Discussion. Although no perfectly preserved specimens are available, this material can be compared to *Oelandia comma* from the Middle Cambrian of Morocco (Geyer 1986). The unusual asymmetrical ar-

rangement of plications is present only on the lateral sides in both types (contra the case in *O. pauciplicata* and *Latouchella jingheensis* where individual ribs cross the dorsum only to die out on the opposite lateral side). The shells are further similar in the degree of coiling and in early ontogeny. However, the lack of well preserved large specimens showing the sub-apical extension of the aperture as in adult *O. comma* from Morocco (Geyer 1986), makes the comparison tentative. The Early Cambrian (Botoman) age is also considerably older than the Middle Cambrian age of *O. comma*.

Genus *Latouchella* Cobbold, 1921

Type species. *Latouchella costata* Cobbold, 1921.

Composition. Type species, *L. arcuata* Gubanov *et al*. in press and *L. ostenfeldense* n. sp. Otherwise uncertain.

1921   *Latouchella* n.sp. Cobbold, p. 366.
1960   *Latouchella* Cobbold, 1921 – Knight *et al*. p. 172 (*pars*).
1998   *Latouchella* Cobbold, 1921 – Gubanov & Peel, p. 17.
2004   *Latouchella* Cobbold, 1921 – Gubanov *et al*., p. 209.

Discussion. *Latouchella* has been widely applied to Early and Middle Cambrian cap-shaped or coiled helcionelloids. Gubanov & Peel (1998) redescribed the type species from the Lower Cambrian of Shropshire, England, and restricted the genus to relatively strongly coiled forms with a smooth dorsum combined with plications on the lateral surfaces (Gubanov & Peel 1998, 1999). Although much needed, a complete revision of the various forms attributed to *Latouchella* has never been attempted, and also is considered to be beyond the scope of the present work.

Latouchella ostenfeldense n. sp.
Fig. 7A–G

Holotype. MGUH 26995 (Fig. 7B). Phosphatic internal mould from GGU sample 314835, upper Bastion Formation, North-East Greenland.

Etymology. From the common occurrence at C.H. Ostenfeld Nunatak.

Diagnosis. Species of *Latouchella* with low, tightly coiled shell with weak co-marginal plications on the lateral sides.

Material. Figured material: MGUH 26994, 26997, 26998 from GGU sample 314933, MGUH 26995 from GGU sample 314835, MGUH 26996 from GGU sample 314804. 108 additional internal moulds from GGU samples 314804, 314835, 314904, 314906, 314908, 314910, 314919, 314931 and 314933.

Description. Shell planispiral, relatively low (height about 45% of shell length), coiled through about one whorl. Early growth stages moderately compressed laterally, with an elongated oval aperture, but in larger specimens the shell expands more rapidly in the lateral directions and the length/width ratio of the aperture decreases (from about 2.0 to 1.5). Faint co-marginal plicae present on the lateral fields but in small specimens the dorsum appears smooth. Plicae appear to be symmetrical on both lateral sides. In larger specimens the lateral plicae are more obvious and, although subdued, appear to cross the dorsum, resulting in a slightly wavy profile. The protoconch is hemispherical and laterally compressed (0.29 mm long, 0.15 mm wide). No micro-ornamentation have been observed on the internal moulds. External shell surface not known.

Discussion. *Latouchella ostenfeldense* n. sp. is distinguished from *L. costata* by the less strongly developed lateral plications and in the lower and more elongated profile of the shell. It differs from *L. arcuata* in being more strongly coiled. The species is distinguished from *Igorella ungulata* Missarzhevsky in: Rozanov *et al.*, 1969 from the Early Cambrian of Siberia by the more strongly coiled shell and weaker co-marginal plications and from *Cyrtodiscus kuruktagensis* Yu, 1986 from North China by the single whorl of coiling.

Occurrence. Early Cambrian of North-East Greenland.

Genus *Asperconella* Landing & Bartowski, 1996

Type species. *Asperconella troyensis* (Resser, 1938). Monotypic.

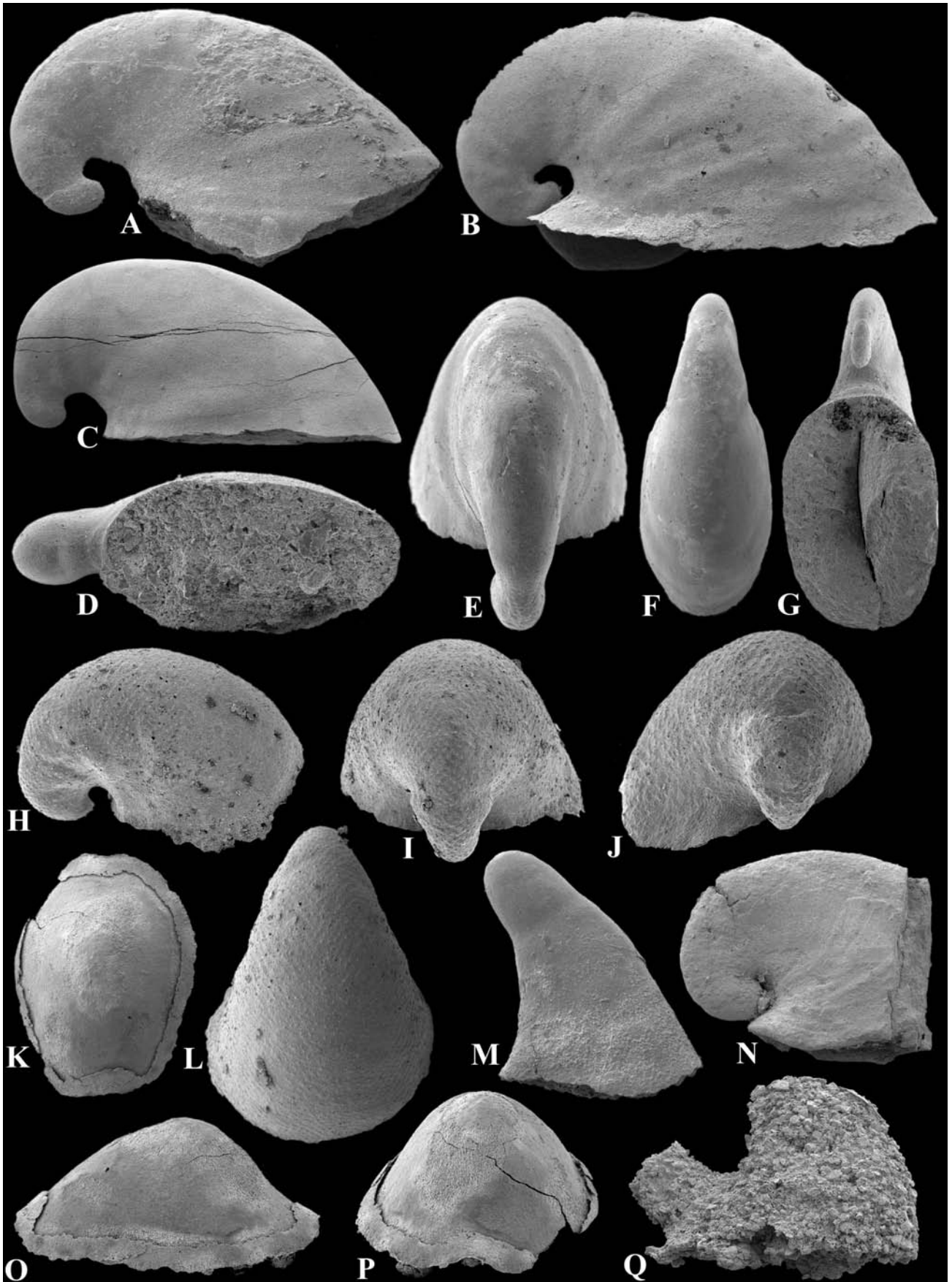1996 *Asperconella* n.sp. Landing & Bartowski, p. 753.

