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Extending the diversity of grasping spines in middle Cambrian stem-group Chaetognathifera

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ABSTRACT


Elements of *Fimbulispina laurentica* gen. et sp. nov. from the Fimbuldal Formation (middle Cambrian, Miaolingian Series, Drumian Stage) of North Greenland (Laurentia) are interpreted as the circum-oral grasping spines of a stem-group chaetognathiferan. Association of the elements into the arrays known from fossil and recent free swimming chaetognathans (arrow worms) has not been observed. The elements differ from the simple, hollow, cones characteristic of contemporary protoconodont elements in displaying a transversely convex posterior face, a deeply channelled anterior face, a pair of internal lath-like structures and two basal cavities. In terms of their overall cross-section they are reminiscent of elements of *Dakorhachis thambus* from the Weeks Formation (Miaolingian Series) of Utah. Seen collectively, the morphological variation displayed by these elements attests to the diversity of 'graspers' in stem-group chaetognathiferans.

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CHAETOGNATHS (arrow worms) have been regarded as the oldest lineage of pelagic predators, with an age range throughout the Phanerozoic, and form a key zooplankton element of the present day food chain (Vannier *et al.* 2007, Park *et al.* 2024). Their record through geological time is scant despite their great abundance in present-day oceans, but Cambrian Lagerstätten have yielded exceptionally preserved specimens that have been assigned confidently to the group (Chen & Huang 2002, Chen *et al.* 2002, Vannier *et al.* 2007, Briggs & Caron 2017, Shu *et al.* 2017, Caron & Cheung 2019, Vinther & Parry 2019, Park *et al.* 2024). Notable amongst these are *Ankalodous sericus* Shu, Conway Morris, Han, Hoyal Cuthill, Zhang, Cheng & Huang, 2017 from the Qiongzhusi Formation (Cambrian Series 2, Stage 3) of Yunnan, China and *Capinatator praetermissus* Briggs & Caron, 2017. The latter is based on almost 50 specimens up to 10 cm long from the middle Cambrian Burgess Shale (Miaolingian Series, Wuliuan Stage) of British Columbia, which is also about the maximum length attained by a few modern chaetognaths. The arrays of spines on each side of the mouth of *C. praetermissus* (Fig. 1A) can be compared directly in morphology to the grasping spines of present day chaetognaths such as

Sagitta Quoy & Gaimard, 1827 (Szaniawski 1982, Vannier *et al.* 2007). Grasping spines in *A. sericus* are up to 7 mm long and occur in bundles of six or seven, whereas individual spines in *C. praetermissus* may be 8–9 mm long and can occur in arrays of about 25 spines (Fig. 1).

Other Cambrian chaetognathiferans, such as *Amiskwia* Walcott, 1911 from the Burgess Shale (Conway Morris 1977, Vinther & Parry 2019, Bekkouche & Gąsiorowski 2022) and *Timorebestia* Park, Nielsen, Parry, Sørensen, Lee, Kihm, Ahn, Park, de Vivo, Smith & Harper, 2024 from the Sirius Passet Lagerstätten of North Greenland (Park *et al.* 2024) do not preserve arrays of circum-oral spines.

The chitinous composition of the circum-oral grasping spines in Chaetognatha provides a potential for preservation in the fossil record and it is generally accepted that the curved, slender spines of the widely distributed protoconodonts *Protohertzina* Missarzhevsky, 1973 and *Phakelodus* Miller, 1984 are the circum-oral grasping spines of ancestral chaetognaths, as proposed by Szaniawski (1982, 1983), Andres (1988) and Azmi (1996). Arrays of laterally juxtaposed, fused elements of these genera occur in the Cambrian fossil record (Müller & Andres 1976, Müller & Hinz 1991, Dong 1993, Dong & Bergström 2001, Vannier *et al.* 2007, Lee 2013, Dong & Zhang 2017) and are also reported from Ordovician and younger strata (Landing 1977, Doguzhaeva *et al.* 2002, Tolmacheva *et al.* 2008). Arrays of spines assigned to other protoconodont genera are much less well

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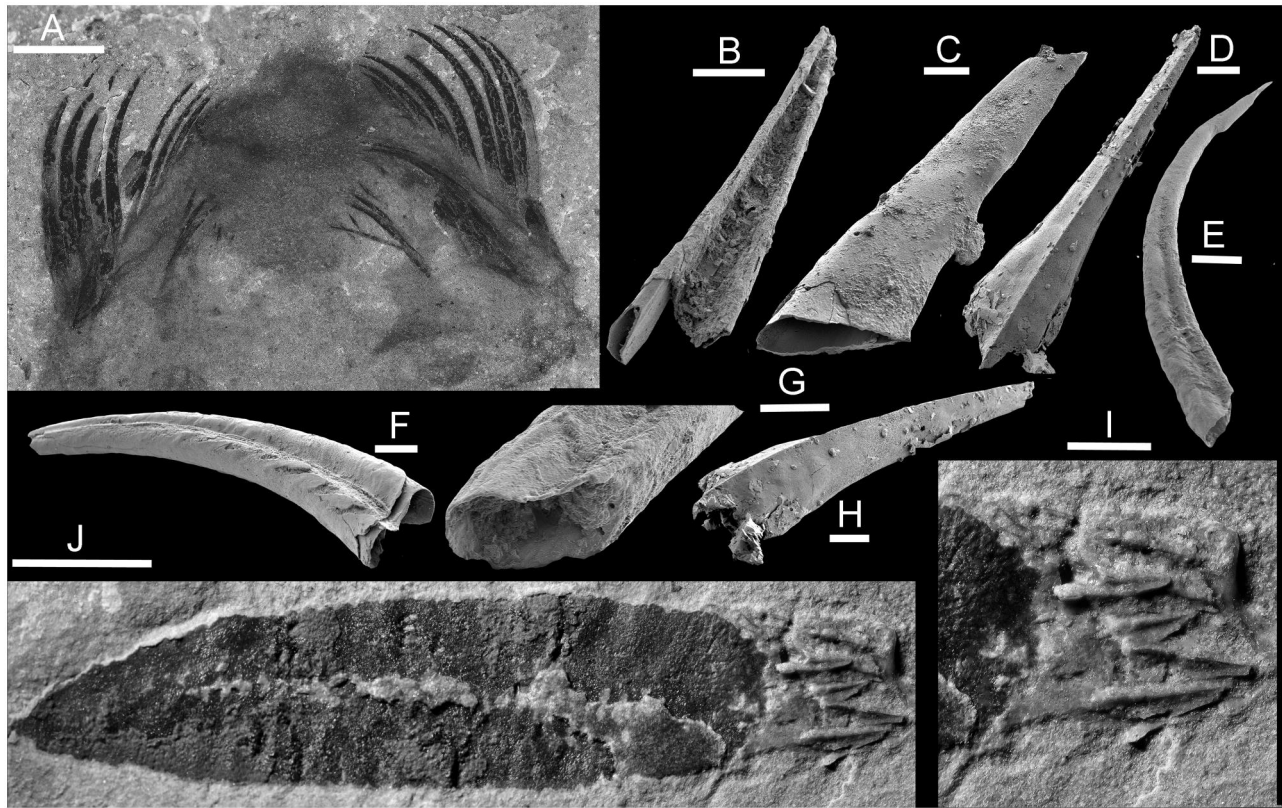


