The problematic fossil *Triplicatella* from the Early Cambrian of Greenland, Canada, and Siberia

Christian B. Skovsted, John S. Peel, and Christian J. Atkins

Abstract: The cap-shaped Early Cambrian fossil *Triplicatella*, previously known only from Australia, is reported from the upper Lower Cambrian of North and North-East Greenland, western Newfoundland, and Siberia. The occurrence of *Triplicatella* in Laurentia strengthens faunal ties between Laurentia and the Australian margin of Gondwana in late Early Cambrian times and supports hypotheses advocating the close proximity for the two palaeocontinents. Two new species, ***Triplicatella sinuosa*** n. sp., and ***T. peltata*** n. sp. are described, morphological details of which help elucidate the functional morphology and taxonomic affinity of the group. Three opercular types attributable to *Triplicatella* are left in open taxonomy. The postulated affinity of *Triplicatella* to hyoliths is confirmed, although the genus can not be placed within either of the two orders of hyoliths currently recognized.

Résumé : Le présent article décrit le fossile *Triplicatella* (Cambrien précoce), à forme de calotte, connu antérieurement seulement en Australie, trouvé dans le Cambrien inférieur supérieur dans le nord et le nord-est du Groenland, l'ouest de Terre-Neuve et en Sibérie. L'occurrence de *Triplicatella* dans la Laurentia renforce les liens fauniques entre la Laurentia et la bordure australienne du continent Gondwana à l'époque du Cambrien précoce et soutient les hypothèses en faveur d'un rapprochement des deux paléocontinents. Deux nouvelles espèces, ***Triplicatella sinuosa*** n. sp. et ***T peltata*** n. sp. sont décrites; leurs détails morphologiques aideront à élucider la morphologie fonctionnelle et l'affinité taxonomique du groupe. La taxonomie de trois types operculaires attribuables à *Triplicatella* est laissée ouverte. L'affinité postulée de *Triplicatella* aux Hyolithes est confirmée bien que le genre ne puisse être placé dans l'un ou l'autre des ordres de Hyolithes actuellement reconnus.

[Traduit par la Rédaction]

Introduction

Microscopic remains of organisms with mineralized hard parts from the Lower Cambrian, so-called "small shelly fossils," have been intensively studied for some 35 years (e.g., Rozanov et al. 1969; Missarzhevsky 1989; Bengtson et al. 1990; Gravestock et al. 2001). Although many of these fossils represent disarticulated parts of larger skeletons and remain poorly understood in terms of function and taxonomic affinity, they may be useful for biostratigraphy and palaeogeographic reconstructions. One example is the small, cap-shaped fossil *Triplicatella* Conway Morris in Bengtson et al. (1990), a fossil originally described from the upper Lower Cambrian of Australia. This article reports the occurrence of *Triplicatella* in the upper Lower Cambrian of Greenland, eastern Canada, and Siberia, the first records of the genus outside Australia.

Early studies of the palaeogeography of the Early Cambrian indicated that palaeocontinents were isolated during this period, and their fossil faunas largely endemic (e.g., McKerrow et al. 1992). Later contributions, based on both palaeontological and palaeomagnetic data, have shown that the continents were probably more closely juxtaposed in the Early Cambrian (e.g., Dalziel 1997; Brock et al. 2000; Gubanov 2002). During ongoing investigations of the late Early Cambrian faunas of North-East (by CBS) and North Greenland (by CJA), evidence for a strong faunal connection between Australia and Laurentia has been documented (Skovsted and Peel 2001; Gubanov et al. in press; Malinky and Skovsted 2004; Skovsted and Holmer in press; Skovsted in press; C.J. Atkins, unpublished observation, 2003). The occurrence of *Triplicatella* in the Lower Cambrian of both North and North-East Greenland adds to this growing body of evidence. The peculiar and well-preserved Laurentian species of *Triplicatella* further yield new information on the morphology of the fossil. In light of this new information, the functional morphology of *Triplicatella* and its taxonomic affinities are discussed later in the text. During this study *Triplicatella* has also been recognized in Siberia, and a single specimen is described herein.

Geological setting

Cambrian strata crop out through Arctic Canada and eastward across northern Greenland to Peary Land (Fig. 1), as

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C.B. Skovsted, J.S. Peel, and C.J. Atkins. Department of Earth Sciences, program for Palaeobiology, Uppsala University, Norbyvägen 22 SE-75236, Uppsala, Sweden.

[1]Corresponding author (e-mail: Christian.Skovsted@geo.uu.se).