Discussion. Several generic names have been applied to relatively strongly coiled, bilaterally symmetrical helcionelloid molluscs with a pitted internal shell surface, or rather, to corresponding internal moulds ornamented by minute spines or tubercles. A circular to slightly oval cross-section combined with minute processes arranged in V-shaped rows on internal moulds is common to *Anhuiconus* Zhou & Xiao, 1984,

Asperconella Landing & Bartowski, 1996 and *Daedalia* Parkhaev in: Gravestock *et al.*, 2001. Of these genera the first two are coiled with the apex overhanging the posterior apertural margin while *Daedalia* Parkhaev is higher and less strongly coiled. *Punctella* Zhong, 1977 and *Tuberoconus* Yue in: Xing *et al.*, 1983 differ from the fossils mentioned above by an apparently random organisation of tubercles on internal moulds. A comparable lack of organisation of tubercles is also present in specimens of *Anhuiconus microtuberosus* Zhou & Xiao, 1984 described from Australia (Parkhaev in: Gravestock *et al.* 2001). The tubercles in the Australian material also appear to be much smaller than in the Chinese type material of the species (Zhou & Xiao 1984). In general morphology *Asperconella* appear very similar to the Chinese specimens of *Anhuiconus*, and the two may proove to be synonymous. However, available illustrations of the Chinese material (Zhou & Xiao 1984) do not allow a detailed comparison of the distribution of tubercles, or the morphology of the apex, and specimens from North-East Greenland are therefore referred to the better known *Asperconella*.

Asperconella troyensis (Resser, 1938)
Fig. 7H–J, L.

1886 *Stenotheca rugosa* (Hall, 1847) – Walcott, p. 128 (*pars*), pl. 12, figs 1d–e, *non* pl. 12, figs 1a–c.

Fig.7. Helcionelloid molluscs from North-East Greenland. A–G, *Latouchella ostenfeldense* n. sp. A, G, internal mould MGUH 26994; A, lateral view, ×40; G, apertural view, ×30. GGU sample 314933, C.H. Ostenfeld Nunatak. B, internal mould MGUH 26995, lateral view, ×32. GGU sample 314835, Albert Heim Bjerge. C, internal mould MGUH 26996, lateral view, ×40. GGU sample 314804, Albert Heim Bjerge. D, internal mould MGUH 26997, apertural view, ×80. GGU sample 314933, C.H. Ostenfeld Nunatak. E–F, internal mould MGUH 26998; E, oblique dorsal view, ×60; F, dorsal view, ×40. GGU sample 314933, C.H. Ostenfeld Nunatak.
H–J, L, *Asperconella troyensis* (Resser, 1938). GGU sample 314804, Albert Heim Bjerge. H–I, L, internal mould MGUH 26999; H, lateral view, ×35; I, oblique dorsal view, ×40; L, dorsal view, x40. J, internal mould MGUH 27000, oblique dorsal view, ×65.
K, O–P, Helcionelloid indet. Internal mould MGUH 27001; K, apical view, ×42; O, lateral view, ×55; P, view of sub-apical surface, ×55. GGU sample 314807, Albert Heim Bjerge.
M, *Stenotheca* sp. Internal mould MGUH 27002, lateral view, ×90. Sample 314908, C.H. Ostenfeld Nunatak.
N, *Anabarella australis* Runnegar *in* Bengtson *et al.*, 1990. Phosphatized shell MGUH 26693, lateral view, ×65. GGU sample 314835, Albert Heim Bjerge.
Q, *Yochelcionella* sp. Internal mould MGUH 27003, lateral view, ×45. Sample 314808, Albert Heim Bjerge.

1890 *Stenotheca rugosa* (Hall, 1847) – Walcott, p. 617 (*pars*), pl. 74, figs 1h–i, *non* pl. 74, figs 1, 1a–h.
1938 *Stenothecoides troyensis* n.sp. Resser, p.25.
1996 *Asperconella troyensis* (Resser) – Landing & Bartowski, p. 753 (*pers*), figs 5.1, 10.1, *non* figs 5.2– 5.4, 5.6.

Holotype. United States National Museum 96484 (Resser 1938). Locality information not available.

Material. Two almost complete phosphatic internal moulds from GGU sample 314804, MGUH 26999, 27000.

Discussion. Two specimens closely comparable to *Asperconella troyensis* (Resser, 1938) were found in the samples from Greenland. Landing & Bartowski (1996) erected *Asperconella* to contain *Stenothecoides troyensis* Resser, 1938. These authors illustrated four acid-isolated specimens from the Browns Pond Formation of New York State, only one of which has the characteristic ornamentation of V-shaped rows with spine-like processes (Landing & Bartowski 1996, fig. 5.1–5.2, 10.1). The authors interpreted this specimen as a phosphatized shell with prominent external ornamentation, and based the description of the genus and the only species, *A. troyensis*, on this assumption. Judging from the published pictures of the specimen and from comparison to unfigured topotype material (personal observation 2001), the specimen is more likely to represent a well preserved internal mould than a secondarily phosphatized shell. This view is corroborated by a hand specimen lacking all external ornamentation beyond simple growth lines (Walcott 1886, pl. 12, fig. 1d). Three figured specimens lacking the characteristic ornamentation (Landing & Bartowski 1996, fig. 5.3–5.4, 5.6) most likely represent worn internal moulds of the same species, or an unrelated form. The poor preservation of a specimen labelled *A. troyensis* from Ville Guay of Québec (Landing *et al.* 2002, fig. 8.6–8.7) precludes taxonomic evaluation.

In general morphology, internal moulds of *Asperconella troyensis* appear very similar to *Anhuiconus microtuberosus* Zhou & Xiao, 1984 from North China. The two forms could be conspecific, but the poor quality of the published illustrations of the Chinese material makes direct comparison difficult. *Asperconella troyensis* differs from *Tuberoconus paucipapillae* Yue in: Xing *et al.*, 1983 from China, *Punctella maidipingensis* Zhong, 1977 from China and Siberia (Missarzhevsky 1989) and specimens identified as *A. microtuberosus* Zhou & Xiao, 1984 from South Australia (Parkhaev in: Gravestock *et al.* 2001) by the V-shaped arrangement of tubercles, and from *Daedalia daedala* Parkhaev

in: Gravestock *et al.*, 2001 by the lower and more strongly coiled shell.

Occurrence. Lower Cambrian of the north-eastern USA and North-East Greenland.

Helcionelloid indet.
Fig. 7K, O–P

Material. Nine internal moulds from GGU samples 314802, 804, 807, 835. Figured material: MGUH 27001.

Discussion. The shell is elongated, low (height about ½ the shell length) and cap-shaped with the apex slightly displaced from the centre (Fig. 7O). The aperture is oval (width about 3/5 of shell length) with a shallow sinus developed on the sub-apical margin (Fig. 7P). The protoconch is not clearly delineated. These simple cap-shaped shells are reminiscent of *Protoconchoides* Shaw, 1962 (Geyer 1994), and in size and dimensions they are most similar to *P. varians* (Walcott, 1886) from Quebec and Vermont. However, the Greenland specimens are not considered well enough preserved for taxonomic evaluation. The specimens differ from *Mackinnonia taconica* by the lack of rugae and polygonal micro-ornamentation on internal moulds as well as in the lower and wider shell.

Genus *Stenotheca* Salter in: Hicks, 1872

Type species. *Stenotheca cornucopia* Salter in: Hicks, 1872.

Composition. See Parkhaev in: Gravestock *et al.* (2001) for a discussion of the many species refereed to this genus.

Stenotheca sp.
Fig. 7M.

Material. MGUH 27002, a fragmentary internal mould from GGU sample 314908.