Fig. 1. A, *Capinatator praetermissus* Briggs & Caron, 2017, ROMP 64271, holotype, Burgess Shale, Cambrian, Miaolingian Series, Wuliuan Stage, British Columbia. Anterior of head with clusters of grasping spines (Photo: D.E.G. Briggs). B–H, protoconodonts from the Fimbuldal Formation, Cambrian, Miaolingian Series, Drumian Stage, North Greenland. B, *Fimbulispina laurentica* gen. et sp. nov., PMU 18225 from GGU sample 315006, anterior face, see also Fig. 5H. C, *Phakelodus* cf. *elongatus* (An, 1983), oblique basal view, PMU 18226 from GGU sample 218645. D, H, *Paibiconus?* sp., PMU 18227 from GGU sample 218645, anterior and anterolateral views. E–G, *Gapparodus* sp. from GGU sample 216845, E, G, PMU 18228 lateral and basal views, F, PMU 18229. I, J, *Dakorhachis thambus* Conway Morris, Smith, Hoyal Cuthill, Bonino & Lerosey-Aubril, 2020, UU15101.01, holotype, Weeks Formation, Cambrian, Miaolingian Series, Guzhangian Stage, House Range, Utah. J, dorsal view, I, detail of teeth in internal and external views (Photos: R.D.A. Smith). Scale bars: 50 μ m (B, G); 100 μ m (C–E); 1 mm (A); 2 mm (I); 5 mm (J).

known, although Vannier *et al.* (2007) described associations of five spines of *Mongolodus* Missarzhevsky, 1977 from China; see also Azmi (1996) and McIlroy & Szaniawski (2000).

Most Cambrian protoconodont taxa are known only from individual elements that may be common constituents in residues after the treatment of limestone samples in weak acids, but usually lack any indication that they formed parts of the closely juxtaposed arrays seen in *Ankalodous*, *Capinatator*, *Phakelodus* and *Protohertzina*. However, variation in protoconodont morphology (Fig. 1C–H) suggests that they may have been derived from animals following different life styles than the free-swimming chaetognaths with which they are generally compared (Conway Morris *et al.* 2020). *Dakorhachis thambus* Conway Morris, Smith, Hoyal Cuthill, Bonino & Lerosey-Aubril, 2020 provides one model. It was tentatively interpreted as a stem-group chaetognathiferan by Conway Morris *et al.* (2020), although Bekkouche & Gąsiorowski (2022) preferred interpretation as a

scolidophoran (see also Zhang *et al.* 2023). *Dakorhachis thambus* was interpreted as benthic on account of its apparent segmentation and lack of the fins characteristic of free-swimming forms (Conway Morris *et al.* 2020). Specimens from the Weeks Formation (Miaolingian Series) of Utah have a maximum observed length of 28 mm and retain a circum-oral circling of at least six spines approximately 3 mm long (Fig. 1I, J). Conway Morris *et al.* (2020) reported that the spines (referred to as teeth) were triangular in cross-section, with a convex outer surface and a concave inner surface.

This paper extends the morphological spectrum of protoconodont-like grasping elements from the middle Cambrian in describing *Fimbulispina laurentica* gen. et sp. nov. from the Fimbuldal Formation of North Greenland (Miaolingian Series, Drumian Stage). The typical hollow, conical morphology described by Szaniawski (1983) in individual protoconodont elements (Fig. 1C–H) is replaced in *F. laurentica* with elements that display a deeply channelled anterior face, a pair of

internal lath-like structures (Fig. 1B) and paired basal cavities. *Fimbulispina laurentica* is known only from discrete elements that invite comparison with the circum-oral grasping spines of *Dakorhachis*, prompting review of its status as a stem-group chaetognathiferan.

Materials and methods

Samples were collected during 'North Greenland (1978–85)', a mapping and regional geology project of Grønlands Geologiske Undersøgelse (the Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark.

GGU sample 218645 was collected by J.R. Ineson on 7 July 1979 from the western side of Gustav Holm Dal, western Peary Land (Fig. 2; 82°20.3'N, 39°45'W) from just above the middle of a unit of dark, bituminous limestones forming the recessive middle unit of the Fimbuldal Formation in its type section (Ineson & Peel, 1997, figs 44, 45); Cambrian, Miaolingian Series, Drumian Stage. I collected GGU sample 315006 on 27 June 1984 from dark, recessive limestone forming the middle part of the Fimbuldal Formation on the southwest side of the glacier feeding into Navarana Fjord, Freuchen Land (Fig. 2; 82°16.7'N, 41°20'W).

Specimens were hand-picked from residues after digestion of limestone samples in 10% acetic acid.

Following examination using a Zeiss Supra 35VP scanning electron microscope (SEM; Zeiss, Oberkochen, Germany) operating at 5 kV, the images were assembled in Adobe Photoshop 7 and CS4 (Adobe Systems, San Jose, California, U.S.A.).

Geological background

The Fimbuldal Formation was described by Ineson & Peel (1997) as composed of alternating units of recessive, dark weathering, dolostone and dominant cliff-forming units of pale dolostone that attain a thickness of about 180 m at the type locality in westernmost Peary Land. Fossils are abundant in dark weathering limey dolostones near the middle of the formation in that area and include agnostoids indicative of the *Ptychagnostus punctuosus* Biozone (Miaolingian Series, Drumian Stage; Robison 1984, Ineson & Peel 1997).

The mollusc *Pseudomyona groenlandica* Peel, 2021 was described from GGU sample 315006 by Peel (2021). *Fimbulispina laurentica* is associated with a variety of small shelly fossils, including the protoconodonts *Gapparodus* Abaimova, 1978 (Fig. 1E–G), *Phakelodus* Miller, 1984 (Fig. 1C) and *Paibiconus?* Dong, 1983 (Fig. 1D, H) in GGU samples 218645 and 315006 from the Fimbuldal Formation.

