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Source: Acta Palaeontologica Polonica, 54(3) : 513-523

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2009.0026

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Trachyplax arctica, a new multiplated problematic fossil from the lower Cambrian of North Greenland

CECILIA M. LARSSON, JOHN S. PEEL, and ANETTE E.S. HÖGSTRÖM



Larsson, C.M., Peel, J.S., and Högström, A.E.S. 2009. *Trachyplax arctica*, a new multiplated problematic fossil from the lower Cambrian of North Greenland. *Acta Palaeontologica Polonica* 54 (3): 513–523. DOI: 104202/app.2009.0026.

A new scleritome-bearing organism with eight sclerite types, *Trachyplax arctica* gen. et sp. nov., is described from the lower Cambrian Paralledal Formation of North Greenland. The originally calcareous sclerites are now silicified; no microstructures are preserved. The dominant sclerite type (*A*; maximum dimension 19.3 mm) is bilaterally symmetrical, strongly arched, with an oval shield showing co-marginal growth lines and a projecting rostrum with prominent radial ornamentation. A similar sclerite morphology can be identified in Silurian–Carboniferous multiplacophoran molluscs but the remaining sclerite types, which also display a combination of concentric and radial ornamentation, find no clear equivalents. Two models for scleritome reconstruction are presented, based on the relative abundance of the sclerites, but neither promotes a satisfactory assignment to a higher taxon. Despite the morphological dissimilarities, possibly reflecting the age discrepancy, reference to the Multiplacophora is most attractive and entails a substantial extension of the known geological range of that group.

Key words: *Trachyplax*, Problematica, sclerites, scleritome, Multiplacophora, Cambrian, Greenland.

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Received 6 March 2009, accepted 21 July 2009, available online 17 July 2009.

Introduction

In the Cambrian, as in other geological systems, the disarticulated remains of invertebrate animals are common fossils. Often, as in the trilobites, the individual plates or sclerites can be easily identified and reconstructed into complete exoskeletons (scleritomes). In other cases, such as sponges, echinoderms, and chancelloriids, the affinity of the remains is clear but reconstruction into complete individuals and identification of species may be difficult. Not infrequently, however, the affinity of individual sclerites or associations of sclerites in Cambrian fossil assemblages is problematic and the reconstruction of the original scleritomes is a morphological jig-saw puzzle fraught with possibilities for speculation, but also for self-deception. In such cases, rare occurrences of complete or partially complete scleritomes of multiplated species in Cambrian lagerstätten prove to be an invaluable source of information concerning the true nature and affinity of problematic taxa. A familiar example is provided by *Halkieria*, originally described as isolated sclerites from the Cambrian of Denmark (Poulsen 1967) and subsequently reconstructed by Bengtson and Conway-Morris (1984). Discovery of articulated specimens of *Halkieria evangelista* Conway Morris and Peel, 1995 from the lower Cambrian Sirius Passet lagerstätte of North Greenland not only served to test the reconstruction based entirely on the isolated minute blade-like sclerites but, surprisingly, also introduced additional skeletal elements in the form of prominent anterior and posterior shields not foreseen by the model.

In this paper we describe as *Trachyplax arctica* gen. et sp. nov. a complex assemblage of isolated sclerites, composed of at least 8 morphological types, from the Paralleldal Formation (Cambrian Series 2, Stage 4) of North Greenland. We have no obvious point of reference in our attempts to identify the animal or reconstruct the scleritome, and are drawn into simple morphological comparisons with the sclerites of a number of multiplated organisms, many of which are themselves problematic. Noteworthy amongst these is the group Multiplacophora proposed by Hoare and Mapes (1995) which Vendrasco et al. (2004) interpreted as ancestral molluscs.

Institutional abbreviations.—GGU, Grønlands Geologiske Undersøgelse, (Geological Survey of Greenland, now part of the Geological Survey of Denmark and Greenland, Copenhagen); MGUH, type collection of the Geological Museum, Copenhagen, part of the Natural History Museum of Denmark.

Material and methods

All specimens are derived from GGU sample 274907, collected from dark, silicified, cherty limestone forming the lower part of the Paralleldal Formation on the north side of Paralleldal, central Peary Land, North Greenland (82°17'

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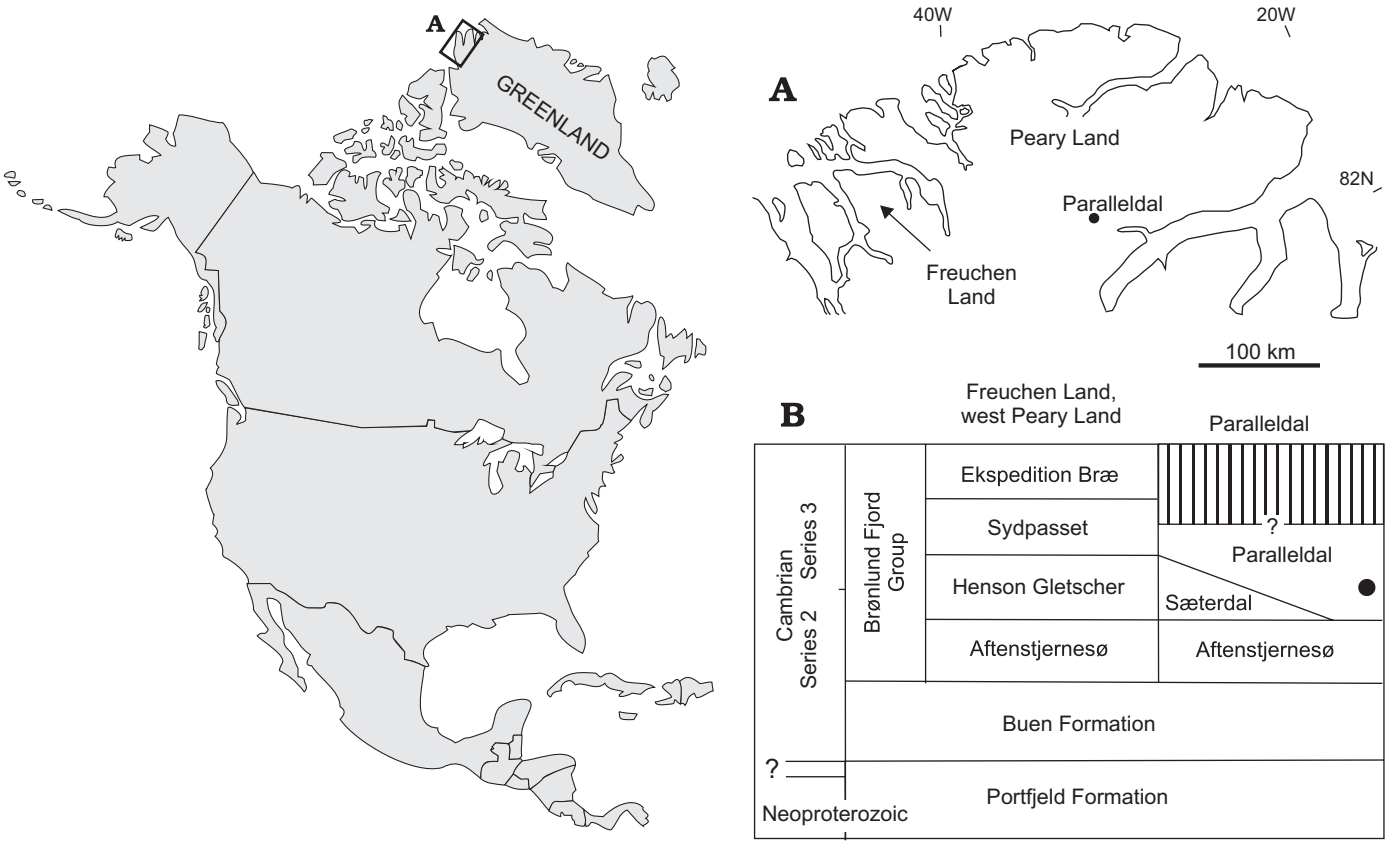


Fig. 1. Derivation of *Trachyplax arctica* gen. et sp. nov. **A**. Locality in North Greenland. **B**. Stratigraphy: Brønlund Fjord Group, Paralleldal Formation, indicating horizon of collection (filled circle).

