The problematic fossil *Mongolitubulus* from the Lower Cambrian of Greenland

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Spines referred to the problematic phosphatic Small Shelly Fossil *Mongolitubulus* Missarzhevsky, 1977 are described from the Lower Cambrian of Greenland. The type species, *M. squamifer*, is reported from the Henson Gletscher Formation of North Greenland, while *M. henrikseni* sp. nov. is described from the Bastion Formation of North-East Greenland. Co-occurring small plates with broken spine bases suggest that *Mongolitubulus henrikseni* may have been a bivalved(?) arthropod with a carapace bearing multiple spines, but it is uncertain if this restoration can be extended to the type species.

Key words: Small Shelly Fossils, problematica, Cambrian, Greenland.

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The transition from the Precambrian to the Cambrian is marked by a sudden influx of so-called Small Shelly Fossils (SSF) representing one of the greatest evolutionary diversifications of life during earth history (Bengtson 1994a). A variety of shell morphologies appears, witnessing the widespread acquisition of protective external calcification or phosphatisation in organisms commonly represented by fossils up to 1 mm or so in maximum dimension (Rozanov, Missarzhevsky, Volkova, Voronova, Krylov, Keller, Korolyuk, Lendzion, Michniak, Pykhova & Sidorov 1969; Qian & Bengtson 1989; Bengtson, Conway Morris, Cooper, Jell & Runnegar 1990; Bengtson 1994b). Some SSF are more or less readily assigned to animal groups familiar from the later fossil record, such as the variety of molluscs (Bengtson et al. 1990; Peel 1991; Gubanov & Peel 2000), but others are problematic both in terms of their morphology and affinity. As with fossils in general, the nature of some of these SSF may be obscured by taphonomic changes but a widespread trend for individual organisms to include a variety of dissimilar skeletal elements, or sclerites, within a single apparatus, or scleritome, provides an additional complication to restoration and interpretation. For example, the single blade-like fossil *Halkieria* described by Poulsen (1967) from the Lower Cambrian of Bornholm was subsequently interpreted as a sclerite in a multi-element scleritome by Bengtson & Conway

Morris (1984). Only with the description of articulated halkieriids from the Lower Cambrian Sirius Passet fauna of North Greenland by Conway Morris & Peel (1990, 1995) could the true nature of the beast be ascertained, although its affinity remains controversial.

Peel & Blaker (1988) reported the occurrence of the microscopic Small Shelly Fossil *Mongolitubulus squamifer* Missarzhevsky, 1977 in limestones of the Henson Gletscher Formation from southern Freuchen Land, central North Greenland, of late Early Cambrian age (Fig. 1). Their preliminary description concentrated on the identification of a species originally described from the Lower Cambrian of Mongolia by Missarzhevsky (1977) but later described from Kazakhstan (Missarzhevsky & Mambetov 1981) and reported from the Melville Peninsula, West Antarctica (Gazdzicki & Wrona 1986). Subsequently, *Mongolitubulus* has been reported from a number of other Lower Cambrian localities, worldwide (Meshkova 1985; Wrona 1989; Esakova & Zhegallo 1996; see also Bengtson et al. 1990). Peel & Blaker (1988) presented evidence of increased variation in surface ornamentation and morphology in the 1–2 mm long tubular fragments, but their well preserved material, first fully described herein, indicated that the tubes are hollow spines, closed at one end.

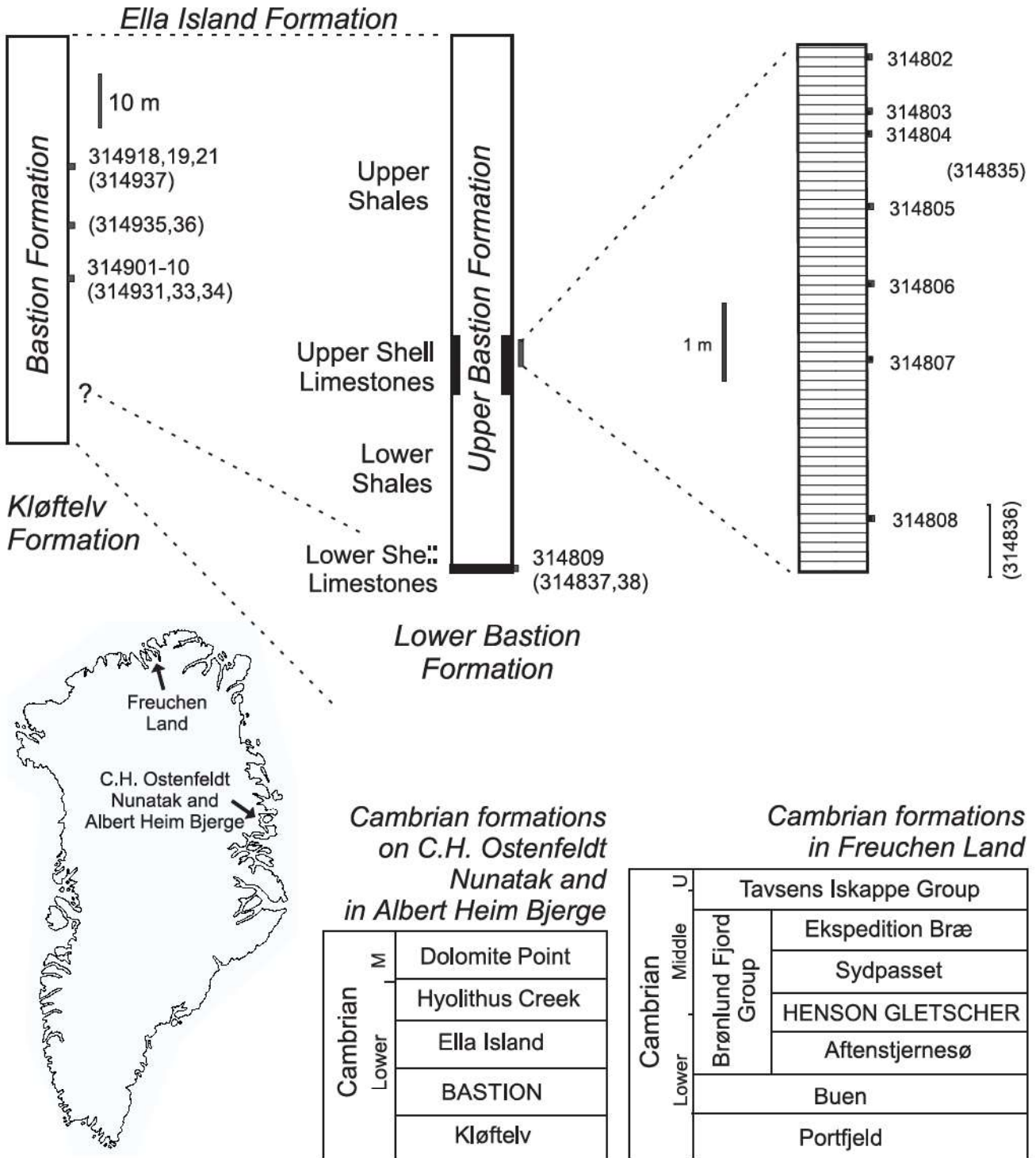Fossils similar to *Mongolitubulus squamifer* have recently been recovered in abundance in residues re-