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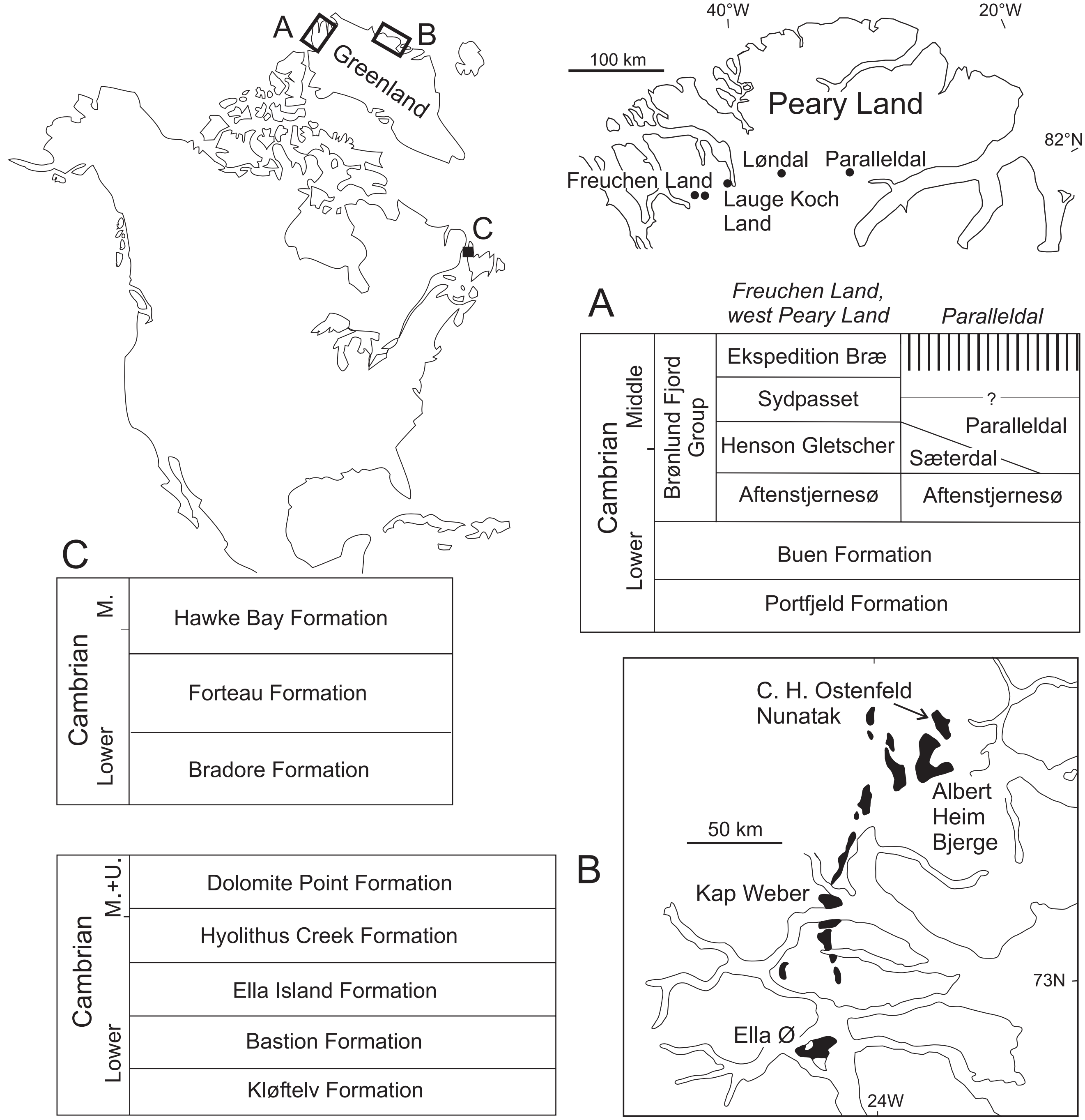
Fig. 1. Map of North America and Greenland with Laurentian occurrences of *Triplicatella* indicated. (A) Map and simplified stratigraphic column for North Greenland with fossil localities indicated. (B) Map and simplified stratigraphic column for North-East Greenland with lower Palaeozoic outcrop areas (in black) and fossil localities indicated. (C) Simplified stratigraphic column for the Early Cambrian of western Newfoundland.



part of the Franklinian Basin succession of the Canadian Arctic Islands (Trettin 1991; Peel and Sønderholm 1991). Scattered outcrops also occur within the Caledonide orogen, which fringes the eastern coast of Greenland. To the southwest, these circum-Laurentian Cambrian outcrops continue in Labrador and western Newfoundland within the Appalachian orogen of eastern North America (Williams 1995).

In North Greenland, *Triplicatella* was collected from the Aftenstjernesø Formation, the basal formation of the Brønlund Fjord Group, which records the northward progradation of shallow-water carbonate sedimentation over the outer-shelf deposits of the underlying Buen Formation. The stratigraphy of the Brønlund Fjord Group was described in detail by Ineson and Peel (1997; see also Higgins et al. 1991*a*, 1991*b* and Blaker and Peel 1997). At its type locality in southern Lauge Koch Land this mainly dolostone formation is about 62 m thick, but it varies from 30 to 130 m within the Freuchen Land – southern Peary Land area. Fossils are derived from the basal phosphoritic carbonates of the formation (Member A of the Brønlund Fjord Formation of Christie and Peel 1977 and Frykman 1980; thickness 2–5 m) and include trilobites (*Bonnia*, *Calodiscus lobatus* and fragments of *Wanneria*), a variety of molluscs (many of which also occur in North-East Greenland, i.e., Skovsted in press) and other shelly fossils. Bendix-Almgreen and Peel (1988) described sclerites of *Hadimopanella apicata*, which also occurs in the Bastion and Ella Island formations of North-East Greenland (C.B. Skovsted, unpublished observation, 2003).

In North-East Greenland, *Triplicatella* is derived from the Bastion Formation (thickness 150 m at Albert Heim Bjerge; Fig. 1), which is dominated by glauconite-rich sandstones and siltstones in the lower part and by shales with minor carbonate beds and nodules in the upper part. Body fossils have only been found in the upper part of the formation (Poulsen 1932; Cowie and Adams 1957; Gubanov et al. in press; Skovsted 2003*b*, in press; Skovsted and Holmer 2003, in press; Skovsted and Peel 2001), but Pickerill and Peel (1990) described trace fossils from the lower part. Cambrian strata in North-East Greenland form part of a thick succession of shallow-marine Proterozoic to Ordovician sediments deposited on the Laurentian shelf prior to the Caledonian orogeny (Cowie 1971; Peel 1982; Stouge et al. 2001).

Cambrian strata in western Newfoundland (Fig. 1) are described by Schuchert and Dunbar (1934), North (1971), James and Stevens (1982), and Knight et al. (1995). *Triplicatella* was collected from the Forteau Formation, comprising some 216 m of shales and siltstones, with minor sandstones and limestones.

Samples

All samples are carbonates that were digested in buffered acetic acid (10%). Greenland fossils described herein result from collections made during regional geological investigations conducted by the Grønlands Geologiske Undersøgelse (GGU, Geological Survey of Greenland, now Geological Survey of Denmark and Greenland), Copenhagen, Denmark, between 1978 and 1988.

GGU sample 218894 was collected by P. Frykman on 10th July 1979 from 1.6 m below the top of Member A of the Aftenstjernesø Formation, Brønlund Fjord Group, on the western side of Løndal, Peary Land (Fig. 1A). GGU sample 271469 was collected by JSP at locality JSP 19780625-1, from 1.3 m below the top of Member A of the Aftenstjernesø Formation in easternmost Lauge Koch Land, on the west side of J.P. Koch Fjord, (Fig. 1A). This is the type locality of the Aftenstjernesø Formation described by Ineson and Peel (1997, pp. 39–46, figs. 23, 24A, 25). GGU sample 271717 was collected by JSP from the top of Member A of the Aftenstjernesø Formation at locality JSP 19780714-1 on the western side of Løndal, western Peary Land (Fig. 1A).

GGU samples 314807–314809 and 314835 were collected by JSP and M.P. Smith from near the middle of a reference section through the Bastion Formation at Albert Heim Bjerge, northern Hudson Land, North-East Greenland described by Cowie and Adams (1957) (Fig. 1B). GGU samples 314904, 314906, 314908–314910, and 314933 were collected by JSP and M.P. Smith from the upper part of the Bastion Formation of the nearby C.H. Ostenfeld Nunatak (Fig. 1B). Details of the stratigraphic position of these samples are given by Skovsted and Peel (2001) and Skovsted and Holmer (2003).