N 31°9.2' W) by J.S.P. on 26th July 1980 (Fig. 1). The formation was defined and described by Ineson and Peel (1997: 78–81) and the collection locality is illustrated in their fig. 75; this is the same locality as GGU sample 274908 in Blaker and Peel (1997: fig. 8B). The rich fauna includes silicified remains of originally calcareous brachiopods (Popov et al. 1997), helcionelloid and stenothecid molluscs and trilobites (Blaker and Peel 1997; Atkins and Peel 2004, 2008; Stein and Peel 2008). Overlying pale-weathering dolomites assigned to the same formation have yielded archaeocyathids of late early Cambrian (Toyonian; Cambrian Series 2, Stage 4) age (Debrenne and Peel 1986) and *Salterella* Billings, 1861 (Peel and Yochelson 1982). They interdigitate with and overlie the dark, cherty dolomites due to the northern progradation of the shallower water, pale dolomite facies. The Paralleldal Formation forms part of the Brønlund Fjord Group, a succession of lower–middle Cambrian dolomite, limestone and subordinate siliciclastic sediments that accumulated in platform margin to outer shelf environments on the southern margin of the North Greenland segment of the Franklinian Basin (Peel and Sønderholm 1991; Ineson and Peel 1997).

Individual slabs were etched in weak hydrochloric acid and the residue yielded about 200 silicified, isolated, sclerites which are interpreted as originally calcareous due to the similarity in preservation to contemporaneous molluscs and brachiopods. Eight different sclerite morphologies are recognised, here referred to as types *A–H* respectively (Table 1 for details). Sclerite types *B–D* and *G–H* exist in two series that are arbitrarily described as left and right morphs, although their orientation in life is not known. Specimens were coated with ammonium chloride sublimate prior to photography with a Nikon Digital Sight DS-5M camera mounted on a Leica MZ75 microscope. Length, height, and width (mm) were measured with digital slide callipers to an accuracy of one decimal point, and represent true measurements rather than estimates (Tables 1–3). Terminology and standard measurements are shown in Fig. 2.

Table 1. Sclerite count per sclerite type, showing: number of complete/partly damaged specimens; LM, left morphs; RM, right morphs; fragments referred to each type.

Sclerite type	Complete or partly damaged	LM	RM	Fragments	Total number
A	67	–	–	11	78
B	8	5	3	–	8
C	7	5	2	–	7
D	18	8	10	–	18
E	11	–	–	6	17
F	30	–	–	5	35
G	11	–	–	–	11
H	12	–	–	–	12
uncertain	14	–	–	–	14

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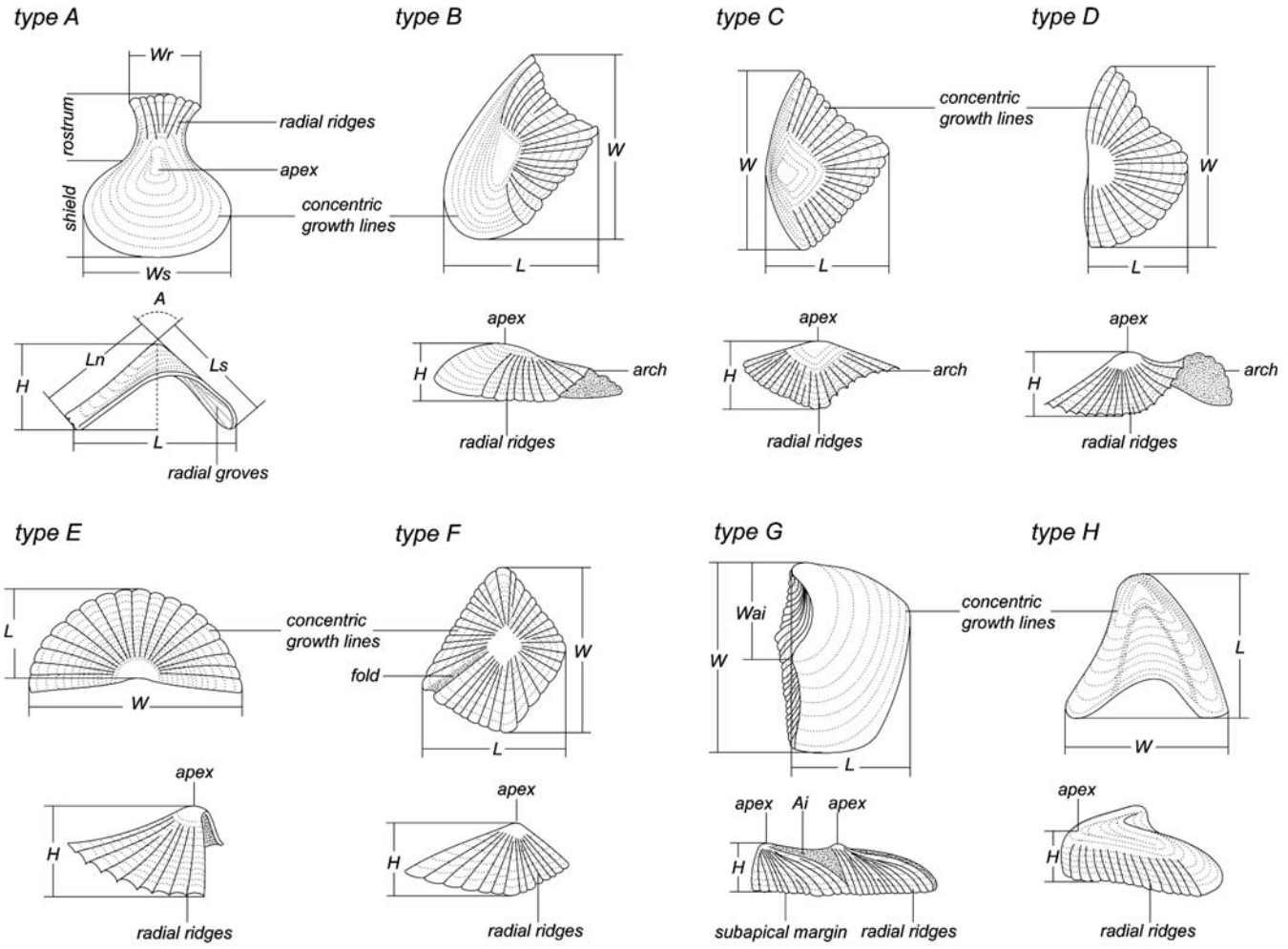


Fig. 2. Schematic drawing showing measured parameters and descriptive terminology used for sclerite types *A–H*. Abbreviations: A, apical angle; Ai, apex interarea; L, length; Lr, length of rostrum; Ls, length of shield; H, height; W, width; Wai, width of apex interarea; Wr, width of rostrum; Ws, width of shield. Not to scale.

Systematic palaeontology

Incertae sedis

Genus *Trachyplax* nov.

Type species: *Trachyplax arctica* sp. nov., by monotypy.

Etymology: From Greek *trachy*, rough; *plax*, plate.

Diagnosis.—Large (up to 19. 3 mm), robust, calcareous sclerites growing by marginal accretion; external surfaces display concentric growth lines encircling the elevated apex and radial ridges originating from the apex and spreading over parts of, or the whole, sclerite, surface (new ridges being introduced between older ones). Eight sclerite types identified (*A–H*, see below) of which *A* is selected as the defining element: it is bilaterally symmetrical in presumed dorsal view, divided into an oval shield and an elongate, subrectangular rostrum, but strongly arched in lateral perspective.

Discussion.—The nature and form of the scleritome is not known. The holotype of the type species, and thus the defining element of the new genus, is selected from the most distinctive and most abundant sclerite morph, type *A*; all elements are described below.

Stratigraphic and geographic range.—*Trachyplax arctica* is currently known only from the Paralleldal Formation (Cambrian Series 2, Stage 4) of Paralledal, southern Peary Land, North Greenland.

Trachyplax arctica gen. et sp. nov.

Figs. 2–5.

Etymology: With reference to the arctic provenance of the material.

Type material: Holotype, MGUH 29087 from GGU sample 274907, sclerite type A. Figured paratypes, MGUH 29088–29102 from the same collection as holotype.

Type locality: North side of Paralleldal, central Peary Land, North Greenland (82°17' N 31°9.2' W).

Type horizon: Lower part of the Paralleldal Formation, late Early Cambrian (Toyonian; Cambrian Series 2, Stage 4).

Diagnosis.—As for genus.

Descriptions.—Eight calcareous sclerite types are recognised, of which type *A*, the most common (Table 1 for num-

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Table 2. Size measurements for sclerite type *A*, measurements only made on sclerites considered complete enough for the parameter in question: A, apical angle; H, height; L, length; Lr, length of rostrum; Ls, length of shield; M, estimated mean value; max, maximum value; min, minimum value; n, number of sclerites measured for the parameter in question; Wr, width of base; Ws, width of shield. All measurements in mm, except A, which is in °.