Fig. 1. Derivation of fossiliferous GGU samples within the Bastion Formation of Albert Heim Bjerge and C. H. Ostenfeldt Nunatak, North-East Greenland. For location see discussion in the text. Sample numbers in parentheses are derived from localities immediately adjacent to the measured sections. The map and accompanying tables indicate the known distribution of *Mongolitubulus* in Greenland (for explanation see text).

maining after acetic acid digestion of limestone samples from the Upper Bastion Formation of North-East Greenland (Fig. 1). These fossils appear to be slightly older than the late Early Cambrian records of *M. squamifer* from North Greenland, and show a different morphology, both as regards ornamentation and the preserved basal area. The new material is described herein as *Mongolitubulus henrikseni* sp. nov., named in honour of State Geologist Niels Henriksen (Geological Survey of Denmark and Greenland, incorporating the former Geological Survey of Greenland) in recognition of his career-long commitment to Greenland geology. More than 1000 specimens of *Mongolitubulus henrikseni* sp. nov. are available from North-East Greenland, which is notable when compared to other occurrences of this problematic fossil. It is evident that *Mongolitubulus* as currently known is not an entire organism but a resistant spine forming part of a larger skeletal element, or perhaps several different kinds of element, within the exoskeleton of a larger animal, or possibly several different animals. Thus, *Mongolitubulus* spines in themselves are an incomplete foundation for the full description of a biological species. Nevertheless, the wide distribution and potential stratigraphic utility of the spines justify the description of the new species, while accompanying spinose plates offer clues as to its true identity.

Geological background

Specimens of *Mongolitubulus squamifer* Missarzhevsky, 1977 described by Peel & Blaker (1988) and herein were derived from GGU sample 301351, collected by J.S. Peel and M.R. Blaker in 1985 from a reference section through the Henson Gletscher Formation in southern Freuchen Land, central North Greenland (Ineson & Peel 1997, Figs 21, 32, 33), about 18 m above the base of the formation. This is the same locality described by Blaker & Peel (1997, Fig. 8A, locality 1; Fig. 10) and from which they described the trilobites *Ogygopsis batis* (Walcott, 1916), *Cheiruroides* sp. A, *Kootenia radiata* Blaker & Peel, 1997 and *Kootenia* cf. *K. 'longa'* Ju, 1983.

The Henson Gletscher Formation was defined and fully described by Ineson & Peel (1997) and represents a widely distributed and richly fossiliferous formation of dark carbonates with subsidiary sandstones within the Brønlund Fjord Group of North Greenland. The latter is a carbonate-dominated unit within the Franklinian Basin succession of North Greenland (Higgins et al. 1991a, b; Surlyk 1991; Ineson & Peel 1997). On a regional scale, the Henson Gletscher For-

mation is strongly diachronous, ranging in age from late Early Cambrian to late Middle Cambrian. It is entirely late Early Cambrian (Dyeran = *Bonnia-Olenellus* Zone in North American usage) in the mentioned reference section in southern Freuchen Land, but in the type area, approximately 50 km to the east, the formation continues into the Middle Cambrian (*Ptychagnostus gibbus* Zone). Exposures along the north coast contain Middle Cambrian faunas (*Glossopleura* Zone and younger) but the Lower Cambrian is not demonstrated (Peel 1994).

Specimens of *Mongolitubulus henrikseni* sp. nov. were all obtained from limestone samples collected from the shale dominated Upper Bastion Formation in two regions of North-East Greenland. The section in the south-west part of Albert Heim Bjerge, northern Hudson Land, is about 98.5 m thick and was fully described by Cowie & Adams (1957, pp. 50–58, 154–155) with a summary by Peel (1982). Samples from this area were collected by J. S. Peel and M.P. Smith during 1988 from the Cowie & Adams (1957) locality and its immediate vicinity (see also Pickerill & Peel 1990). Peel and Smith also collected a suite of samples from a previously undescribed section through the Bastion Formation (c. 75 m thick) at the northern tip of C.H. Ostenfeldt Nunatak, within Wordie Gletscher, some 35 km north of the Albert Heim Bjerge locality. The formation here is not well exposed, especially in the lower part, and the subdivision proposed by Cowie & Adams (1957) at Albert Heim Bjerge could not be recognised.

