

Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland

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A small, but diverse fauna of molluscs is described from the lower beds of the Holm Dal Formation (late Middle Cambrian) of central North Greenland. Species of Helcionellacea and Hypseloconellacea dominate, although only individuals of the former superfamily are numerically common, as are examples of a single stenothecoid species. Paragastropoda and Hyolitha are rare faunal elements. A single new genus (*Perssuakiella*) and 5 new species are described: *P. troelseni*, *Latouchella holmdalense*, *L. pearylandica*, *Stenothecoides groenlandica* and *Costipelagiella kochi*.

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Molluscs are a generally uncommon element within the fauna of the Holm Dal Formation (late Middle Cambrian) of central North Greenland (Fig. 1). Less than fifty specimens are available for study from grainstones in the lower part of the formation, compared with the many hundreds of specimens of both trilobites and brachiopods described elsewhere in this volume (Robison; Zell & Rowell). In terms of diversity, however, the discrepancy is less strongly marked. Thirteen molluscan species are recognised, compared with 14 species of inarticulate brachiopods and 58 species of trilobites (Figs 2–4). Many of the molluscan taxa are known only from single specimens; taking into account the effects of variable preservation this has often resulted in such material being described in open nomenclature.

Most of the Holm Dal molluscs are simple cap-shaped, or isostrophically coiled univalves which can be referred to the Class Monoplacophora Knight 1952. In recent years, however, the scope of this taxon has been subject to so much debate that it can not be employed meaningfully without qualification as to content (compare Runnegar & Jell 1976, Yochelson 1979; Runnegar & Pojeta 1985; Salvini-Plawen 1985; Wingstrand 1985; Geyer 1986). Thus, the term is not employed in the present context and relevant taxa are assigned either to the Superfamily Helcionellacea or to the Superfamily Hypseloconellacea.

The molluscan fauna of the Holm Dal Formation is unusual in that it contains representatives of both Helcionellacea and Hypseloconellacea. Members of the latter superfamily are typical of Upper Cambrian inner shelf sequences, particularly in central North America (Berkey 1898; Stinchcomb 1986). They are not commonly associated with Helcionellacea, individuals of which are more characteristic of Lower and Middle Cambrian strata. The association of members of the two

superfamilies confirms the late Middle Cambrian age (*Lejopyge laevigata* Interval-zone of the Swedish standard zonation; early Dresbachian of much of North America) suggested on the basis of the trilobite faunas by Robison (this volume).

Relatively few studies exist of molluscs of Middle and Late Cambrian age, although a number of taxa have been recorded as minor elements of trilobite-dominated faunas. Few of these taxa are adequately described or illustrated, causing difficulties in the comparison of Holm Dal molluscs with published literature. Exceptions are provided by recent studies of Middle Cambrian molluscs from Australia (Runnegar & Jell 1976), Spain and Morocco (Geyer 1986) and a large Upper Cambrian fauna from the Antarctic (Yochelson et al. 1973; Webers et al. in press). A sequence of papers by Stinchcomb (1975, 1980, 1986, see also Stinchcomb & Echols 1966) has illuminated problems associated with hypseloconellacean-dominated faunas of Late Cambrian to Early Ordovician age in Missouri. Unfortunately, only material from the latter study shows more than slight similarity to the Holm Dal fauna.

In view of the paucity of described contemporaneous material, it is not unexpected that little relationship can be established between the molluscan fauna of the Holm Dal Formation and faunas from other areas. A single taxon of uncertain generic position compares well with a Dresbachian species from the Missouri area (*Kiringella? washingtonense* Stinchcomb 1975).

Repositories. – Type and figured specimens are deposited in the type collection of the Geological Museum, Copenhagen, Denmark (MGUH prefix). Other material is retained in the collections of the Geological Survey of Greenland, Copenhagen (GGU prefix).

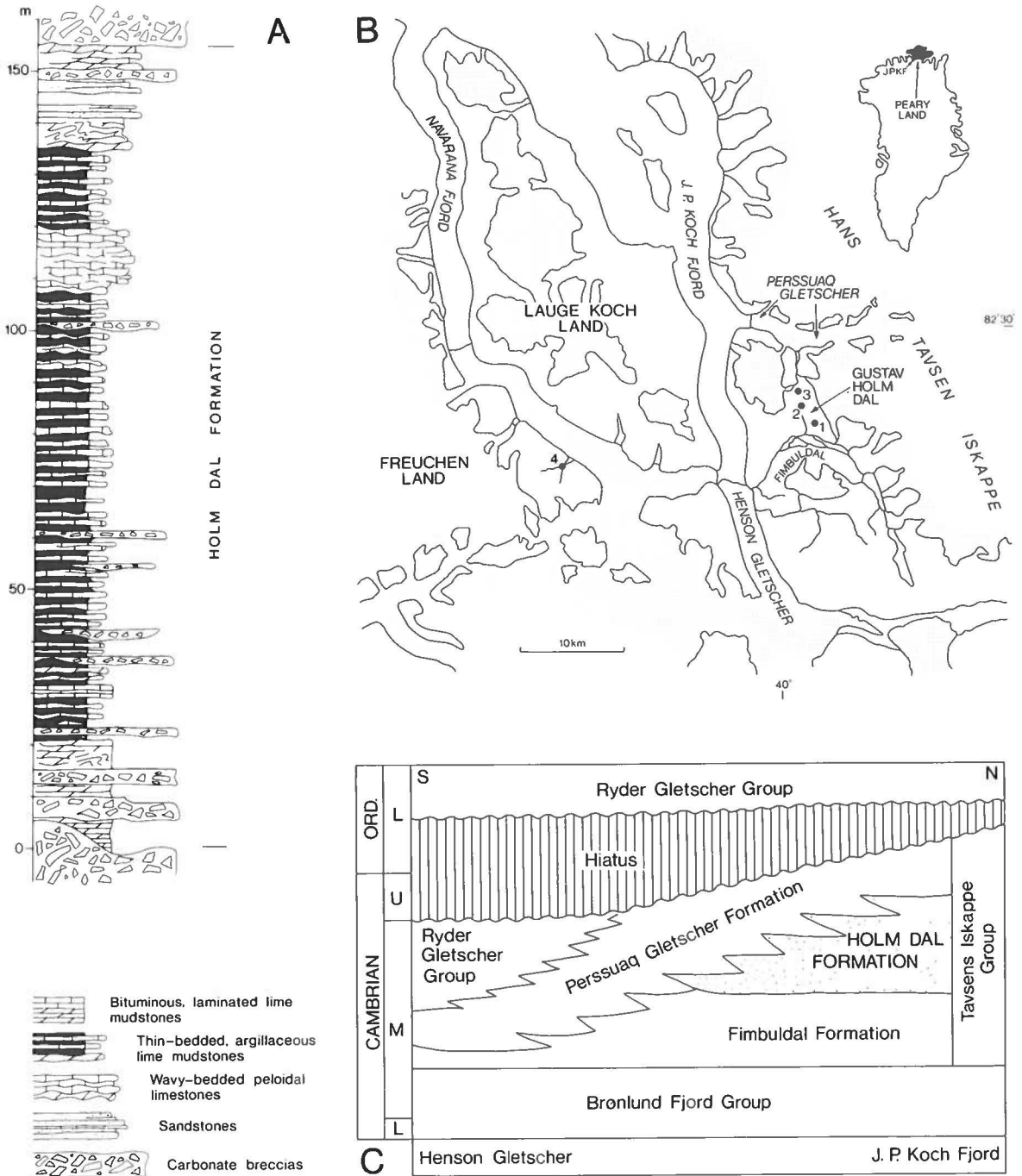


Fig. 1. Derivation of molluscs from the Holm Dal Formation, central North Greenland. A, stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central North Greenland. Peary Land and J. P. Koch Fjord (JPKF) are indicated on the small inset map of Greenland. Collection localities within the Holm Dal Formation are numbered 1 to 4: 1, the type locality (Fig. 1A) and adjacent area, GGU collections in the sequence 225528–225567; 2, east side of Gustav Holm Dal, GGU collections 225586, 271403, 271404, 271408, 271414, 271417; 3, east side of Gustav Holm Dal, GGU collections 225592–225595; 4, south-east Freuchen Land, GGU collections 315007, 315009, 315011–315013. Not all collections and localities have yielded molluscs. C, stratigraphic relationship of the Holm Dal Formation (from Ineson, this volume).

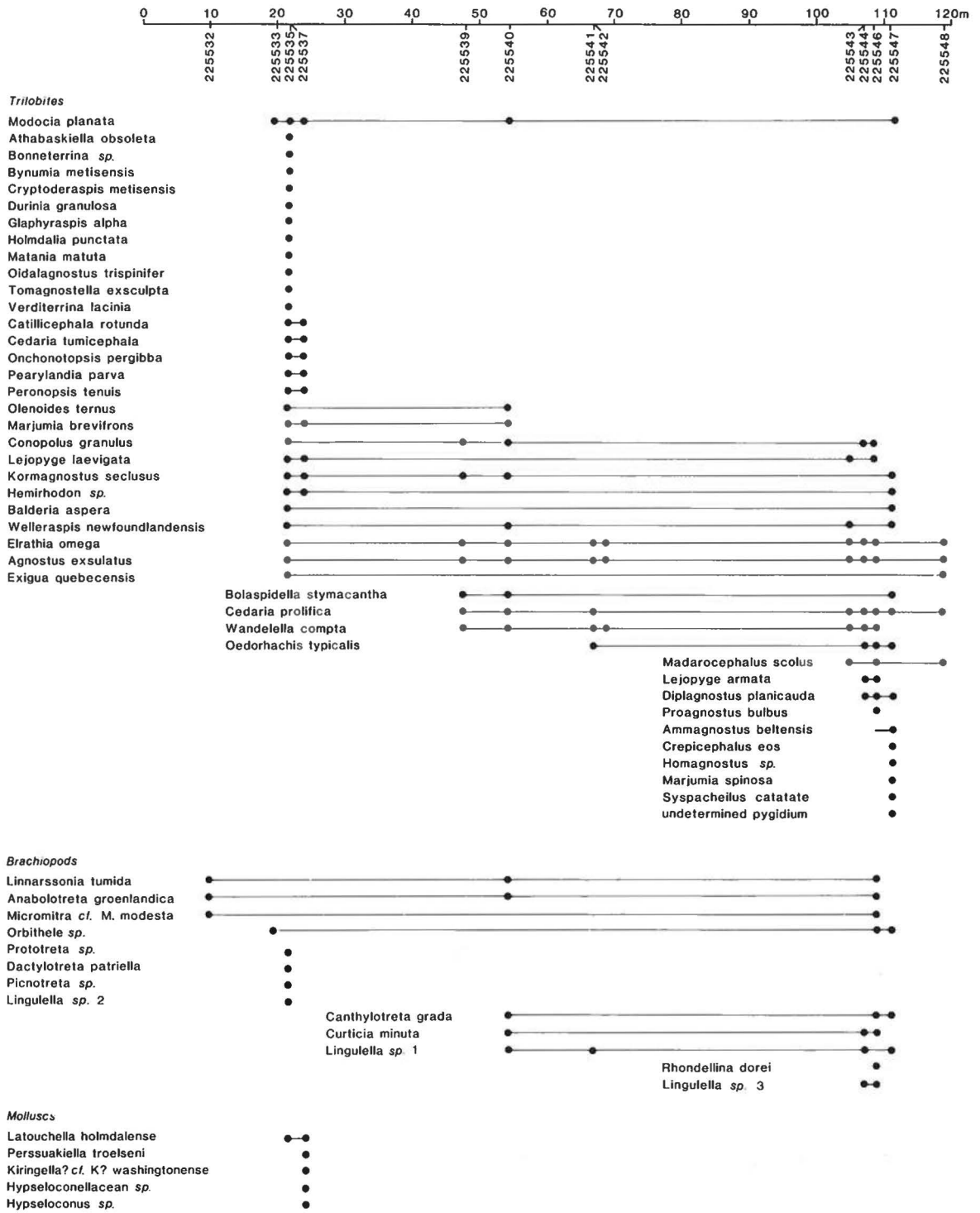


Fig. 2. Stratigraphic distribution of trilobites, brachiopods and molluscs from the type section of the Holm Dal Formation (Fig. 1A, locality 1 in Fig. 1B). Six-digit numbers are GGU collection numbers. The formation is almost 155 m thick in its type section; scale indicates height above base of formation.