Size measurements for sclerite type *A*							
	A	L	H	Ls	Ws	Lr	Wr
M	122	9.2	3.1	7.1	7.9	4.9	3.2
min	90	4.8	1.5	2.6	3.5	2.8	1.9
max	140	19.3	7.9	15.9	19.5	8.6	5.8
n	31	20	19	23	26	20	15

Table 3. Size measurements for sclerite types B–H, measurements only made on sclerites considered complete enough for the parameter in question: H, height; L, length; M, estimated mean value; max, maximum value; min, minimum value; n, number of sclerites measured for the parameter in question; W, width; Wai, width of apex interarea. All measurements in mm.

Sclerite type	Type of value	Size measurements for sclerite types *B–H*			
		L	W	Wai	H
B	M	4.2	5.9	–	1.5
	min	3.7	4.3	–	1.3
	max	5.3	7.0	–	1.8
	n	8	7	–	8
C	M	4.0	5.4	–	1.3
	min	2.8	3.9	–	0.9
	max	4.7	6.9	–	1.8
	n	6	6	–	6
D	M	3.0	5.0	–	–
	min	2.3	3.9	–	–
	max	4.2	7.2	–	–
	n	10	6	–	–
E	M	4.9	7.6	–	–
	min	3.5	5.9	–	–
	max	7.1	10.8	–	–
	n	7	9	–	–
F	M	5.8	5.1	–	1.4
	min	3.5	3.0	–	0.6
	max	9.9	8.5	–	2.4
	n	27	26	–	26
G	M	5.2	8.5	3.5	2.1
	min	4.0	6.4	2.4	1.2
	max	7.0	10.2	4.6	2.7
	n	8	7	7	8
H	M	4.0	4.5	-	2.1
	min	3.3	3.8	-	1.5
	max	5.4	5.8	-	2.5
	n	7	7	-	7

bers), is considered to be the taxonomic defining element. Individual sclerites are robust, ranging in maximum dimension up to 19.3 mm; their internal surfaces are poorly known, usually matrix covered. All eight morphologies display a raised apex or apices (as in type *G*, Fig. 2), marginal accretionary growth reflected by external concentric growth lines, radial ridges originating from the apex or apices and spreading over parts of or the entire external sclerite surface with new ridges being introduced between older ones (Fig. 2); a spiral component is often visible in the ornamentation of larger sclerites. Enantiomorphic symmetry pairs are present in types *B–D* and *G–H*; these are arbitrarily interpreted as right and left morphs. Differences between left and right morphs are obvious within types *B–D* (accounted for in Table 1), but less clear for types *G–H* (therefore not specified in Table 1).

Type *A* (Figs. 2: type *A*, 3A–D; Tables 1, 2 for all measurements) consists of bilaterally symmetrical sclerites divided into shield and rostrum by a centrally placed apex; rate of growth is highest in shield. Five exceptionally large sclerites attain a shield width (*Ws*) of about 18 mm (Fig. 3D). The shield is suboval with facetted margins, plate-like, and relatively smooth, apart from facetted concentric growth lines (Fig. $3A_1$, B_1, C, D). Internal surfaces may show a radial groove pattern (Fig. $3A_2$, B_2). The rostrum is elongate, subrectangular, and widest most distal to the apex (*Wr*); it is covered by radial ridges, but growth lines are barely visible. In lateral view the sclerite is strongly arched with the shield and rostrum forming an apical angle (*A*) with each other (Figs. 2: type *A*, $3A_3$) of about 120° (Table 2).

Types *B–C* (Figs. 2: types *B* and *C*, 4A–D; Tables 1 and 3) are asymmetrical with left and right morphs. The sclerites can be divided through the apex into a smooth and a ridged portion. In type *B* (Figs. 2: type *B*, 4A, B) the smoother portion of the sclerite is convex with a crescentic outline (Fig. $4A_1$, A_2); the ridged portion describes an undulating angular fan forming an arch on one side (Fig. $4A_3$). In type *C* (Figs. 2: type *C*, 4C, D) the smoother portion of the sclerite is narrow, slightly convex with a rounded outline (Fig. 4C, D_1); the ridged portion describes an undulating fan forming an arch on one side (Fig. $4D_2$).

Type *D* sclerites (Figs. 2: type *D*, 4E, F; Tables 1 and 3) are asymmetrical, with a fan-like outline with both left and right morphs and concentric growth lines; the apex is situated about halfway along the straight side (Fig. $4E_1$, F) and ornament consists of radial ridges on an undulating fan which forms an arch on one side (Fig. $4E_2$–E_4).

Type *E* (Figs. 2: type *E*, 4G; Tables 1, 3) is bilaterally symmetrical with a fan-like outline displaying radial ridges and concentric growth lines; the apex is situated halfway along the relatively smooth vaulted side (line of symmetry runs perpendicular to the straight side from apex to sclerite edge) (Fig. $4G_1$, G_2). The sclerite is also strongly concave along the radial ridges (Fig. $4G_3$).

Type *F* (Figs. 2: type *F*, 5A, B; Tables 1, 3) is subpyramidal with radial ridges present on their entire surface; the ridges may be twisted in the apical region on larger sclerites (Fig. 5B). Some specimens have a prominent radial fold running from the apex to the sclerite margin (Fig. $5A_1$).

Type *G* (Figs. 2: type *G*, 5C, D; Tables 1, 3) is asymmetrical with left and right morphs. It is a subhemispherical, convex sclerite interpreted as a fusion of two plates (Fig. 5C, D_1).

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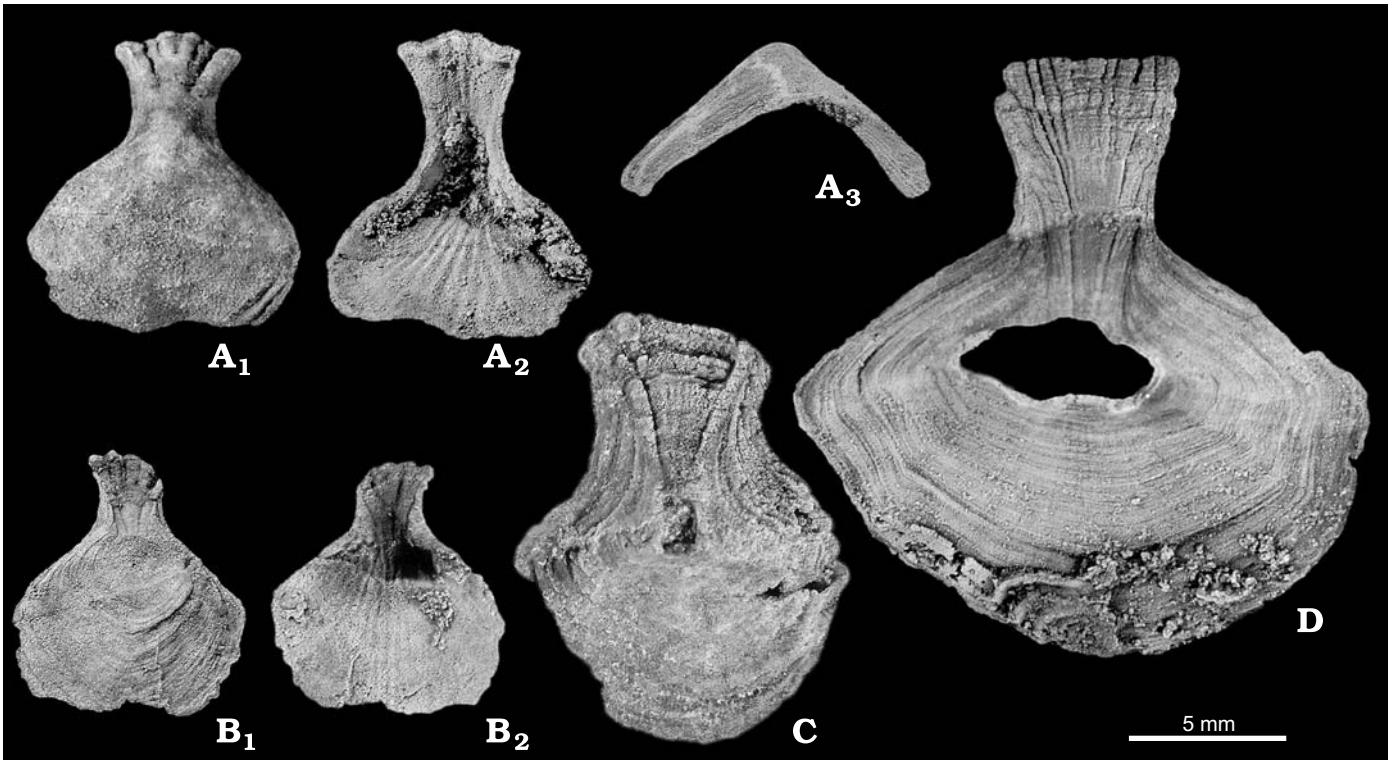


Fig. 3. Multiplated problematic fossil *Trachyplax arctica* gen. et sp. nov., **A**–**D**. Sclerite type *A*. **A**. MGUH 29087, holotype, in external, dorsal view (A_1), internal view exposing radial grooves (A_2), and lateral view (A_3). **B**. MGUH 29088, in external, dorsal view (B_1) and internal view exposing radial grooves (B_2). **C**. MGUH 29089, in external, dorsal view. **D**. MGUH 29090, large specimen in external, dorsal view.