The fossils occur together with a diverse and well-preserved fauna of Small Shelly Fossils of early to mid Dyeran age (late Early Cambrian). The associated fauna includes trilobites, brachiopods, helcionelloid molluscs, hyoliths, phosphatocopid and bradoriid arthropods, as well as a whole range of problematic fossils such as mobergellans, lapworthellids and hyolithelminths. Crack out-collections of trilobites, brachiopods, hyoliths, and other fossils have also been described by Poulsen (1932) and listed by Cowie & Adams (1957).
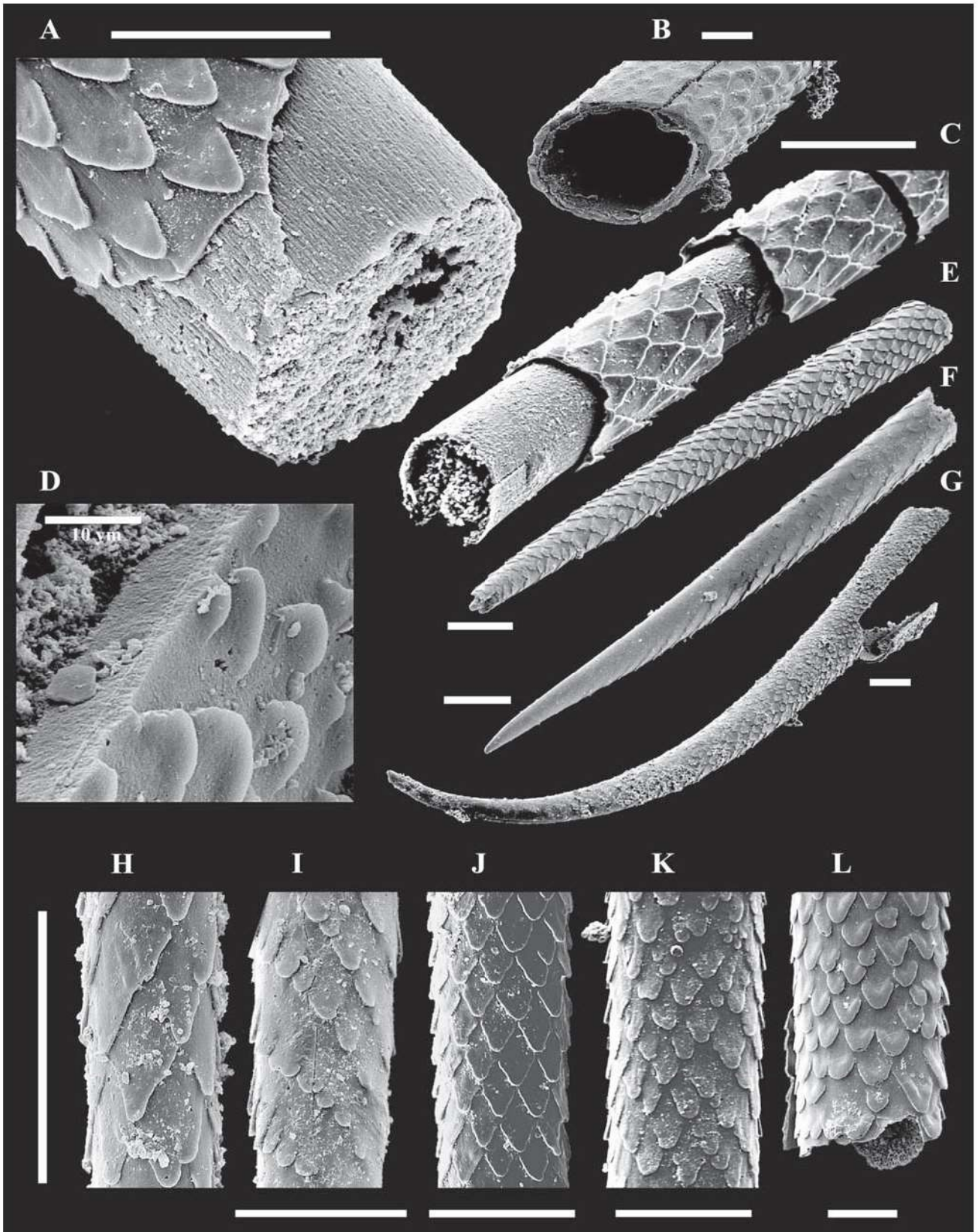
Systematic descriptions

Genus *Mongolitubulus* Missarzhevsky, 1977

Type species. – *Mongolitubulus squamifer* Missarzhevsky, 1977 from the Lower Cambrian of Mongolia.

Mongolitubulus squamifer Missarzhevsky,1977
Fig. 2

1977 *Mongolitubulus squamifer* Missarzhevsky, sp. nov., pp. 13–14, pl. 1, figs 1, 2

1985 *Mongolitubulus squamifer*, Meshkova, pl. 46, figs 1–3

1988 *Mongolitubulus squamifer*, Peel & Blaker, pp. 56–58, fig. 2

1988 *Rhombocorniculum* n. sp., Landing, pp. 687, fig. 11.6

1989 *Mongolitubulus squamifer*, Missarzhevsky, pp. 45–47, pl. XXXI, figs 1, 3

Figured material. – MGUH 26009 – 26019 from GGU sample 301351 from the Henson Gletscher Formation (Brønlund Fjord Group) in central North Greenland.

Additional material. – MGUH 18.288 – 18.289 figured by Peel & Blaker (1988, fig. 2) and about 170 additional specimens were also recovered from the acetic acid-resistant residue of GGU sample 301351.

Diagnosis. – Long, slowly tapering spines with sharply pointed apex, although the basal region is not known. Ornamentation of adapically directed, rounded to diamond-shaped scales usually covering the entire outer surface except for the smooth apex. Scales are contiguous with the surface of the spine, becoming elevated above it adapically; they commonly form highly regular chequered patterns or spiralling ridges.

Description. – Spines of *Mongolitubulus squamifer* have a circular cross-section and taper uniformly towards the pointed apex. This pointed apex is preserved in 8.5% of 176 specimens from GGU sample 301351, but no specimen shows any evidence of the original morphology of the opposite, antapical, end of the fossil. Specimens recovered range between 0.5 and 2 mm in length, and the diameter of the widest part of the fragments varies from 0.07 to 0.23 mm. Most elements are straight or gently curved with a straight tip (Figs 2E-F), but one specimen has a highly recurved tip (Fig. 2G).

M. squamifer from GGU sample 301351 shows a high degree of variation in surface ornamentation both between specimens and between different parts of the same specimen. Typically, the ornamentation consists of inclined, rhomboid, scale-like, protuberances, with the antapical termination of the scale grading into the smooth surface of the spine and the adapical termination being raised above this surface. Diamond-shaped (Fig. 2J) and rounded scales (Figs 2K-L) co-occur and intergrade in the material. Diamond-shaped scales usually form highly regular patterns while rounded scales show a less perfect arrangement. In some specimens, the regular pattern of imbricating scales develops into separated rows of scales towards the apex (Fig. 2H), and eventually into crested ridges spiralling around the spine (Fig. 2I). In the most apical part of the majority of specimens, the ornamentation is subdued, leaving a smooth tip. The smoothness can affect the entire tip, or only one side of it (Fig. 2F). A limited number of large specimens has a much finer, and apparently more irregular ornamentation of rounded scales.