	225528	225529	225530	225552	225561	225563	225564	225565	225567
<i>Trilobites</i>									
<i>Bolaspidella stymacantha</i>	●			●	●		●		
<i>Bynumia metisensis</i>	●	●		●	●	●			
<i>Catillicephala rotunda</i>	●	●		●	●	●	●		
<i>Cedaria tumicephala</i>	●	●			●	●	●	●	
<i>Conopolus granulus</i>	●	●		●	●	●			
<i>Crepicephalus eos</i>	●	●		●	●				
<i>Cryptoderaspis metisensis</i>	●				●				
<i>Durinia granulosa</i>	●				●				
<i>Exigua quebecensis</i>	●			●					
<i>Hemirhodon sp.</i>	●	●		●	●		●		
<i>Holmdalia punctata</i>	●				●				
<i>Kormagnostus seclusus</i>	●	●		●	●	●	●	●	
<i>Marjumia brevifrons</i>	●	●		●	●		●		
<i>Modocia planata</i>	●	●		●	●	●	●		
<i>Oidalgagnostus trispinifer</i>	●	●			●				
<i>Onchonotopsis pergibba</i>	●	●			●	●			
<i>Onchonotopsis physala</i>	●				●				
<i>Pearylandia parva</i>	●	●		●	●	●	●	●	
<i>Proagnostus bulbosus</i>	●	●		●	●	●			
<i>Tomagnostella exsculpta</i>	●	●		●			●		
<i>Ammagnostus beltensis</i>		●							
<i>Elrathia omega</i>		●			●	●			
<i>Homagnostus sp.</i>		●							
<i>Marjumia spinosa</i>		●				●		●	
<i>Olenoides ternus</i>		●			●		●	●	
<i>Peronopsis tenuis</i>		●				●		●	
<i>Tavsenia ditrema</i>		●		●	●	●	●		
<i>Ankoura sp.</i>				●	●	●			
<i>Balderia aspera</i>				●	●				
<i>Blountia sp. 1</i>				●					
<i>Lejopyge laevigata</i>				●	●				
<i>Sypscapeilus catatate</i>				●	●		●		
<i>Welleraspis newfoundlandensis</i>				●	●			●	
<i>Agelagma quadratum</i>					●				
<i>Blountia sp. 2</i>					●				
<i>Hawkinsia? sp.</i>					●				
<i>Kingstonia peltata</i>						●		●	
<i>Aagnostus exsulatus</i>								●	
<i>Brachiopods</i>									
<i>Acrothelid gen. indet.</i>					●				
<i>Linnarssonina tumida</i>									●
<i>Molluscs</i>									
<i>Stenothecoides groenlandica</i>	●	●		●	●	●	●		
<i>Latouchella holmdalense</i>		●			●	●			
<i>Latouchella pearylandica</i>		●			●				
<i>Kiringella? cf. K? washingtonense</i>		?			●	?			
<i>Kiringella sp.</i>					●				
<i>Costipelagiella kochi</i>					●				
<i>Euomphalacean (?)</i>					●				
<i>Hypseloconus sp.</i>		●				?			
<i>Hyalolithids</i>		●	●		●				
<i>Scenella sp.</i>			●						

Fig. 3. Trilobites, brachiopods and molluscs in GGU collections from the lowest part of the Holm Dal Formation in the vicinity of the type section (see Figs 1, 2). Collections are not in stratigraphic sequence.

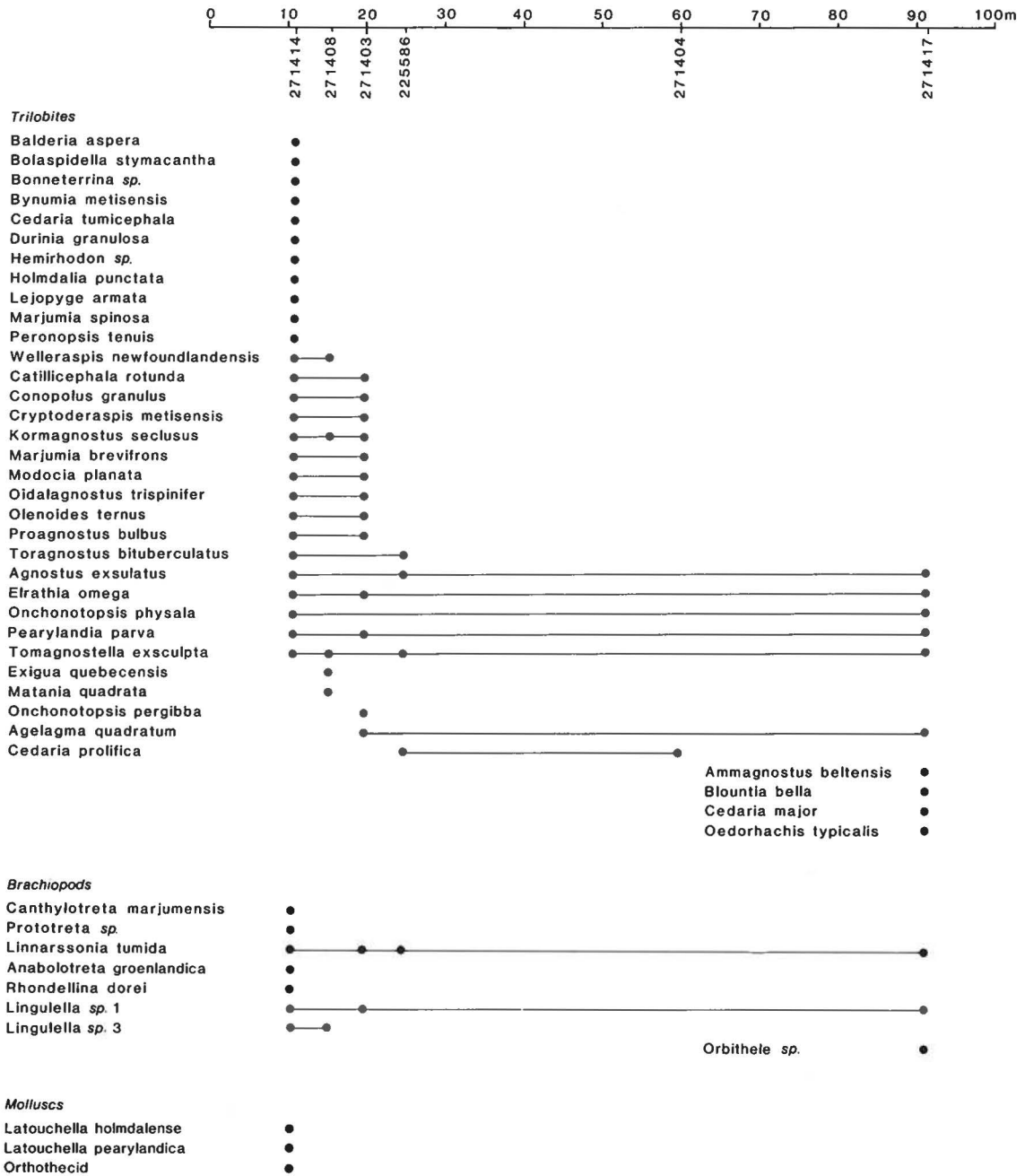


Fig. 4. Stratigraphic distribution of trilobites, brachiopods and molluscs in GGU collections (six-digit numbers) from locality 2 (Fig. 1B) of the Holm Dal Formation. Scale indicates height above the base of the formation.

Stenothecoida

Members of this group are bivalved, with closely fitting calcareous valves, although specimens with conjoined valves are infrequent. At different times considered to be crustaceans, bivalves or univalved molluscs, they are best placed as a separate class within the Mollusca, the *Stenothecoida* Yochelson 1968 (= *Probivalvia* Aksarina 1968; see Yochelson 1969, also Rasetti 1954; Horny 1956; Robison 1964; Koneva 1976).

Stenothecoids are often considered to be very variable in form and this variability may explain the wealth of species recognised in certain studies (e.g. Koneva 1979). Certainly the Holm Dal material described here as a single species includes morphs which elsewhere might be assigned to several taxa.

Genus *Stenothecoides* Resser 1938

Type species. – *Stenotheca elongata* Walcott 1884 (in part)

Stenothecoides groenlandica n. sp.

Figs 5, 6

Derivation of name. – After Grønland (Danish, Greenland).

Holotype. – MGUH 18.671 from GGU collection 225552, illustrated as Fig 5A, H, I

Material. – Fifteen specimens from GGU collections 225528, 225529, 225552, 225561, 225563, 225564 (Fig. 3).

Description. – A species of *Stenothecoides* in which the individual valves vary from about three-quarters as wide as long (Fig. 5A) to less than half as wide as long (Fig. 6A, C). Individual valves may be almost bilaterally symmetrical in young specimens (Fig. 5E) but larger examples are often clearly asymmetric. Apex marginal or slightly overhanging the adapical margin, varying from strongly curved to left or to right in apical view (Fig. 5G) but mainly almost symmetrical; forming the initial, most prominent end of a ridge or fold of variable expression which extends to the abapical margin. In plan view the individual valves tend to be most pointed adapically; greatest width is generally achieved at about one third to one half of the length, viewed in plan view and measured from the adapical margin (Figs 5A, 6C, 6D). Commonly, one abapico-lateral apertural margin is excavated relative to the other in plan view (compare

the left and right sides in Figs 5A, 6C). Commissure apparently flat, lying within a single plane. In abapical view, the valves vary from convex to sub-triangular in cross-section (Fig. 5C), although the median dorsal angulation is usually prominent. Shell thick, with irregularly developed growth lines.

Discussion. – Bivalved specimens of the type described by Yochelson (1969, figs 1, 2), Aksarina & Pelman (1978, pl. 17) and Koneva (1979, pl. 3: 1, pl. 5) have not been observed. Hence, the distinction employed by Yochelson between ventral and dorsal valves, with a horizontal commissure, can not be certainly applied. Illustrations given by Yochelson (1969, fig. 2) of *Stenothecoides knighti* from the Lower Cambrian of the Yukon of conjoined valves in apical view show the apices turned to the left, i.e. the dorsal valve curves anti-clockwise during growth (in dorsal plan view) and the ventral valve curves clockwise (in ventral plan view). This curvature is also seen in Siberian specimens illustrated by Yochelson (1969, fig. 1). Assuming that the same direction of curvature is present in *Stenothecoides groenlandica*, both the valves illustrated in Fig. 5F, G would be interpreted as ventral. Strong curvature with growth, however, is not a feature of most valves.

Koneva (1976) favoured orientation of stenothecoids as bivalves, with the plane of contact between the valves oriented vertically in contrast to the horizontal orientation suggested by Yochelson (1969). Apices in *Bagenovia kazakhstanica* Koneva 1976 from the Lower Cambrian of Kazakhstan, are stated to be occasionally prosogyral. In this interpretation, both the illustrated valves in Fig. 5F, G would be left valves.

Stenothecoides knighti Yochelson 1969 is distinguished from *S. groenlandica* by its well-rounded adapical margin and uniformly oval plan (cf. Yochelson 1969, fig. 2A, B). In *S. groenlandica* the adapical margin is more acute and adults are commonly almost diamond-shaped in plan. *S. labradorica* Resser 1938 from the Lower Cambrian of eastern Canada, as described by Rasetti (1954: 65, pl. 11: 1, 2) is much narrower than typical *S. groenlandica*. The unusually narrow example of *S. groenlandica* illustrated as Fig. 6A-C is differentiated from *S. labradorica* in being less acute adapically, with maximum shell width at about one third, of the length: in *S. labradorica* maximum width is achieved first at half the length.

Stenothecoides elongata (Walcott 1884), redescribed by Rasetti (1954, see also Robison 1964) is more slender and uniformly oval in plan than adult *S. groenlandica*; the species is reminiscent of the juvenile *S. groenlandica* (Fig. 5E) but this is less pointed adapically.