Two apices are placed along the steep, narrow, more or less straight side, radial ridges run from each apex to the sub-apical margin (Fig. $5D_2$). Concentric growth lines are only visible outside the apex interarea of the smoother convex portion of the sclerite.

Type *H* (Figs. 2: type *H*, 5E; Tables 1, 3) is convex, with a subtriangular outline. The apex is placed over the corner opposite the concave base, and the surface between the base and the apex is slightly depressed (Fig. $5E_3$). Radial ridges are present on the two remaining sides (Fig. $5E_1$, E_2). The apex may be somewhat beaked in some sclerites (Fig. $5E_3$).

Stratigraphic and geographic range.—*Trachyplax arctica* is known currently only from the Paralleldal Formation (late Early Cambrian; Toyonian; Cambrian Series 2, Stage 4) of Paralleldal, Peary Land, North Greenland.

Reconstruction

Reconstruction of *Trachyplax arctica* is obstructed by the absence of conjoined sclerites and resultant lack of a firm foundation upon which to re-assemble the scleritome. It cannot be automatically assumed that all the sclerites belong together within the same structure, although a number of lines of evidence support this interpretation. (1) The sclerite types appear to be consistently associated with each other in the individually prepared slabs. (2) Remains of other putative scleritome-bearing organisms are lacking, other than ubiquitous echinoderm plates and chancelloriids. (3) All sclerites carry the same "preservational signature" in general appearance, indicating at least a similar original composition. (4) The different types of sclerites occur in similar size clusters with no real extremes, except for a few large *A* sclerites (Fig. 3G). (5) The sclerites grow by marginal accretion and show similar combinations of external radial ridges and smoother areas. Their morphologies reflect transitions between the proportions of these two features (Fig. 6). Considering these arguments together it is unlikely that the material represents sclerites from more than one type of organism.

The numerical proportions of the different sclerite types do not appear to reflect sorting of different morphologies or size classes. This observation is supported by the size range of other fossils as a whole in the entombing sediment but information concerning orientation of individual fossils within the sediment is not available. The numerous, originally calcareous, brachiopods, however, are invariably disarticulated, as are the vast majority of stenothecid molluscs. Brachiopods, stenothecids, and helcionellid molluscs are generally not fragmented; infrequent silicified archeocyathans are usually compacted. Type *A* sclerites show a wide size distribution and the remainder of the collection contains types with both right and left morphs preserved in relatively equal numbers (Tables 1–3). Thus, the numbers and sizes of the different sclerite types may provide a reasonable estimate of original abundance and be used as parameters for reconstruction.

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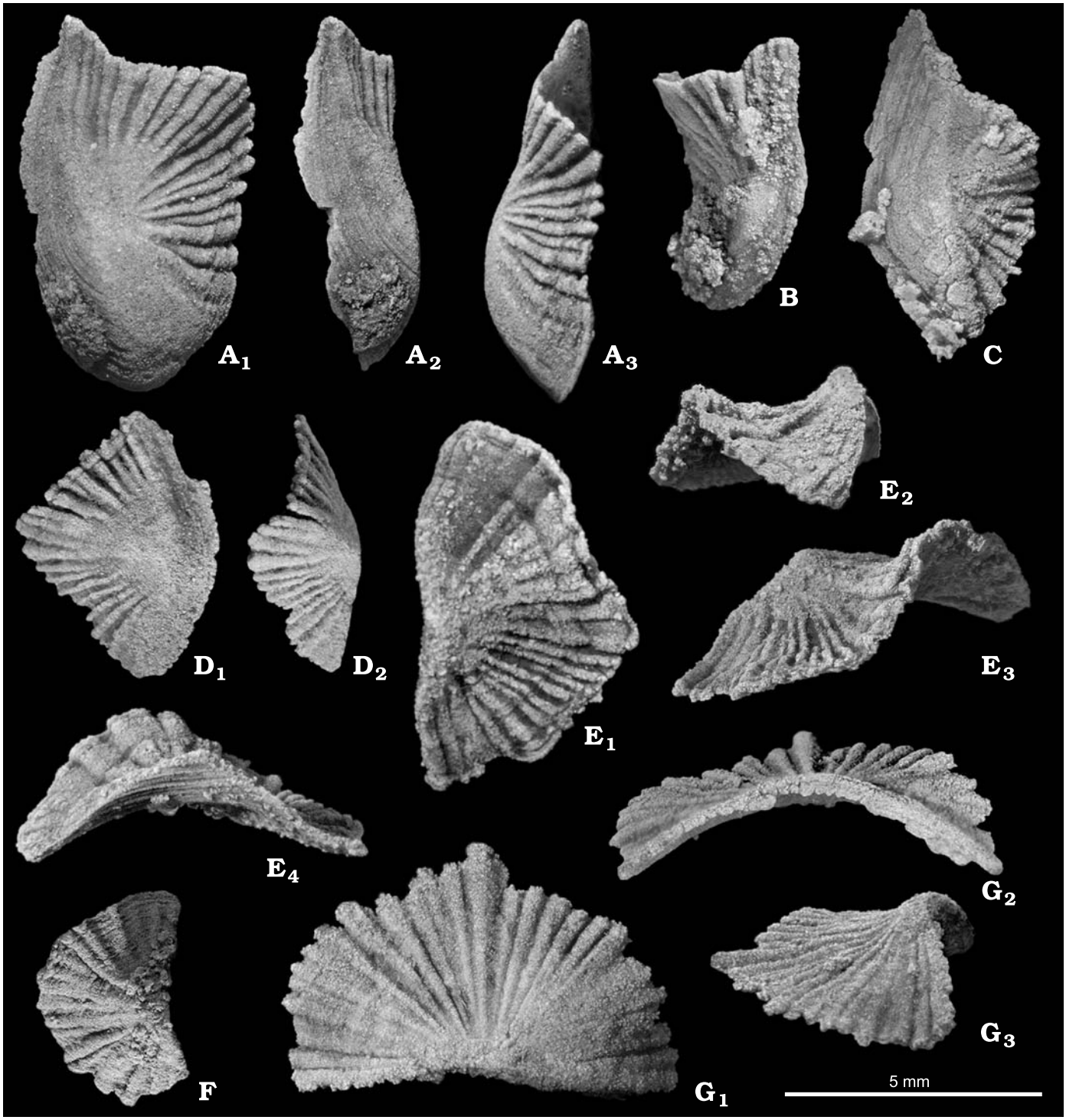


Fig. 4. Multiplated problematic fossil *Trachyplax arctica* gen. et sp. nov., sclerite types *B–E*, all external views. **A**, **B**. Sclerite type *B*, right and left morphs. **A**. MGUH 29091, in dorsal view (A_1), lateral view showing arching edge (A_2), and lateral view (A_3). **B**. MGUH 29092, in dorsal view. **C**, **D**. Sclerite type *C*, right and left morphs. **C**. MGUH 29093, in dorsal view. **D**. MGUH 29094, in dorsal view (D_1) and lateral view showing arching edge (D_2). **E**, **F**. Sclerite type *D*, right and left morphs. **E**. MGUH 29095, in dorsal view (E_1), lateral view, profile (E_2), lateral view showing arching edge (E_3), and lateral view showing straight side (E_4). **F**. MGUH 29096, in dorsal view. **G**. MGUH 29097, sclerite type *E* in external view (G_1), lateral view showing straight side (G_2), and lateral view, profile (G_3).