Some specimens show substantial variation in ornamentation along the length of the spine and, in rare cases, the extremes of variation present in the entire collection appear in different parts of only one specimen. Intra-spine variation appears to have a certain degree of consistency, with smaller, rounded and somewhat irregularly placed scales in the thick, antapical portion of the spine, a more regular pattern of large diamond-shaped scales in mid-length and spiralling ridges that eventually diminish in the apical part (Fig. 2G).

Preservation and microstructure. – Preservation of available specimens of *M. squamifer* is generally very good, and the fossils yield interesting new microstructural information. The spines in GGU sample 301351 are preserved as shiny black or brown phosphate, similar to that of co-occurring phosphatic brachiopods and protoconodonts. The darkness of the colour is typical of the carbonates of the Henson Gletscher Formation as a whole. A two-layered microstructure is apparent from damaged specimens where both shell layers are exposed (Figs 2A-C). The outer layer has a fine, porcellanous texture (Fig. 2D), and the inner layer is less dense, being composed of longitudinally arrang-

Fig. 2. A-L, *Mongolitubulus squamifer* Missarzhevsky, 1977, Henson Gletscher Formation, North Greenland. Scalebars (except D) equal 0.1 mm. All specimens from GGU sample 301351. A, MGUH 26009. Detail of broken spine with fibrous inner shell-layer exposed. B, MGUH 26010. Oblique view of broken spine with crack in outer shell-layer and corresponding soft deformation in inner layer. C, MGUH 26011. Spine with outer shell-layer partly removed. D, MGUH 26012. Broken shell-edge with detail of shell structure. Scalebar equal 0.01 mm. E, MGUH 26013. Tapering straight spine with consistent regular ornamentation. F, MGUH 26014. Sharp spine-tip with subdued ornamentation on the tip itself. G, MGUH 26012. Large curved spine with varied ornamentation. H, MGUH 26015. Detail of ornamentation of spiralling rows of scales. I, MGUH 26016. Detail of ornamentation of crested ridges. J, MGUH 26017. Detail of regular ornamentation of diamond-shaped scales. K, MGUH 26018. Detail of ornamentation with somewhat irregularly placed scales. L, MGUH 26019. Detail of ornamentation of irregularly placed wedge-shaped scales.

ed fibres (Fig. 2A). The scaly surface ornamentation is not reflected in the inner shell layer. The fibrous inner layer was probably not completely mineralised, with a high organic content; in some specimens it seems to have responded to damage by wrinkling, and not breakage, unlike the outer shell layer (Fig. 2B).

Discussion. – *Mongolitubulus squamifer* has hitherto been regarded as a widespread and very variable small shelly fossil from the upper Lower to lower Middle Cambrian, but this record has been re-evaluated in the light of the present recognition of a new species of *Mongolitubulus*, described below.

Mongolitubulus squamifer, as defined herein, is identified from the Lower Cambrian (Botomian) of Mongolia where it was originally described from only 4 specimens (*M. squamifer* of Missarzhevsky 1977, 1989), Massachusetts (*Rhombocorniculum* n. sp. of Landing 1988) and Greenland (*M. squamifer* of Peel & Blaker 1988 and herein), as well as from the lower Middle Cambrian of Turkestan (*M. squamifer* of Meshkova 1985). The illustrated specimen from Turkestan is a relatively large tube with an ornamentation of rounded scales which are regularly arranged in spiralling rows. This morphology is comparable to that of larger specimens of *M. squamifer* in the North Greenland collection (Figs 2K-L). Other published records of *M. squamifer* are dealt with in the discussion of *M. henrikseni* sp. nov., below.

The internal structure of *M. squamifer* from North Greenland resembles superficially that of the button-shaped *Hadimopanella apicata* Wrona, 1982, as described from the Lower Cambrian of North Greenland by Bendix-Almgren & Peel (1988). Both fossils have a dense outer layer. There is no evidence of incremental growth either in *Hadiomopanella* or *Mongolitubulus*. Bendix-Almgren & Peel (1988) speculated that *Hadimopanella* might represent the spicules of an early chordate, but it is now known to form part of the external skeleton of a paleoscolecidan worm

(Hinz, Kraft, Mergl & Müller 1990). The Lower Cambrian spine-like fossil *Rhombocorniculum* Walliser, 1958 has no dense outer layer, and fibrous phosphate was continually deposited basal-internally during the growth of the spine (Walliser 1958, Landing, Nowlan & Fletcher 1980 and Hinz 1987).

Mongolitubulus henrikseni sp. nov.
Fig 3.

1981   *Mongolitubulus squamifer*, Missarzhevsky & Mambetov, p. 79, pl XIV, figs 1, 2
?1986   *Mongolitubulus squamifer*, Gazdzicki & Wrona, p. 611
1989   *Mongolitubulus squamifer*, Wrona, pp. 543–544, pl 8, fig. 5
?1990   Ornamented tube B. Conway Morris & Bengtson in Bengtson et al., p. 158, fig. 102 A-G
?1990   Ornamented tube C. Conway Morris & Bengtson in Bengtson et al., p. 158, fig. 103 A-H
?1996   *Mongolitubulus squamifer*, Esakova & Zhegallo, pp. 103-105, pl. IV, figs 9–13

*Holotype.* – MGUH 26024 from GGU sample 314933, Bastion Formation, North-East Greenland.

Figured material. – MGUH 26020-26032 from GGU samples 314906, 314910, 314931, 314933

Additional material. – More than 1000 fragments of ornamented tubular and spine-like fossils attributable to the genus *Mongolitubulus* occur in acetic acid-resistant residues of limestone samples from the Upper Bastion Formation of North-East Greenland (GGU samples 314804, 314809, 314901, 314902, 314903, 314904, 314906, 314908, 314910, 314931, 314933 and 314934).