Aksarina & Pelman (1978) described several new genera and species of *Stenothecoida* from the Lower Cambrian of Siberia. Most are more slender than *S. groenlandica*. Some of the cambriids (e.g. *Bagenovia* Horny 1956 and *Katunioides* Aksarina in Aksarina & Pelman 1978) are characteristically wide and crudely

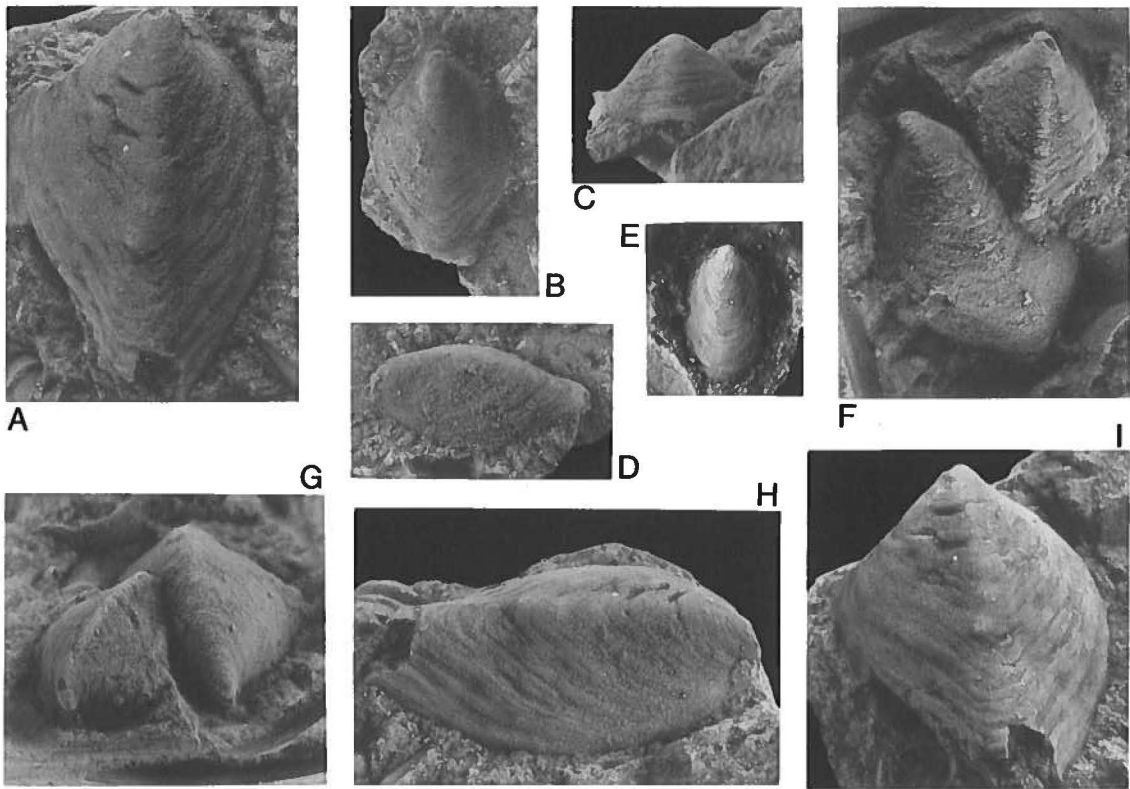


Fig. 5. *Stenothecoides groenlandicus* n. sp.

A, H, I, MGUH 18.671, holotype, from GGU collection 225552, plan, oblique lateral and oblique abapical views of the valve, very slight twisting suggests that this may be a right valve, although the apex is damaged, X 6.6. B, C, D, MGUH 18.672 from GGU collection 225529, plan, abapical and oblique lateral views of an almost symmetrical valve; slight apical twisting suggests that this may be a left valve, X 6.6. E, MGUH 18.673 from GGU collection 225561, juvenile valve, X 6.6. F, G, MGUH 18.674 and 18.675 from GGU collection 225552, plan and apical views of two supposed left valves, X 6.6.

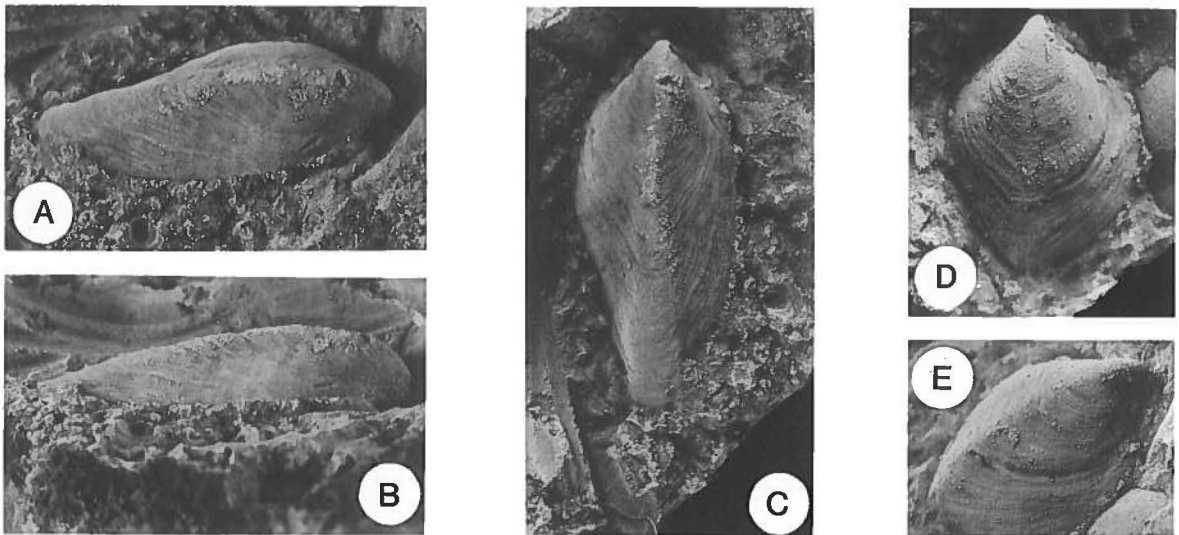


Fig. 6. *Stenothecoides groenlandicus* n. sp.

A-C, MGUH 18.676 from GGU collection 225561, oblique-lateral, lateral and plan views of an unusually narrow, possible right valve, X 6. D, E, MGUH 18.677 from GGU collection 225552, plan and oblique abapico-lateral views, X 6.

diamond-shaped in plan view, but are readily distinguished from *S. groenlandica* by their high shells with a prominent pointed apex. Koneva (1979) described many new stenothecoid species mainly from the Lower Cambrian of Kazakhstan, although it is difficult to assess variation within this material. Several of these species are carinate and thus reminiscent of *S. groenlandica*; they differ in being more pointed adapically.

Helcionellacea

Runnegar & Jell (1976) employed a much wider concept of this monoplacophoran superfamily than that envisaged by Knight et al. (1960), where the Helcionellacea Wenz 1938 was regarded as a superfamily within the Archaeogastropoda. They recognised 7 constituent families, including the Hypseloconidae Knight 1956, although this family is here excluded from the Helcionellacea and placed within the Superfamily Hyseloconellacea Knight 1956, as advocated by Stinchcomb (1986).

Following interpretations of *Yochelcionella* and *Oelandia* proposed by Geyer (1986) and Peel & Yochelson (1987), helcionellaceans are considered to be untorted, endogastrically coiled molluscs which are not closely related to the untorted, exogastrically coiled tryblidians (including Hypseloconellacea). Neither the higher systematic position of the superfamily nor its composition are discussed further in the present context, although the 3 genera discussed below are considered correctly placed at this time.

Genus *Latouchella* Cobbold 1921

Type species. – *Latouchella costata* Cobbold 1921

Latouchella holmdalense n. sp.

Figs 7, 8

Derivation of name. – After Gustav Holm Dal and the Holm Dal Formation.

Holotype. – MGUH 18.678 from GGU collection 225535 (Fig. 7A, B, H), Holm Dal Formation.

Material. – Almost 20 specimens from GGU collections 225529, 225535, 225537, 225561, 225563 and 271414; half these specimens are from GGU 225535 (Figs 2–4).

Description. – Laterally compressed species of *Latouchella* with less than one whorl; the apex strongly curved and overhanging the concave sub-apical surface. Rate

of expansion relatively high such that height is about three quarters of length (left to right in Fig. 7A, D). Aperture convex in lateral view, flattened near the abapical margin but increasing in curvature toward the adapical margin with passage into a prominent sub-apical fold. Dorsal surface with prominent convex plications separated by narrower concave depressions. The plications vary in expression between individuals (compare Fig. 7A, D, E) and die out on the lateral areas as the sub-apical surface is approached. Ornamentation of growth lines crossed by finer spiral striations. Shell seemingly relatively thick.

Discussion. – The prominent fold in the sub-apical margin of *Latouchella holmdalense* (Fig. 7A, B) can be compared to similar structures developed in other helcionellaceans, e.g. *Mellopegma* and *Eotebenna*, two genera described by Runnegar & Jell (1976) from the Middle Cambrian of Australia, and *Oelandia* Westergård 1936, as redescribed by Peel & Yochelson (1987).

In *Latouchella penecyrano* Runnegar & Jell 1976 the fold is equally well developed as in *L. holmdalense*, although this Middle Cambrian species from Australia has strongly developed spiral lirae and only subdued transverse plication. *Latouchella terraaustralis* (Runnegar & Jell 1976), also from the Middle Cambrian of Australia has more widely expanded apertural margins than known material of *L. holmdalense* (but this partly reflects ontogenetic differences since shells become relatively wider with increased growth) and a less pronounced sub-apical fold. The Australian species is distinguished by the narrowness of its more strongly delimited plications relative to the intervening concave areas.

Robison (1964, pl. 92: 11–17) illustrated a suite of specimens from the Wheeler Shale and Marjum Formation of western Utah which he assigned to "*Helcionella*" *arguta* Resser, 1939. The specimens exhibit considerable variation, noted by Robison (1964: 561) and may not constitute a single species. In particular, the specimen illustrated as fig. 14 closely resembles *L. holmdalense* in the degree of coarseness of the rugae and general coiling, but it appears to lack the fold and emargination on the sub-apical surface.

Latouchella holmdalense differs from the type suite of Resser's species in its less coarse ornamentation. The rugae of the latter are broader (measured spirally) and more globose; they are separated by deep and narrow furrows. *Latouchella burlingi* Resser 1939, described from the lower Middle Cambrian of Utah and Idaho, also has broad rugae but these are not so inflated and strongly delimited as in *L. arguta* which is of the same age. All three species combine spiral threads with transverse growth ornamentation, but the resultant reticulation is most conspicuous in *L. arguta*.

Latouchella costata Cobbold 1921, the type species from the Lower Cambrian of Shropshire is less rapidly expanding and has fewer, more prominent plications than *L. holmdalense*.

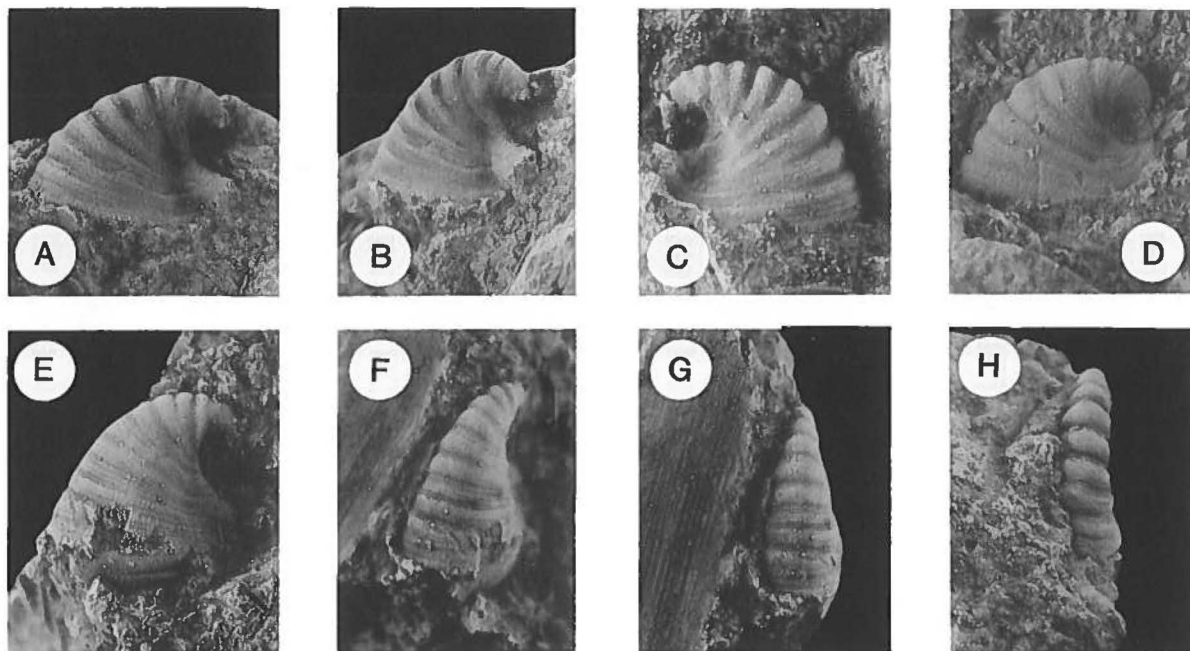


Fig. 7. *Latouchella holmdalense* n. sp.

A, B, H, MGUH 18.678, holotype, in lateral, oblique lateral and abapical views, note the prominent fold on the sub-apical surface. C, MGUH 18.679 in lateral view. D, MGUH 18.680 in lateral view. E-G, MGUH 18.681 in lateral, oblique lateral and abapical views. All specimens from GGU collection 225535, X 10.

Latouchella pearylandica n. sp.

Figs 9–11

Derivation of name. – From Peary Land.

Holotype. – MGUH 18.684 from GGU collection 225561.

Material. – Common in GGU collection 225561, but also present in GGU collections 225529 and 271414 (Figs 3, 4).