All sclerite types can be placed into a relatively simple morphological transition series (as shown in Fig. 6), starting and ending with the symmetrical sclerite types *A* and *E* respectively; the asymmetrical types lie in between. Preferred morphological transitions are interpreted as follows; from sclerite type *A* to *B*, to *C*, to *D*, to *E*; from sclerite type *C* to *F*, to *H*, to *G* through the fusion of two sclerites. Alternatively, type *G* could be derived through the fusion of two type *B*

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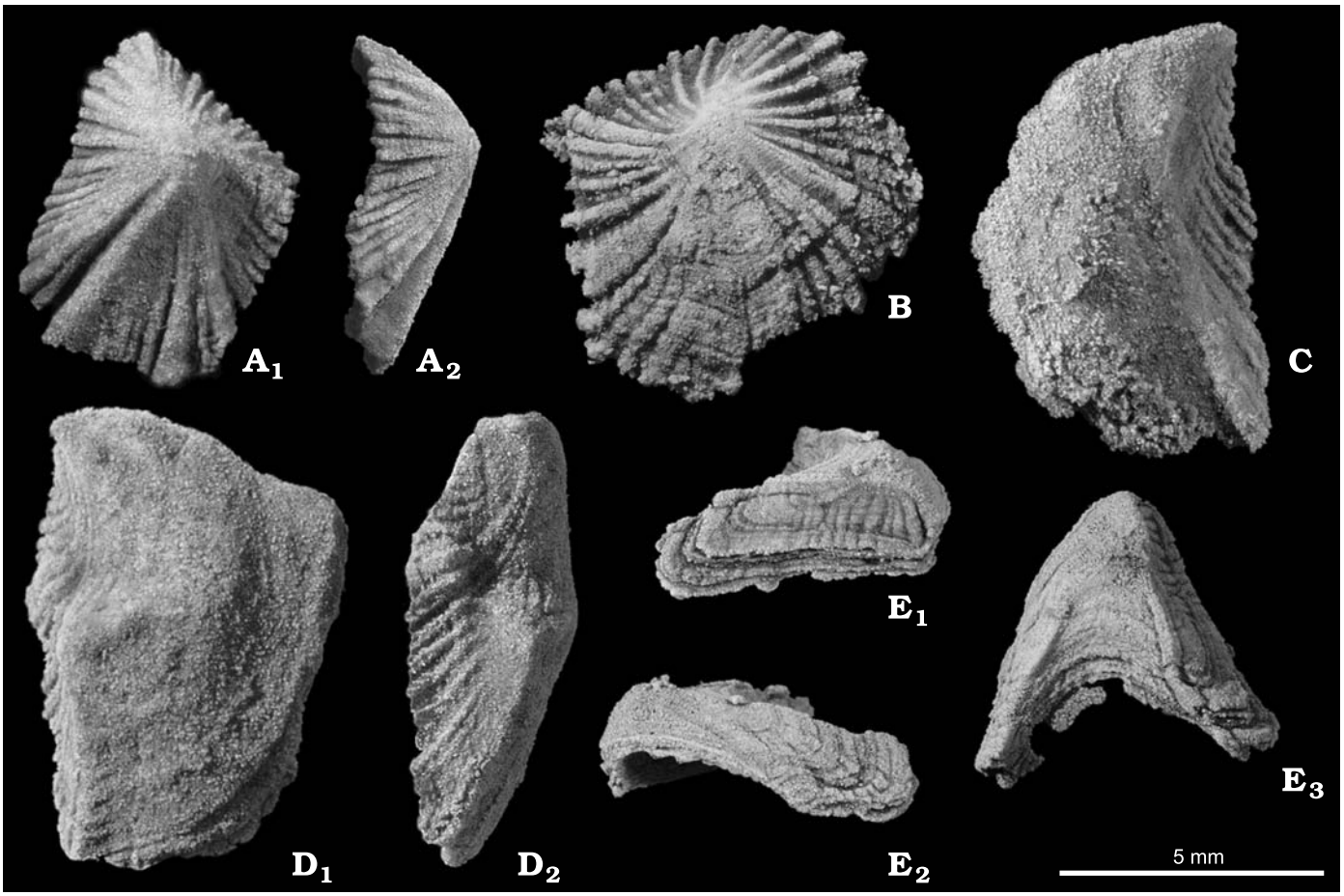


Fig. 5. Multiplated problematic fossil *Trachyplax arctica* gen. et sp. nov., sclerite types *F–H*, all external views. **A**, **B**. Sclerite type *F*. **A**. MGUH 29098, in dorsal view showing fold (A_1) and lateral view (A_2). **B**. MGUH 29099, in dorsal view showing twisted ridges. **C**, **D**. Sclerite type *G*, right and left morphs. **C**. MGUH 29100, in dorsal view. **D**. MGUH 29101, in dorsal view showing apices and apex interarea (D_1) and lateral view showing apices and apex interarea (D_2). **E**. MGUH 29102, sclerite type *H* in lateral view showing radial ridges (E_1, E_2) and external view (E_3).

sclerites, one type *B* and one type *C* sclerite, two type *C* sclerites, or two type *H* sclerites directly derived from sclerite type *D* (Fig. 6).

The difficulties inherent in reconstructing scleritomes of problematic organisms from their disarticulated sclerites are well illustrated by a series of putative reconstructions of *Tannuolina* Fonin and Smirnova, 1967 and *Micrina* Laurie, 1986 presented by Li and Xiao (2004: fig. 3). All of their five reconstructions involve antero-posterior rows (between 1 and 4 in number) of the two sclerites types in an elongate, bilaterally symmetrical, slug-like animal. None of them bears any similarity to the reconstruction of *Micrina* as a bivalved, stem group brachiopod suggested by Holmer et al. (2008) on the basis of articulated *Eccentrotheca* Landing, Nowlan, and Fletcher, 1980 (Skovsted et al. 2008) and *Paterimitra* Laurie, 1986 (Skovsted et al. 2009).

Here we present two alternative reconstructions for *Trachyplax*; the first is primarily based on the numerical proportions of sclerite types (Table 1) as well as the preferred interpretation of morphological transitions between sclerite types (Fig. 6); the second alternative is primarily based on comparisons with multiplacophoran molluscs and similar scleritomes.

Reconstruction 1.—This has its natural starting point in sclerite type *A* since this is by far the most common one. The symmetrical sclerites of type *A* are placed on the dorsal side of an organism, covering a relatively large and homogenous part of the body. Marginal accretionary growth indicates that more or less the entire sclerite was connected to soft tissue and the wider part of the rostrum may have penetrated into the soft parts slightly. The facetted shape of the shield suggests close juxtaposition (Fig. 7A), possibly in a cataphract pattern covering a large (dorsal) area of a bilaterally symmetrical organism, with a slight posterior overlap of the sclerites. Six of the remaining seven sclerite types are placed along the lateral parts of the animal in the reconstruction, while one type (*E*) is located terminally at the posterior end (Fig. 7A). The large number of different sclerite types suggests a high degree of differentiation of the body in addition to the development of distinct anterior and posterior ends, but interpretation of such morphological complexity is currently not possible. The robust character of the thick sclerites offers protection, both in terms of the shallow marine top of-mound environment in which the animal lived and with regard to eventual predation. On account of the strongly arched form of

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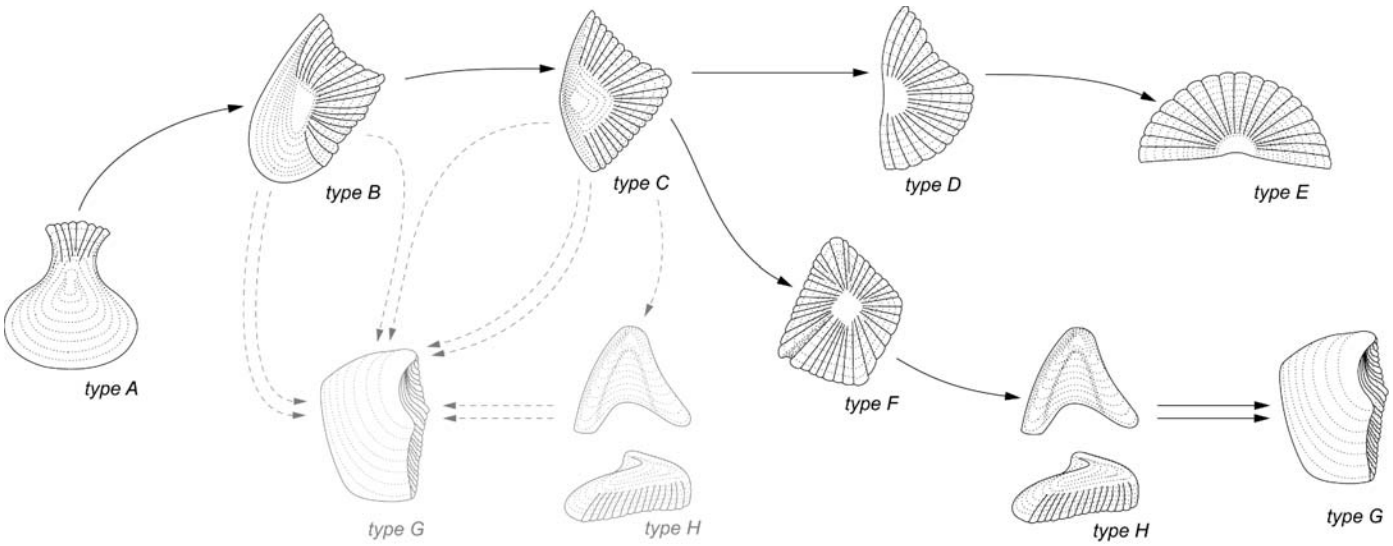


Fig. 6. Schematic illustration showing preferred interpretation of sclerite type transitions in *Trachyplax arctica* gen. et sp. nov., with double lines symbolising fusion of two sclerites resulting in sclerite type *G*, dashed grey-shaded lines symbolising alternative transitions. Not to scale.

type *A* sclerites, the resulting dorsal surface has a bumpy, uneven, surface resulting from the attachment of numerous sclerites. In this respect, this reconstruction of *Trachyplax arctica* resemble stem-group chitons such as *Matthevia* Walcott, 1885 and *Chelodes* Davidson and King, 1874, where the tall sclerites overhang towards the posterior (Runnegar and Pojeta 1985). The latter, however, are arranged in a single row of eight sclerites with the apices lying posterior, and not anterior as in the cataphract pattern of *T. arctica*.