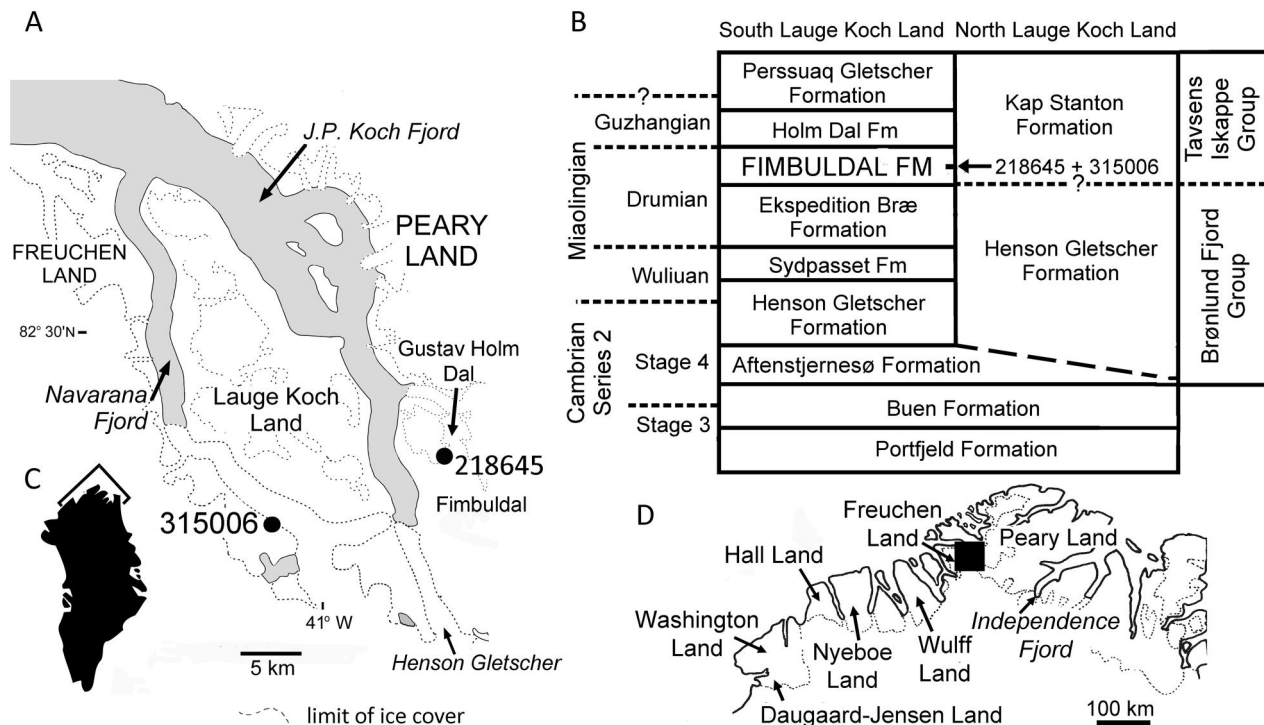


Fig. 2. A, Collection localities for *Fimbulispina laurentica* gen. et sp. nov. (GGU samples 218645 and 315006) western Peary Land and in southern Freuchen Land (located by black square in D). B, Cambrian stratigraphic nomenclature showing derivation of GGU samples 218645 and 315006. C, Greenland, locating toponymic map of North Greenland (D).

Institutional abbreviations

GGU, Grønlands Geologiske Undersøgelse (the Geological Survey of Greenland), now part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. PMU, Palaeontological Collection of the Museum of Evolution, Uppsala University, Uppsala, Sweden. ROM, Royal Ontario Museum (P prefix denotes the Palaeobiology collections), Toronto, Canada. UU, Department of Geology and Geophysics (Research Collections), University of Utah, Salt Lake City, UT, U.S.A.

Systematic palaeontology

Terminology

In standard terminology for protoconodonts, the convex face in lateral view (Fig. 3E, H; left in Fig. 4C) is termed anterior, whereas the concave face in lateral view is termed posterior (Fig. 3G; right in Fig. 4C). These terms are maintained here, although inappropriate in terms of the interpreted grasping mechanical function of the chaetognath elements (Fig. 1; Szaniawski 1982, 2002, Briggs & Caron 2017, Shu *et al.* 2017).

CHAETOGNATHIFERA

Remarks

Conway Morris *et al.* (2020) introduced Chaetognathifera to embrace Chaetognatha and Gnathifera and tentatively placed *Dakorhachis thambus* within its stem-group. Bekkouche & Gąsiorowski (2022) retained Chaetognathifera, but excluded *D. thambus* from their analysis, citing its similarity with scalidophorans; this action is not followed here.

Fimbulispina gen. nov.

Diagnosis

Bilaterally symmetrical, uniformly gently curved element in which the lateral margins of the anterior face are separated by a pronounced median channel that widens towards the base (Figs 3E, H, 4F, 5I). The posterior face is concave in lateral view (upper surface in Fig. 3H, right in Fig. 4C), convex in cross-section, often with a raised central area and a pair of broad longitudinal ridges or folds (Fig. 4G, K) that are related to lath-like mineralized structures within the wall of the element (Figs 3F, 4A, I). Lateral areas of posterior surface become concave in later growth stages (Fig. 4K, N, O). A pair of basal cavities is located one to each side of the median anterior channel.

Etymology

From the Fimbuldal Formation, combined with *spina* (Latin: spine); feminine.

Type species

Fimbulispina laurentica sp. nov., Fimbuldal Formation, North Greenland; Cambrian, Miaolingian Series, Drumian Stage.

Remarks

In protoconodonts such as *Amphigeisina* Bengtson, 1976, *Gapparodus* Abaimova, 1978 (Fig. 1E–G), *Hertzina* Müller, 1959, *Phakelodus* (Fig. 1C) and *Protohertzina*, the element is conical and the anterior face is convex in cross-section, even acutely angular or with a longitudinal median flange as in *Hagionella* Xie, 1990. In contrast, the anterior face of *Fimbulispina* is depressed into a broad, deep channel between the lateral margins. In anterior perspective, this anterior face is bifid with the raised lateral margins flanking the median channel (Figs 3E, 4F). Thus, the cross-section of *Fimbulispina* elements varies from U-shaped (Fig. 3E) to almost W-shaped (Fig. 5L), widening towards the anterior, in contrast to the basically oval to sub-triangular cross-section of the protoconodonts. In contrast to typical protoconodonts, where the conical element has a single hollow central cavity, *Fimbulispina* has two inner cavities located one on each side of the median channel (Fig. 5E, J, L, 6A, C).

Some degraded, preservational variants of *Fimbulispina* in which the posterior surface is not preserved (Figs 4O, 5E, L) superficially resemble *Laiwugnathus* An, 1982, originally described from the Drumian Stage of North China (An 1982, Dong & Zhang 2017) when viewed in posterior perspective. The posterior face in *Laiwugnathus* carries a prominent median keel, sometimes with a cup-shaped basal cavity, and flanking, concave, lateral surfaces. In these preservational variants of *Fimbulispina*, the median fold is an expression of the deep channel on the anterior face (Fig. 5G, L). In contrast, the anterior face in *Laiwugnathus* is convex in cross-section, without a longitudinal channel (An & Mei 1994, pl. 1, fig. 1). A thin section of *Laiwugnathus* illustrated by Dong (2007, pl. 3, fig. 9) does not demonstrate the presence of the paired mineralized laths seen in *Fimbulispina*.