Four specimens of *Triplicatella* were also recovered from residues after acetic acid digestion of limestones of the Lower Cambrian Forteau Formation of western Newfoundland (Fig. 1C). Three of these came from sample JSP1982-01 collected by JSP from a road cut in the Deer Arm Member (4.6 m thick; James and Stevens 1982, p. 68) 12 km east of Rocky Harbour on Highway 73, near the head of Dear Arm, Gros Morne. This member occurs from about 110–115 m above the base of the formation. From the same sample, Peel (1987) described the helcionelloid mollusc *Yochelcionella americana*, while Peel and Berg-Madsen (1988) illustrated internal moulds of *Salterella* cf. *S. maccullochi*. The fourth specimen of *Triplicatella* was derived from sample ICS-1421, collected by A.R. Palmer from the basal layers of a 4 m-thick limestone occurring some 180 m above the base of the formation along the north shore of Bonne Bay. Skovsted (2003*a*) has described internal moulds of *Salterella* from this sample. A single specimen of *Triplicatella* is also described herein from the Tyuser Formation (Early Cambrian, Atdabanian) of Siberia. Sample M31/11 was collected by V.V. Missarzhevsky along the lower reaches of the Lena River at Chekurovka, Siberia (see Rozanov et al. 1969, p. 34; and Skovsted 2003*b* for stratigraphic information).

Palaeogeographical implications

In the late Early Cambrian, a high level of endemism among faunas from different regions of the world has often been assumed, as a result of rapid separation of continents and consequent faunal isolation. This view has been promoted by well-documented differences in trilobite and archaeocyathid faunas and by incomplete knowledge of the fossil record of many other Early Cambrian groups. Post-Tommotian archaeocyathan faunas appear to be highly endemic (Debrenne et al. 1999), but recent studies of trilobites and molluscs have shown that many taxa are widespread in the late Early Cambrian, occurring in Siberia, central Asia, China, Australia and Laurentia (Brock et al. 2000; Geyer and Shergold 2000; Gravestock et al. 2001; Gubanov 2002; Gubanov et al. 2004). The new evidence has promoted palaeocontinental reconstructions with more closely spaced continents in the Early Cambrian than previously had been supposed (e.g., Dalziel 1997; Brock et al. 2000; Gubanov 2002).

The late Early Cambrian faunas of Greenland exemplify this recently recognized strong faunal connection between Early Cambrian regions. At the present time, the best known fauna is that of the Bastion Formation of North-East Greenland, but faunas from the Aftenstjernesø Formation of North Greenland show marked similarities to the former and are probably of a similar age (CJA, unpublished observations, 2003). The fauna of the Bastion Formation shares a number of elements with previously described faunas from Australia: the brachiopod *Eoobolus priscus* (Skovsted and Holmer in press), the ornamented arthropod spine *Mongolitubulus henrikseni* (Skovsted and Peel 2001), the molluscs *Anabarella australis*, *Mackinnonia rostrata*, *Pelagiella subangulata*, *Pojetaia runnegari*, and related species of the genera *Figurina* and *Capitoconus* (Gubanov et al. in press and Skovsted in press), the hyoliths *Microcornus eximius*, *M. petilus*, *Hyptiotheca*

Fig. 2. *Triplicatella* from the Bastion Formation, North-East Greenland. **2A–2K.** *Triplicatella sinuosa* n. sp. GGU sample 314835, Albert Heim Bjerge. (A, B) MGUH 27064 (holotype), viewed from the dorsal edge and from above. (C, D, E) MGUH 27065, from the dorsal edge, from above, and obliquely from the left lateral side. (F, G, J) MGUH 27066, internal surface from above, oblique view, and close-up of left lateral invagination, muscle scar indicated by arrow in J. (H) MGUH 27067, from dorsal edge. (I) MGUH 27068, from dorsal edge. (K) MGUH 27069, fragmentary specimen, close-up of left lateral side with lateral muscle scar. **2L–2O**. *Triplicatella* sp. A. GGU sample 314835, Albert Heim Bjerge. (L, M) MGUH 27070, from above and from ventral margin (oblique). (N, O) MGUH 27071, internal surface from above and from dorsal edge (oblique). **2P–2S.** *Triplicatella peltata* n. sp. GGU sample 314906, C.H. Ostenfeld Nunatak. (P) MGUH 27072, from above. (Q) MGUH 27073, fragmentary specimen, dorsal part from above. (R, S) MGUH 27074, internal surface viewed from above and from the ventrodorsal edge (oblique). Scale bar = 0.5 mm for all pictures, except J, where scale bar = 0.25 mm.

karraculum, *Parkula bounites*, *Conotheca australiensis*, *Cupitheca holocyclata*, and *C. hemicyclata* (Malinky and Skovsted 2004) occur in both the Bastion Formation and in the upper Lower Cambrian of South Australia. Similar strong faunal ties to North China, Siberia, and Antarctica were documented by Skovsted (in press) and Malinky and Skovsted (2004).

Although many Early Cambrian shelly fossils appear to have a considerable longevity (e.g., Landing et al. 2002), the co-occurrence of several species, or closely related forms, in sedimentary rocks on different palaeocontinents appears to indicate that faunal interchange occurred frequently between these areas in the Early Cambrian. Far from being isolated, the late Early Cambrian continents appear to have been closely juxtaposed, sharing many faunal elements.