Reconstruction 2.—This is also based primarily on sclerite type *A* but the criterion for comparison is its perceived resemblance to the first pair of plates (i.e., posterior to the un-paired terminal plates) of *Polysacos vickersianum* Vendrasco, Wood, and Runnegar, 2004 and *Deltaplax* Puchalski, Johnson, Kaufman, and Eernisse, 2009 from the Carboniferous of Indiana (Vendrasco et al. 2004: fig. 1a, c; Puchalski et al. 2009). Similar plates are also present as the B9 and B10 plates of *Diadeloplax paragrapsima* Hoare and Mapes, 1995 from the Carboniferous of Oklahoma (Hoare and Mapes 1995: fig. 5G–I) and *Strobilepis spinigera* Clarke, 1888 (Hall and Clarke 1888; B9 and B10 of Hoare and Mapes 1995: fig. 2) from the Carboniferous of New York State. Type *A* sclerites are placed around the lateral margins of the animal with the shield covering the lateral areas and the rostrum lying on the dorsal surface, directed inwards (Fig. 7B). The reconstruction makes use of the angulated form of sclerite *A* in protecting the thickness of the organism. An alternative is that the shield of the respective *A* sclerites is located on the dorsal surface, with the rostra extending down over the sides of the animal. Placement of the other sclerite types is arbitrary and no comparable plates are recognised in the three named taxa. Disposition of type *A* sclerites in series (as might be expected from the dominance of this element) along the margins of a bilaterally symmetrical organism might be expected to show some evidence of morphological transition along the scleritome, as described by Vendrasco et al. (2004) in *Polysacos*; this is not seen. Neither is there any evidence of left and right morphs, although these might not be recognisable since type *A* sclerites are bilaterally symmetrical, unlike the similar plates in *D. paragrapsima, S. spinigera*, *P. vickersianum*, and *Deltaplax*. The expected morphological variation might be reduced, however, if the animal was more equidimensional than elongate, when the disposition of the type *A* sclerites would be radial (Fig. 7C), the pattern approached in *Protobalanus hamiltonensis* Hall and Clarke, 1888 from the Devonian of New York State (van Name 1926; Dzik 1986).

Comparison to other scleritome-bearing organisms

Trachyplax arctica displays more types of sclerites (eight) than many of the organisms with which comparisons are made. To some extent this large number is a construct of the morphological transitions recognised here between sclerite types; some are similar to each other (especially types *B–C*, Figs. 2, 4A–D, 6) and could be viewed as transition states within one sclerite type. Of particular note is the absence of spines which form a girdle around the periphery of multiplacophorans but are also conspicuous in halwaxiids (Conway Morris and Caron 2007) and the armoured aplacophoran *Acaenoplax* Sutton, Briggs, Siveter, and Siveter, 2001.

Molluscs.—Within the molluscan clade, multiplated scleritomes are found primarily within aplacophorans, polyplacophorans (chitons) and the entirely fossil multiplacophorans. The recent inclusion of multiplacophorans has expanded our view of molluscan body plans and molluscan diversity

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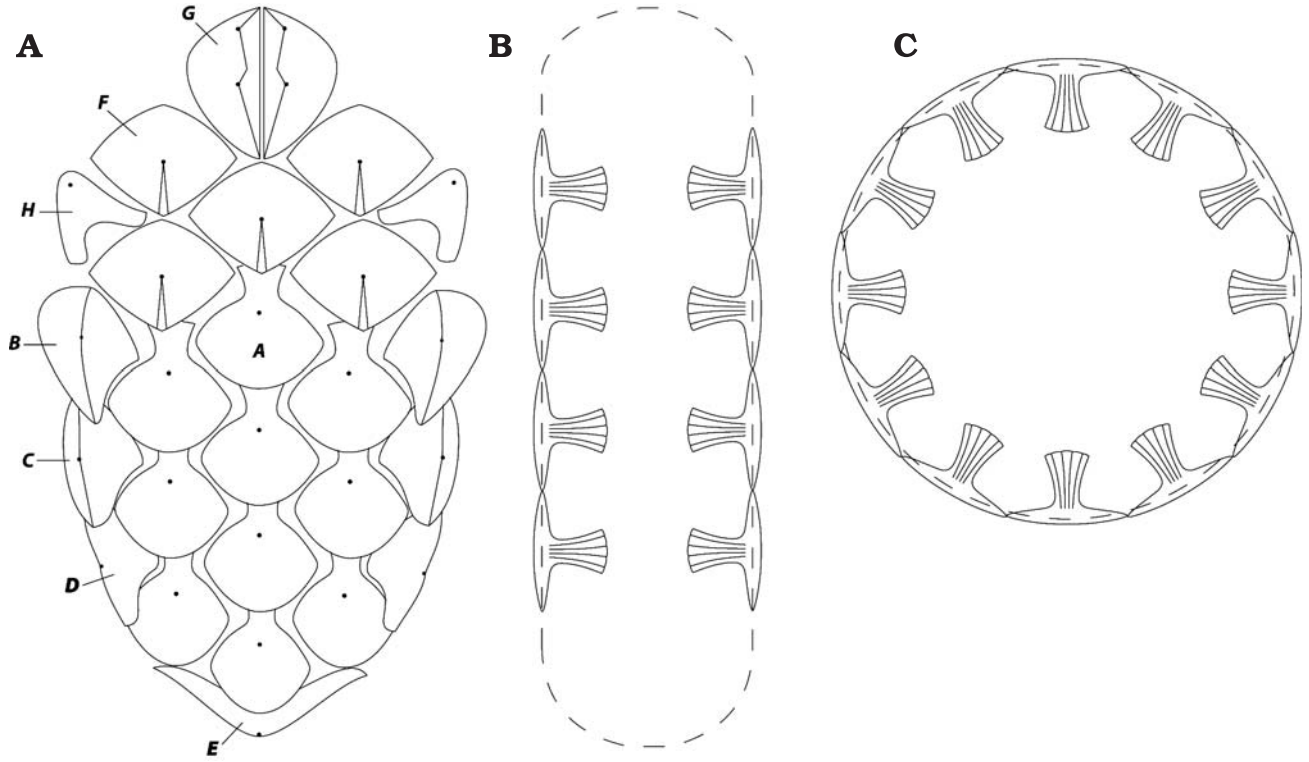


Fig. 7. Reconstructions of *Trachyplax arctica* gen. et sp. nov., not to scale. **A**. Alternative 1, with cataphract arrangement of sclerite type *A*, based on numerical proportions of sclerite types. **B**, **C**. Alternative 2 with type *A* sclerites placed along the lateral margins of a bilaterally symmetrical, elongate organism (**B**) and an equidimensional, radially symmetrical organism (**C**). Randomly chosen number of sclerites.

through time (Hoare and Mapes 1995, 2000; Hoare 2002; Vendrasco et al. 2004; Puchalski et al. 2009). The morphology of stem-group chitons, such as the Cambrian *Matthevia* and *Dycheia* Pojeta and Derby, 2007, and the Ordovician *Chelodes*, is very different from extant species, with high conical shell plates surrounded by a girdle (Vendrasco and Runnegar 2004). The middle Ordovician *Echinochiton* Pojeta, Eernisse, Hoare, and Henderson, 2003 has very large lateral spines around the girdle (Pojeta et al. 2003) and a central series of large sclerites, again an unusual morphology for a chiton. However, the eightfold iteration of dorsal sclerites representing 2 or 3 sclerite types seen in Recent chitons is stable through the fossil record and offers little scope for comparison with the sclerite morphologies present in *T. arctica*.