Description. – Laterally compressed species of *Latouchella* with more slowly expanding shell than *L. holmdalense* and without the sub-apical fold. In preserved material the height is greater than the length (left to right in Fig. 9A), although this may partly be a function

of the growth stage. In lateral view the apertural margin is almost flat, although a very shallow emargination in the lateral area is visible in some specimens (Fig. 9A). Dorsum convex with a tendency to be flattened in some specimens (Fig. 9C). Ornamentation of numerous closely spaced plications of similar width to the intervening troughs; minor secondary plications may be interdigitated between those of the first order in the dorsal area at later growth stages (Fig. 9A).

Discussion. – *Latouchella pearylandica* is easily distinguished from *L. holmdalense* by the fineness of its plication and the taller shell. *L. accordianata* Runnegar & Jell 1976 from the Middle Cambrian of Australia includes forms with similar fineness of plication but individual plications are acute in cross-section, rather than cord-like as in *L. pearylandica*. *L. accordianata* is also less laterally compressed than the Greenland species.



Fig. 8. *Latouchella holmdalense* n. sp. MGUH 18.682 from GGU collection 225561 in lateral and two oblique lateral views, X 20.

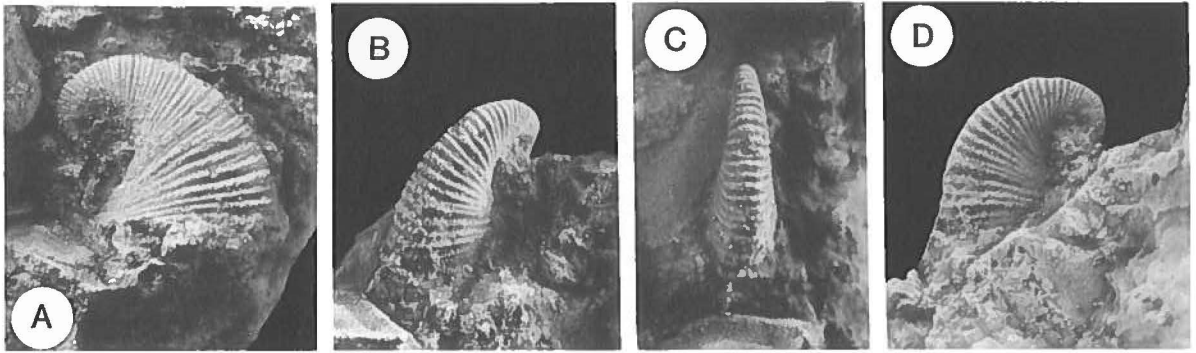


Fig. 9. *Latouchella pearylandica* n. sp. A, MGUH 18.683, lateral view showing a shallow lateral emargination indicated by slight adapertural concavity in the plications, X 10. B, C, D, MGUH 18.684, holotype, in oblique lateral, dorsal and lateral views, X 13. Both specimens from GGU collection 225561.

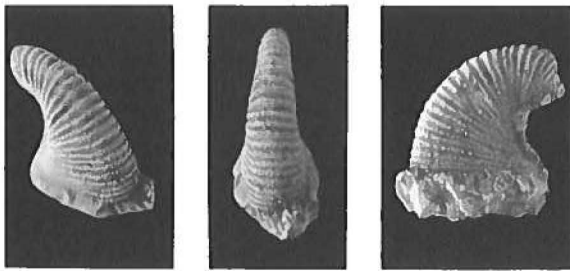


Fig. 10. *Latouchella pearylandica* n. sp. MGUH 18.685 from GGU collection 225561 in oblique lateral, dorsal and lateral views, X 10.

Latouchella iacobinica Geyer 1986 from the Middle Cambrian of Marocco has a similar high form to *L. pearylandica* but coarser ornament. *L. arguta* Resser 1939 and *L. burlingi* Resser 1939 are both readily distinguished by the coarseness of their comarginal ornamentation.

Genus *Perssuakiella* n. gen.

Type species. – *Perssuakiella troelseni* n. gen. n. sp.

Diagnosis. – Small helcionellacean with just less than one whorl in which the globose, uniformly convex early growth stage is succeeded by a brim-like expanded late growth stage which is elongated in the plane of symmetry of the shell. Shell ornamentation of fine growth lines and revolving fine lirae.

Discussion. – *Perssuakiella* is reminiscent of the early stages of at least some species of *Helcionella* Grabau & Shimer 1909, where a smooth protoconch forming about the first half whorl is abruptly succeeded by the first step-like plication. *Perssuakiella* is distinguished from the early growth stage of such species of *Helcionella* by its greater globosity which clearly gives the impression of a small adult rather than a juvenile. *Perssuakiella* resembles *Protowenella* Runnegar & Jell 1976 in the uniformly convex character of the whorl profile, without prominent plications or rugae. The expanded late growth stage seen in the available specimen of *Perssuakiella* is not known in *Protowenella*, although most material assigned to this latter genus is known from phosphatised internal moulds which lack true apertures. One specimen of *Protowenella* in the type collection from the Middle Cambrian of Australia, shows a constriction on the internal mould reminiscent of the brim (which, however, is not constricted) in *Pers-*

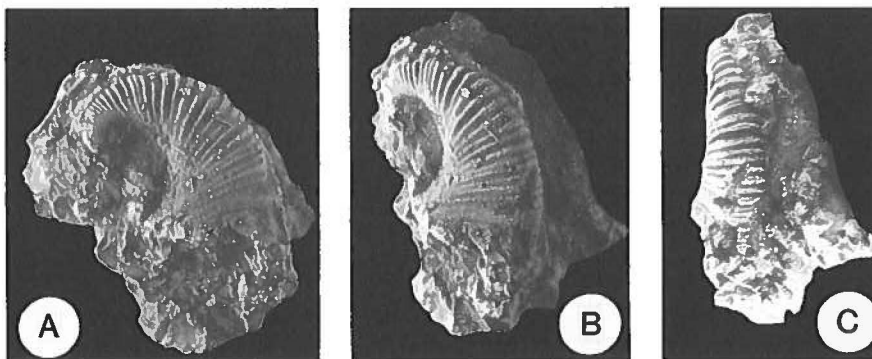


Fig. 11. *Latouchella pearylandica* n. sp. A-C, MGUH 18.686 from GGU collection 225561 in lateral, oblique lateral and dorsal views, note the tendency for plications on the dorsum to divide (B, C), X 9.

suakiella. Conspicuous folds on the internal mould in the umbilical region are also present in *Protowenella* (Runnegar & Jell 1976; Berg-Madsen & Peel 1978). There is no evidence of their presence in *Perssuakiella* as known but they may not be visible on the shell

Protowenella was originally interpreted by Runnegar & Jell (1976) as a monoplacophoran, assigned to the Family Multifariidae Bjaly 1973 of the Superfamily Bellerophontacea M'Coy 1851. Berg-Madsen & Peel (1978), in describing a specimen from the Middle Cambrian of Bornholm, restored *Protowenella* as a monoplacophoran on the basis of possible reconstruction of water circulation patterns within the mantle cavity. They noted that the configuration of water currents was quite distinct from that suggested for bellerophontaceans such as *Knightites* Moore 1941 and *Plectonotus* Clarke 1899 and thus rejected the suggestion that the Bellerophontacea was a superfamily within the Monoplacophora. Placement of *Protowenella* within the Multifariidae was tentatively accepted, but this family was excluded from the Bellerophontacea.

While clearly helcionellid, *Perssuakiella* partly bridges the morphological gap between this family and *Protowenella*, suggesting that the latter may also be a member of the Helcionellacea. Some material identified as *Protowenella* in the literature possibly represents early growth stages of *Helcionella* or related genera.

The reconstruction of the mantle cavity in *Protowenella* suggested by Berg-Madsen & Peel (1978) requires some modification to accord with this helcionellacean model (see discussion of *Yochelcionella* by Geyer 1986 and of *Oelandia* by Peel & Yochelson 1987). The umbilico-lateral spiral folds in *Protowenella* are still interpreted as marking the location of the inhalant currents to the mantle cavity but the exhalant current is now expected to have emerged below the coiled earlier portion of the shell (sub-apical margin) instead of at the dorsal (abapical) margin.

Perssuakiella troelseni n. gen. n. sp.

Fig. 12

Material. – MGUH 18.687 from GGU collection 225537, holotype and only known specimen (Fig. 2).

Derivation of name. – For Johannes C. Troelsen, in recognition of his contribution to the study of Lower Palaeozoic geology in North Greenland.

Description. – Small helcionellacean, the type and only known species of *Perssuakiella*, with just less than one full whorl. Umbilici narrow; apex unknown. Early growth stage with globose, uniformly convex dorsum, lacking rugae or plications; passing abruptly into a more widely expanded, brim-like, final growth stage. The

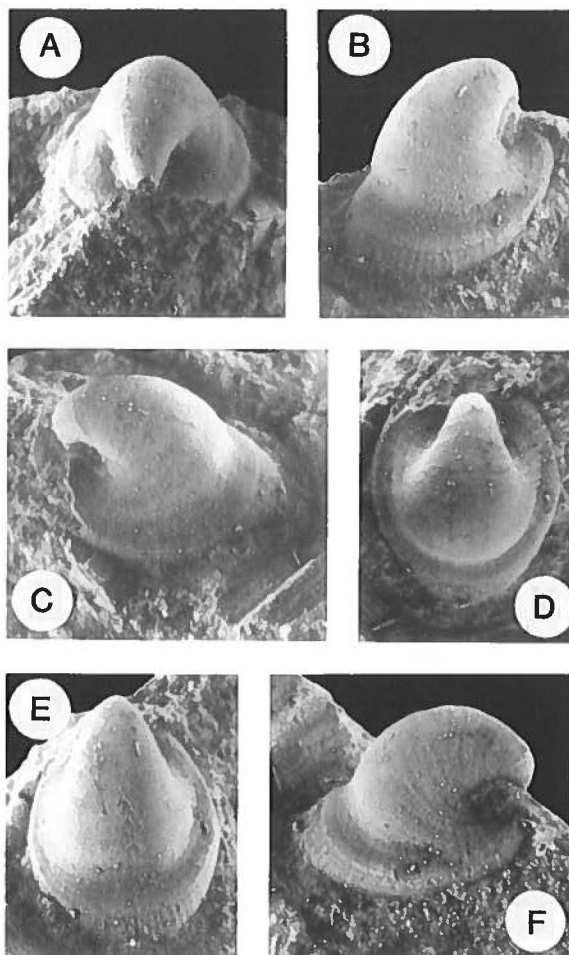


Fig. 12. *Perssuakiella troelseni* n. sp. A-F, MGUH 18.687 from GGU collection 225537, holotype, X 15. A, oblique adapico-dorsal view; B, C, F, oblique lateral views, note the concave upper surface to the marginal brim, falsely giving the impression of a constriction, and the prominent growth line at the adapical margin of the outer surface of the brim; D, dorsal view, note the upper surface of the brim; E, oblique dorsal view.

initial expansion of the shell in this brim produces a concave surface which delimits the upper (adapical) surface of the brim (Fig. 12F). A prominent growth line marks the adapertural margin of the concave surface, after which there is an angular junction with the outer surface of the brim. This outer surface expands more rapidly than the initial, globose, growth stage, but less rapidly than the first increase in shell expansion producing the upper surface of the brim. Aperture tangential; initially elongate but becoming equidimensional just prior to the brim. In the final preserved growth stage the aperture is elongate and about one fifth longer than the shell width in plan view (Fig. 12D).

Dorsum with suggestion of a shallow median sinus in early growth stages; apertural margin slightly convex in

lateral view in the final preserved growth stage, such that shallow emarginations are present in both the dorsal and sub-apical margins.

Ornamentation of growth lines crossed by fine spiral lirae; the latter most prominent on the outer surface of the brim.

Discussion. – The only known specimen is well preserved in limestone, and clearly shows the fine reticulate ornamentation. For comparison, see discussion of genus, above.

Genus *Scenella* Billings 1872

Type species. – *Scenella reticulata* Billings 1872

Discussion. – Yochelson & Gil Cid (1984; see also Stanley 1986) transferred *Scenella* from the Phylum Mollusca to the Suborder Chondrophorina of the Phylum Coelenterata (Class Hydrozoa), mainly on the basis of their description of a new species (*S. morenensis*) from the Lower Cambrian of Spain. This species was subsequently transferred to a new genus, *Marocella*, of uncertain systematic position by Geyer (1986: 96), while *Scenella* was maintained as a mollusc (Geyer 1986: 90–91; see also Berg-Madsen & Peel 1986).

As with many Cambrian molluscs, the systematic position of *Scenella* is the subject of debate in the literature. Apart from interpretation as a chondrophorine (Yochelson & Gil Cid 1984), *Scenella* has been interpreted as a gastropod (historical placement revived by

Harper & Rollins 1982; see also Starobogatov 1970), a helcionellacean monoplacophoran (Runnegar & Jell 1976) and a possible tryblidiidan monoplacophoran (Geyer 1986). The relationship to *Helcionella* Grabau & Shimer 1909 expressed by Runnegar & Jell (1976: 116) currently seems most acceptable. As noted by Yochelson & Gil Cid (1984), material with muscle scars assigned to *Scenella* by Rasetti (1954; see also Knight & Yochelson 1960) is best excluded from the genus.