Discussion. A tall and erect, laterally compressed internal mould with a slightly inclined apex. The adapical end of the fossil probably represents a very narrow aperture, but a slight sub-apical flexure of the aperture probably represents breakage of the internal mould. This specimen is similar to species of *Stenotheca* Salter in: Hicks, 1872 and *Anuliconus* Parkhaev in: Gravestock *et al.*, 2001 from the Lower Cambrian

of Australia (Runnegar & Jell 1976; Bengtson *et al*. 1990; Parkhaev in: Gravestock *et al*. 2001), but the limited information available precludes taxonomic identification.

Genus *Anabarella* Vostokova, 1962

Type species. *Anabarella plana* Vostokova, 1962.

Composition. Type species and *A. australis* Runnegar in Bengtson *et al*., 1990.

Anabarella australis Runnegar in: Bengtson *et al*., 1990
Fig. 7N

1990   *Anabarella australis* n.sp. Runnegar in: Bengtson *et al*., pp. 244, 251, fig. 163A, fig. 64A–G.
1990   *Anabarella argus* n.sp. Runnegar in: Bengtson *et al*., p. 251, fig. 164H–N.
1996   *Anabarella australis* Runnegar in: Bengtson *et al*. – Elicki, p. 152, pl. 6, figs 1–2.
2000   *Anabarella australis* Runnegar in: Bengtson *et al*. – Parkhaev, pl.4, figs 13–14.
2001   *Anabarella australis* Runnegar in: Bengtson *et al*. – Parkhaev in: Gravestock *et al*., p. 185, pl. 42, figs 1–14
in press *Anabarella australis* Runnegar in: Bengtson *et al*. – Gubanov *et al*. p. X, fig. 1.1–17

Holotype. South Australian Museum (Adelaide) SAMP 29017, from the base of Parara Limestone, Lower Cambrian, Horse Gully, Yorke Peninsula, South Australia.

Material. Figured material: MGUH 26693 from GGU sample 314835. 21 additional specimens from GGU samples 314804, 314835, 314904, 314908 and 314933.

Discussion. Gubanov *et al*. (*in press*) described *Anabarella australis* from the Bastion Formation of North-East Greenland and discussed the affinity of the material to other occurrences of the genus. No additional information is presented here, but it is illustrated for completeness of the fauna.

Occurrence. Late Early Cambrian of Australia, Germany and Greenland.

Genus *Yochelcionella* Runnegar & Pojeta, 1974

Type species. *Yochelcionella cyrano* Runnegar & Pojeta, 1974.

Composition. The numerous species referred to *Yochelcionella* were reviewed by Hinz-Schallreuter (1997).

Yochelcionella sp.
Fig. 7Q.

Material. MGUH 27003, a dolomitic internal mould from GGU sample 314808.

Discussion. Small, laterally compressed internal mould of a helcionelloid mollusc. The apex is slightly inclined towards towards the assumed apertural plane. Based on the well defined sub-apical snorkel this internal mould can be placed in the genus *Yochelcionella*, but the poor preservation of the specimen precludes specific identification.

Genus *Pelagiella* Matthew, 1895

Type species. *Cyrtolithes atlantoides* Matthew, 1894.

Composition. See Parkhaev in: Gravestock *et al*. (2001) for a recent review of the large number of species of *Pelagiella* proposed in the literature.

Discussion. *Pelagiella* and a few similar Early Cambrian genera have strongly anisometrically, coiled shells and are thus reminiscent of gastropods. However, Wenz (1938) noted non-gastropod features, and some subsequent authors have regarded *Pelagiella* as untorted, and therefore not a gastropod (e.g. Knight *et al*. 1960; Runnegar 1981; Peel 1991). Linsley & Kier (1984) formally proposed the Class Paragastropoda to include, among other Palaeozoic molluscs, *Pelagiella* and the similarly constructed Early Cambrian *Aldanella* Vostokova, 1962. Other authors have maintained the gastropod affinity of *Pelagiella* (e.g. Missarzhevsky 1989; Parkhaev 2001; Landing *et al*. 2002).

Asymmetrical coiling has been demonstrated in some of the earliest known helcionelloids (e.g. *Archaeospira* Yu, 1979, see Qian & Bengtson 1989 and *Oelandiella* Vostokova, 1962, see Gubanov & Peel 2000). Gubanov & Peel (2000) suggested that *Aldanella* could represent a similar adaptation within the Helcionelloida, and this interpretation may also apply to *Pelagiella*. Linsley & Kier (1984) regarded *Pelagiella* as untorted based on the morphology of the aperture in relation to the coiling axis. Muscle scars reported in specimens of *Pelagiella* from New Brunswick, Canada (Runnegar 1981) and Morocco (Landing *et al*. 2002), although possibly representing evidence for a retractile mollusc, do not provide unequivocal evidence for

a gastropod affinity of the genus. Similar muscle scars are present in Palaeozoic, untorted cyrtonellid tergomyans (Peel 1991). Presently, *Pelagiella* is perhaps best regarded as an asymmetrically coiled but untorted helcionelloid mollusc.

Pelagiella subangulata (Tate, 1892)
Fig. 8A–J.

1892 *Ophileta subangulata* n.sp. Tate, p. 184, pl. 2, figs 8a–b.
1990 *Pelagiella subangulata* (Tate, 1892) – Bengtson *et al*. p. 254, figs 167, 168A–D, 169A–F, H–L.
2001 *Pelagiella subangulata* (Tate, 1892) – Parkhaev in: Gravestock *et al*., p. 193, pls 44–45.

Lectotype. South Australian Museum SAMT1234a (designated by Runnegar in: Bengtson *et al*. 1990).

Material. MGUH 27004 and 27006 from GGU sample 314835, MGUH 27005 and 27007 from GGU sample 314807 and MGUH 27008 from GGU sample 314918. In addition, 747 specimens from GGU samples 314804, 314806–314809, 314835, 314837, 314904, 314906, 314908–314910, 314918–314919, 314931 and 314933 as well as three specimens from sample 842 (coll. C. Poulsen).

Discussion. Internal moulds of *Pelagiella* are by far the most common molluscan remains in the acid-resistant residues of the Bastion Formation. Species of *Pelagiella* are generally very variable, and specific assignment of internal moulds can only be regarded as tentative. However, a small number of phosphatized specimens preserving fine growth lines are available from Greenland (Fig. 8J). An external shell ornament of arched ridges converging to form a V-shaped pattern on the shell periphery (Figs 8A–C) is also preserved. Comparable ornamentation of V-shaped ridges is present in *P. subangulata* from the Late Early Cambrian of Australia (Runnegar in: Bengtson *et al*. 1990), and in *P. primaeva* (Billings, 1871) from the Taconic Allochthon of the United States and Canada (Walcott 1886, 1890; Lochman 1956; Landing & Bartowski 1996; Landing *et al*. 2002). As the latter species is in need of revision, the Greenland specimens of *Pelagiella* are here referred to the Australian form, *P. subangulata*. The V-shaped ridges of the Greenland *Pelagiella* appear higher than those illustrated in the Australian specimens (Bengtson *et al*. 1990, pl. 167), but in view of the great variability of *P. subangulata* (Runnegar in: Bengtson *et al*. 1990, Parkhaev in: Gravestock *et al*. 2001) and the small number of speci-

mens from Greenland preserving the shell ornament, the specimens from the two collections are regarded as conspecific.

Parkhaev (in: Gravestock *et al*. 2001) included in *P. subangulata* a species from China, *P. emeishanensis* He *in* Xing *et al*., 1983, and four species of *Pelagiella* from the Early Cambrian of Germany (Elicki 1994, 1996). The figured specimens from China and Germany are similar to the Australian species, but the poor preservation does not allow detailed comparison.

Occurrence. Early to Middle Cambrian of Australia, Late Early Cambrian of North-East Greenland.