Function and affinity of *Triplicatella*

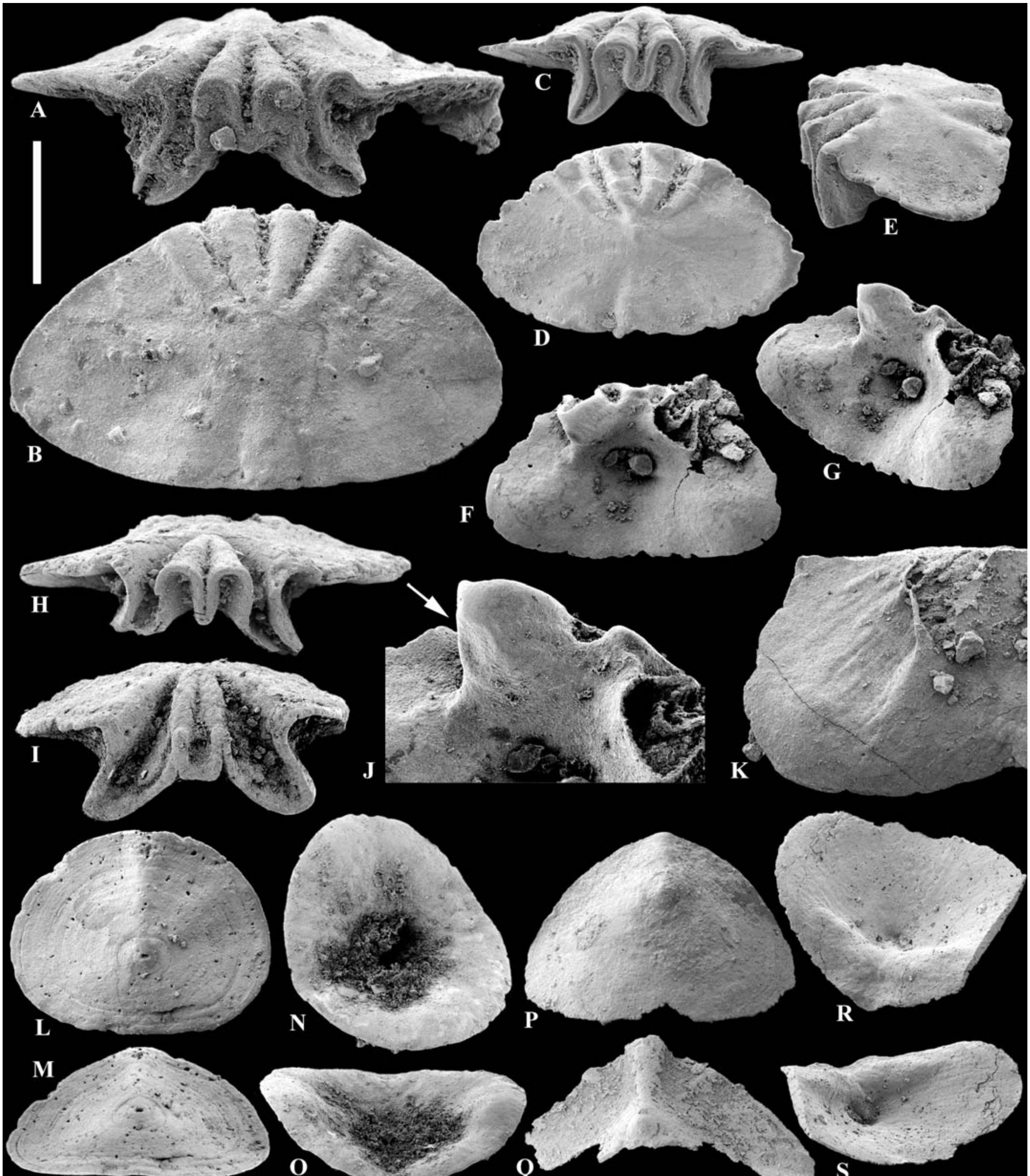
The cap-shaped shells of *Triplicatella* are subtriangular in outline and are characterized by one to four folds developed on two opposite margins of the shell. The phosphatic composition of the type species, *T. disdoma* Conway Morris in Bengtson et al. 1990 from Australia, was interpreted as secondary by Conway Morris, who also noted (Bengtson et al. 1990, p. 232) that the shape of *Triplicatella* and the configuration of possible muscle scars on the interior surface support comparison with hyolith opercula. However, no co-occurring hyolith conch with an aperture matching the crenulated margin of the shells was found (Bengtson et al. 1990, p. 232). Conway Morris mentioned the possibility of a multi-sclerite reconstruction of *Triplicatella*, but favoured an opercular function for the fossil. Evidence in support of the opercular reconstruction was recently published by Demidenko (in Gravestock et al. 2001, pl. 10, fig. 7). This single specimen from South Australia appears to represent a partial internal mould of a hyolith-like conch with a specimen of *T. disdoma* sealing the aperture. Unfortunately, Demidenko failed to describe the specimen in the text, although similarly preserved, undescribed material confirms that the configuration is not a chance event (A. Yates, personal communication, 2003). The published illustration of the articulated specimen does not allow a description of the conch itself. Although the margin of the preserved part of the conch appears to follow the shape of the operculum, in an internal mould this may be a preservational effect. Thus, *Triplicatella* is clearly constructed in a way similar to hyoliths, even though the conch is yet to be fully described. No conchs attributable to the genus were found together with the presently described material from Greenland, Canada, and Siberia.

In his description of *Triplicatella disdoma*, Conway Morris arbitrarily designated one side of the shell bearing three folds as posterior and the opposite side as anterior (Bengtson et al. 1990, p. 232). The supposedly anterior side always appears to be more strongly curved in plan view than the posterior (Bengtson et al. 1990, figs. 157–158; Figs. 2B, 3J, 4A, 5 herein). It is here interpreted as corresponding to the dorsal side of hyolith opercula. Following the terminology used to describe hyolith opercula, the terms “dorsal” (for the supposedly anterior side) and “ventral” are used throughout this work.

Hyolithida and Orthothecida

The opercula of the two main groups of hyoliths, the orders Hyolithida Syssoiev, 1957 and Orthothecida Marek, 1966, differ in several characters. The opercula of hyolithids are divided into a convex cardinal shield (corresponding to a continuation of the ventral wall of the conch, the ligula) and a dorsal lip. Folds are often developed on the lateral margins of the operculum to accommodate the proximal part of the helens, paired skeletal components of uncertain function characteristic of hyolithids. The opercula of hyolithids also have two sets of internal processes; a set of teeth-like structures (cardinal processes) situated close to the dorsal margin and a set of ridge-like structures (clavicles) running from the cardinal processes towards the ventral side. Diverse muscle scar patterns are present in certain hyolithid opercula, and Marek (1963, 1967) and Marti-Mus and Bergström (2001) suggested that some at least (including scars associated with the cardinal processes) were involved in controlling the movement of the operculum with reference to the conch. Other scars were interpreted by Marti-Mus and Bergström (2001) as structures involved in controlling the position and movement of the helens. For a different opinion on the function of hyolithid muscles see Runnegar et al. (1975).

The operculum of orthothecids is planar; its outline corresponding to the internal surface of the conch, and it is not divided into clearly defined areas. The orthothecid skeleton does not appear to have included any structures comparable to the hyolithid helens (e.g., Marek 1966, 1967). Orthothecids also lack clavicles on the internal surface of the operculum, but usually posses blade-like cardinal processes (Marek 1966, 1967). No muscle scars are known from the opercula of orthothecids. A distinguishing feature of orthothecid opercula (Marek 1966, 1967) is the presence of radial folds (plicae of Marek 1967, p. 63) developed on the ventral margin of the shell. The ventral folds were thought by Marek (1967) to have “biological significance,” but no specific interpretation was presented. If the folds left open slits even when the



operculum closed the conch (as envisaged by Marek 1967, text-fig. 7), the structures could have served as inhalant–exhalant structures. This may be problematic when hyoliths, as usually reconstructed, lay in a ventral resting position on the sea floor (e.g., Runnegar et al. 1975; Marek and Yochelson 1976), but would be less problematic if the shell is reconstructed with the apex buried in the sediment.