In addition to the type material from North Greenland, a specimen from the Huaqiao Formation of Hunan Province described by Bagnoli *et al.* (2008, fig. 3H) as *Phakelodus?* sp. is referred to *Fimbulispina* gen. nov. Both records are of Drumian age and

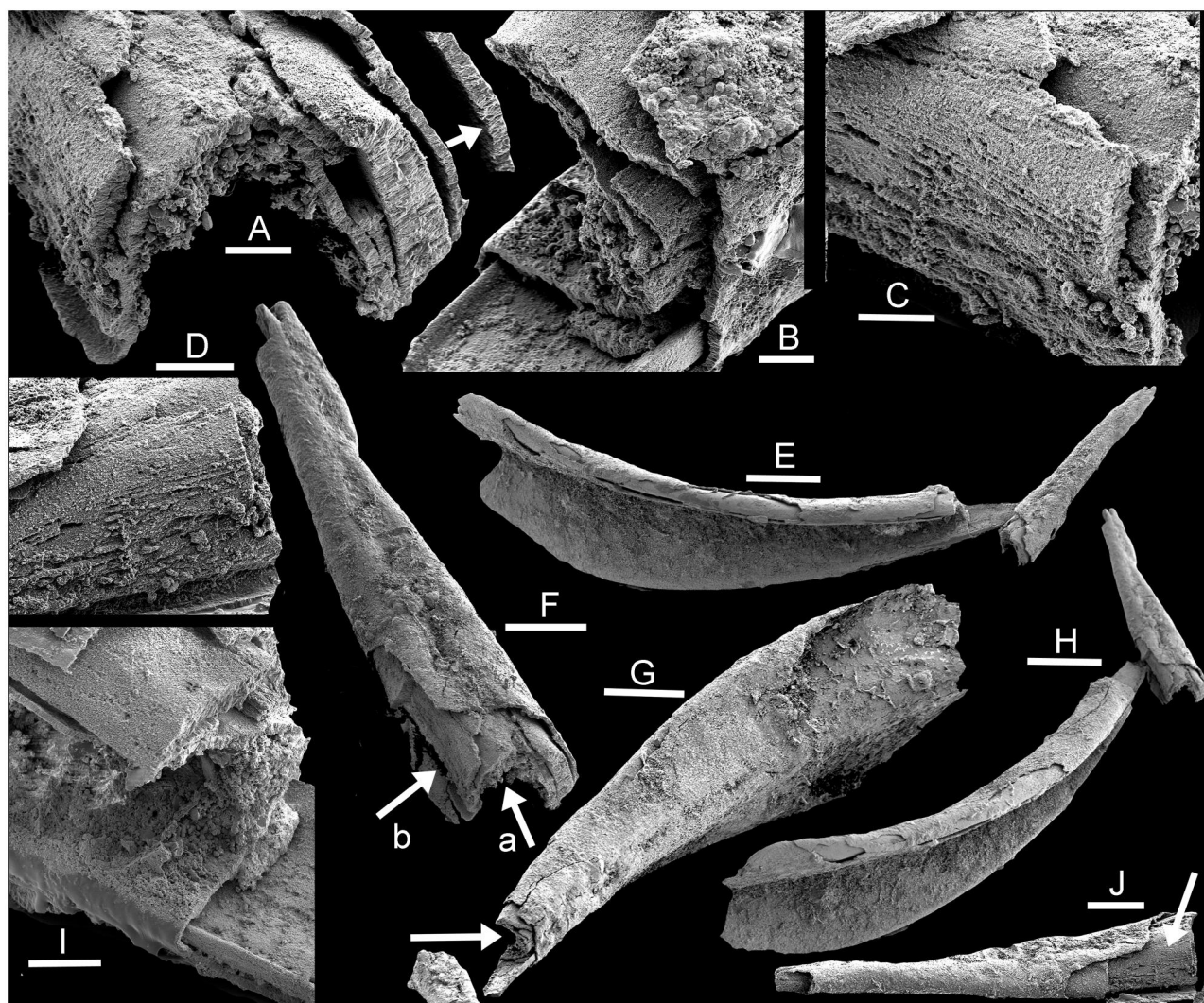


Fig. 3. *Fimbulispina laurentica* gen. et sp. nov., PMU 18230 from GGU sample 315006, holotype, Fimbuldal Formation, Cambrian, Miaolingian Series, Drumian Stage, southern Freuchen Land, North Greenland. A, basal cross-section of broken apical fragment (arrow a in F) with detail of outer encrusted layer. B, I, cross-section of broken apex of main specimen (arrow in G). C, D, fibrous surface of lath (arrow b in F, arrow in J). E, H, oblique anterior views showing concave anterior face and slightly displaced broken apex. F, broken apex of element, detail of H. G, oblique posterior view. J, broken apex in lateral view, arrow locates D. Scale bars: 20 µm (a–D); 30 µm (I); 100 µm (F, J); 200 µm (E, G, H).

therefore slightly older than *Dakorhachis* from the Guzhangian Weeks Formation.

***Fimbulispina laurentica* sp. nov.**
(Figs 1B, 3–6)

Etymology

Reflecting its occurrence in the palaeocontinent Laurentia.

Holotype

PMU 18230 from GGU sample 315006, Fimbuldal Formation, Freuchen Land, North Greenland; Cambrian (Miaolingian Series, Drumian Stage).

Referred material

In addition to the holotype, PMU 18225, PMU 18231–PMU 18239, paratypes from the same sample as the holotype. PMU 18240 from GGU sample 218645, Gustav Holm Dal, western Peary Land, North Greenland; Cambrian (Miaolingian Series, Drumian Stage).

Description

The element is bilaterally symmetrical, sub-triangular to tear-shaped (Fig. 4G, O) and uniformly gently curved. The anterior face is convex in lateral view (left side in Fig. 4C); in anterior view it is bifid with the lateral margins separated by a pronounced median