Class Bivalvia Linnaeus, 1758

Discussion. In 1932 Poulsen described and figured *Fordilla troyensis* Barrande, 1881 from Hyolithus Creek of Andrée Land, North-East Greenland. In the acid-resistant residues investigated for this study *F. troyensis* is rare, occurring in two samples only. At the same time 188 bivalve specimens, including a single specimen from Hyolithus Creek (sample 842), were found to belong to the widespread *Pojetaia* Jell, 1980. Thus, in Greenland, the two common Early Cambrian bivalve genera occur similarly preserved in the same samples.

Fig.8. Molluscs from North-East Greenland, all specimens except I, M and P from the Albert Heim Bjerge area. A–J, *Pelagiella subangulata* (Tate, 1892). A–C, phosphatised external shell MGUH 27004, GGU sample 314835; A, view from the spire, ×40; B, dorsal view, ×32; C, oblique dorsal view, ×40. D–F, phosphatic internal mould MGUH 27005, GGU sample 314807; D, view from the spire, ×25; E, dorsal view, ×25; F, oblique dorsal view, ×30. G, J, phosphatised external shell MGUH 27006, GGU sample 314835; G, apertural view, ×45; J, oblique view from the spire, ×45. H, phosphatic internal mould MGUH 27007, GGU sample 314807, view from the spire, ×30. I, phosohatic internal mould MGUH 27008, GGU sample 314919 C.H. Ostenfeld Nunatak, apertural view, ×40.
K–Q, *Pojetaia runnegari* Jell, 1980. K, O, phosphatised, articulated shell MGUH 27009, GGU sample 314835; K, right lateral view, ×40; O, umbonal view, ×40. L, phosohatised right valve MGUH 27010, GGU sample 314835, lateral view, ×20. M, phospahtised internal mould of left valve MGUH 27011, GGU sample 314919 C.H. Ostenfeld Nunatak, lateral view, ×25. N, Q, phosphatic internal mould of articulated shell MGUH 27012, GGU sample 314835; N, right lateral view, ×50; Q, umbonal view, ×50. P, phosphatic internal mould of articulated shell MGUH 27013, GGU sample 314919 C.H. Ostenfeld Nunatak, posterior view, ×50.
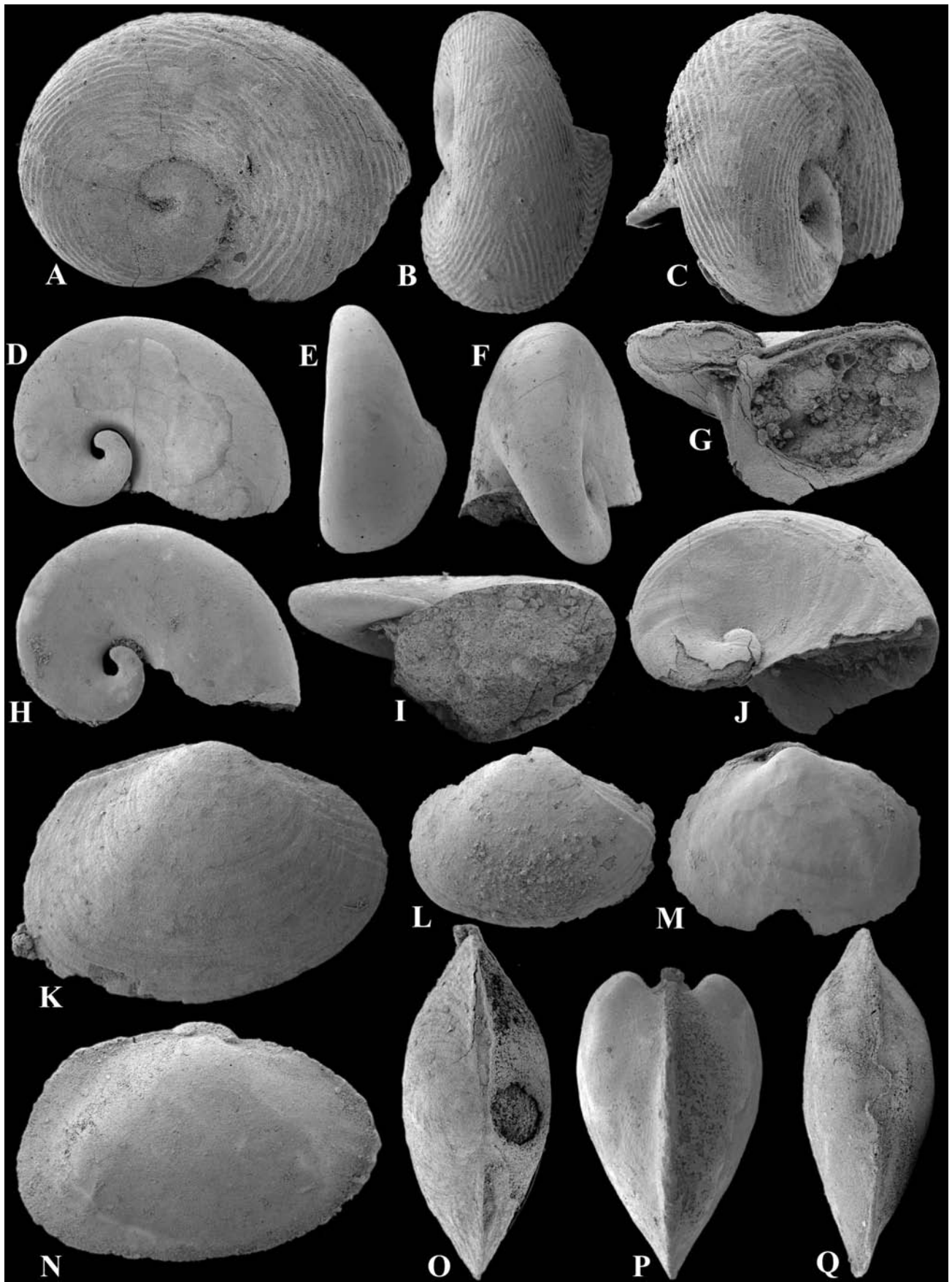
Order and Family uncertain

Genus *Pojetaia* Jell, 1980

Type species. *Pojetaia runnegari* Jell, 1980. Monotypic. For a discussion on other proposed species of the genus, see Parkhaev (in: Gravestock *et al*. 2001).

Discussion. *Pojetaia* Jell, 1980 is known from many Early and Middle Cambrian localities (see Geyer & Streng 1998 and Parkhaev (in: Gravestock *et al*. 2001 for recent reviews) in addition to Australia from where it was first described (Jell 1980). A number of species have been proposed, all of which are distinguished by very small differences (compiled by Geyer & Streng 1998, table 1). Most of the species have been claimed to fall within the range of variability of *P. runnegari* from Australia, and consequently synonymised with the type species (Runnegar in: Bengtson *et al*. 1990; Parkhaev in: Gravestock *et al*. 2001).

Pojetaia runnegari Jell, 1980
Fig. 8K–Q.

1980   *Pojetaia runnegari* n.sp. Jell, p. 234, fig. 1A–F, fig. 2A–I, fig. 3C–K.
2001   *Pojetaia runnegari* Jell – Parkhaev in: Gravestock *et al*., p. 201 (*cum syn*.), pls 49–50.

Holotype. National Museum of Victoria (Australia) P59669. Internal mould from the lower part of the Lower Cambrian Parara Limestone of Horse Gully, York Peninsula, South Australia.

Material. Figured material: MGUH 27009, 27010 and 27012 from GGU sample 314835 and MGUH 27011 and 27013 from GGU sample 314919. 182 additional specimens from GGU samples 314804, 314835, 314906, 314918, 314919, 314933. One specimen from sample 842.