Diagnosis. – Long, parallel-sided or very slowly ta-

Fig. 3. A-M, *Mongolitubulus henrikseni* n. sp. Bastion Formation, North-East Greenland. All specimens, unless otherwise stated from GGU sample 314906. Scalebars (except A-B, H, K-M) equal 0.2 mm. A, MGUH 26020. Detail of natural cross-section of shell and scales. Scalebar equal 0.01 mm. B, MGUH 26021. Detail of broken shell-edge of spine-base showing internal lamination. Scalebar equal 0.01 mm. C, MGUH 26022. Curved spine with partly subdued ornamentation. D, MGUH 26023 from GGU sample 314933. Spine showing morphology of the spine-tip. E, MGUH 26024 from GGU sample 314933. Holotype. Slightly curved spine-tip. F, MGUH 26025. Non-tapering spine-fragment. G, MGUH 26026. Spine-base with natural (?) fold on flaring base. H, MGUH 26027 from GGU sample 314910. Large spine-base with broadly flaring basal area, and long spine attached. Scalebar equal 0.5 mm. I, MGUH 26028 from GGU sample 314931. Broad spine-base with smooth outer surface. J, MGUH 26029. Spine-base with artificially (?) rounded edges showing bend on the spine close to basal part. K, MGUH 26030. Detail of ornamentation of broad scales with longitudinal wrinkles. Scalebar equal 0.1 mm. L, MGUH 26031. Detail of ornamentation of small and widely spaced scales. Scalebar equal 0.1 mm. M, MGUH 26032 from GGU sample 314933. Detail of partly subdued ornamentation on curved spine. Scalebar equal 0.1 mm.
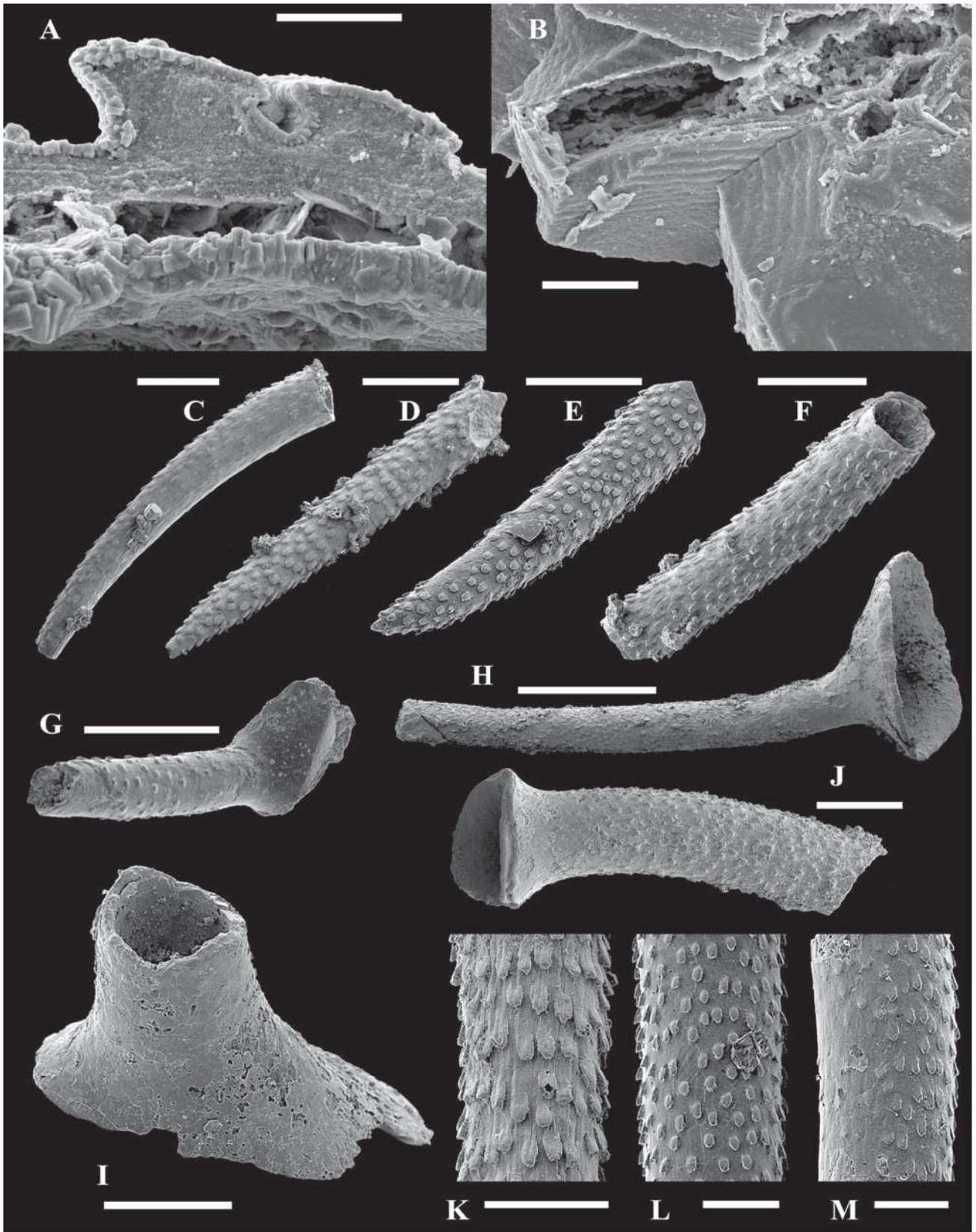
pering spines. Degree of tapering increases close to the apical termination forming a conical apex. Basal (antapical) part flaring widely. Ornamentation of adapically directed rounded scales covers all parts of the spines except the flaring base. Consistently irregular distribution of scales on all scale-bearing parts of the spines.

Description. – Species of *Mongolitubulus* with circular cross-section and straight to slightly curved form (Fig. 3). All specimens of the slowly tapering spines are fragmentary, but either the pointed tip (Figs 3D-E) or the flaring base (Figs 3G-J) may be preserved. Close to the flaring base most specimens are bent through approximately 20 degrees (Fig. 3J). One aberrant specimen has a bend of 76 degrees.

The diameter of preserved fragments varies from 0.08 to 0.24 mm. There is a substantial variation in the diameter of both apical and basal elements. There are also elements which do not show any sign of tapering, and many spines are equidimentional over much of their length. The longest specimen recovered (lacking both apex and base) is 3 mm long with a diameter varying from 0.19 mm at the apical end to 0.21 mm antapically.

The base of the spine is preserved in 9% of 500 counted specimens and is very distinct. The diameter of the base increases very rapidly as it leaves the near-parallel sided spine, in some cases to 4 or 5 times the diameter of the spine (Fig. 3H). In all specimens, the edges of the expanded base are broken, and the true dimensions of this part of the fossil can not be ascertained. In a few specimens the large base grades into an almost flat, or slightly convex plate with broken edges (Fig. 3I).