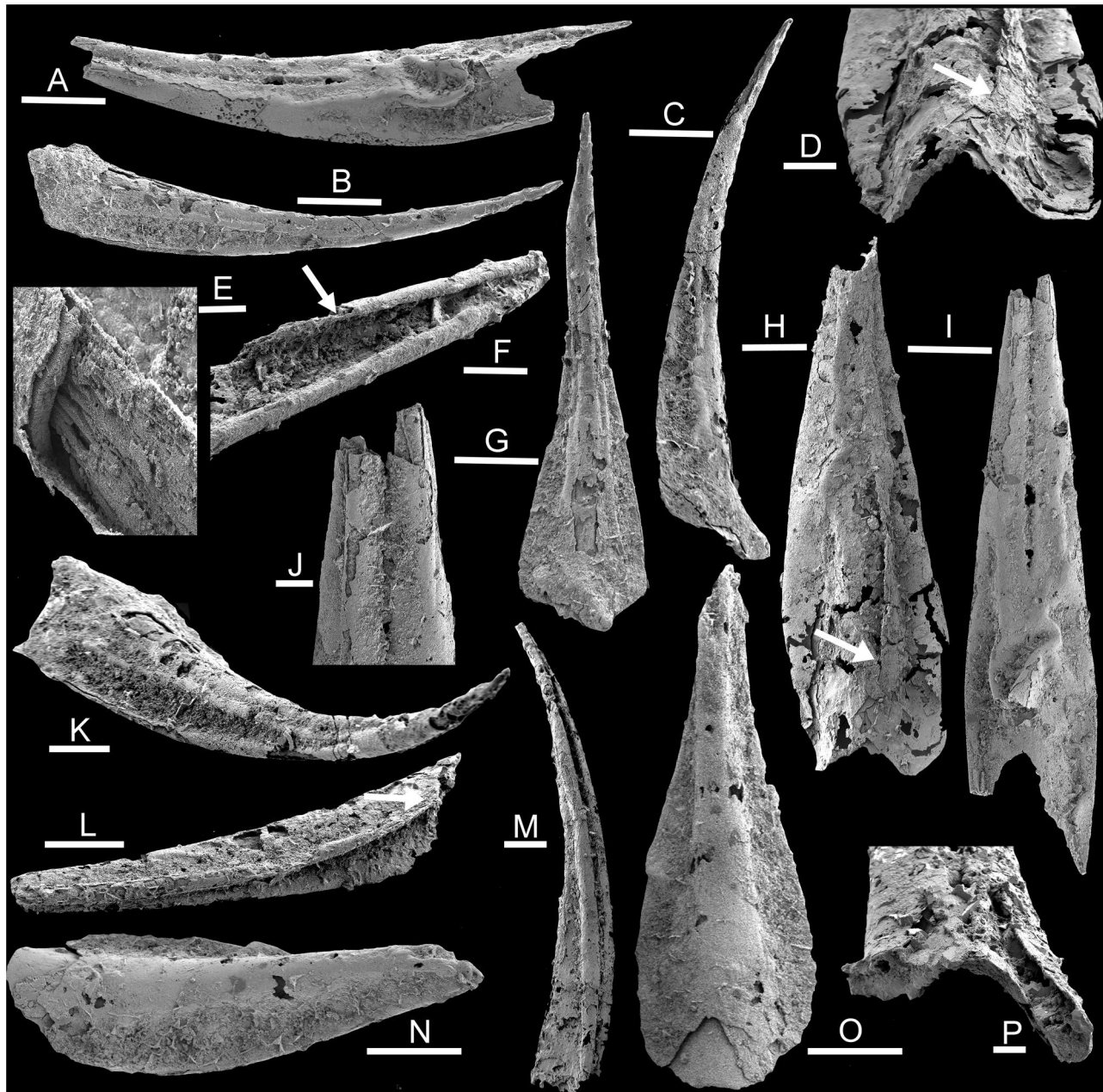


Fig. 4. *Fimbulispina laurentica* gen. et sp. nov., Fimbuldal Formation, Cambrian, Miaolingian Series, Drumian Stage; GGU sample 315006, southern Freuchen Land, North Greenland. **A, I, J**, PMU 18231 showing diagenetic fracture of outer encrusted layer between inner laths in posterolateral (A) and posterior (B) views, with detail of apex (J). **B, C, G, K**, PMU 18232, posterolateral (B), lateral (C), posterior (G) and oblique apical (K) views. **D, H**, PMU 18233, posterior face (H) with termination of edge of internal lath (D, arrow also in H). **E, F**, PMU 18234, oblique anterior view (F) with detail of fibrous surface texture of lath (E, located by arrow in F). **L**, PMU 18235, lateral view of crushed specimen showing termination of lath (arrow). **M**, PMU 18236, lateral view of crushed specimen. **N, O**, PMU 18237, posterior (O) and oblique lateral (N) views. **P**, PMU 18238, cross-section with outer surface formed by encrustation. Scale bars: 20 μm (E); 30 μm (J); 50 μm (P); 100 μm (D, K); 200 μm (A, B, C, F–I, L, M, O).

concavity or channel that widens towards the base (Figs 3E, H, 4F, 5I, K). The posterior surface is concave in lateral view (right side in Fig. 4C); it is convex in cross-section, usually with a raised central area that may show a pair of broad longitudinal folds (Fig. 4G, 1, K), and flanks that may become concave during growth as the lateral margins are approached (Fig. 4K, O).

The element is initially pointed (Fig. 4C, G, K) and sub-circular, later oval, in cross-section, with a U-shaped channel on the anterior face (Figs 1B, 3A, 4F, 5A). The median channel widens and becomes more V-shaped, but still rounded medially in later growth stages, with flattened lateral margins (Figs 4D, 5F, 5I, K). At the latest growth stage, the anterior face of the elements as