Discussion. Specimens of *Pojetaia* from the Bastion Formation of North-East Greenland are oval with relatively strongly projecting and almost centrally placed umbones on internal moulds (Fig. 8K–N). The posterior auricle is less well defined, and the posterior-dorsal angle larger (130–140 degrees) in the Greenland collection than in most illustrated specimens of *P. runnegari* from Australia. Two hinge-teeth are present in both valves. Although the Greenland specimens differ from the Australian ones in a few characters (e.g. sub-central umbones, larger posterior-dorsal angle) they appear to lie within the range of variability of *P. runnegari* (*sensu* Bengtson *et al*. 1990 and

Parkhaev in: Gravestock *et al*. 2001), and are placed in that species. The variability of the Greenland *Pojetaia* is not well known due to preservational limits. Comparison to a large collection of well preserved bivalves from the Lower Cambrian Forteau Formation of Newfoundland (unpublished information) suggests that the intraspecific variablility of Early Cambrian bivalves could be considerable. In the Newfoundland material, morphological variation exceeding that of the seven species of *Pojetaia* (*sensu* Geyer & Streng 1998) is found in a single sample.

The collection of *Pojetaia* from Greenland includes a relatively high proportion of disarticulated valves and internal moulds of single valves (89%), compared to collections from Australia (Jell 1980: 23.5%, and Runnegar & Bentley 1983 claimed that almost all specimens were articulated). This probably reflects the transported origin of the calcareous components in the Bastion Formation.

Occurrence. Early Cambrian of Australia, Mongolia, North China, South China, Transbaikalia, Germany and North-East Greenland.

Genus *Fordilla* Barrande, 1881

Type species. *Fordilla troyensis* Barrande, 1881.

Composition. Type species and *F. sibirica* Krasilova, 1977.

Discussion. The affinity of *Fordilla* to present day bivalves have been questioned (e.g. Yochelson 1981), but today it is more or less accepted (see Pojeta 2000 and references therein). The genus is distinguished from *Pojetaia* by more excentrically placed umbones, by the organisation of muscle scars, and by the development of the earliest growth stages (see below).

Fordilla troyensis Barrande, 1881
Fig. 9A–F.

1881   *Fordilla troyensis* n.sp. Barrande, p. 391, pl. 361.
1975   *Fordilla troyensis* Barrande – Pojeta, p. 368 (*cum. syn*.), pl. 1, figs 1–4, pls 2–5.
1986   *Fordilla troyensis* Barrande – Jermak, p.184
1988   *Fordilla troyensis* Barrande – Jermak, p. 179, pls 26–28.
?1994   *Fordilla troyensis* Barrande – Elicki, fig. 4/13.

Lectotype. Latex replica, Unites States National Museum 207687, of the lectotype from the Lower Cambrian of Troy, New York State. Illustrated in Pojeta
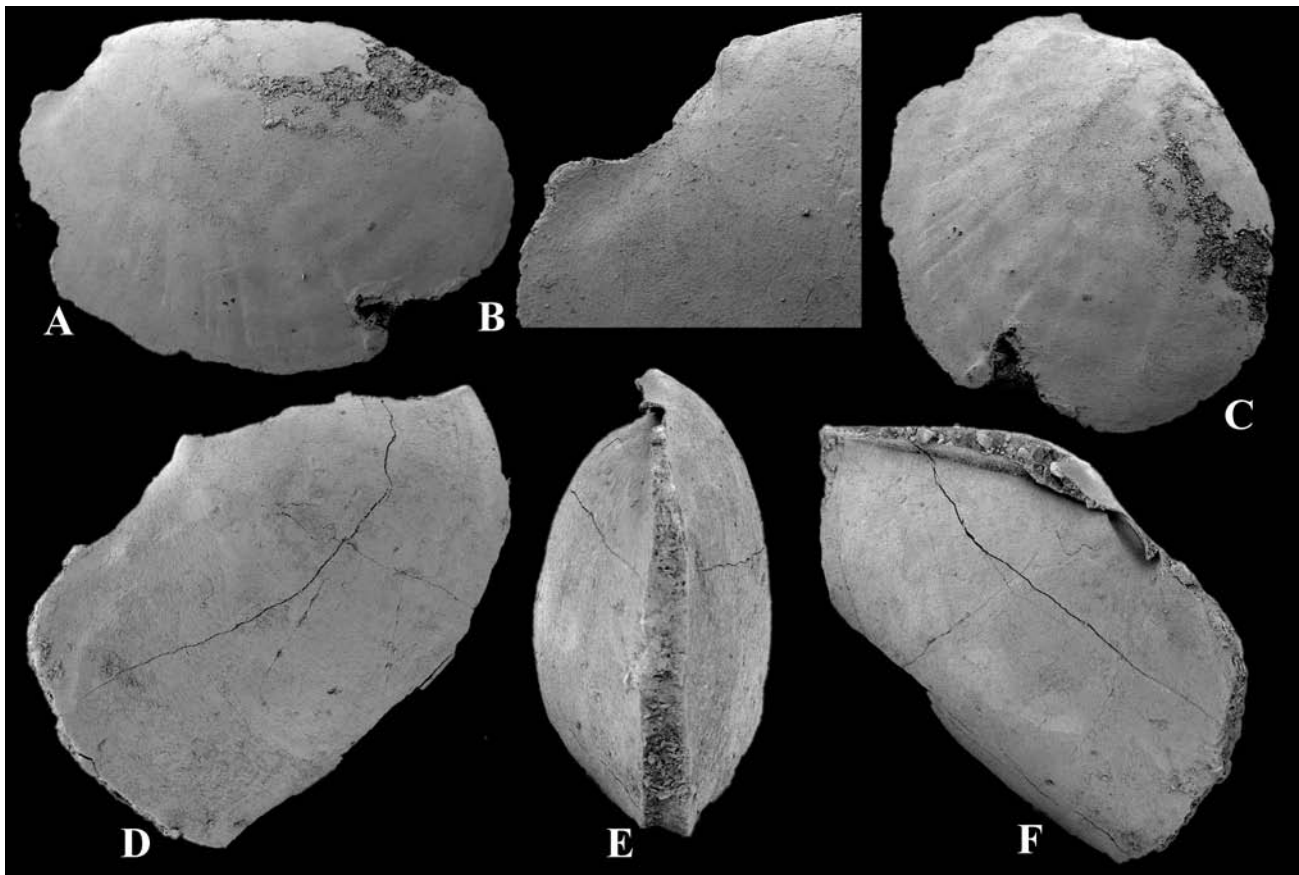
Fig. 9. A–F, *Fordilla troyensis* Barrande, 1881 both specimens from C.H. Ostenfeld Nunatak, North-East Greenland. A–C, phosphatic internal mould of left valve MGUH 27014, GGU sample 314919; A, lateral view, ×22; B, umbonal region, lateral view, ×50; C, oblique lateral view, ×22. D–F, phosphatic internal mould of damaged articulated specimen MGUH 27015, GGU sample 314918; D, left lateral view, ×35; E, anterior view, ×35, F, right lateral view, ×35.

1975, pl. 4, figs 1–2.

Material. MGUH 27014 from GGU sample 314919 and MGUH 27015 from GGU sample 314918. Nine additional specimens from GGU samples 314918 and 314919.

Discussion. Internal moulds recovered from two samples are oval and sometimes show radiating furrows formed by the migration of muscle scars (Fig. 9A, C). The hinge-line is not well preserved, but the umbonal region of the valves preserves small tubercles (Fig. 9A–B, D), presumably moulds of the internal cavity of the protoconch. *Fordilla troyensis* is known from North America (New York State, Newfoundland, North Greenland, North-East Greenland), Bornholm, Siberia and possibly Germany (see reviews in Pojeta 1975, 2000). In North America the species is mainly known from crack-out material (Pojeta 1975), although acid-isolated material from Siberia has been illustrated (Jermak 1986, 1988). The material from North-East Greenland is referred to *F. troyensis* based on the shape of the valves, and the arrangement of muscle scars.

Occurrence. The Early Cambrian of New York State, Newfoundland, North-East Greenland, North Greenland, Bornholm, Siberia and possibly Germany.

Acknowledgements

References

Barrande, J. 1881: Systême Silurien du centre de la Boheme. Acephales. 6. Paris and Prague, 342 pp.

Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A. & Runnegar, B.N. 1990: Early Cambrian fossils from South Australia. Association of Australasian Palaeontologists, Memoir 9, 364 pp.

Billings, E. 1871: On some new species of Palaeozoic fossils. Canadian Naturalist 6, 213–233, 240.

Billings, E. 1872: On some fossils from the primordial rocks of Newfoundland. Canadian Naturalist 6, 465–479.

Brasier, M.D. 1984: Microfossils and small shelly fossils from the Lower Cambrian Hyolithes Limestone at Nuneaton, English Midlands. Geological Magazine 121, 229–253.

Brock, G.A. & Cooper, B.J. 1993: Shelly fossils from the Early Cambrian (Toyonian) Wirrealpa, Aroona Creek, and Ramsay limestones of South Australia. Journal of Paleontology 67, 758–778.

Brock, G.A., Engelbretsen, M.J., Jago, J.B., Kruse, P.D., Laurie, J.R., Shergold, J.H., Shi, G.R. & Sorauf, J.E. 2000: Palaeobiogeographic affinities of Australian Cambrian faunas. Association of Australasian Palaeontologists, Memoir 23, 1–61.

Budd, G.E. & Jensen, S. 2000: A critical reappraisal of the fossil record of the bilaterian phyla. Biological Reviews 75, 253–295.

Cobbold, E.S. 1921: The Cambrian horizons of Comley (Shropshire) and their Brachiopoda, Pteropoda, Gastropoda, etc. Quarterly Journal of the Geological Society of London 76, 325–386.

Cobbold, E.S. 1934: The Cambrian genus Stenotheca. Geological Magazine 71, 463–468.

Cowie, J.W. & Adams, P. J. 1957: The geology of the Cambro–Ordovician rocks of central East Greenland. Part I: Stratigraphy and Structure. Meddelelser om Grønland 153, 193 pp.

Cuvier, G. 1797: Tableau élementaire del'historie naturelle des animaux. 710 pp. Paris.

Dalziel, I.W.D. 1997: Neoproterozoic-Plaeozoic geography and tectonics: review, hypothesis, environmental speculation. Geological Society of America Bulletin 106, 243–252.

Duff, K.L. 1975: Palaeoecology of a bituminous shale – the Lower Oxford Clay of central England. Palaeontology 18, 443–482.

Elicki, O. 1994: Lower Cambrian carbonates from eastern Germany: Palaeontology, stratigraphy and palaeogeography.
Neues Jahrbuch für Geologie und Paläontologie Abhandlungen B 191, 69–93.

Elicki, O. 1996: Die Gastropoden und Monoplacophoren der unterkambrischen Görlitz-Fauna. Freiberger Forschungshefte C 464, 145–173.

Esakova, N.V. & Zhegallo, E.A. 1996: Biostratigrafiya i fauna nizhnego kembriya Mongolii (Lower Cambrian biostratigraphy and fauna of western Mongolia). Trudy, Sovmestnaya Rossiysko-Mongol´skaya paleontologicheskaya ekspeditsiya 46, 214 pp. Moscow: Nauka (in Russian).

Feng Weimin, Qian Yi & Rong Zhiquan 1994: (Study of Monoplacophora and Gastropoda from the Lower Cambrian Xinji Formation in Ye Xian, Henan). Acta Micropalaeontlogica Sinica 11, 1–19 (in Chinese).

Geyer, G. 1986: Mittelkambrische Mollusken aus Marokko und Spanien. Senkernbergiana letaea 67, 55–118.

Geyer, G. 1994: Middle Cambrian molluscs from Idaho and early conchiferan evolution. In: Landing, E. (ed.): Studies in Stratigraphy and Paleontology in Honor of Donald W. Fisher. New York State Museum Bulletin 481, 69–86.

Geyer, G. & Streng, M. 1998: Middle Cambrian pelecypods from the Anti-Atlas, Morocco. Revista Espanola de Paleontología n° extra Homenaje al Professore Gonzalo Vidal, 83–96.

Golikov, A.N. & Starobogatov, Ya.I. 1988: Voprosy filogenii i sistematiki perednezhabernykh bryukhonogikh mollyuskov (Problems of phylogeny and systematics of prosobranch gastropods). Trudy, Zooloicheskiy institut AN SSSR 176, 4–77 (in Russian).

Gravestock, D.I., Alexander, E.M., Demidenko, Yu.E., Esakova, N.V., Holmer, L.E., Jago, J.B., Lin Tianrui, Melnikova, L.M., Parkhaev, P.Yu., Rozanov, A. Yu., Ushatinskaya, G.T., Zang Wenlong, Zhegallo, E.A. & Zhuravlev, A.Yu. 2001: The Cambrian biostratigraphy of the Stansbury Basin, South Australia. Transaction of the Palaeontological Institute 282, 344 pp. Moscow: IAPC Nauka/Interperiodica.

Gubanov, A.P. 1998: The Early Cambrian molluscan evolution and its palaeogeographic implications. Acta Universitatis Carolinae, Geologica 42, 419–422.

Gubanov, A.P. 2002: Early Cambrian palaeogeography and the probable Iberia – Siberia connection. Tectonophysics 352, 153–168.

Gubanov, A.P. & Peel, J.S. 1998: Redescription of the type species of Latouchella Cobbold, 1921 (Mollusca) from the Lower Cambrian of Comley, England. GFF 120, 17–20.

Gubanov, A.P. & Peel, J.S. 1999: Oelandiella, the Earliest Cambrian helcionellid mollusc from Siberia. Palaeontology 42, 211–222.

Gubanov, A.P. & Peel, J.S. 2000: Cambrian monoplacophoran molluscs (Class Helcionelloida). American Malacological Bulletin 15 (2), 139–145.

Gubanov, A.P. & Peel, J.S. 2001: Latest Helcionelloid molluscs from the Lower Ordovician of Kazakhstan. Palaeontlogy 44, 681–694.

Gubanov, A.P., Fernández Remolar, D.C. & Peel, J.S. 2004: Early Cambrian molluscs from Sierra de Córdoba (Spain). Geobios 37, 199–215.

Gubanov, A.P., Skovsted, C.B. & Peel, J.S. in press: Anabarella australis (Mollusca, Helcionelloida) from the Lower Cambrian of Greenland. Geobios.

Hall, J. 1847: Description of the organic remains of Lower Paleozoic division of the New York System. Paleontology of New York 1, 338 pp.

Hall, J. 1872: Notes on some new or imperfectly known forms among the Brachiopoda. etc. Annual Report to the Regents of the University of the State of New York, Report 23, Appendix G, 244–247.

Hambrey, M.J. & Spencer, A.M. 1987: Late Precambrian glaciation of central East Greenland. Meddelelser om Grønland Geoscience 19, 50 pp.

He Tinggui & Yang Xianhe 1982: (Lower Cambrian Meishucun Stage of the western Yangtze stratigraphic region and its small shelly fossils. Bulletin of Chengdu Institute of Geology and Mineral Resources, Chinese Academy of Sciences 3, 69–95 (in Chinese).

Hicks, H. 1872: On some undescribed fossils from the Mendevian Group. Quarterly Journal of the Geological Society of London 28, 173–185.

Hinz-Schallreuter, I. 1997: Einsaugstutzen oder Auspuff? Das Rätsel um *Yochelcionella* (Mollusca, Kambrium). Geschiebekunde aktuell 13, 105–122.

Holmer, L.E., Skovsted, C.B. & Williams, A. 2002: A stem group brachiopod from the Lower Cambrian – support for a *Micrina* (halkieriid) ancestry. Palaeontology 45, 875–882.

Jell, P.A. 1980: Earliest known pelecypod on Earth – a new Early Cambrian genus from South Australia. Alcheringa 5, 85–93.

Jermak, P.P. 1986: Rannekembrijskie fordillidy (Bivalvia) severa Sibirskoj platformy (Early Cambrian Fordillidae (Bivalvia) from the northern Siberian Platform). Trudy Sibirskoe Otdelenie Institut Geologogii i Geophysiki Akademiya Nauk SSSR 669, 183–188 (in Russian).