The tip of the spine is preserved in 4 % of available specimens. In most specimens the rate of tapering increases close to the tip forming a conical apex, but the scaly ornamentation persists to the very tip of the spine (Figs 3D-E).

The characteristic ornamentation consists of small scale-like processes that diverge from the body of the spine adapically and cover the entire outer surface of most elements. Only the flaring part of the base consistently lacks ornamentation is (Figs 3I-J). In a few curved elements the small scales disappear, or fuse to form faint ridges on the inside of the curvature (Figs 3C, 3M). The scales are slightly inflated, generally rounded and in most cases clearly separated from each other, although they sometimes intergrow or overlap.

The arrangement of the scales is commonly uniform but without any underlying pattern; it can differ both between specimens and between different parts of the same specimen. Almost regular patterns are sometimes observed in small patches, but these patterns never persist on a larger scale (Figs 3K-M). Close to the smooth base the scales are generally smaller and less densely spaced (Figs 3G, 3J). Scales are sometimes connected by tiny longitudinal folds or wrinkles, but in most specimens the area between scales is perfectly smooth (Figs 3K-L).

Preservation and microstructure. – The shell material of the available spines is most often preserved as translucent, shiny phosphate. In appearance, this shell material resembles that of co-occurring lingulate brachiopods (*Eoobolus prisca* Poulsen, 1932 and *Botsfordia* sp.) with a presumed original phosphatic composition. Part of the material has a thin (approximately 0.001 mm thick) film of secondarily precipitated phosphate covering all surfaces. Its rather coarse crystalline texture and habit of covering obviously broken surfaces reveal its secondary nature (Fig. 3A).

Broken edges of a number of specimens reveal a two-layered structure (Fig. 3A). A void or partial separation sometimes occurs between the layers in specimens as preserved, probably reflecting taphonomic loss of original organic material. In several instances, secondary mineral growth occurs between the layers. The outer layer is thicker than the inner, and is composed of finely laminated phosphate (Fig. 3B). The lamination is parallel to the surface of the spine; individual laminae are thickest near the outer surface, and become successively thinner towards the inner surface of the spine. The scales of the surface ornamentation are an integral part of the outer shell-layer, and are not reflected on the inner layer. The thin inner shell-layer shows no evidence of internal lamination. It is more coarsely crystalline (recrystallised?) and less dense than the outer shell-layer (Fig. 3A). No evidence of pores or other perforations of the shell layers have been identified.

Discussion. – *Mongolitubulus henrikseni* sp. nov. is distinguished from the type species *M. squamifer* Missarzhevsky, 1977 by its more parallel-sided form, with tapering confined just to the immediate area of the apex (Figs 3D-E). Furthermore, spines of *M. henrikseni* are usually ornamented to the apex whereas those of *M. squamifer* generally become smooth as the apex is approached. The ornamentation of the type species forms a regular pattern, with dense and frequently diamond-shaped scales arranged in spirals. In *M. henrikseni* the scales are randomly and more widely spaced without the diamond form. It is emphasized that individual spines, or parts of spines, of both species may resemble material assigned to the other species in terms of ornamentation. In viewing the large samples as a whole, however, the differences in ornamentation between species are distinct.

Fossils here assigned to *M. henrikseni* sp. nov. have been described from the medial Lower Cambrian (Adtabanian) of Kazakhstan (*M. squamifer* of Missarzhevsky & Mambetov 1981). They occur together with tubular fossils referred to *Torrelella explicata* Missarzhevsky & Mambetov, 1981 which have a widely expanding base similar to that seen in *M. henrikseni*.

Illustrated specimens identified as *M. squamifer* from Antarctic glacial erratics of Early Cambrian age by Gazdzicki & Wrona (1986) and Wrona (1989), seem to belong to *M. henrikseni*. The age of the glacial erratics was interpreted by Wrona (1989) as Botomian (equivalent largely to the Dyeran of North American usage) but some of the contained fossils are stated to occur only in the older Atdabanian. Tubes identified as *M. squamifer* were described from the Botomian of Mongolia by Esakova & Zhegallo (1996). They have an irregular ornamentation of rounded scales similar to that of *M. henrikseni*, and are tentatively referred to that species. Conway Morris and Bengtson (in Bengtson et al. 1990) described two ornamented tubes (Ornamented tube forms B and C), from the Lower Cambrian Adtabanian equivalent of Australia, attributable to *M. henrikseni*. They compared Ornamented tube form B to specimens of *Tumuliolynthus macrospinosus* Jiang & Huang, 1986 from the Lower Cambrian of China. Landing & Bartowski (1996) described fragments of ornamented tubular fossils from the Lower Cambrian (mid Dyeran) Browns Pond Formation of New York State, USA. Their material is badly preserved, but one of the illustrated specimens (Landing & Bartowski 1996, Fig 9.10) is reminiscent of *M. henrikseni*.

In Greenland *M. henrikseni* seems to occur in older strata than does *M. squamifer* but accompanying faunas are not yet well known. However, a correlation of the Upper Bastion Formation with the lower Botomian (lower to mid Dyeran) is suggested. Strata of the Henson Gletscher Formation in southern Freuchen Land yielding *M. squamifer* appear to be of younger Botomian to Toyonian age (mid to late Dyeran) but, as noted above, the formation is strongly diachronous.

All occurrences of *M. squamifer* as here defined appear to be of Botomian or younger age while known occurrences of *M. henrikseni* seem to be older, Adtabanian or early Botomian age.

Functional morphology of *Mongolitubulus*

Missarzhevsky (1977) originally described *M. squamifer* as a protoconodont, an opinion essentially maintained throughout his later publications (e.g. Missarzhevsky 1989). Recently, Esakova & Zhegallo (1996) questionably assigned the genus to the Conodonta but the spines described herein instead give the impression of a defensive rather than grasping function. The scale-like processes diverge from the main axis of the spine towards the pointed apical end of the fossil, quite contradictory to what would be expected if *Mongolitubulus* were part of a grasping apparatus. The ornamentation does not help in holding or seizing prey, but rather it serves to hamper an active hunter from 'biting down' the spine towards the main portion of the organism.