Scenella sp.

Fig. 13

Material. – MGUH 18.688 from GGU collection 225530, Holm Dal Formation (Fig. 3).

Description. – A single well preserved specimen, lacking the apex, is placed here. The shell is oval in plan view (Fig. 13B) with a length:width ratio of 5:4; original height was probably a little more than half the length. The apex was located eccentrically to produce a sub-apical surface (right in Fig. 13C) which was shorter and more steeply inclined than the dorsal surface (left in Fig. 13C). All surfaces slope away from the apex with convex curvature. Shell ornamentation consists of a fine and even reticulation of radial and concentric elements.

Discussion. – This is a higher shell, lacking the conspicuous overhanging apex of *Marocella* Geyer 1986. In addition, all surfaces are convex in the Holm Dal speci-

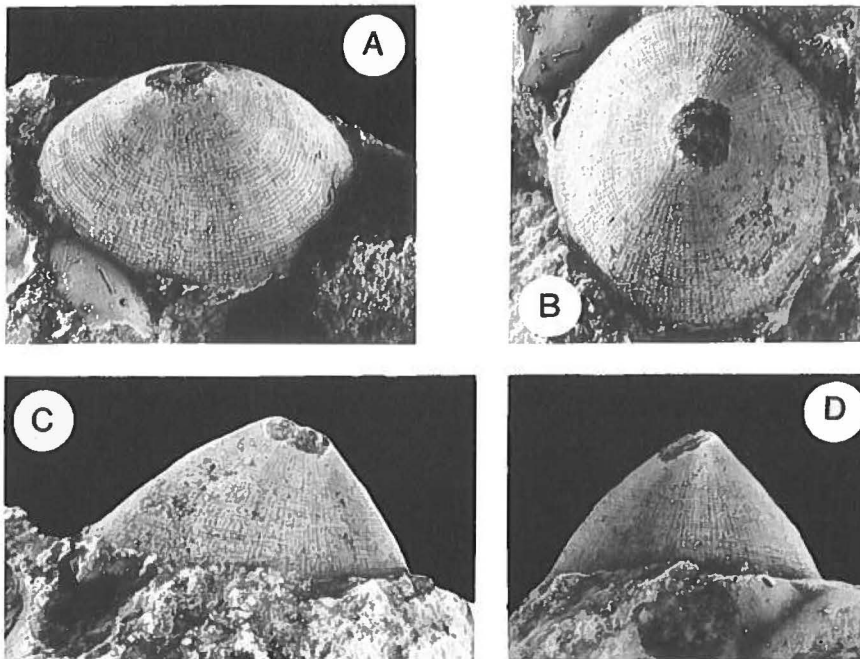


Fig. 13. *Scenella* sp. MGUH 18.688 from GGU collection 225530, X 8. A, oblique dorso-lateral view; B, plan view showing the eccentric (broken) apex located nearer to the top of the illustration; C, lateral view; D, profile when viewed from the sub-apical margin.

men (Fig. 13C, D). *Scenella barrandei* (Linnarsson 1879) from the Middle Cambrian of Baltoscandia is also distinguished by its more eccentric apex and less strongly convex surfaces.

Scenella sp. compares closely with the paratype of the type species from the Lower Cambrian of Conception Bay, Newfoundland, figured by Knight (1941, pl. 2: 5c). This is a smaller specimen than the lectotype in which the convex curvature of all shell surfaces is replaced near the aperture by concave curvature as the shell expands. Periodic coarser concentric ornamentation serves to distinguish *S. reticulata* from *Scenella* sp., where growth ornamentation is uniformly developed.

Hypseloconellacea

Tall monoplacophorans from Upper Cambrian and Lower Ordovician strata in North America have traditionally been referred to the genus *Hypseloconus* Berkeley 1898. Assigned species show a variety of forms but one face is typically concave and the other convex when the coiled shell is viewed in lateral aspect (Fig. 14B). In other species groups all surfaces of the shell sloping away from the apex are flat; lateral compression is common, such that the aperture is often elongate, oval or narrowing at one end.

In more recent years several additional taxa have been differentiated, among which the Antarctic *Knightoconus* Yochelson et al. 1973 is conspicuous on account of its proposed relevance to the question of the origin of the Cephalopoda (Yochelson et al. 1973). The genus *Shelbyoceras* Ulrich et al. 1943, originally described as a cephalopod, has also been re-interpreted as an unusually tall monoplacophoran related to *Hypseloconus* (Stinchcomb & Echols 1966, Stinchcomb, 1980). Recently, Stinchcomb (1986) introduced six new genera – *Cambrioconus*, *Orthoconus*, *Cornuella*, *Protoconus*, *Archeoconus* and *Gasconadeoconus* – which he placed within the new Superfamily Hypseloconellacea. His study indicates the presence of a much greater diversity of taxa within this previously neglected and poorly understood group.

During the same general period, Soviet palaeontologists have also described a number of new monoplacophoran taxa; these have included several relatively tall shells, although comparisons with *Hypseloconus* have generally not been made. An exception is the study by Rozov (1975) where a new Order Kiringellida contained a new Family Romaniellidae containing both *Hypseloconus* and its stated synonym *Romaniella* Doguzhaeva 1972. Since the only other taxon placed within the family is the new genus *Nyuella* there seems little justification for accepting Romaniellidae in preference to the Hypseloconidae Knight 1956, even though the stated synonymy of *Romaniella* and *Hypseloconus* is not accepted here.

Common to many of these Upper Cambrian to Lower Ordovician monoplacophoran taxa is difficulty in restoration and interpretation of the living animal. Muscle scars are known in most recently described taxa. However, interpretation of the significance of the patterns is speculative and frequently is based upon comparison with geologically younger taxa (such as *Pilina* Koken 1925 and *Tryblidium* Lindström 1880) which need not be close phylogenetic relatives. The question of recognising anterior *contra* posterior is fraught with problems and there exists great uncertainty as to whether or not the apex in the generally slightly coiled, cap-shaped shells always lies anteriorly (as in the Recent *Neopilina*), if it may be posterior in some groups or if its position has no greater meaning within the phylogeny of the monoplacophorans. The direction of coiling of the shell also needs to be considered. Coiling may be exogastric, i.e. with the earlier coiled portion anterior (as is the case in *Pilina* and *Tryblidium*), or endogastric with the earlier coiled portion lying posterior (as in gastropods). However, differential growth of the apertural margins can place the apex anterior or posterior irrespective of the direction of coiling.

An example of the difficulties associated with restoration is provided by the genus *Kiringella* which Rozov (1968) proposed for cap-shaped shells of medium size from the Upper Cambrian of Siberia in which the apex was located slightly eccentrically. He described six pairs of muscle scars forming a U-shape in plan view, of which two pairs forming the prongs of the U-shape were fused into a large composite pair judged to lie posterior to the apex. Thus the apex was interpreted by Rozov (1968) as lying nearer to the anterior margin of the shell in *Kiringella* as is also the case with *Pilina* and *Tryblidium*. Yochelson et al. (1973) rejected this interpretation of *Kiringella*. By comparison with the same *Pilina* and *Tryblidium* (Lindström 1884, Lemche & Wingstrand 1959, Peel 1977, Wingstrand 1985), Yochelson et al. interpreted the large composite pair of muscle scars in *Kiringella* as anterior. Hence, the apex was considered to be displaced toward the posterior and the shell re-oriented 180 degrees with respect to the interpreted orientation of Rozov (1968). Stinchcomb (1980) arrived at the same conclusion as Yochelson et al. (1973) following a slightly different line. He noted that the open end of the U-shape of muscle scars lies anterior in *Pilina* which would also suggest that the apex in *Kiringella* was posterior and not anterior as was originally suggested by Rozov (1968).

Muscle scars in *Hypseloconus* have been described by Stinchcomb (1980) who noted a U-shaped band of 6 pairs of discrete scars when the shell is viewed in plan view which he interpreted as opening anteriorly (as in *Pilina*). The typical shell form in *Hypseloconus* is thus apparently endogastric, although in lateral view the apex is located near the anterior. The anterior surface is convex and the posterior surface is concave. This shell form is unusual among monoplacophoran molluscs and

suggests a coiling direction opposite to the exogastric coiling seen in *Pilina* and *Tryblidium*. Therefore, a natural speculation might be that the tryblidiacean and the hypseloconellacean stocks are not closely related. While both are reasonably interpreted as untorted molluscs (monoplacophoran in a loose sense) such an apparently fundamental difference in shell form is otherwise difficult to reconcile.

The dilemma can be resolved, however, by comparison with another untorted mollusc, the helcionellacean *Yochelcionella ostentata* Runnegar & Jell 1976 from the Middle Cambrian of Australia (Runnegar & Jell 1976: fig. 11C). Shell form in *Y. ostentata* is very reminiscent of that in *Hypseloconus*, with well developed concave and convex surfaces in lateral aspect (the latter carries the tubular snorkel characteristic of *Yochelcionella*). Indeed, Pojeta & Runnegar (1976) interpreted the convex side as anterior (as in *Hypseloconus*) based on a reconstruction of mantle cavity structure (see Runnegar & Pojeta 1985 for a full review), although Geyer (1986) and Peel & Yochelson (1987) preferred to reconstruct the convex surface as posterior on the basis of an alternative mantle cavity reconstruction. This difference from *Hypseloconus* is not important in the present context, however, since *Yochelcionella* as an helcionellacean is only distantly related to the tryblidiaceans and hypseloconellaceans. Of relevance, however, is the ontogenetic form of *Yochelcionella ostentata* (Runnegar & Jell 1976: fig. 11C) which clearly demonstrates that the tall shell undergoes a change in coiling direction during growth. Adopting the orientation of Geyer (1986) and Peel & Yochelson (1987), with the snorkel located posteriorly, it can be seen that the initial part of the shell is coiled endogastrically as in other helcionellaceans. After formation of the snorkel, coiling gradually changes to exogastric with the development of the prominent

anterior concave surface characteristic of the adult of the species but typical of helcionellaceans in general.

The apparently anomalous coiling of *Hypseloconus* can be resolved with that of the tryblidiaceans by invoking similar allometric growth to that clearly demonstrated in *Y. ostentata*, an interpretation which allows similar orientation of muscle fields in *Hypseloconus* and, for example, *Pilina*.

Early growth stages are not known in most tall hypseloconellaceans. An exception is provided by Antarctic *Knighthoconus* figured by Webers et al. (in press) in which the endogastrically coiled apex overhangs the convex surface (in lateral view) of the exogastrically coiled adult.

Family Hypseloconidae Knight 1956

Genus *Hypseloconus* Berkey 1898

Type species. – *Hypseloconus recurvus* Berkey 1898

Hypseloconus sp.

Figs 8, 14

Material. – MGUH 18.689 from GGU collection 225529 and MGUH 18.690 from GGU collection 225537, Holm Dal Formation (Figs 2, 3). A poor specimen, possibly *Hypseloconus* sp., is present in GGU collection 225563.

Discussion. – Two poorly preserved fragments are figured here. The smallest is an internal mould of the early stages of a very tall hypseloconellacean species with a slightly elongate aperture, angulated below the convex surface (left in Fig. 14B). The apex and aperture are broken.

The largest specimen (Fig. 15) preserves much of the latest growth stage but intermediate and early stages are broken away. The shell was also a tall slowly expanding cone, apparently elongate in cross-section at the earliest preserved stage although the preserved aperture is equidimensional. The apertural margin below the convex surface is not preserved but Stinchcomb (1980, 1986) has noted that the aperture commonly narrows in this direction which he interpreted as anterior. Adherent patches of shell retain fine growth lines.

There is no morphological or ontogenetic overlap between the two specimens, although both indicate tall, relatively slowly expanding hypseloconellacean species.

Hypseloconus bonneterrense Stinchcomb 1975 from the Dresbachian Bonneterre Formation of Missouri is

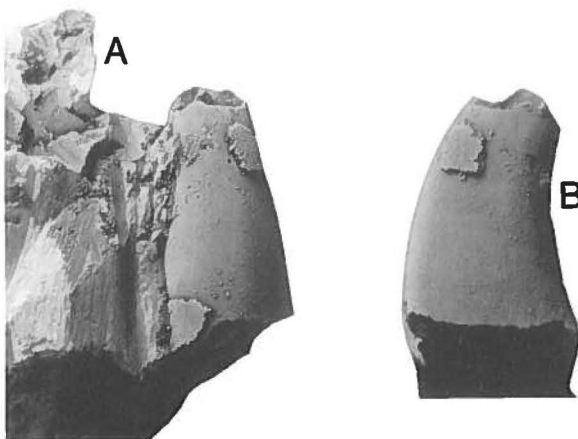


Fig. 14. *Hypseloconus* sp. MGUH 18.689 from GGU collection 225529, X 5. A, profile viewed from the abapical margin, i.e. left in B; B, lateral view, note the convex and concave surfaces characteristic of *Hypseloconus*.