In 2001, the range of the aplacophorans was tentatively extended into the Silurian by the discovery of the exceptionally preserved vermiform *Acaenoplax hayae* Sutton, Briggs, Siveter, and Siveter, 2001, from the middle Silurian Herefordshire Lagerstätte, England, with seven isolated dorsal valves in addition to the mineralised spicules traditionally covering the aplacophoran body (for a different view on the affinity of *Acaenoplax* see Steiner and Salvini-Plawen 2001). The dorsal plates of *A. hayae* are placed in a single row, occur in basically three types [no. 1: cap-like anterior; nos. 2–6: saddle-like oval to subcircular with short spines on the posterior half except for no. 2; no. 7 (dorsal and ventral): subrectangular], are bilaterally symmetrical and grow by marginal accretion (Sutton et al. 2001, 2004). Apart from the mode of growth, the plates of *A. hayae* show little resemblance to the sclerites of *T. arctica*.

The three rows of robust calcareous sclerites showing morphological transitions and the relatively high number of sclerite types (five and lateral spines) seen in multiplacophorans such as *Polysacos vickersianum* readily promote comparison with *T. arctica*. Especially noteworthy is the similarity between sclerite type *A* (Fig. 3) and sclerite no. 2 of *P. vickersianum*, although comparison in terms of scleritome models is problematic. The type *A* sclerite in the present material is the most common type (Table 1) whereas sclerite no. 2 in *P. vickersianum* is one of the rarer types (see fig. 1 in Vendrasco et al. 2004, for the numerical proportions in the scleritomes of *Polysacos* and *Strobilepis* Clarke, 1888). Furthermore, there are no indications of spines or spine-like sclerites within the present material from Greenland where the scleritome also seems to have been significantly larger than in recognised multiplacophorans (although these are from the Silurian–Permian and geologically much younger than *T. arctica*).

Microstructural studies have shown that multiplacophorans possess a similar porous structure of the outer layer, a projecting layer (articulamentum) with possible aesthete canals as living polyplacophorans; this has been taken as a convincing argument for linking multiplacophorans with polyplacophorans within the aculiferan clade (Vendrasco et al. 2004). Unfortunately no microstructures and very few surface structures are preserved in the silicified Greenland material.

DOI: 104202/app2009.0026

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Protobalanus Whitfield, 1888 from the Devonian of New York State (Hall and Clarke 1888; Whitfield 1889; van Name 1925, 1926) and *Hercolepas* Withers, 1915 from the Silurian of Gotland (Aurivillius 1892) have been compared to a number of scleritome-bearing organisms; at first hand they appear as barnacle-like sessile organisms but with differentiated anterior and posterior ends of the scleritome. Dzik (1986) included them within his greatly expanded polyphyletic definition of machaeridians, rejected by Adrain (1992). Vendrasco et al. (2004) included *Protobalanus* and *Hercolepas* in the Multiplacophora, together with *Strobilepis*, *Diadeloplax* Hoare and Mapes, 1995, *Aenigmatectus*, Hoare and Mapes, 1996 and *Polysacos*; *Deltaplax* also belongs here (Puchalski et al. 2009). *Protobalanus* and *Hercolepas* have not been re-described in modern times but placement within the Multiplacophora, as suggested by Vendrasco et al. (2004), seems justified; their reinvestigation may well enhance understanding of the present material.

Tommotiids.—Articulated scleritomes of the tommotiids *Eccentrotheca* and *Paterimitra* were only recently described from the lower Cambrian of Australia by Skovsted et al. (2008, 2009). Unexpectedly, they appear to have been tube dwelling organisms, possibly related to phoronids. There are no indications of similar sclerite forms in the present material and little to suggest a tube-like morphology for the scleritome. Holmer et al. (2008) depicted the bivalved scleritome of *Micrina* as a sessile stem group brachiopod, in contrast to the previous halkieriid inspired reconstruction (Holmer et al. 2002; Li and Xiao 2004). *Eccentrotheca*, *Paterimitra*, and *Micrina* are now seen as attached organisms that deviate greatly from the general picture of slug-shaped, bilaterally symmetrical scleritomes (Li and Xiao 2004; Skovsted et al. 2009). However, tommotiids such as *Dailyatia* Bischoff, 1976 from the lower Cambrian of Australia are very unlike the tube forming genera, and show a diverse set of sclerite morphotypes that may appear similar to some of the Greenland sclerite types described herein. Especially the larger sclerites of type *F* with their spiral component (Fig. 5B) are reminiscent of some sclerite types of *Dailyatia* (Bischoff 1976). Morphological similarities apart, the large size difference (tommotiids are consistently microscopic) as well as the difference in mineralogy (calcareous *Trachyplax* versus phosphatic *Dailyatia*) preclude any obvious relationship at this time between *Trachyplax* and the tommotiids; both are early Cambrian in age.

Other taxa.—The scant fossil record of annelids reflects partly their dominantly soft anatomy with few preservable hard parts apart from jaws and slightly sclerotised setae. Annelids are represented in the Cambrian in Lagerstätte such as the Sirius Passett biota of North Greenland (Conway Morris and Peel 2008) and the Burgess Shale (Conway Morris 1979) of British Columbia, although they are curiously absent from the Chengjiang Lagerstätte of China. Hard calcified plates are present in one group, the machaeridians, recently discovered to be annelids (Vinther et al. 2008). Machaeridian plates show little similarity with those of *Trachyplax* and the machaeridian skeleton is substantially different from that envisaged for the Greenland form. There is a consistent arrangement of 2–4 longitudinal series of posteriorly overlapping plates attached to alternate body segments, an antero-postero differentiation of the plates is also present, as well as differences between the inner and outer longitudinal series (Högström 1997; Högström and Taylor 2001).

Halkieriids and wiwaxiids were recently joined in the group "Halwaxiida" by Conway Morris and Caron (2007), based on their very similar sclerites, and united by the intermediate *Orthrozanclus reburrus* Conway Morris and Caron, 2007, which possesses one shell similar to those found in *Halkieria evangelista* (Conway Morris and Peel 1995). Unfortunately, they show little similarity to *Trachyplax* either in sclerite morphology or structure and our two reconstructions differ substantially from the halwaxiid scleritome concept. However, Paterson et al. (2009) assigned to the supposed halkieriid *Oikozetetes* Conway Morris, 1995 an arched, shell similar to *Trachyplax* type *A* from the Cambrian of Australia but no fossil remains reminiscent of other *Trachyplax* sclerites were reported.

Yong and Lian-fang (1996) described the microfossil *Qintheca pectonloides* Yong and Lian-Fang, 1996 from the lower Cambrian of Shuijingtuo Formation, Zhenba, Shanxi, China. There are morphological similarities between the type *A* sclerite of *Trachyplax* and *Q. pectonloides*, but *Q. pectonloides* is substantially smaller than *T. arctica* and its mineralogy is not accounted for in the description, making further comparisons speculative.

Conclusions

The sclerites described herein as *Trachyplax arctica* likely belong together within a single structure representing an unusual scleritome with a large number of sclerite types; although the total number of sclerites within that scleritome is unknown. Unfortunately, it is currently unrealistic to assign *Trachyplax arctica* to any described group. The presented reconstructions represent two possible scleritome configurations, although both should be regarded as contributions to an ongoing discussion of the relationships of *Trachyplax*. Alternative 1 (Fig. 7A) is based primarily on the numerical distribution of the different sclerite types and their distinct morphologies and hence very speculative, raising questions concerning for example the functional morphology. Alternative 2 (Fig. 7B, C) refers to comparisons with other scleritome bearing taxa, but no other known taxon seem to have as many different types of sclerites. Closest similarity appears to be with the multiplacophorans and especially comparisons with *Protobalanus*, *Hercolepas*, and *Aenigmatectus* may be fruitful. The earliest multiplacophorans are known from the Silurian whereas the present material is from the lower Cambrian. As such, the Greenland scleritome clearly enhances the role of multiplacophorans in early molluscan evolution, if the inherent assumption that *Trachyplax arctica* is a multiplacophoran can be made.

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Acknowledgements

We thank Glenn A. Brock (Macquarie University, Sydney, Australia) and one anonymous referee for helpful journal reviews. JSP acknowledges support from GGU (GEUS) during the collection and preparation of the *Trachyplax* samples. CML's doctoral studies are financed by Uppsala University. Financial support from the Swedish Research Council (Vetenskapsrådet) to JSP and AESH is gratefully acknowledged.

References

Adrain, J.M. 1992. Machaeridian classification. *Alcheringa* 16: 15–32.