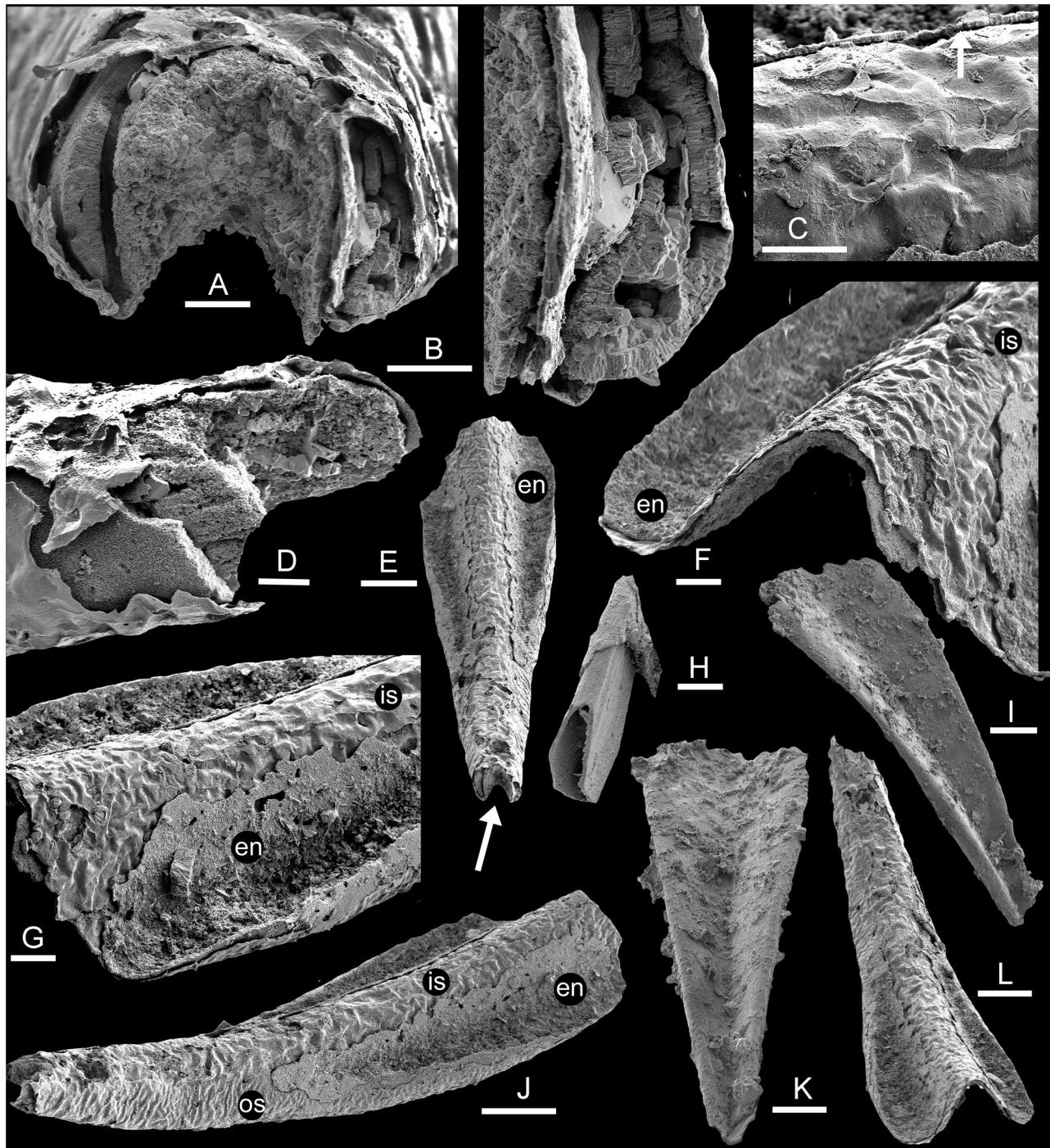


Fig. 5. *Fimbulispina laurentica* gen. et sp. nov., Fimbuldal Formation, Cambrian, Miaolingian Series, Drumian Stage, southern Freuchen Land, North Greenland. A–G, J, L, PMU 18239 from GGU sample 315006, element with wrinkled layer. A, cross-section of broken apex (arrow in E) with detail of recrystallized lath (B). C, detail of wrinkled layer with overlying outer encrusted layer (arrow). D, lateral view of tip (arrow in E). E, J, L, oblique posterior views (arrow in E locates A and D). F, G, detail of basal margin. Abbreviations: en, encrusted layer; is, inner surface of wrinkled layer; os, outer surface of wrinkled layer. H, PMU 18225 from GGU sample 315006, protruding lath with striated surface, see also Fig. 1B. I, K, PMU 18240 from GGU sample 218645, anterior (K) and oblique anterior (I) views. Scale bars: 20 μm (B, C); 30 μm (A, D); 50 μm (F–H); 60 μm (L); 100 μm (I, K); 200 μm (E, J).

preserved is a low W-shape in cross-section (Fig. 5F, L). The lateral transitions from the anterior face to the posterior face are rounded (Fig. 4D, P) to angular (Fig. 4K). The posterior face is raised medially and may show a pair of broad longitudinal folds or broad ridges (Fig. 4G,

1, K) that reflect lath-like, robust, mineralized structures within the wall of the cone (Figs 3F, 4A, I). The mineralized zones and resultant folds are most conspicuous in the early growth stages, and fade away as the base is approached. As a result of degradation of the thin

element wall and diagenetic compaction, the mineralized laths may be exposed at the apex (Figs 3F, H, 4A, I, J). A pair of internal cavities, one on each side of the median channel (Fig. 6C), is present in the proximal part of the element (Fig. 5J, L).

Remarks

The holotype of *Fimbulispina laurentica* (Fig. 3) has a length of about 2 mm and a maximum width perpendicular to the plane of symmetry of about 600 μm , which is substantially smaller than the grasping spines in ‘crack-out’ specimens of *Ankalodous sericus* (length up

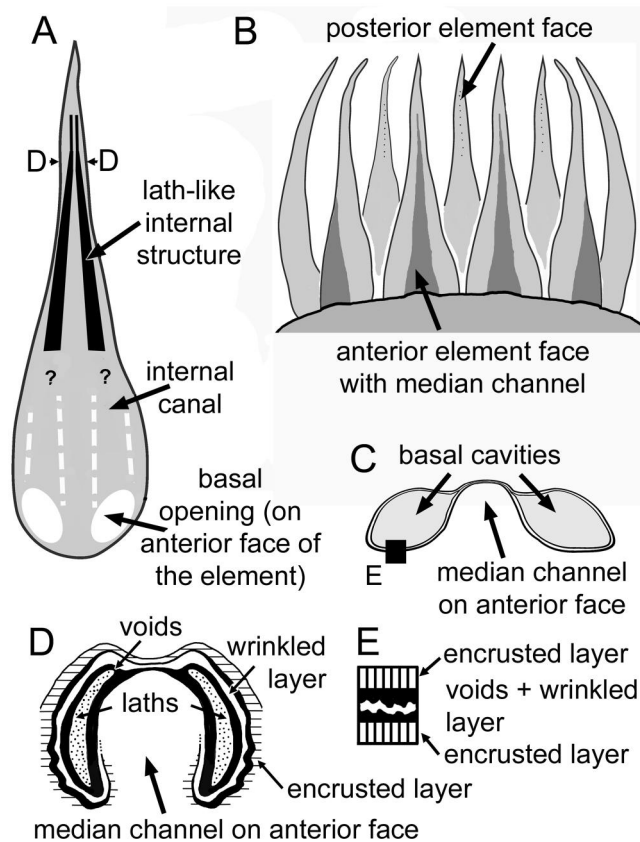


Fig. 6. *Fimbulispina laurentica* gen. et sp. nov. **A**, schematic interpretation of morphology based on posterior view. **B**, arbitrary reconstruction of postulated circum-oral grasping apparatus. **C**, schematic transverse section of the original organic wall in the basal (anterior) part of the element. The original organic walls are not retained in specimens as preserved (Figs 3A–C, 4P); they are represented by voids and a phosphatized wrinkled layer between thin layers of encrusting diagenetic calcium phosphate that occur on the out surface of the element and within the basal cavities (see D, E). **D**, schematic transverse section through apical (posterior) part of element, as preserved, with calcium phosphate encrusting the degraded element wall (voids and wrinkled layer); located at D–D in A. **E**, schematic cross-section of element wall, as preserved, with calcium phosphate encrusting the degraded element wall (represented by voids and wrinkled layer) on the element exterior and within the basal cavity; located at E in C.

to 7 mm) and *Capinatator praetermissus* (length 8–9 mm; Fig. 1A). However, this size is comparable to protoconodonts and other fossils from the same acid residues, and other early–middle Cambrian sample residues from Greenland. Most elements within the available samples are broken, which suggests bias in preservation, including transport, or preparation. Conway Morris *et al.* (2020) noted that teeth in *Dakorhachis thambus* are up to 3 mm in length (Fig. 1I, J).

Bagnoli *et al.* (2008) tentatively assigned three problematic specimens from the Huaqiao Formation (Drumian Stage) of Hunan, South China to *Phakelodus?* sp., noting a superficial similarity to two elements of *Phakelodus tenuis* (Müller, 1959) that were joined longitudinally along their posterior face, but diverged anteriorly (Bagnoli *et al.* 2008, fig. 3H). *Phakelodus tenuis* was described by Müller & Hinz (1991, p. 34) as having ‘long, slender, and simple cones[that] are gently and evenly recurved. The angle of divergence exceedingly low’. *Phakelodus* often occur in clusters of more than 20 laterally juxtaposed individual cones (Müller & Hinz 1991, pl. 2; see also Fig. 1A), interpreted by Szaniawski (1982) as chaetognath grasping spines.