The differences between orthothecid and hyolithid opercula have led to different interpretations of the function of the opercula. While hyolithid opercula in life position were stationary at the aperture of the conch, only opening at the ventral margin (Marek 1967; Marti-Mus and Bergström 2001), the opercula of orthothecids were small enough to fit inside the conch and apparently were capable of vertical movement within it (Marek 1966; Marek and Yochelson 1976). While hyolithids apparently relied on muscles to move the operculum and conch in relation to each other (Marti-Mus and Bergström 2001), orthothecids may have relied on hydrostatic mechanisms to manipulate their skeletal parts.

Construction and functional morphology of *Triplicatella*

The external surface of *Triplicatella* can not be divided into distinct morphological zones, and no modifications of the lateral margins indicate the presence of helens or any other appendages. The prominent folds characteristic of *Triplicatella* make the operculum far from planar, and the internal surface lacks both clavicles and cardinal processes. However, in one of the species from Greenland described later in the text (*T. sinuosa* n. sp.), folds on the dorsal margin of the operculum are developed to such an extreme degree as to be superficially similar to genuine hyolith processes (Figs. 2A–2I). In other species of *Triplicatella* (*T. disdoma*, *T. peltata* n. sp., and *Triplicatella* sp. A and B), there are no invaginations extending downwards on the dorsal opercular margin, but rather a single positive fold developed to varying degrees. In *T. peltata*, and to a lesser extent in *T. disdoma*, the interior surface has two ridges developed on either side of the central dorsal fold, apparently formed by secondary thickening of the shell (Figs. 3K–3N; Bengtson et al. 1990, figs. 158I, 158J).

Possible muscle scars are present in *Triplicatella sinuosa*, *T. disdoma* and *T. peltata*. In *T. sinuosa*, possible muscle scars are present close to the tips of the dorsal invaginations (Figs. 2G, 2J) and close to the dorsolateral margins of the shell (Fig. 2K). In *T. disdoma*, elongated depressions (interpreted as possible muscle scars by Conway Morris in Bengtson et al. 1990, p. 232) bounded by ridges occupy the same position on the shell interior as the wide internal ridges in *T. peltata*. The latter species has possible muscle scars inserted below the ridges, close to the centre of the shell (Figs. 3K–3N).

In ventral view, the prominent folds of *Triplicatella sinuosa* are reminiscent of cardinal processes and also occupy a similar position close to the dorsal margin. In hyolithids, the downward extension of cardinal processes is thought to reduce the length of muscles controlling the movement of the operculum and helens (Marti-Mus and Bergström 2001), and the prominent folds of *T. sinuosa* could serve a similar general purpose. However, the structures are formed by invaginations of the opercular margin and are clearly not homologous to genuine cardinal processes. In life, the cardinal processes of hyolithids were inserted into the conch at a distance from the dorsal margin and were attached to the dorsal surface of the conch by soft tissue (Marti-Mus and Bergström 2001). The dorsal side of the folds in *T. sinuosa* must have followed closely the internal surface of the conch, leaving little space for soft tissue, and the possible muscle scars are situated on the ventral side of the folds. This location is similar to the position of hyolithid muscle scars interpreted to have a role in controlling the movement of the helens, skeletal structures that are absent in *Triplicatella*. The understanding of the organization of *Triplicatella* is further complicated by the absence of dorsal invaginations and the presence of internal ridges formed by secondary thickening of the shell in *T. peltata* and *T. disdoma*, as well as differences in position and morphology of muscle scars among all species of the genus. Presently, the functional morphology and soft anatomy of *Triplicatella* remain poorly understood, but the common occurrence of muscle scars indicates that the animals relied on muscular action, rather than hydrostatic pressure, to manipulate their skeletal parts.

The gentle ventral folds present in all species of *Triplicatella* are similar to orthothecid plicae and could have had a similar function in water circulation. Interpretation of the prominent dorsal folds as inhalant/exhalant structures is also possible and would be more compatible with the conventional ventral-down reconstruction of hyoliths. An alternative interpretation of the elaborate dorsal folds of *T. sinuosa* could then be as structures that separated exhalant and inhalant currents. However, the great variability of the dorsal folds seems to preclude this interpretation, as certain specimens have open and some sealed channels between the folds (e.g., compare Figs. 2H and 2I).

Affinity of *Triplicatella*

Although the affinity of *Triplicatella* to hyoliths seems well established, the genus is difficult to place within the existing taxonomy of the group. *Triplicatella* resembles orthothecid opercula in several characters: the absence of clavicles and helens and the presence of folds on the ventral margin of the shell. However, the opercula of *Triplicatella* differ from orthothecids in the non-planar margin of the shell, in the absence of true cardinal processes and ithe presence of muscle scars. Muscle scars and a non-planar operculum are instead characters shared with hyolithids. Thus, the unique construction of *Triplicatella* means that the genus can not be securely placed in either Hyolithida or Orthothecida and is also difficult to reconcile with the early evolution of hyoliths as outlined by Dzik (1994). Presently *Triplicatella* could perhaps be best placed within an informal (and probably polyphyletic) group of Early Cambrian "hyolith-like" small shelly fossils, presumably including the ancestors of the post-Early Cambrian hyolith groups. Malinky and Skovsted (2004) discussed a range of other Early Cambrian fossils in a similar taxonomic position with regards to hyoliths. The similarities of *Triplicatella* to orthothecids suggests that the operculum may have had a similar function, being moveable within the distal end of the conch. In identifying possible conchs of *Triplicatella*, it should then be noted that this functional interpretation does not require a close match between the crenulated margin of the operculum and that of the conch.

Systematic palaeontology

REPOSITORY: All specimens from Greenland are deposited in the Geological Museum in Copenhagen, Denmark (MGUH). Specimens from western Newfoundland are deposited in the Provincial Museum of Newfoundland and Labrador, St. John's, Newfoundland (NFM). The specimen from Siberia is deposited in Naturhistoriska Riksmuseet, Stockholm, Sweden (NRM-PZ).

Phylum uncertain
Class Hyolitha Marek, 1963
Order and Family uncertain
Genus *Triplicatella* Conway Morris in Bengtson et al. 1990.
Type species. *Triplicatella disdoma* Conway Morris in Bengtson et al. 1990.