Atkins, C.J. and Peel, J.S. 2004. New species of *Yochelcionella* (Mollusca: Helcionelloida) from the Lower Cambrian of North Greenland. *Bulletin of the Geological Society of Denmark* 51: 1–9.

Atkins, C.J. and Peel, J.S. 2008. *Yochelcionella* (Mollusca, Helcionelloida) from the lower Cambrian of North America. *Bulletin of Geosciences* 83: 23–38.

Aurivillius, C.W.S. 1892. Über einige Ober-Silurische cirripeden aus Gotland. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar* 18: 1–25.

Bengtson, S. and Conway-Morris, S. 1984. A comparative study of Lower Cambrian *Halkieria* and Middle Cambrian *Wiwaxia*. *Lethaia* 17: 307–329.

Bischoff, G.C.O. 1976. *Dailyatia*, a new genus of the Tommotiidae from Cambrian strata of SE. Australia (Crustacea, Cirripedia). *Senckenbergiana Lethaea* 57: 1–33.

Blaker, M.R. and Peel, J.S. 1997. Lower Cambrian trilobites from North Greenland. *Meddelelser om Grønland, Geoscience* 35: 1–145.

Conway Morris, S. 1979. Middle Cambrian polychaetes from the Burgess Shale of Brittish Columbia. *Philosophical Transactions of the Royal Society, London B* 285: 227–274.

Conway Morris, S. and Caron, J.B. 2007. Halwaxiids and the early evolution of the lophotrochozoans. *Science* 315: 1255–1258.

Conway Morris, S. and Peel, J.S. 1995. Articulated halkieriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* 347: 305–358.

Conway Morris, S. and Peel, J.S. 2008. The earliest annelids: Lower Cambrian polychaetes from the Sirius Passet Lagerstätte, Peary Land, North Greenland. *Acta Palaeontologica Polonica* 53: 137–148.

Debrenne, F. and Peel, J.S. 1986. Archaeocyatha from the Lower Cambrian of Peary Land, central North Greenland. *Rapport Grønlands Geologiske Undersøgelse* 132: 39–50.

Dzik, J. 1986. Turrilepadida and other Machaeridia. *In*: A. Hoffman and M.H. Nitecki (eds.), *Problematic fossil taxa*, 116–134. Oxford University Press, New York.

Hall, J. and Clarke, J.M. 1888. Trilobites and other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portate, Chemung and Catskill Groups. *New York Geological Survey, Paleontology* 7: 1–236.

Hoare, R.D. 2002. European Paleozoic Polyplacophora, Multiplacophora, and Turrilepadida in United States repositories. *Journal of Paleontology* 76: 95–108.

Hoare, R.D. and Mapes, R.H. 1995. Relationships of the Devonian *Strobilepis* and related Pennsylvanian problematica. *Acta Palaeontologica Polonica* 40: 111–128.

Hoare, R.D. and Mapes, R.H. 2000. New data on the genus *Diadeloplax* Hoare and Mapes, 1995. *Journal of Paleontology* 74: 976–978.

Holmer, L.E., Skovsted, C.B., Brock, G.A., Valentine, J.L., and Paterson, J.R. 2008. The Early Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod. *Biology Letters* 4: 724–728.

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

Högström, A.E.S. 1997. Machaeridians from the Upper Wenlock (Silurian) of Gotland. *Palaeontology* 40: 817–831.

Högström, A.E.S. and Taylor, W.L. 2001. The machaeridian *Lepidocoleus sarlei* Clarke, 1896, from the Rochester Shale (Silurian) of New York State. *Palaeontology* 44: 113–130.

Ineson, J.R. and Peel, J.S. 1997. Cambrian stratigraphy of North Greenland. *Geology of Greenland Survey Bulletin* 173: 1–120.

Li, G. and Xiao, S. 2004. *Tannuolina* and *Micrina* (Tannuolinidae) from the Lower Cambrian of Eastern Yunnan, South China, and their Scleritome reconstruction. *Journal of Palaeontology* 78: 900–913.

Paterson, J.R., Brock, G.A., and Skovsted, C.B. 2009. *Oikozetetes* from the early Cambrian of South Australia: implications for halkieriid affinities and functional morphology. *Lethaia* 42: 199–203.

Peel, J.S. and Sønderholm, M. 1991. Sedimentary basins of North Greenland. *Grønlands Geologiske Undersøgelse Bulletin* 160: 1–164.

Peel, J.S. and Yochelson, E.L. 1982. A review of *Salterella* (Phylum Agmata) from the Lower Cambrian in Greenland and Mexico. *Rapport Grønlands Geologiske Undersøgelse* 108: 31–39.

Pojeta, J. Jr, Eernisse, D.J., Hoare, R.D., and Henderson, M.D. 2003. *Echinochiton dufoei*: A new spiny Ordovician chiton. *Journal of Paleontology* 77: 646–654.

Popov, L., Holmer, L.E., Rowell, A.J., and Peel, J.S. 1997. Early Cambrian brachiopods from North Greenland. *Palaeontology* 40: 337–354.

Poulsen, C. 1967. Fossils from lower Cambrian of Bornholm. *Matematisk-Fysiske Meddelelser udgivet Af Det Kongelige Danske Videnskabernes Selskab* 36: 1–48.

Puchalski, S.S., Johnson, C.C., Kaufman, E.G., and Eernisse, D.J. 2009. A new genus and two new species of multiplacophorans (Mollusca, Polyplacophora, Neoloricata), Mississippian (Chesterian), Indiana. *Journal of Paleontology* 83: 422–430.

Runnegar, B. and Pojeta, J. 1985. Origin and diversification of the Mollusca. *In*: E.R. Trueman and M.R. Clarke (eds.), *The Mollusca*, 1–57. Academic Press, New York.

Skovsted, C.B., Brock, G.A., Paterson, J.R., Holmer, L.E., and Budd, G.E. 2008. The scleritome of *Eccentrotheca* from the Lower Cambrian of South Australia: Lophophorate affinities and implications for tommotiid phylogeny. *Geology* 36: 171–174.

Skovsted, C.B., Holmer, L.E., Larsson, C.M., Högström, A.E.S., Brock, G.A., Topper, T.P., Balthasar, U., Pettersson Stolk, S., and Paterson, J.P. 2009. The scleritome of *Paterimitra*: an Early Cambrian stem group brachiopod from South Australia. *Proceedings of the Royal Society of London B* 276: 1651–1656.

Stein, M. and Peel, J.S. 2008. *Perissopyge* (Trilobita) from the lower Cambrian (Series 2, Stage 4) of North America and Greenland. *GFF* 130: 71–78.

Steiner, G. and Salvini-Plawen, L. 2001. Invertebrate evolution—*Acaenoplax*—polychaete or mollusc? *Nature* 414: 601–602.

Sutton, M., Briggs, D.E.G., Siveter, D.J., and Siveter, D.J. 2001. An exceptionally preserved vermiform mollusc from the Silurian of England. *Nature* 410: 461–463.

Sutton, M.D., Briggs, D.E.G., Siveter, D.J., and Siveter, D.J. 2004. Computer reconstruction and analysis of the vermiform mollusc *Acaenoplax hayae* from the Herefordshire Lagerstätte (Silurian, England), and implications for molluscan phylogeny. *Palaeontology* 47: 293–318.

van Name, W.G. 1925. The supposed Paleozoic barnacle *Protobalanus* and its bearing on the origin and phylogeny of the barnacles. *American Museum Novitates* 197: 1–8.

van Name, W.G. 1926. A new specimen of *Protobalanus*, supposed Paleozoic barnacle. *American Museum Novitates* 227: 1–6.

Vendrasco, M.J. and Runnegar, B. 2004. Late Cambrian and Early Ordovician stem group chitons (Mollusca: Polyplacophora) from Utah and Missouri. *Journal of Paleontology* 78: 675–689.

Vendrasco, M.J., Wood, T.E., and Runnegar, B.N. 2004. Articulated Palaeozoic fossils with 17 plates greatly expands disparity of early chitons. *Nature* 429: 288–291.

Vinther, J., Van Roy, P., and Briggs, D.E.G. 2008. Machaeridians are Palaeozoic armoured annelids. *Nature* 451: 185–188.

Whitfield, R.P. 1889. Description of a new form of fossil, Balanoid Cirripede, from the Marcellus shale of New York. *Bulletin American Museum of Natural History* 2: 66–69.

Yong, L. and Lian-Fang, D. 1996. New Small Shelly Fossils from the Lower Cambrian Shuijingtuo Formation of Zhenba, Shaanxi. *Acta Micropalaeontologica Sinica* 13: 57–64.

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