A variety of bivalved Cambrian arthropods with phosphatic shells carrying long spines have been described in the literature (see for example Hinz 1986, pl 3.8; Hinz-Schallreuter 1998). In Greenland, the bivalved *Isoxys volucris* Williams, Siveter & Peel, 1996 from the early Cambrian Sirius Passet fauna of North Greenland has posterior and anterior spines which may exceed the length of the main portion of the carapace (Williams, Siveter & Peel 1996). This probably unmineralized form is many times larger than *Mongolitubulus*, occurs in older strata and lacks any hint of the characteristic scaly ornamention. However, Melnikova (1996, 2000) associated *Mongolitubulus*-like spines from the Botomian and early Middle Cambrian of Siberia with the bradoriid *Tubuterium ivantsovi* Melnikova, 2000. Regardless of its phylogenetic relationship to *T. ivantsovi*, the North-East Greenland material of *Mongolitubulus* fits well with the interpretation of *Mongolitubulus* as a detached defensive spine, possibly of phosphatocopiid or bradoriid origin. The flaring base of the spine would then represent the connection of the spine to the general carapace wall.

Tubuterium ivantsovi from Siberia was considered to have one long ornamented spine on each valve (Melnikova 1996, 2000). The spines were supposed to have been attached to a knob on the antero-dorsal part of the shell and were bent backwards and slightly upwards. The large morphological variation present in *Mongolitubulus* from both North and North-East Greenland may suggest differentiation in spines and spine function, possibly the result of a carapace having numerous spines attached to it. Several species of bradoriids and small phosphatocopiids occur together with *Mongolitubulus* in North-East Greenland, but there are are no spinose forms among these, and no likely candidates for association with the *Mongolitu-*
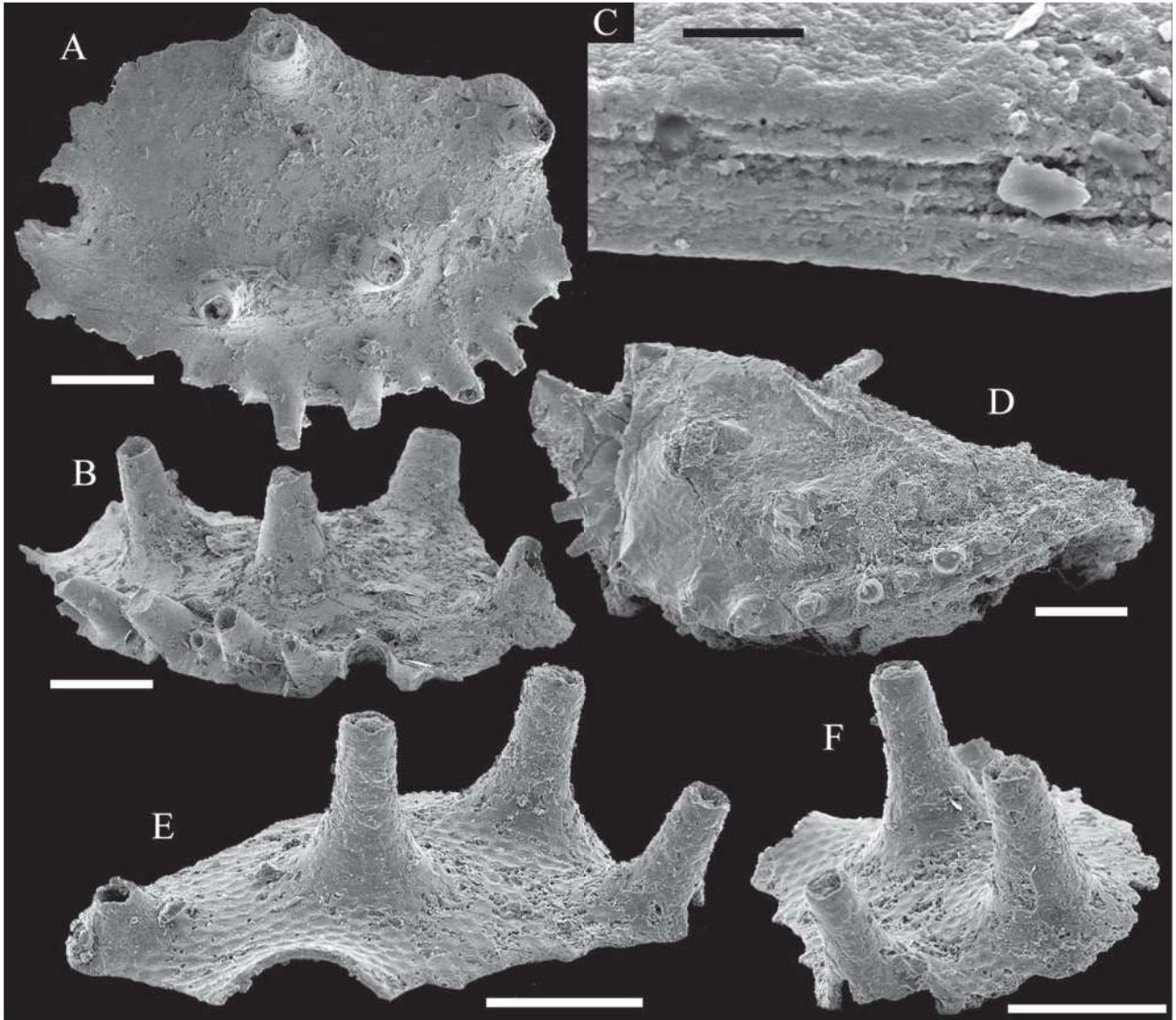
Fig. 4. A-F, Fragments of presumed spinose bivalved arthropod associated with spines of *Mongolitubulus henrikseni* sp. nov. All scalebars (except C) equal 0.1 mm. A-B, MGUH 26033 from GGU sample 314906. Side and oblique ventral view of left (?) valve showing bases of 7 ventral-marginal and 5 central spines. C, MGUH 26034 from GGU sample 314908. Detail of broken shell-edge showing etched internal lamination. Scalebar equal 0.005 mm D, MGUH 26035 from GGU sample 314908. Oblique side-view of left (?) valve with 10 ventral-marginal and 2 (3?) central spines. E-F MGUH 26036 from GGU sample 314908. Oblique views of isolated central portion of shell with reticulated ornamentation on shell and 4 central spines.

bulus spines. However, shells bearing spines in excess of 3 mm in length (the size of the largest available specimen of *M. henrikseni)* would certainly be much larger than any of the hitherto retrieved carapaces, and the large, thin shells of the presumed *Mongolitubulus* carapace could possibly have been destroyed taphonomically. Phosphatocopids are known to grow to at least 10 mm in length (Hinz-Schallreuter 1993) and the largest of the smaller (less than a few mm) specimens commonly found in acid-macerated samples are only regarded as large juve-

niles (Hinz-Schallreuter 1998). The small phosphatocopiids present in the North-East Greenland material could possibly represent juvenile, non-spinose growth stages of *Mongolitubulus*.