Triplicatella Conway Morris in Bengtson et al. 1990, pp. 231–232.

DISCUSSION: As discussed earlier in the text, *Triplicatella* is mainly known from the operculum, while the conch is still undescribed. Although an affinity to hyoliths is assumed, no assignment of the genus to any specific group within that class is attempted.

The variability of different species of *Triplicatella* appears to be considerable. The degree of convexity, the surface ornamentation, and even the number of folds on the dorsal margin are variable features in *T. disdoma* from Australia (Conway Morris in Bengtson et al. 1990). This appears also to be the case in *T. sinuosa* n. sp. from Greenland, where, for example, the development of the dorsal folds differs between specimens (compare Figs. 2H and 2I). The great variability of the shells results in uncertainty regarding the taxonomic position of forms represented by small numbers of specimens, and four different forms from Greenland, Newfoundland, and Siberia are here left in open nomenclature.

Triplicatella sinuosa n. sp.
Figs. 2A–2K, 3A–3F.

HOLOTYPE: MGUH 27064 from GGU sample 314835, upper Bastion Formation of Albert Heim Bjerge, North-East Greenland.

DIAGNOSIS: Species of *Triplicatella* with the operculum transversely oval and subtriangular. Four strongly developed folds on the dorsal margin accompany three ventral invaginations, which project far below the floor of the internal surface. The two lateral invaginations curve outwards towards the corresponding lateral margins.

ETYMOLOGY: From the sinuous curve described by the shell margins.

MATERIAL: MGUH 27064 – MGUH 27069 from GGU sample 314835 and 89 additional specimens from GGU samples 314808, 314835, and 314908, Bastion Formation, North-East Greenland. MGUH 27075 – MGUH 27077 from GGU samples 218894 and 271717 and 20 additional specimens from GGU samples 218894, 217469, and 271717, Aftenstjernesø Formation, North Greenland.

DESCRIPTION: The shell is transversely elongated (width 0.5–3 mm), oval, and subtriangular in outline. The apex is shifted slightly towards the dorsal margin. Ventral margin has three weakly developed symmetrical folds, and the dorsal margin has four prominent folds with three corresponding ventral invaginations extending downwards far below the level of the shell (Figs. 2A, C, D). The central invagination is normal to the shell surface. The left and right lateral invaginations extends further (about twice as far) as the central one, and curve towards the lateral ends of the shell. Length of each lateral invagination is about 25% of the width of the fossil. All three invaginations are usually open folds, but in some specimens, they are reduced to narrow slits (Fig. 2H). Viewed from the dorsal edge the folds and invaginations usually form a rounded sinuous curve shaped like the letter “M” (Figs. 2A, 2C, 3A, 3C), but more compressed forms occur (Fig. 2I). Viewed from the interior, the lateral invaginations form ridges that run on both sides of a central depression. Towards the dorsal margin the ridges develop into stout spines. The outer surface is ornamented by concentric growth lines, and the internal surface is smooth with a deep central depression between the lateral ridges. Shallow circular depressions are present on the internal surface close to the tips of the lateral invaginations (Fig. 2J). Vaguely defined circular depressions are also present between the internal ridges and the dorsolateral margins; sometimes ornamented by faint ridges (ca. 50 μm across; Fig. 2K).

DISCUSSION: The transversely elongated shell and the four dorsal marginal folds distinguish *Triplicatella sinuosa* n. sp. from all other species of the genus. The shallow depressions on the internal surface of the dorsal invaginations and the circular depressions on the dorsolateral margins are interpreted as muscle scars. The function of these and other structures in *T. sinuosa* was discussed earlier in the text.

OCCURRENCE: Bastion Formation of Hudson Land, North-East Greenland, and Aftenstjernesø Formation of Peary Land, North Greenland. Age: late Early Cambrian.

Triplicatella peltata n. sp.
Figs. 2P–2S, 3G–3O, 4A–4C.

HOLOTYPE: MGUH 27078 from GGU sample 218894 of the Aftenstjernesø Formation of Løndal, western Peary Land, North Greenland.

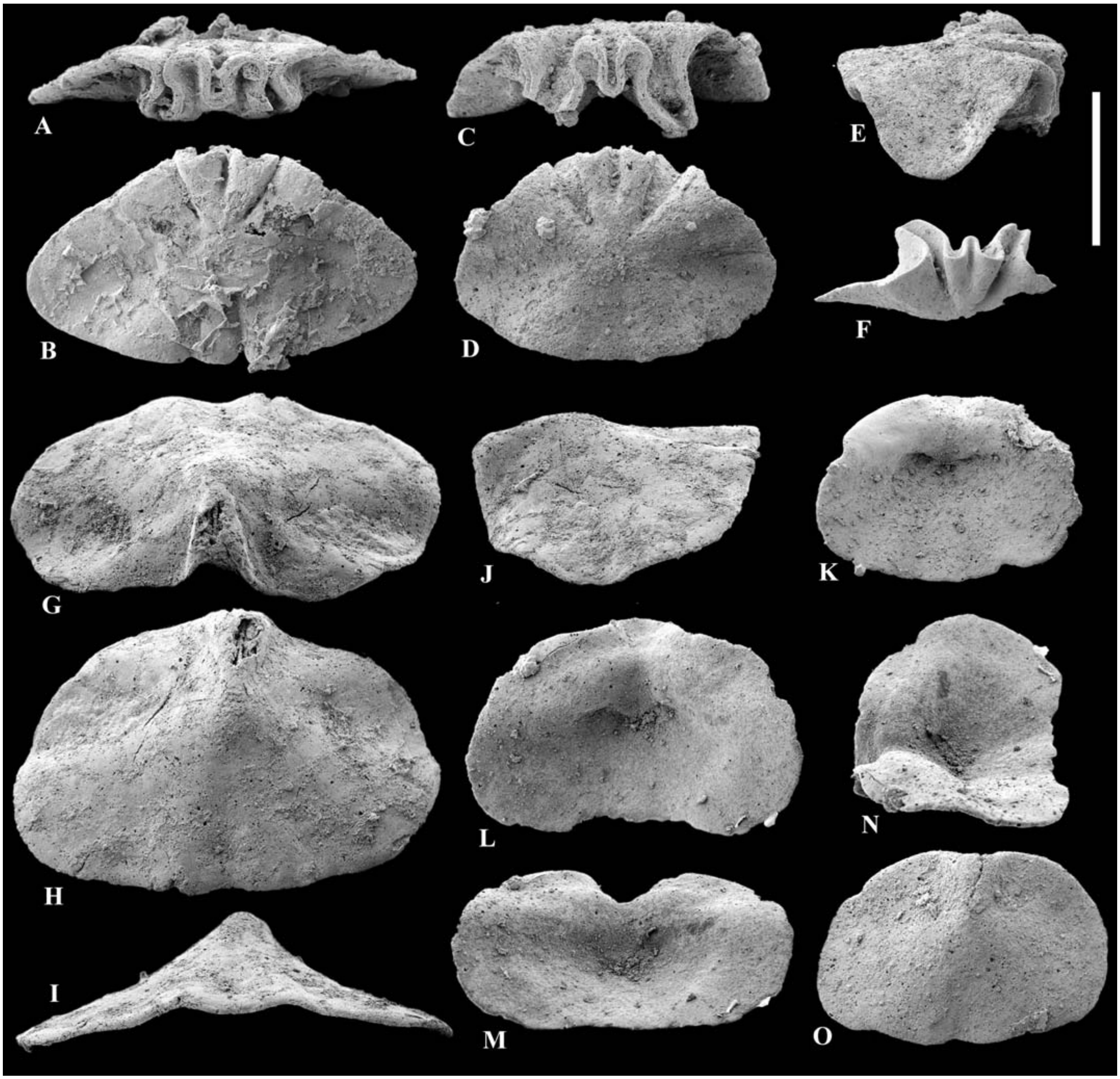
DIAGNOSIS: Species of *Triplicatella* with convex operculum; subtrapezoidal to subtriangular in outline. One dorsal and two weakly developed ventral marginal folds.