Jermak, P.P. 1988: Strovenie zamoznogo apparata, mikrostruktura rakovinie i obraz chizni rannekembrijskie fordillid (Bivalvia). Trudy Sibirskoe Otdelenie Institut Geologogii i Geophysiki Akademiya Nauk SSSR 720, 179–184 (in Russian).

Kerber, M. 1988: Mikrofossilien aus Unterkambrischen Gesteinen der Montagne Noire, Frankreich. Palaeontographica A 202, 127–203.

Knight, J.B., Cox, L.R., Keen, A.M., Batten, R.L., Yochelson, E.L. & Robertson, R. 1960: Systematic descriptions. In: Moore, R.C. (ed.): Treatise on Invertebrate Paleontology, I, Mollusca 1, 169–310. Lawrence: Geological Society of America and University of Kansas Press.

Kouchinsky, A.V. 2000: Shell microstructures in Early Cambrian molluscs. Acta Palaeontologica Polonica 45, 119–150.

Krasilova, I.N. 1977: Fordillidy (Bivalvia) iz nizhnego paleozoya Sibirskoy platformy (Fordillidae (Bivalvia) from the Lower Paleozoic of the Siberian platform). Palaeontologicheskii Zhurnal 1977 (2), 42–48 (in Russian, translated to English in Paleontological Journal 11, 172–178).

Landing, E. & Bartowski, K. E. 1996: Oldest shelly fossils from the Taconic allochthon and late Early Cambrian sea levels in Eastern Laurentia. Journal of Paleontology 70, 741–761.

Landing, E., Geyer, G. & Bartowski, K.E. 2002: Latest Early Cambrian Small Shelly Fossils, trilobites, and Hatch Hill dysarerobic interval on the Québec continental slope. Journal of Paleontology 76, 287–305.

Li Yuwen & Zhou Benhe 1986: (Discovery of old fossil bivalves in China and its significance). Scientia Geologica Sinica 1986 (1), 38–45 (in Chinese).

Lindström, A. & Peel, J.S. 2003: Shell repair and mode of life of *Praenatica gregaria* (Gastropoda) from the Devonian of Bohemia (Czech Republic). Palaeontology, 623–633.

Linnaeus, C. 1758: Systema naturae per tria regna naturae. Edit. decima 1, Laurentii Salvii, Stockholm.

Linsley, R.M. & Kier, W.M. 1984: The Paragastropoda: A proposal for a new Class of Paleozoic Mollusca. Malacologia 25, 241–254.

Liu Diyong 1979: (Earliest Cambrian Brachiopods from southwest China). Acta Palaeontologica Sinica 18, 505–511 (in Chinese).

Lochman, C. 1956: Stratigraphy, paleontology and paleogeography of the *Elliptocephala asaphoides* strata in Cambridge and Hoosick Quadrangles, New York. Bulletin of the Geological Society of America 67, 1331–1396.

MacKinnon, D.I. 1985: New Zealand late Middle Cambrian molluscs and the origin of Rostroconchia and Bivalvia. Alcheringa 9, 65–81.

Matthew, G.F. 1894: Illustrations of the fauna of the St. John Group. Transactions of the Royal Society of Canada 11 part 4, 85–129.

Matthew, G.F. 1895: The *Protolenus* fauna. Transactions of the New York Academy of Sciences 14, 101–153.

Missarzhevsky, V.V. 1977: Konodonty (?) i fosfatnye problematiki kembriya Mongolii i Sibiri. (Conodonts(?) and phosphatic problematica from the Cambrian of Mongolia and Siberia). In: Bespozvonochnye Paleozoya Mongolii, 10–19. Trudy Sovmestaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya (in Russian).

Missarzhevsky, V.V. 1981: Rannekembriyskie khiolity I gastropody Mongolii (Early Cambrian hyoliths and gastropods of Mongolia). Palaeontologicheskii Zhurnal 1981, 21–28 (in Russian).

Missarzhevsky, V.V. 1989: Drevnejshie skeletnye okamenelosti i startigrafiya pogranichnykh tolshch dokembriya i kembriya (Oldest skeletal fossils and stratigraphy of Precambrian and Cambrian boundary beds). Trudy Akademia Nauk SSSR 443, 238 pp. (in Russian).

Missarzhevsky, V.V. & Mambetov, A.M. 1981: Stratigrafiya i fauna progranichnykh sloev kembiya i dokembriya Malogo Karatau. (Stratigraphy and fauna of the Precambrian–Cambrian boundary beds of Malyj Karatau). Trudy Geologischeskogo Instituta Akademia nauk SSSR, Leningrad 326, 92 pp. (in Russian).

Palmer, A.R. 1998: A proposed nomenclature for stages and series for the Cambrian of Laurentia. Canadian Journal of Earth Science 35, 323–328.

Palmer, A.R. & Repina, L.N. 1993: Through a glass darkly: taxonomy, phylogeny and biostratigraphy of the Olenellina. University of Kansas, Paleontological Contributions 3, 35 pp.

Parkhaev, P.Yu. 2000: Funktsional´naya morphologiya odnostvorchatykh mollyuskov – gel´tsionellid. Chast' 1 (The functional morphology of the Cambrian univalved molluscs – Helcionellids, part 1). Palaeontologicheskii Zhurnal 2000 (4), 32–39 (in Russian, English translation in Paleontological Journal 34, 392–399).

Parkhaev, P.Yu. 2001a: Funktsional´naya morphologiya odnostvorchatykh mollyuskov – gel´tsionellid. Chast' 2 (The functional morphology of the Cambrian univalved molluscs – Helcionellids, part 2). Palaeontologicheskii Zhurnal 2001 (5), 20–26 (in Russian, English translation in Paleontological Journal 35, 470–475).

Parkhaev, P.Yu. 2001b: *Trenella bifrons* – novyy gel´tsionellidnyy mollyusk iz botomskogo yarusa Yuzhnoy Avstralii (*Trenella bifrons*: A new Helcionelloid mollusc from the Lower Cam-

brian of South Australia). Paleontologicheskii Zhurnal 2001 (6), 22–24 (in Russian, English translation in Paleontological Journal 35, 585–588).

Parkhaev, P.Yu. 2002: Filogeniya i sistematik kembriyskikh odnostvorchatykh mollyuskov (Phylogeny and systematics of Cambrian univalve molluscs). Paleontologicheskii Zhurnal 2002 (1), 27–39 (in Russian, English translation in Paleontological Journal 36, 25–36).

Peel, J.S. 1977: Systematics and palaeontology of the Silurian gastropods of the Arisaig Group, Nova Scotia. Det Kongelige Danske Videnskabernes Selskab Biologiske Skrifter 21 (2), 89 pp.

Peel, J.S. 1979: *Protowenella* (Mollusca) from the Cambrian of Greenland. Rapport Grønlands Geologiske Undersøgelse 91, 92 only.

Peel, J.S. 1980: Yochelcionellids from the Early and Late Cambrian of North Greenland. Rapport Grønlands Geologiske Undersøgelse 101, 44 only.

Peel, J.S. 1988a: *Yochelcionella americana* (Mollusca) from the Lower Cambrian of Newfoundland. Canadian Journal of Earth Science 24, 2328–2330.

Peel, J.S. 1988b: Molluscs of the Holm Dal Formation(late Middle Cambrian), central North Greenland. Meddelelser om Grønland Geoscience 20, 145–168.

Peel, J.S. 1989: A Lower Cambrian *Eotebenna* (Mollusca) from Arctic North America. Canadian Journal of Earth Science 26, 1501–1503.

Peel, J.S. 1991: The Classes Tergomya and Helcionelloida, and early molluscan evolution. Grønlands Geologiske Undersøgelse, Bulletin 161, 11–65.