The comparison by Bagnoli *et al.* (2008) with two laterally conjoined elements of *Phakelodus* agrees with the longitudinal bifid structure of the anterior face of *Fimbulispira*, and *Phakelodus?* sp. from South China is assigned to *Fimbulispira*. It differs from *F. laurentica* in having a narrower, V-shaped channel on the anterior face and lacking the tendency to develop concave lateral flanks on the posterior face, but both these characters may indicate a juvenile portion of the element.

Kouchinsky *et al.* (2011, fig. 27I–K) described an unassigned single element from the Kuonamka Formation of northern Siberia in which the posterior face was channelled medially and the anterior face inflated medially. The trilobed cross-section is reminiscent of some specimens of *Fimbulispina* but these differ in having a channelled anterior face and medially inflated posterior face.

Preservation and internal structure

Available material of *Fimbulispina laurentica* has been diagenetically phosphatized, probably in several events, which has enabled extraction of the elements from the host carbonate using weak acetic acid. Preservational variants resulting from differential phosphatization have been enhanced by the etching process. Voids and thin laminar cavities in the

extracted specimens were filled with diagenetic calcium carbonate prior to etching but probably reflect an original organic wall to the element (Wierzbowski *et al.* 2021). Remains of the original organic layers have not been detected.

The outermost layer preserved in most specimens is a thin, diagenetic phosphate encrustation, often just 2–3 μm thick, with a uniform structure of crystals oriented perpendicular to the inner surface (Fig. 3A). Its outer surface generally appears to be relatively smooth and continuous, although patches with spheroids and attached sediment grains may be seen in detail (Figs 3B, 4F). The way in which this outer layer drapes over underlying structures, such as large scale wrinkles (Fig. 4A, I) or the internal laths (Figs 3A, 4A, G, I, J) suggests partial degradation, and possibly an earlier phosphatization event, of the thin organic wall prior to the crystallization of the outer phosphate encrustation. Only minimal fracturing of the encrusting layer due to compaction occurred after the formation of the encrustation, although holes, breakage and exfoliation due to incomplete encrustation or sample preparation are present (Fig. 4D, H, P). A narrow gap underneath the outer encrustation represents the thin outer surface of the organic wall of the element. In one specimen (Fig. 5A–G, J, L) a heavily wrinkled layer, varying in thickness from about 5 to 10 μm , occurs beneath this narrow gap and represents a phosphatized, degraded organic layer. The rise and fall of the wrinkles in this specimen does not affect the planar undersurface of the overlying encrusting layer (arrow in Fig. 5C, G, J), indicating that the degradation induced wrinkling was smoothed out before phosphate encrustation.

Cross-sections of the early growth stages in broken specimens indicate that the longitudinal ridges or folds visible on the posterior face of elements (Figs 3F, 4A, I, J, K) relate to two mineralized lath-like structures within the element wall (Figs 3A–D, F, I, 5A, 6A, D). The laths are shallowly crescentic in cross-section, corresponding to the curvature of the outer lateral walls of the element (Figs 3A, 5A), with a thickness of about one fifth of their maximum dimension in cross-section (Fig. 5A). Their terminations in cross-section are indicated by the course of the overlying thin wrinkled layer that wraps around them (Figs 5A, 6D). The laths are separated from each other along their posterior margin (uppermost in Figs 5A, 6D), although the currently phosphatized, wrinkled element wall continues across this median area of the element from one lath to the other on the posterior face (uppermost in Figs 5A, 6D). On the

anterior face (lower surface in Fig. 5A), the laths underlie the lateral margins to the diagnostic central channel of *Fimbulispira* (Figs 3A, 4F, 5A) and the wrinkled layer forms a continuous cover to the longitudinal laths on the medial and lateral areas of the element and within the anterior channel (Fig. 5A, B). The laths are most prominent in the apical half of the element and in corroded specimens they may protrude through the apex (Fig. 4A, I, J). A similar feature is seen in *Gapparodus bisulcatus* (Müller, 1959) from the Furongian Series of Sweden illustrated by Müller & Hinz-Schallreuter (1998, fig. 2.8) where it represents diagenetic phosphate growth within the central cavity of the element.

Preservation of the laths varies. In one specimen (Figs 1B, 5H), the outer surface of the phosphate internal mould of the lath is smooth and longitudinally striated, whereas the inner surface of the currently hollow lath is granular, indicating that the lath as preserved is a phosphatic replacement of the original structure. In a second specimen (Fig. 5A, E) the laths are replaced by phosphate crystals radiating inwards from the overlying shell layer following dissolution of the original lath material. In the right lath (Fig. 5A, detail in B), the radial phosphate crystals are coarser, with a core containing large euhedral crystals, whereas the texture in the left lath is finer and compact, suggesting different periods of replacement. In this specimen (Fig. 5A–G, J, L), the outer surface of the early growth stage is uniformly oval in cross-section with a deep, U-shaped anterior channel (Figs 5A (located by arrow in 5E), 6D). After mid-length the convex lateral surfaces of the posterior face (uppermost in Fig. 5E, J, L), as preserved, become concave on each side of the rounded, median ridge as the base is approached. The change in shape follows the reduction and ultimate disappearance of the laths in the later growth stages. However, in this specimen (Fig. 5C, E–G, J, L), the true surface of the posterior face of the element is not preserved, presumably due to incomplete phosphatization or subsequent loss, such that the visible wrinkled layer forming the median ridge is the inner surface of the layer on the anterior face ('is' in Fig. 5F, G). This layer curves under the lateral concave surfaces of the specimen such that its outer surface ('os' in Fig. 5J) forms the lateral edge of the element. The phosphatized outer surface (os) is more finely wrinkled than the inner surface (is) and overlies this inner surface adaptically (Fig. 5J). The presence of the outer encrusted layer ('en' in Fig. 5G, J) overlying the wrinkled layer of the element wall in the lateral concave areas indicates that these

concavities are preservational relics of a pair of internal basal cavities lying one on each side of the median channel on the anterior face (Fig. 6C). An alternative interpretation might be that the lateral concave areas were open U-shaped longitudinal channels in the posterior face, but the uniformly convex surface of the posterior face of other elements (Fig. 4A) argues against this.

Szaniawski (1982, 1983) noted the close similarity of the internal structure of extant chaetognaths and well-preserved Cambrian protoconodont elements, illustrating three layers in the element wall. In the currently described material of *Fimbulispina* the surfaces of the elements have been diagenetically encrusted with calcium phosphate. The original element walls were likely organic, as in protoconodonts, but no trace of this organic material remains following diagenesis and sample preparation. The wall, as preserved, is represented by a void that may contain a phosphatized surface suggesting a three-layer structure (Fig. 5F, G, J, 6D).

Nature of the laths

The lath-like internal structures are interpreted tentatively as original solid elements within the element wall that were recrystallized during diagenesis, perhaps indicating compositional variation within the layered wall structure. As such, they could be compared to the dominant continuous middle layer in circular cross-sections of *Phakelodus tenuis* and chaetognaths as described by Szaniawski (1983). They all display a longitudinal fibrous structure (Figs 3C, D, 4E; Szaniawski 1983, fig. 2A), also illustrated by Müller & Hinz-Schallreuter (1998, fig. 4.2) in *Gumella cuneata* Müller & Hinz, 1991. The laths may also represent infilling during growth of the apical part of the inner canals representing the adapical extension of the basal cavities (Fig. 6A). In both cases they would serve to strengthen the tips of the elements in their grasping function. The uniform occurrence of the laths in available material supports both of these interpretations. Unfortunately, the transition between the laths and the internal canals is obscured by poor preservation.