ETYMOLOGY: Latin *pelta*, small shield, from the shield-like appearance of the shells.

MATERIAL: MGUH 27078 – MGUH 27081 from GGU sample 218894, and 29 additional specimens from GGU samples 218894 and 217469, Aftenstjernesø Formation, North Greenland. MGUH 27072 – MGUH 27074 from GGU sample 314906, and 16 additional specimens from GGU samples 314904, 314906, 314908, 314909, 314910, and 314933, Bastion Formation, C.H. Ostenfeld Nunatak, North-East Greenland. NFM F-453 from sample JSP1982-01 and NFM F-454 from sample ICS 1421, upper Lower Cambrian Forteau Formation, near the head of Dear Arm, Gros Morne, western Newfoundland.

DESCRIPTION: The shell is convex, subtrapezoidal to oval and only very weakly triangular in outline (width 0.8–2 mm). The shell apex is displaced towards the dorsal margin. The

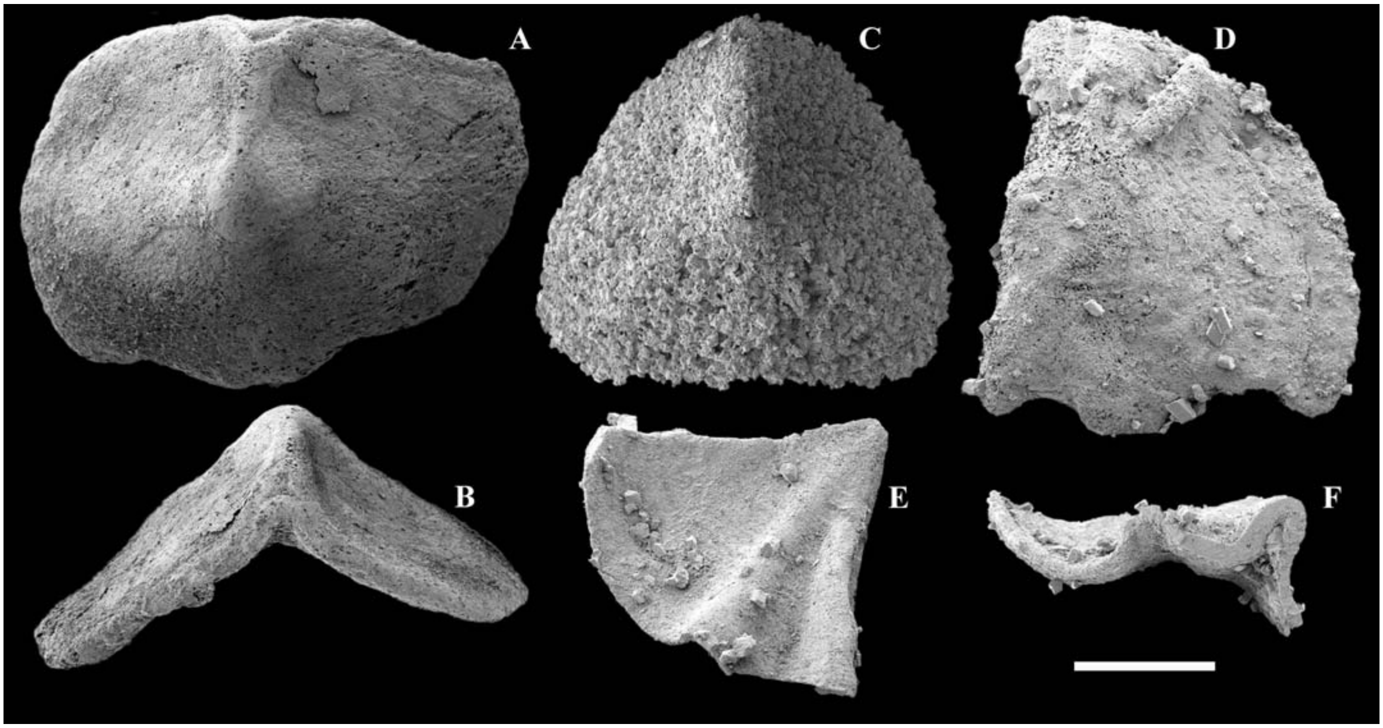
Fig. 3. *Triplicatella* from the Aftenstjernesø Formation, North Greenland. **3A–3F.** *Triplicatella sinuosa* n. sp. Løndal, western Peary Land. (A, B) MGUH 27075, GGU sample 271717, viewed from the dorsal edge and from above. (C, D, E) MGUH 27076, GGU sample 218894, viewed from dorsal edge, from above, and from right lateral side (oblique). (F) MGUH 27077, GGU sample 271717, fragment, oblique view of dorsal edge. **3G–3O.** *Triplicatella peltata* n. sp. GGU sample 218894, Løndal, western Peary Land. (G, H, I, J) MGUH 27078 (holotype), viewed from dorsal edge (oblique), from above, from ventral edge, and from left lateral side. (K) MGUH 27079, internal surface from above. (L, M, N) MGUH 27080, internal surface from above, from ventral edge (oblique), and from left lateral side (oblique). (O) MGUH 27081, viewed from above. Scale bar = 0.5 mm.



dorsal margin exhibits one prominent fold and the ventral margin two weakly developed folds separated by a shallow trough. The dorsal fold rises sharply above the low dorsolateral fields, almost reaching the shell apex in lateral view. External ornamentation of weakly defined concentric growth lines. The internal surface is smooth with a deep central depression. Two broad lateral ridges converge between the central depression and the dorsal margin. Indented below the lateral ridges, close to their point of convergence are two small pits (Figs. 3K, 3N).