Peel, J.S. & Yochelson, E.L. 1987: New information on *Oelandia* (Mollusca) from the Middle Cambrian of Sweden. Bulletin of the Geological Society of Denmark 36, 263–273.

Pelman, Yu.L. 1977: Early and Middle Cambrian inarticulate brachiopods from the Siberian Platform. Nauka, Novosibirsk, 168 pp. (in Russian).

Pojeta, J.Jr. 1975: *Fordilla troyensis* Barrande and early pelecypod phylogeny. Bulletins of American Paleontology 67, 363–384.

Pojeta, J., Jr. 2000: Cambrian Pelecypoda (Mollusca). American Malacological Bulletin 15, 157–166.

Poulsen, C. 1932: The Lower Cambrian faunas of East Greenland. Meddelelser om Grønland 87, 66 pp.

Qian Yi & Bengtson, S. 1989: Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. Fossils and Strata 24, 156 pp.

Resser, C.E. 1938: Fourth contribution to nomenclature of Cambrian fossils. Smithsonian Miscellaneous Collections 97 Number 10, 43 pp.

Rozanov, A.Yu., Missarzhevsky, V.V., Volkova, N.A., Voronova, L.C., Krylov, I.N., Keller, B.M., Korolyuk, I.K., Lendzion, K., Michniak, R., Pykhova, N.G. & Sidorov, A.D. 1969: Tommotskij yarus i problema nizhnej grantisy kembriya. (The Tommotian Stage and the Cambrian lower Boundary problem). Trudy Geologocheskogo Instituta Akademia Nauk SSSR 206, 380 pp. (in Russian).

Runnegar, B. 1981: Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs. Lethaia 14, 311–322.

Runnegar, B. 1996: Early evolution of the Molusca: The fossil record. In: Taylor, J. (ed.): Origin and evolutionary radiation of the Mollusca, 77–87. Oxford: Oxford University Press.

Runnegar, B. & Bentely, C. 1983: Anatomy, ecology and affinities of the Australian early Cambrian bivalve *Pojetaia runnegari* Jell. Journal of Paleontology 57, 73–92.

Runnegar, B. & Jell, P.A. 1976: Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. Alcheringa 1, 109–138.

Runnegar, B. & Pojeta, J., Jr. 1974: Molluscan phylogeny: The paleontological viewpoint. Science 186, 311–317.

Runnegar, B. & Pojeta, J., Jr. 1980: The monoplacophoran mollusc *Yochelcionella* identified from the Lower Cambrian Pennsylvania. Journal of Paleontology 54, 635–636.

Schiøler, P. 1989: Non-toxic low-cost heavy liquid separation in the Geological Survey of Greenland. Rapport Grønlands Geologiske Undersøgelse 145, 11–13.

Shaler, N.S. & Foerste, A.F. 1888: Preliminary description of North Attleboro fossils. Harvard Museum of Comparative Zoology Bulletin 16, 27–41.

Shaw, A.B. 1962: Paleontology of northwestern Vermont IX, fauna of the Monkton Quartzite. Journal of Paleontology 36, 322–345.

Skovsted, C.B. 2003: Mobergellans (Problematica) from the Cambrian of Greenland, Siberia and Kazakhstan. Paläontologische Zeitschrift 77, 429–443.

Skovsted, C.B. & Holmer, L.E. 2003: The Early Cambrian stem group brachiopod *Mickwitzia* from Northeast Greenland. Palaeontologica Polonica 48, 11–30.

Skovsted, C.B. & Holmer, L.E. in press: Early Cambrian brachiopods from North-East Greenland. Palaeontology.

Skovsted, C.B. & Peel, J.S. 2001: The problematic fossil *Mongolitubulus* from the Lower Cambrian of Greenland. Bulletin of the Geological Society of Denmark 48, 135–147.

Starobogatov, Ya.I. 1970: K sistematike rannepaleozoyskikh Monoplacophora (Systematics of early Paleozoic Monoplacophora). Paleontologicheskii Zhurnal 1970, 6–17 (in Russian, translated in Palaeontological Journal 1970, 293–302).

Stouge, S., Boyce, D.W., Christiansen, J., Harper, D.A.T. & Knight, I. 2001: Vendian – Lower Ordovician stratigraphy of Ella Ø, North-East Greenland: new investigations. Geology of Greenland Survey Bulletin 189, 107–114.

Tate, R. 1892: The Cambrian fossils of South Australia. Transactions of the Royal Society of South Australia 15, 183–189.

Voronova, L.G., Drosdova, N.A., Esakova, N.V., Zhegallo, E.A., Zhuravlev, A.Yu., Rozanov, A.Yu., Sayutina, T.A. & Ushatinskaya, G.T. 1987: Lower Cambrian fossils of the Mackenzie Mountains (Canada). Trudy Paleontologicheskyi institut, Akademia nauk SSSR 224, 1–88, 32 pls. (in Russian).

Vostokova, V.A. 1962: Kembriyskie gastropody Sibirskoy platformy i Taymyra (Cambrian gastropods of the Siberian Platform and Taimyr). In Sbornik statey po paleontologii i biostratigrafii (Collection of papers on Palaeontology and Biostratigraphy) 28, 51–74. Leningrad: Nedra (in Russian).

Walcott, C.D. 1886: Second contribution to the studies on the Cambrian faunas of North America. Bulletin of the United States Geological Survey 30, 369 pp.

Walcott, C.D. 1890: The fauna of the Lower Cambrian or *Olenellus* Zone of North America. 10th Annual Report of the United States Geological Survey, 509–763.

Walcott, C.D. 1908: Cambrian Brachiopoda: Descriptions of new genera and species. Smithsonian Miscellaneous Collections 53, 231–422.

Walcott, C.D. 1910: *Olenellus* and other genera of the Mesonacidae. Smithsonian Miscellaneous Collections 53, 53–137.

Wenz, W. 1938: Gastropoda. In: Schindewolf, O.H. (ed.): Handbuch der Paläozoologie, Band 6. Berlin: Borntraeger.

Westergård, A.H. 1936: *Paradoxides oelandicus* beds of Öland. Sveriges Geologiska Undersökning, serie C 294, 1–6.

Xing Yusheng, Ding Qixiu, Luo Huilin, He Tinggui & Wang Yanggong 1983: (The Sinian–Cambrian boundary of China). Bulletin of the Institute of Geology, Chinese Academy of Geological Sciences 10, 262 pp. (in Chinese).

Yochelson, E.L. 1981: *Fordilla troyensis* Barrande: The oldest known pelecypod may not be a pelecypod. Journal of Paleontology 55, 113–125.

Yu Wen 1979: (Earliest Cambrian monoplacophorans and gastropods from western Hubei with their biostratigraphical significance). Acta Palaeontologica Sinica 18, 233–270 (in Chinese with English summary).

Yu Wen 1986: (Lower Cambrian univalved mollusca from Kurutag, Xinjiang). Acta Palaeontologica Sinica 25, 13–62 (in Chinese with English summary).

Yu Wen 1987: Yangtze Micromolluscan fauna in Yangtze region of China with notes on Precambrian–Cambrian boundary. Nanjing Institute of Geology and Palaeontology, Academia Sinica, 255 p, 68 pls. Nanjing: Nanjing University Publishing House.

Yu Wen & Ning Hui 1985: (Two Cambrian monoplacophorans from borehole, Xinjiang). Acta Palaeontologica Sinica 24, 47–50 (in Chinese).

Zhong Hua [Chen Menge] 1977: (Preliminary study of the ancient fauna of South China and its stratigraphic significance). Scientia Geologica Sinica 1977, 118–128 (in Chinese).

Zhou Benhe & Xiao Ligong 1984: (Early Cambrian monoplacophorans and gastropods Huainan and Huoqiu counties, Anhui Province). Professional Papers of Stratigraphy and Palaeontlogy, Chinese Academy of Geological Sciences 13, 125–140 (in Chinese).