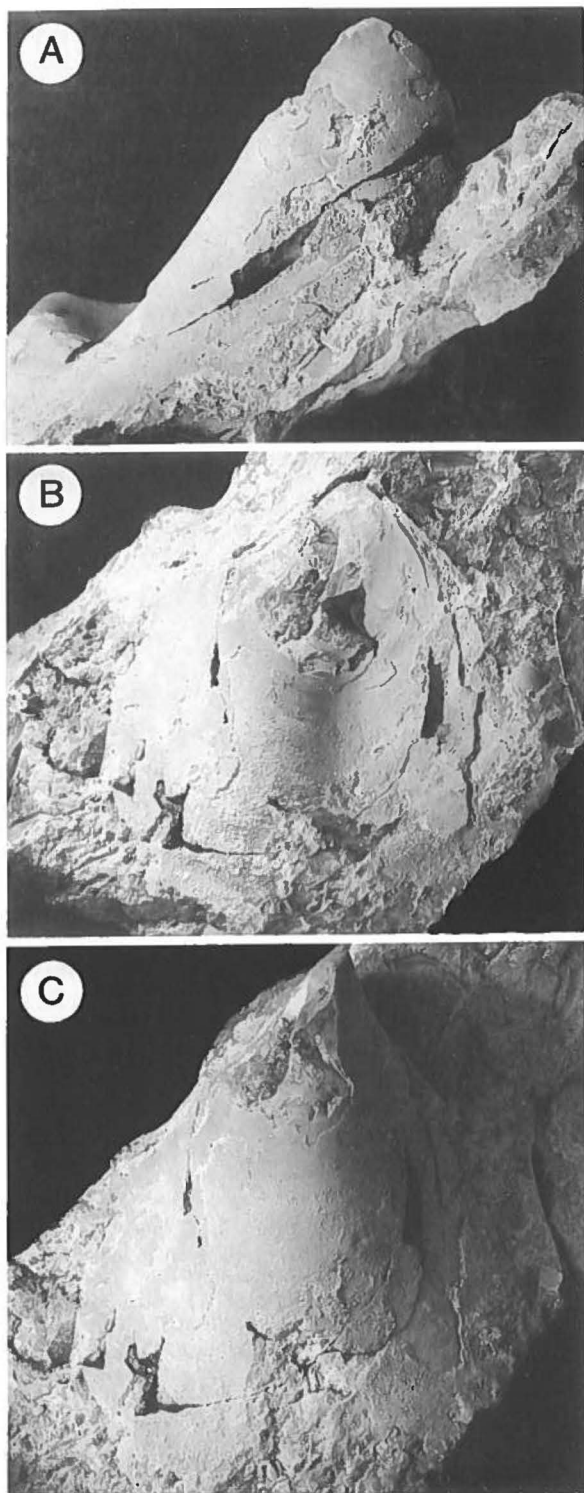


Fig. 15. *Hypseloconus* sp. MGUH 18.690 from GGU collection 225537, only aperture preserved, X 4. A, lateral view showing the pronounced concave surface (left) interpreted as posterior; B, apical view showing the equidimensional plan of the aperture as preserved; C, oblique view of expanded aperture.

similar in form to the Greenland material, although the specimen in Fig. 14 appears to be even more slowly expanding. The larger Greenland specimen has a more flared aperture; this could be an ontogenetic effect since the Missouri specimens are somewhat smaller.

Cornuella parva Stinchcomb 1986 from the Upper Cambrian Eminence Formation of Missouri is distinguished by its small size, greater curvature of the very tall shell and more cord-like growth ornament. *Orthoconus striatus* Stinchcomb 1986, also from the Eminence Formation, lacks the apertural flare of the Greenland material and has prominent spiral ornamentation. *Knightoconus* Yochelson et al. 1973 from the Upper Cambrian of the Antarctic has a similar tall shell but early stages seem to be more circular in cross-section than the smallest of the two Greenland specimens (Fig. 8). The internal septa considered by Yochelson et al. to be characteristic of *Knightoconus* have not been observed in available specimens from the Holm Dal Formation. *Shelbyoceras* Ulrich et al. 1943 has a tall septate shell with longitudinal striations, apparently lacking the flared aperture of the Holm Dal material (Stinchcomb 1980).

Hypseloconellacean sp.

Fig. 16

Material. – MGUH 18.691 from GGU 225537, from the type locality of the Holm Dal Formation (Fig. 2).

Description. – The single specimen placed here is a mainly exfoliated internal mould and associated partial external mould; the apertural margin is not preserved. It is a large (length about 20 mm), high, laterally compressed form; height was probably somewhat less than the length of the complete shell (left to right in Fig. 16B) while width (left to right in Fig. 16A, C) is about two-thirds of length. The apex is displaced slightly from the centre, thus lying slightly closer to the margin interpreted as adapical (right in Fig. 16B). Slight apical overhang produces a shallow concavity in the lateral profile of the sub-apical surface just below the apex and corresponding shallow convexity in the dorsal (abapical) surface. In plan view (Fig. 16F) the shell is broadest near the adapical margin, where the apertural margin is uniformly rounded; the aperture narrows abapically where dorso-lateral shallow excavations on the internal mould, running from the apex to the apertural margin (Fig. 16E-G), delimit a dorsal fold (slight lateral crushing on the right side in Fig. 16F possibly emphasises delimitation of the fold).

The shell was apparently ornamented solely with concentric growth lines, traces of which are preserved on the internal mould (Fig. 16D, E, G). Muscle scars are not preserved.

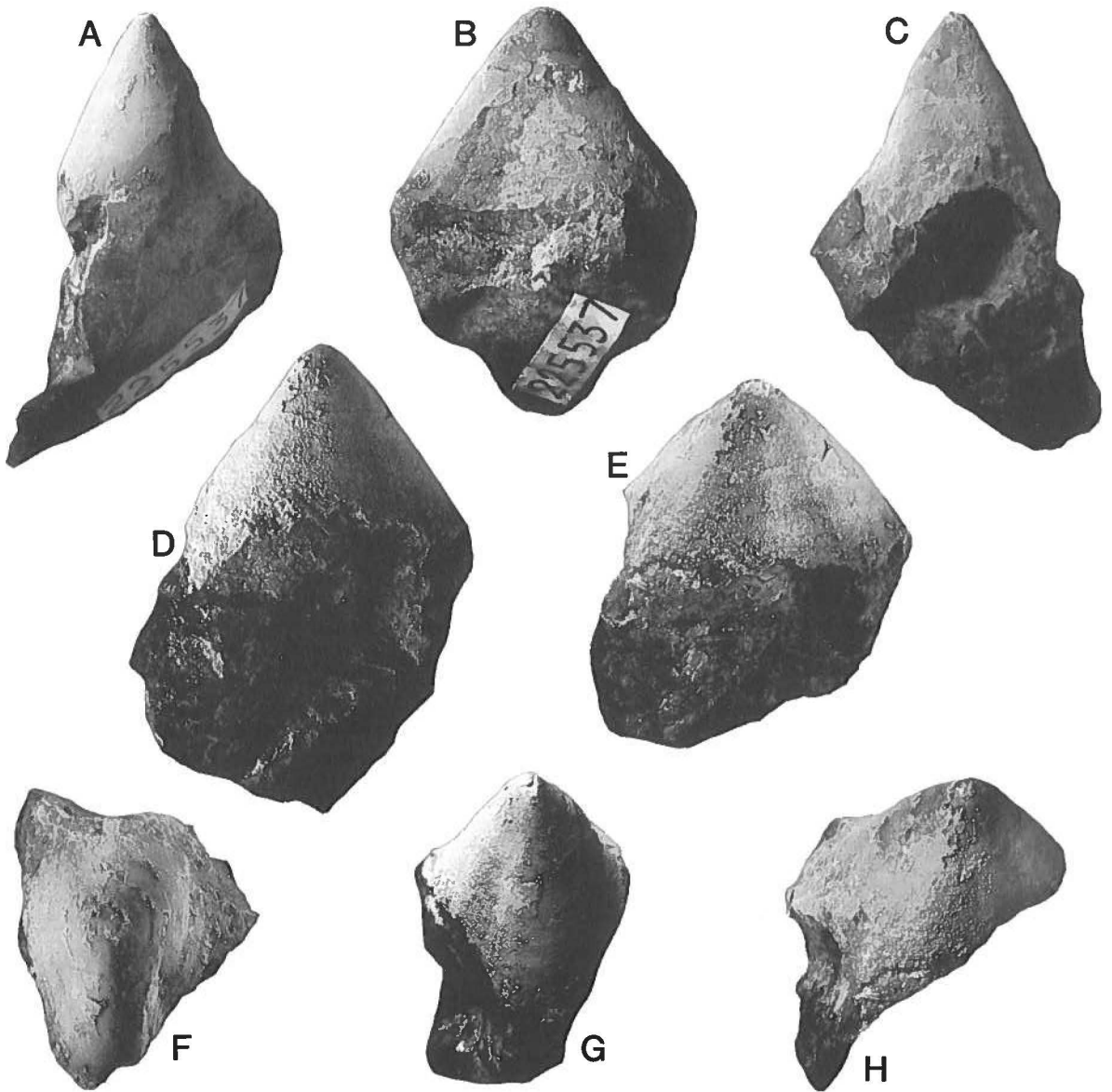


Fig. 16. Hypseloconellacean sp. MGUH 18.691 from GGU collection 225537, internal mould with traces of partly exfoliated shell, X 2. A, profile viewed from abapical margin i.e. from left in B, note slight crushing of fold (right); B, lateral view with the slightly crushed fold to the left, note slight concave curvature of sub-apical surface (right); C, profile viewed from adapical margin i.e. from right in B; D, lateral view with concave sub-apical surface to left; E, oblique lateral view of same side as D showing fold to right; F, apical (plan) view showing apical fold (bottom) and uniformly convex sub-apical apertural margin; G, as E but with increased dorsal obliquity; H, as E but with increased apical obliquity.

Discussion. – *Kiringella ayaktchica* Rozov 1968, the type species of *Kiringella* Rozov 1968 from the Upper Cambrian Mansiysk horizon of the Siberian platform, is a smaller species with a generally lower shell lacking the dorsal fold. However, illustrations given by Rozov (1968, fig. 3) suggest considerable variation in the form of the cone within limits possibly including the Greenland specimen. *Kiringella kultavasaensis* Doguzhaeva 1972 from the Lower Ordovician of the Urals is similar

in height and degree of lateral compression to Hypseloconellacean sp. but the concave sub-apical surface is longer than the convex dorsal surface in the Soviet species.

Yochelsonella compressa Flower 1968 from the Lower Ordovician of New York State is a taller species than Hypseloconellacean sp., with greater lateral compression. The Greenland specimen resembles *Gasconadeoconus waynesvillensis* Stinchcomb 1986 from the Lower

Ordovician of the central United States in the presence of the dorsal fold, but Stinchcomb (1986) considered this genus to be characterised by radial ornamentation. *G. waynesvillensis* was only illustrated from a single aspect (considered anterior by Stinchcomb) to show the fold and the slope of the lateral areas; the latter are shallowly concave near the apex and not slightly convex as in *Hypseloconellacean* sp. (Fig. 16A). In addition, the apex in *G. waynesvillensis* is stated to lie closer to the margin bearing the fold, whereas the fold in *Hypseloconellacean* sp. from the Holm Dal Formation lies at the margin farthest from the apex. The Missouri species also tends to be higher than long, whereas the opposite relationship exists in the Greenland specimen.

The question of orientation, discussed above, is not clearly resolved in this hypseloconellacean from the Holm Dal Formation. By comparison with *Gasconadeoconus* and species of *Hypseloconus*, the narrow abapical margin and fold should indicate the anterior margin. The apex, however, lies slightly closer to the opposite (presumed posterior) margin. In the absence of additional material permitting assessment of variation in the position of the apex and details of musculature, the species can not be more precisely assigned.

Kiringella sp.

Fig. 17

Material. – MGUH 18.692 from GGU collection 225561, a single internal mould, Holm Dal Formation (Fig. 3).

Description. – Small cap-shaped shell with eccentric apex, known only from a single internal mould. In plan view the apertural margin is pear-shaped, with greatest width near the adapical margin (bottom in Fig. 17A), narrowing toward the abapical margin. Slope from apex

to adapical margin is steeper than that toward the abapical margin (Fig. 17B); these surfaces, and the lateral surfaces are flat (Fig. 17C). Dorsal surface between apex and abapical margin is slightly angulated. Internal mould with poorly delimited structures on both lateral areas (dark shadows on left and right sides in Fig. 17A) which may represent muscle scars, although confirmative detail lacking; form of these possible scars suggests a U-shaped distribution open toward the abapical margin. Shell ornamentation unknown.