Six small phosphatic plates of unknown affinity, but possibly representing an undescribed phosphatocopid, bradoriid or other arthropod with abundant, hollow spines have been retrieved from two samples from North-East Greenland (GGU 314906, 314908) also containing *Mongolitubulus* spines (Figs 4A-F). The number of spine bases varies from four to thirteen,

but all specimens are clearly broken. The spines lack ornamentation and are substantially smaller in diameter than even the smallest *Mongolitubulus* spines recovered. One specimen (Figs 4E-F) has a reticulated pattern on the shell itself, but all others appear to be smooth. A similar pattern is illustrated in the bivalved arthropod *Isoxys auritus* from the Lower Cambrian of China illustrated by Williams et al. (1996, Figs 5–5,6,7), but this species has only anterior and posterior spines. The margins of the small plates are broken, but in the two largest specimens (Figs 4A-B and 4D) one edge, defined by a large number of small spines, could represent a natural (ventral?) margin. The microstructure of the shell is visible on the broken edge of one specimen (Fig. 4C), and the internal lamination, although badly preserved, appears to be similar to that of co-occurring *Mongolitubulus* spines (compare Fig. 3B).

If these problematic plates are indeed juvenile specimens of *Mongolitubulus henrikseni*, it follows that the organism should be restored with larger spines occupying central positions on the plate (perhaps each plate representing one of two valves in a bivalved arthropod) and smaller spines distributed along at least one margin. The variation in morphology of the spines present in both collections from North-East and North Greenland is consistent with this interpretation, although there is as yet no evidence that the spines of *M. squamifer* and *M. henrikseni* are similarly disposed or even that they represent parts of similar organisms. Spines occupying different positions on the shell are likely to have slightly differing morphologies and/or ornamentation and these differences may be consistent. Some support for this reconstruction may be gained from the smallest recovered specimen of *Mongolitubulus* with the basal region preserved. Contrary to the case in all larger specimens, the base of this specimen exhibits a fold along a line close to the spine itself, possibly representing a portion of the presumed margin of the shell (Fig. 3G).

Mongolitubulus and related organisms

Ornamented tubular Small Shelly Fossils are known from many Lower and Middle Cambrian localities (see reviews in Bengtson et al. 1990 and Melnikova 1996). These fossils (*Mongolitubulus* Missarzhevsky, 1977, *Tommotitubulus* Fedorov, 1986, *Kazakhstanotubulus* Gridina, 1991, *Rushtonites* Hinz, 1987 and *Rhombocorniculum* Walliser, 1958) are quite variable and their affinities have been debated. Unfortunately, some of these taxa are poorly known and their vari-

ability, geographic and chronologic distributions are insufficiently constrained.

Mongolitubulus appears to be most closely related to *Rushtonites*. The two fossils appear to be clearly distinguishable from *Rhombocorniculum, Nicolarites, Tommotitubulus* and a group of spine-like fossils with an ornamentation of minute spinose processes rather than scales: *Kazhakstanotubulus,* Ornamented tube form A of Conway Morris & Bengtson (in Bengtson et al. 1990), and "*Rushtonites*" *asiatica* (Landing 1991).

Rushtonites spinosus from the Lower Cambrian of Rushton, England is similar to *Mongolitubulus henrikseni* in many respects and the genus *Rushtonites* may prove to be a junior synonym of *Mongolitubulus*. Both fossils are long and slightly curved spines with a pointed apex, a broadly flaring base (see Brasier, 1989, pl. 7.2, picture 5) and a thin shell-wall. *Rushtonites* differs from *Mongolitubulus* in that its ornamentation consists of intergrowing scales and ridges forming a cellular structure, rather than distinct and separated scales, and in the details of the internal structure of the shell (Hinz 1987). Butterfield & Nicholas (1996) compared organic walled spines from the Middle Cambrian of the Mackenzie Mountains, Canada to *R. spinosus*.

Brasier (1989) synonymised *Rushtonites* with *Rhombocorniculum*, but the two fossils are not obviously related when ultra-structure and mode of formation are taken into consideration. In *Rushtonites*, there appears to be no indications of incremental growth either in the microstructure or ornamentation (Hinz 1987; Brasier 1989). In *Rhombocorniculum* fibrous phosphate was continually deposited basal-internally during the growth of the spine (Walliser 1958, Landing et al. 1980 and Hinz 1987).

As discussed above, Melnikova (1996, 2000) interpreted the spines associated with *Tubuterium ivantsovi* as being similar to *Mongolitubulus*. She mentioned that the ornamentation of the spines differed from the original description of *M. squamifer*, and noted similarities to *Rushtonites* (referred to erroneously as *Rushtonia* in Melnikova 2000). *T. ivantsovi* was interpreted by Melnikova as having one curved spine on each valve of the carapace. While this configuration does not preclude the great morphological variation seen in spines of both *M. squamifer* and *M. henrikseni*, it offers a less attractive interpretation than the multi-spined plate or valve hypothesis. Both fossils are therefore tentatively regarded as belonging to some multi-spinose shell, possibly an arthropod carapace.

Based only on comparison of ornamentation, *Rushtonites spinosus* could prove to be more closely related to, or perhaps even identical with the spines associated with *T. ivantsovi*. Thus, *Tubuterium* may be a junior subjective synonym of *Rushtonites* but, in the ab-

sence of direct study of the relevant specimens, no firm base for this suggestion is available. In particular, more information is required about morphological variation within both taxa.

Nicolarites spasskyi Vassiljeva, 1994 is a problematic small shelly fossil from the Lower Cambrian of Yakutia (Vassiljeva 1994). It is composed of a convex shield with two spines attached. The spines and the shield are covered with short processes. The spines in *N. spasskyi* are much shorter than in *Mongolitubulus*, and the small processes are more spine-like. The two fossils may not be related at all, but *N. spasskyi* could possibly serve as an alternative model for a reconstruction of *Mongolitubulus*. The affinity and function of *Nicolarites*, however, remain obscure.

Acknowledgements

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