Alternatively, while the form of the laths is very consistent, they may just represent diagenetic infilling of the internal canals (Fig. 6A) that took place at a very early stage, prior to the degradational wrinkling in the overlying organic layer. Diagenetic phosphatization in tubular or conical Cambrian small shelly fossils is often restricted to the innermost (apical)

portions of the shell cavity (Creveling *et al.* 2014). Diagenetic phosphate growth within the central cavity of *Gapparodus bisulcatus* described by Müller & Hinz-Schallreuter (1998, fig. 2.8) produced an inner core that also extended beyond the worn tip of the outer element layers, as in some specimens of *Fimbulispina laurentica* (Fig. 4G).

Discussion

While the general morphology and presumed organic composition support assignment to the protoconodonts in a general sense, the deep channel in the anterior face and the presence of a pair of basal cavities, together with the pair of lath-like mineralized structures, distinguish *Fimbulispina* from typical forms such as *Amphigeisina*, *Gapparodus* (Fig. 1F, G), *Hertzina*, *Phakelodus* and *Protohertzina*, which have a single internal cavity within a conical element. However, neither are these features of *Fimbulispina* present in present day chaetognaths. As fully described by Szaniawski (1982, 1983), typical protoconodonts and chaetognaths have a three-layer structure dominated by a fibrous middle layer.

Conway Morris *et al.* (2020) noted that at least six narrowly triangular teeth up to 3 mm in length are present in *Dakorhachis thambus* (Fig. 1I, J) from the Weeks Formation (Guzhangian Stage) of Utah (Lerosey-Aubril *et al.* 2018), somewhat greater than the maximum observed length of the spines of *Fimbulispina laurentica* (2 mm). All specimens of *D. thambus* have been flattened, although the resistant teeth are at least partially preserved in three dimensions. Longitudinal curvature, if any, of the teeth is not apparent from the illustrations of the specimens as preserved, but in part this may be a diagenetic effect resulting from the general flattening. In transverse cross-section, each tooth of *D. thambus* has a convex surface, interpreted as the outer surface by Conway Morris *et al.* (2020), and a concave surface interpreted as inner. The cross-section is comparable in shape to that of *Fimbulispina*, but the longitudinal curvature of the elements of *Fimbulispina* demonstrates that the anterior face with its concave cross-sectional surface (Fig. 3E, H) would be the outer surface of the element if the elements are interpreted as a circlet of grasping spines around the mouth (Fig. 6B). In both cases, the longitudinal median fold of the elements can be interpreted as an adaptation to strengthen the spine in its grasping function. In *Fimbulispina* this is complemented by the strengthening of the apex of the element

by the internal laths; lath-like structures and a basal cavity are not present in *D. thambus*.

As with most protoconodont taxa, there is no solid evidence that elements of *Fimbulispina* were organized into circum-oral arrays of the type described in *Ankalodous sericus* and *Capinatator praetermissus* (Fig. 1A; Briggs & Caron 2017; Shu *et al.* 2017). A simple pattern of grasping elements is proposed in *Fimbulispina* (Fig. 6B), following the distribution seen in *D. thambus*, but this arrangement is speculation. Most other typical protoconodonts may have had a similar distribution of elements. It should be noted, however, that the well-preserved Cambrian chaetognathiferans *Amiskwia* from the Burgess Shale (Vinther & Parry 2019, Bekkouche & Gąsiorowski 2022) and *Timorebestia* from the Sirius Passet Lagerstätten of North Greenland (Park *et al.* 2024) do not preserve arrays of circum-oral spines, demonstrating the diversity in feeding mechanisms within stem-group chaetognathiferans. There is no evidence of secondary elements associated with *Fimbulispina* spines that can be compared with the small jaw elements of *Amiskwia* and *Dakorhachis* (Vinther & Parry 2019, Caron & Cheung 2019, Conway Morris *et al.* 2020, fig. 4). However, colour differences between the circum-oral spines and the small jaw elements in illustrations of *Dakorhachis* by Conway Morris *et al.* (2020) suggest a compositional difference that may have resulted in differential preservation.

The circum-oral distribution of the six(?) grasping elements, trunk annulation and the circular cross-section prompted Bekkouche & Gąsiorowski (2022) to exclude *Dakorhachis* from their cladistic analysis of chaetognathiferans in favour of a possible scalidophoran affinity. However, the morphological intermediate position of *Fimbulispina* between typical protoconodonts and *Dakorhachis* promotes rejection of this exclusion. A hexaradiate circum-oral distribution of small, multicuspidate grasping denticles on an extensible introvert is preserved in the large, stem-group loriciferan *Sirilorica carlsbergi* Peel, 2010 from the Sirius Passet Lagerstätte (Cambrian Series 2) of North Greenland (Peel 2010, Peel *et al.* 2013), but these are unlike the large elongate circum-oral elements of *Dakorhachis*. Furthermore, the annulated body of *Dakorhachis* is quite unlike the loricate abdomen of *Sirilorica* and lacks an introvert.

Zhang *et al.* (2023) referred to *Dakorhachis* in describing *Iotuba chengjiangensis* Zhang, Smith & Ren, 2023 from the Chengjiang Lagerstätte (Cambrian Series 2) of China as an early pleistoannelid. They reconstructed *Iotuba* as a slender annulated worm

with the head flanked by fascicles and pallisades of slender radial spines forming a chaetal cephalic cage, but concluded that limited preservation precluded further comparison with *Dakorhachis*. Circum-oral elements in *Dakorhachis* are fewer in number and proportionately much larger and robust than those in *Iotuba*. In the latter, Zhang *et al.* (2023, fig. 6a, b) restored the spines as curving outwards with downward directed tips in connection with their cage function. In contrast the spines in chaetognaths (Fig. 1A) and *Fimbulispina* (as restored herein, Fig. 6B) curve with their tips directed in towards the mouth, reflecting their grasping function.

Elements of *Fimbulispina laurentica* show features reminiscent of both protoconodonts and *Dakorhachis* but the distinctive channelled anterior face and paired interior canals indicate that *Fimbulispina* represents a separate evolutionary lineage of ‘graspers’. Assuming that all described protoconodonts in a loose sense are correctly grouped together phylogenetically, the stem-group Chaetognathifera clearly embraces a wide morphological range of grasping spines arranged in a variety of patterns. The unique spines of *Fimbulispina* extend this diversity. The form and mode of life of their host remain unknown, but a benthic existence as proposed for *Dakorhachis* by Conway Morris *et al.* (2020) seems likely.

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Data archiving statement

This published work and the nomenclatural acts it contains have been registered in ZooBank: <https://zoobank.org/C01DBE57-0D8A-4DBC-AD62-45DC90E-6D05A>.

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