Discussion. – If the shadow-structures present on the internal mould are correctly interpreted as muscle scars, the open end of the U-shaped pattern would be interpreted as anterior, with the apex lying nearer to the posterior margin of the shell. This would justify placement in *Kiringella*, following Yochelson et al. (1973), although Webers et al. (in press) employ a more loose interpretation.

Kiringella sp. is a lower shell than *K. ayaktchica* Rozov 1968 from the Upper Cambrian of the Siberian platform and narrows more strongly toward the supposed anterior. It is lower than *Hypseloconellacean* sp. (Fig. 16) and lacks the pronounced curvature of *Hypseloconus* sp. (Fig. 14).

Kiringella? sp. cf. *K? washingtonense* (Stinchcomb 1975)

Figs 18, 19

Material. – MGUH 18.693 from GGU collection 225537, MGUH 18.694 from GGU collection 225561, Holm Dal Formation (Figs 2, 3).

Description. – A large (length about 20 mm) cap-shaped shell with a sub-central apex and with the height probably somewhat less than the length; width about

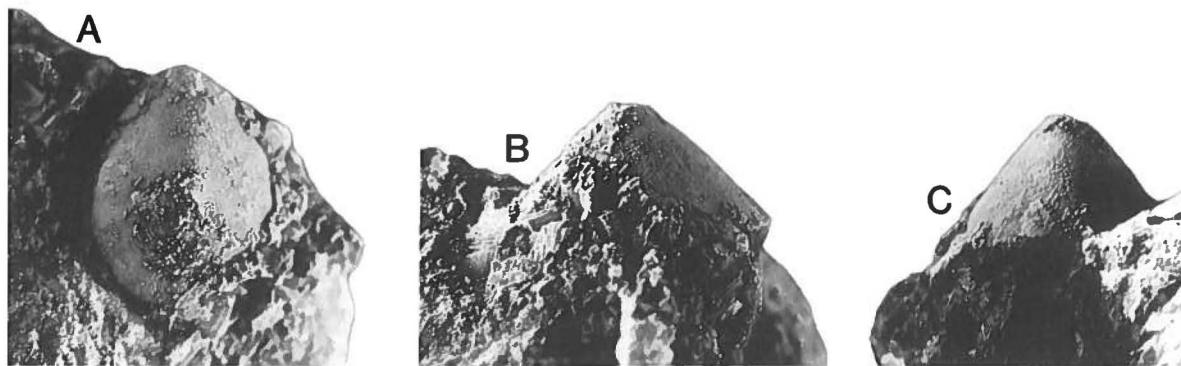


Fig. 17. *Kiringella* sp. MGUH 18.692 from GGU collection 225561, X 7. A, apical (plan) view showing apex located nearer to the presumed posterior (lower) margin, note shadows of possible muscle scars to left; B, lateral view with apex located nearer to left margin of illustration; C, profile of lateral surfaces viewed from the presumed anterior (top in A).

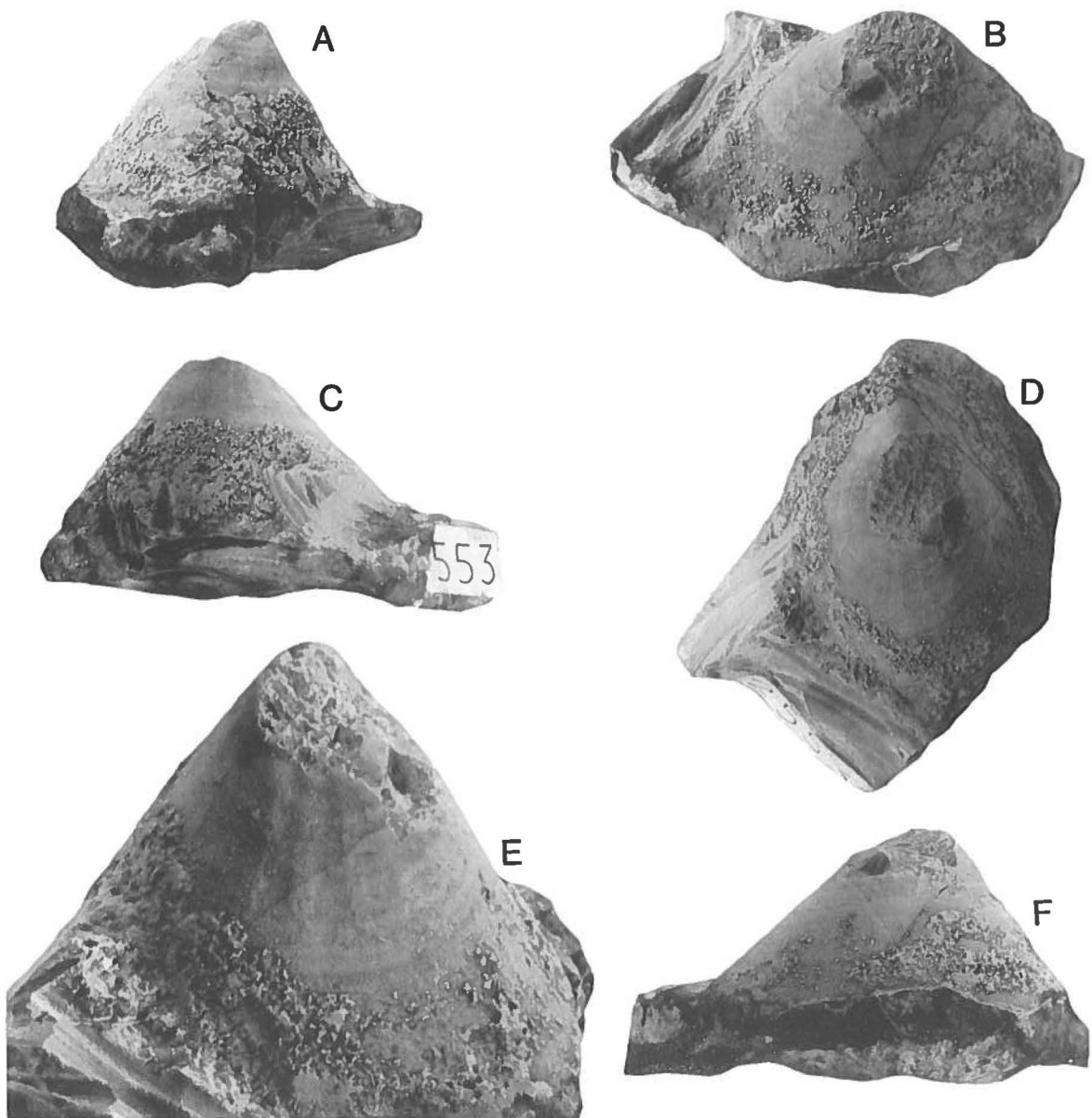


Fig. 18. *Kiringella?* sp. cf. *K? washingtonense* (Stinchcomb 1975)
 MGUH 18.693 from GGU collection 225537, internal mould with broken apex, X 2 unless stated. A, profile of lateral surfaces viewed from sub-apical surface; B, oblique lateral view, same side as in F; C, lateral view, note steeper sub-apical surface; D, apical (plan) view with the angulated sub-apical surface at the top of the illustration, note the radial structures on the dorsal surface; E, oblique view of dorsal surface showing flat-topped radial ridges on the internal mould interpreted as possible muscle scars, X 4; F, lateral view with sub-apical surface to right.

three-quarters of length. Nature of earliest growth stages not known. The apex is eccentric and the sub-apical surface is more steeply inclined than the dorsal (abapical) surface (Figs 18F, 19C). The aperture is widest at the adapical margin, where the apertural margin is uniformly convex in plan view; it narrows toward the abapical margin such that the abaxial margin is angular in plan view (Figs 18D, 19A). All preserved

surfaces of the shell are essentially flat, sloping away from the apex towards the aperture, but it is likely that slight concavity is developed on the lateral surfaces and on the sub-apical surface near the apex.

Shell ornamentation consists entirely of concentric growth lines (Fig. 19). Occasional coarser elements and traces of the finer growth lines may be discerned on moulds of the shell interior (Figs 18, 19).

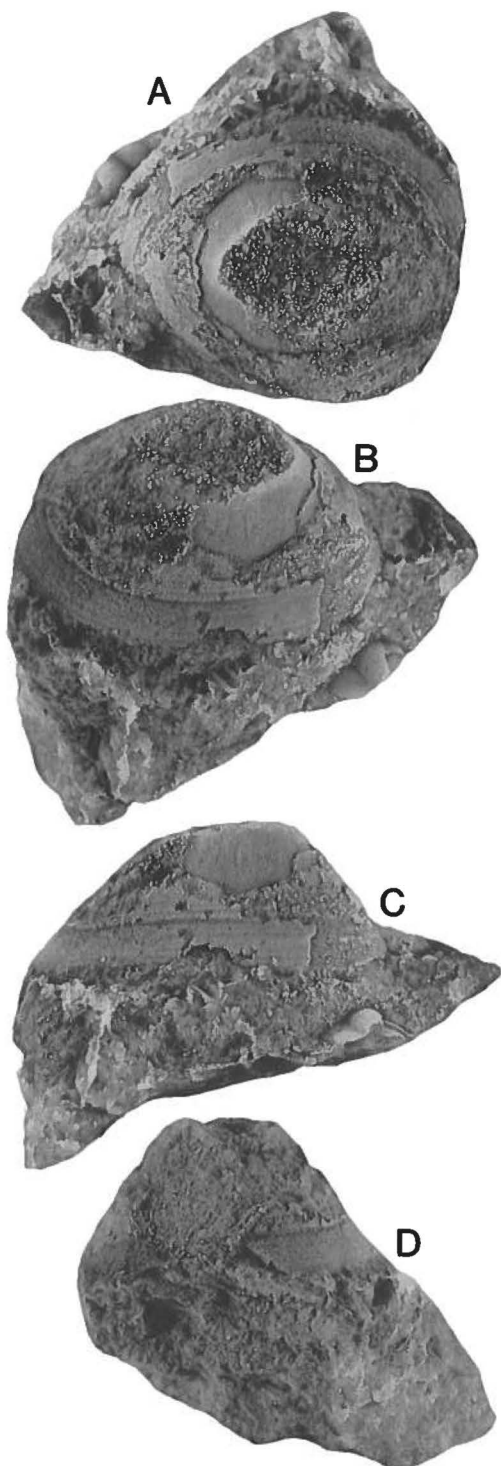


Fig. 19. *Kiringella?* sp. cf. *K? washingtonense* (Stinchcomb 1975)

MGUH 18.694 from GGU collection 225561, partly exfoliated internal mould with broken apex, X 4. A, slightly oblique plan view, note the angulation on the sub-apical surface (left); B, oblique lateral view showing ornamentation; C, lateral view showing the steeper sub-apical surface (right); D, profile view showing slope of lateral surfaces, viewed from right in A.

One specimen has radial, flat-topped ridges preserved on the internal mould on its dorsal surface (Fig. 18D, E). Five (possibly 6) ridges are visible; adaperturally they terminate abruptly about half way from the aperture to the apex but their adapical margins are not preserved.

Discussion. – The largest specimen placed here is an internal mould lacking the apex, but preserving impressions of growth ornamentation and the radiating ridges described above (Fig. 18). The angulation extending from the apical region to the apertural margin on the sub-apical surface is conspicuous. The second specimen is smaller but retains much of the shell; it also lacks the apical area but shows the angulation on the sub-apical surface and well developed growth ornamentation near the aperture (Fig. 19).

The radiating ridges on the internal mould (Fig. 18E) are interpreted as muscle scars although it is not possible to ascertain the total complement of muscle scars present or their distribution. In view of the restricted distribution of the 5 or 6 preserved scars it is likely that two or more additional pairs of scars were originally present.

In terms of shape of the shell the Greenland material compares well with Stinchcomb's (1975) species from the Dresbachian Bonnetterre Formation of Missouri which was originally referred to *Hypseloconus*. The generic placement of the species is uncertain, due to the lack of reliable information concerning muscle scars. However, the species is much lower spired and lacks the prominent curvature generally associated with *Hypseloconus*. Reference to *Kiringella* is not without problems; the partially preserved elongate muscle scars in the larger Greenland specimen (Fig. 18E) strongly suggest that the angular, sub-apical surface is anterior and the apex thus lies closer to the anterior margin. This is in conflict with *Kiringella ayakchica* where the elongate muscles lie on the sub-apical surface suggesting that the apex lies nearer to the posterior margin (following the interpretation of Yochelson et al. 1973 which is diametrically opposed to that of Rozov 1968). The issue can not be resolved on the basis of available information; hence even the tentative assignment to *Kiringella* is made without conviction.