DISCUSSION: *Triplicatella peltata* n. sp. is distinguished from *T. disdoma* by the presence of only two folds on the ventral margin, by the dorsal fold not reaching above the shell apex, and by the presence of two pits on the internal surface close to the centre of the shell. The species is distinguished from

Fig. 4. *Triplicatella* from the Forteau Formation of Gros Morne, Newfoundland. **4A–4C.** *Triplicatella peltata* n. sp. (A, B) NFM F-453, view from above and from dorsal edge. (C) NFM F-454, sample ICS 1421, view from above. **4D–4F.** *Triplicatella*? sp., from 12 km east of Rocky Harbour. (D) NFM F-455, view from above. (E, F) NFM F-456, view from above and from edge of fragment. All except C from sample JSP1982-01. Scale bar = 0.5 mm.



T. sinuosa by the presence of only one fold on the dorsal margin and from other forms attributable to the genus by the subtrapezoidal outline. Specimens from the Bastion Formation of North-East Greenland with subtrapezoidal to subtriangular outline, shell apex shifted towards the dorsal margin, and prominent converging ridges on the internal surface (Figs. 2P–2S) are brought to *T. peltata* in spite of the less well-defined dorsal fold. In the material from North-East Greenland the ventral folds were not clearly observed, but two incipient additional folds on the dorsal margin, on either side of the main fold, were noted in a single specimen (Fig. 2Q). Two specimens from the Forteau Formation of western Newfoundland are placed in this species based on the well-defined dorsal fold, despite the poor preservation of the lateral and ventral margins (Figs. 4A–4C).

The presence of two folds on the ventral margin of this species is unique within *Triplicatella*, but recalls the situation seen in many orthothecid opercula (Marek 1966, 1967). It should be noted that the development of the ventral folds is variable in other species of *Triplicatella*, and in, for example, *Triplicatella* sp. A (Figs. 2L, 2M), they are present only in a rudimentary form.

OCCURRENCE: Aftenstjernesø Formation of Peary Land and Lauge Koch Land, North Greenland, Bastion Formation, North-East Greenland and Forteau Formation of western Newfoundland. Age: late Early Cambrian.

Triplicatella sp. A
Figs. 2L–2O.

MATERIAL: MGUH 27070 – MGUH 27071, GGU sample 314835 and 22 additional specimens from GGU samples 314807 and 314835. All from the upper Lower Cambrian Bastion Formation, Albert Heim Bjerge, North-East Greenland.

DESCRIPTION: The shell is small and very low with an almost circular outline (width 0.5–1.2 mm). The dorsal margin is rounded and the ventral margin only slightly more straight (Fig. 2L). The apex is shifted slightly towards the ventral margin. The dorsal margin has one broad and low fold, and the ventral margin is almost horizontal, but sometimes with three vestigial folds (Fig. 2M). The internal surface is poorly known, but no ridges or depressions have been observed beyond a slight thickening of the lateral margins (Fig. 2O). Outer surface ornamented by concentric growth lines.

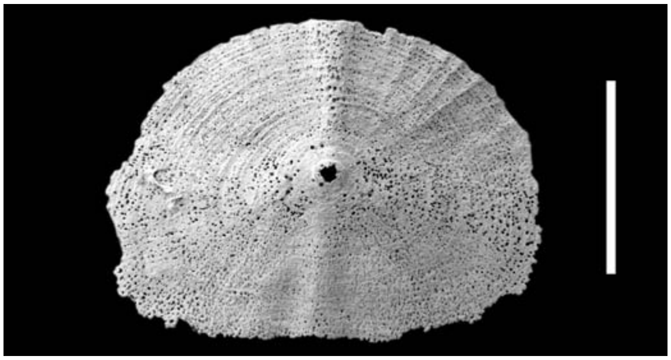
DISCUSSION: This form differs from all other species of *Triplicatella*, except *Triplicatella* sp. B, in the very low profile of the shell and from the latter form by the more rounded shape and the ventral position of the apex.

Triplicatella sp. B
Fig. 5.

MATERIAL: NRM-PZ X3565 (Naturhistoriska Riksmuseet, Stockholm) from the Lower Cambrian (lower Atdabanian) Tyuser Formation of North Siberia.

DESCRIPTION: A very low shell with a rounded dorsal margin and an almost straight ventral margin (width 1.25 mm). The apex is located just dorsally of the centre of the shell. Dorsal margin with one low and rounded fold, the ventral margin with three weakly developed folds. The surface of the shell

Fig. 5. *Triplicatella* sp. B. Tuyser Formation, Chekurovka, North Siberia. NRM-PZ X3565. Scale bar = 0.5 mm.



ornamented by fine concentric growth lines and fine radiating ridges on the lateral fields. The internal morphology is not known.

DISCUSSION: This single specimen differs from other species of the genus, except *Triplicatella* sp. A, in the low profile of the shell, and from the latter form in the straight ventral and rounded dorsal margins. This specimen appears to be the oldest known representative of the genus. Due to the fragility of the specimen, it could not be turned over for photography of the internal surface.

***Triplicatella*? sp.**
Figures 4D–4F.

MATERIAL: NFM F-455 and NFM F-456 from the upper Lower Cambrian Forteau Formation, near the head of Deer Arm, Gros Morne, western Newfoundland.

DESCRIPTION: Two fragments, both apparently broken along the dorso-ventral axis of a probably low and convex shell (Figs. 4B–4C). One specimen has an upturned lateral rim (Fig. 4C). The specimens appear to share well developed marginal folds, but the morphology and number of folds is impossible to determine as both specimens are broken along the folds.

DISCUSSION: The incomplete state of these specimens from western Newfoundland makes assignment to *Triplicatella* uncertain. The specimens occur in Newfoundland together with *Triplicatella peltata*, but appear to differ from this species by the higher number of and more strongly pronounced folds. The low profile and pronounced folds makes the fragments reminiscent of a single specimen from Australia referred to *T. disdoma* (Conway Morris in Bengtson et al. 1990, figs. 158L–158N).

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