Kiringella? sp. cf. *K? washingtonense* differs from *Kiringella* sp. in having its apex located nearer to the presumed anterior margin (Fig. 18D); in the latter, the apex is located nearer to the presumed posterior margin (Fig. 17A).

Paragastropoda

Linsley & Kier (1984) proposed the Class Paragastropoda to accommodate a number of anisostrophically coiled, non-torted molluscs, many of which (Superfam-

ilies Onychochilacea, Macluritacea, ?Euomphalacea grouped in a new Order Hyperstrophina) traditionally have been considered to be gastropods (Knight et al. 1960). A second new order, Orthostrophina, contained the single Superfamily Pelagiellacea Knight 1956, species of which may be numerically conspicuous in Cambrian faunas.

Historically, pelagiellaceans have often been referred to the gastropods, largely on account of their anisotrophically coiled shells. Knight et al. (1960) excluded *Pelagiella* from the Gastropoda but Runnegar and Jell (1976) recognised the superfamily within the archaeogastropod Prosobranchia.

Superfamily Pelagiellacea Knight 1956
Family Pelagiellidae Knight 1956

Genus *Costipelagiella* Horny 1964

Type species. – *Costipelagiella zazvorkai* Horny 1964

Costipelagiella kochi n. sp.

Fig. 20

Derivation of name. – For Lauge Koch, explorer, cartographer, geologist, whose studies and collections in the early part of this century established the framework for North Greenland geology and palaeontology.

Material. – MGUH 18.695 from GGU collection 225561, holotype and only known specimen, Holm Dal Formation (Fig. 3).

Description. – A small; dextrally coiled, almost planispiral shell with about one and a third whorls. Whorl overlap is slight such that sutural indentation is deep. Protoconch globose, smooth, with abruptly rounded adapical termination. The cross-section of the whorl is imperfectly known in detail; in standard orientation

with the axis of coiling placed vertically the whorl profile is clearly wider than high (compare Fig. 20C, D). The upper whorl profile is shallowly convex, such that the apex is not visible in lateral view (Fig. 20D). The outer whorl surface is uniformly rounded, without angulation; the basal surface is not known. Ornamentation of growth lines which become costate around the outer whorl face during the last half whorl. Ornamentation delimits a broad, shallow sinus in the outer lip (Fig. 20B, C).

Discussion. – The costate growth lines suggest that this species be placed in *Costipelagiella* Horny 1964, described from the Middle Cambrian of Czechoslovakia, although this form differs in terms of whorl profile from *Costipelagiella kochi*. The type species, *C. zazvorkai* Horny 1964, was also described from a single specimen which differs from the Holm Dal specimen by virtue of its less rounded whorl profile and slightly elevated spire. The upper whorl surface in *C. zazvorkai* is flattened, passing relatively abruptly onto the outer whorl face which slopes in toward the base. The outer whorl face in *C. zazvorkai* appears concave near the aperture (cf. Horny 1964, pl. 2: 2, 3). In these characters the type species is readily distinguished from *C. kochi* which has convex upper and outer whorl surfaces. In addition, the peripheral sinus of *C. zazvorkai* is deeper than in *C. kochi* and its adapical margin on the upper whorl surface is more abruptly defined.

Costipelagiella kochi is readily distinguished from many species of *Pelagiella* by its rounded whorl profile. The upper whorl surface in *Pelagiella* is commonly strongly flattened and there is rapid transition around a peripheral angulation onto a globose basal surface (cf. *Pelagiella deltoides* Runnegar & Jell 1976 and *P. sp. cf. P. lorenzi* Kobayashi 1939 of Geyer 1986).

Robison (1964) described internal moulds referred to *Pelagiella* from the Marjum Formation (late Middle Cambrian) of Utah which show a similar, rounded, whorl profile to *C. kochi*. The rate of expansion in the Marjum Formation species is lower, however, and the spire is slightly elevated.

Pelagiella corinthiana Runnegar & Jell 1976 from the Currant Bush Limestone (Middle Cambrian) of Australia

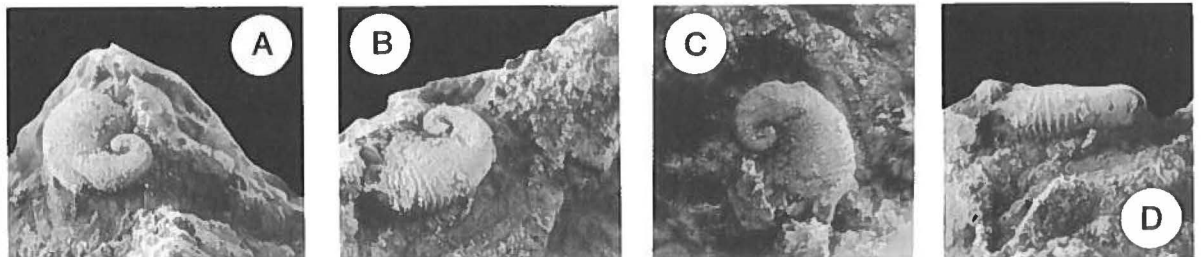


Fig. 20. *Costipelagiella kochi* n. sp. MGUH 18.695 from GGU collection 225561, X 20. A, B, oblique apico-lateral views; C, apical view; D, lateral view.

lia has a similar whorl profile to *C. kochi* but appears to be more rapidly expanding; details of ornamentation were not given by Runnegar & Jell (1976).

Lochman (1940) gave the name *Pelagiella bridgei* to a similarly rounded species from the Bonnetterre Formation of Missouri but her illustrations seem to indicate a sinistral shell with slightly raised spire.

Open coiled euomphalacean (?)

Fig. 21

Figured material. – MGUH 18.696 from GGU collection 225561 (Fig. 3).

Discussion. – This single specimen is so poorly preserved that identification even as a mollusc is tenuous. However, the gentle curvature and presence of longitudinal angulations invite comparison with open-coiled members of the Superfamily Euomphalacea de Koninck 1881. Possible traces of transverse growth lines are present. There is some resemblance to the Devonian genus *Odontomaria* Roemer 1876 but similar open coiled forms have been described recently from the Upper Cambrian by Yochelson (1987) and Yochelson & Stinchcomb (1987). Of these, *Spirodentalium* Walcott 1890 has a whorl profile with grooves (Yochelson 1987: fig. 1.3), while the Greenland specimen has angulations. *Macluritella? walcotti* (Howell 1946) of Yochelson & Stinchcomb (1987: fig. 1) has a pronounced triangular cross-section to the whorl not seen in the specimen from Holm Dal.

Hyolitha

Opinions differ as to the relationships of the Hyolitha and consequently as to its systematic status. Runnegar et al. (1975) suggested similarities between hyoliths and sipunculoid worms, but preferred to separate the former as a new phylum. Marek & Yochelson (1976) presented arguments for considering the Hyolitha to be a class within the phylum Mollusca. Sysoyev (1984) rejected these models and proposed a new phylum Hyolithozoes with affinities to bryozoans, brachiopods and phoronids. Discussion of the issue lies outside the present context, although the established term Hyolitha is retained for the systematic unit.

Most authors recognise two major subdivisions within the Hyolitha, the orders Orthothecida and Hyolithida. Sysoyev (1984: 8) divided his phylum into two classes, Orthothecimorpha and Hyolithomorpha. Peel & Yochelson (1984) subsequently assigned the Order Toxeumorphorida of Shimansky (1962) to the Hyolitha, to include some unusually large Carboniferous-Permian hyoliths.

Order Orthothecida Marek 1966

Orthothecid sp.

Fig. 22

Figured material. – MGUH 18.697 and 18.698 from GGU collection 271414 (Fig. 4).



Fig. 21. Open coiled euomphalacean (?) MGUH 18.696 from GGU collection 225561, X 4. A, note spiral twisting and angulations; B, note traces of possible transverse growth lines at left.

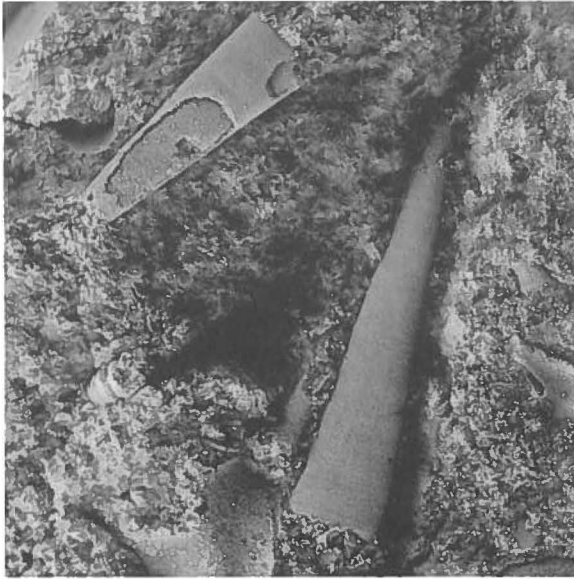


Fig. 22. Orthothecid sp. MGUH 18.697 (left) and MGUH 18.698 from GGU collection 271414, X 8. Note the fine growth lines on the ventral surface of both specimens.

Discussion. – Both of the available small specimens show the ventral surface which is shallowly convex; transverse growth lines indicate a simple orthotheciform aperture without ligua. The dorsal surface is not seen but is clearly more convex than the ventral. No apical to apertural curvature is discernible along the exposed length of both conchs which expand uniformly at 10 degrees. It is not known if the conchs are internally septate.

The flattened ventral surface and inflated dorsum suggest comparison with the families Allathecidae *Miszarzhevskii* 1969 and *Chelsonellidae* Malinky 1987 but lack of information concerning the dorsal surface prevents closer determination.

Order Hyolithida Sysoyev 1957

Hyolithid sp.

Figs 23, 24

Figured specimens. – MGUH 18.699 from GGU collection 225561, MGUH 18.700 from GGU sample 225530 (Fig. 3).

Discussion. – One fragmentary specimen (Fig. 23) lacks the apex and has the dorsal surface buried in sediment. The exposed ventral surface is shallowly convex with growth lines and weak comarginal rugae indicating a short ligua. In transverse cross-section, the height of the

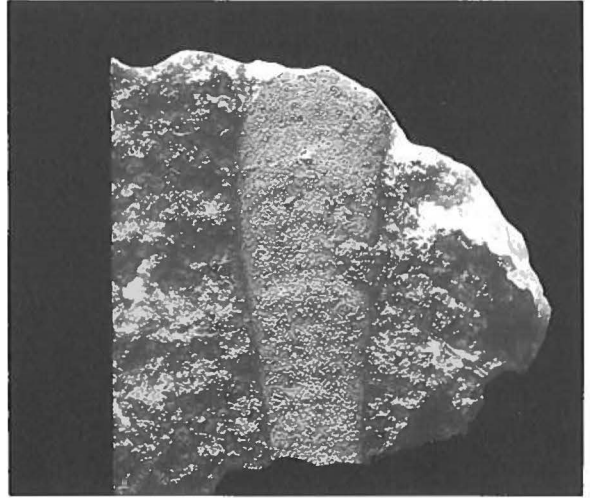


Fig. 23. Hyolithid sp. MGUH 18.699 from GGU collection 225561, ventral surface note short ligua, X 8.

conch is seen to be about half of its width and the dorsum is uniformly convex. A poorly preserved specimen from GGU collection 225529, exposed in lateral aspect but without apex or aperture, may belong here.

The second illustrated specimen preserves the dorsal surface, although the aperture and apex are broken (Fig. 24). The conch is more rapidly expanding than the specimen in Fig. 23 and ornamentation consists of fine cords separated by smooth areas of shell.

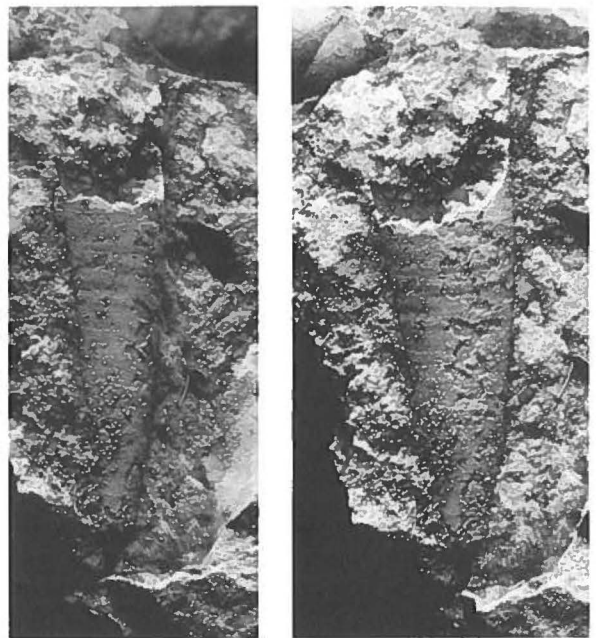


Fig. 24. Hyolithid sp. MGUH 18.700 from GGU collection 225530, dorsal surface showing ornament, X 8.

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