

Musculature and shell microstructure of the ancestral bivalve *Fordilla* (Mollusca) from the lower Cambrian of Greenland (Laurentia)

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Shell microstructure and exquisite details of muscle attachment scars are preserved on the surface of internal moulds in the bivalve *Fordilla troyensis* from the Aftenstjernesø Formation (Cambrian Series 2, Stage 4) of North Greenland (Laurentia). Subsidiary muscles developed in commarginal series that extend laterally from the anterior and posterior adductor muscles probably controlled the centrally emergent foot. Their position close to the ventral margin indicates that only slight withdrawal and limited manipulation of the foot was possible, confirming that *Fordilla* was not a burrower. The pattern suggests derivation of *Fordilla* from a clamping mollusc with shell muscles distributed around the shell margin. No such pattern of serially repeated muscles close to the shell margin is currently known in the few available records of helcionelloid muscle scars, but *Postacanthella* has a commarginal U-shaped muscle scar reflecting its limpet-shaped shell form. Shell microstructure in *Fordilla troyensis* is closely similar to *Pojetaia*, with central areas of the valves dominated by a laterally continuous imbricate lamellar structure with a width of 10–20 μm between successive crests. Imbricate lamellae with about half this spacing form a marginal zone with crests lying perpendicular to the valve edge. The hinge line lacks teeth, although a single tooth is present in each valve of the related *Fordilla sibirica* and *Fordilla germanica*. The site of the simple ligament is coarsely striated. Comparative material of *Fordilla troyensis* is illustrated from New York State, North-East Greenland and Denmark. • Key words: Bivalvia, muscle scars, microstructure, Cambrian Stage 4, Greenland, Laurentia.

PEEL, J.S. 2023. Musculature and shell microstructure of the ancestral bivalve *Fordilla* (Mollusca) from the lower Cambrian of Greenland (Laurentia). *Bulletin of Geosciences* 98(4), 265–287 (14 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received November 4, 2023; accepted in revised form December 31, 2023; published online December 31, 2023; issued December 31, 2023.

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The evolution of Class Bivalvia from univalved molluscs in the Cambrian is unresolved, with two Cambrian bivalved groups generally recognised as potential stem lineages (Cope 1997, 2000; Carter *et al.* 2000, 2011; Fang & Sánchez 2012; Cope & Kříž 2013; Ponder *et al.* 2020; Peel 2021a). The Order Fordillida Pojeta, 1975 contains *Fordilla* Barrande, 1881 (Fig. 1A–C) and *Pojetaia* Jell, 1980 (Fig. 1D, E, H, I) and has its first record in the early Cambrian. Only the nominate genus *Tuarangia* MacKinnon, 1982 (Fig. 1F, G), originally described from the late middle Cambrian (Miaolingian Series; Guzhangian Stage) of New Zealand (MacKinnon 1982, 1985), about 20 Ma later, is present within the Order Tuarangiida MacKinnon, 1982. The youngest known specimens of *Tuarangia* occur together with *Pojetaia* in the Miaolingian Series (Guzhangian Stage) of Denmark (Berg-Madsen 1987, Hinz-Schallreuter 2000, Peel 2021a). Various other supposed Cambrian Bivalvia were reviewed by Runnegar & Pojeta (1992), Pojeta (1975, 1978, 2000), Geyer & Streng (1998) and Elicki & Gürsu (2009). Most were rejected from Bivalvia but others, such as *Buluniella*

Jermak [Ermak], 1986, *Camya* Hinz-Schallreuter, 1995 and *Arhouria* Geyer & Streng, 1998 remain as probable Bivalvia, although they are not well known.

A pragmatic response to uncertainties concerning the ancestral bivalve was advanced by Carter *et al.* (2011) when they recognised a Grade Euprotobranchia, the Superorder Euprotobranchia of Nevesskaja (2009), to accommodate both the orders Fordillida and Tuarangiida. The decision echoed the opinion of Waller (1990) that shell microstructure of *Pojetaia* does not resemble modern bivalves and that fordillids comprise a separate bivalve clade. While euprotobranchs were considered likely to be ancestral to crown group bivalves, the two orders were not considered to form a monophyletic entity (Carter *et al.* 2011). The establishment of the paraphyletic Euprotobranchia maintained the separation of *Fordilla* and *Pojetaia* from *Tuarangia* as lineages of stem group bivalves, an action that had prompted Runnegar & Pojeta (1992) to exclude *Tuarangia* from the Bivalvia, see also Peel (2021a). However, Pojeta (2000) considered *Tuarangia* to be a bivalve if claims of musculature proposed

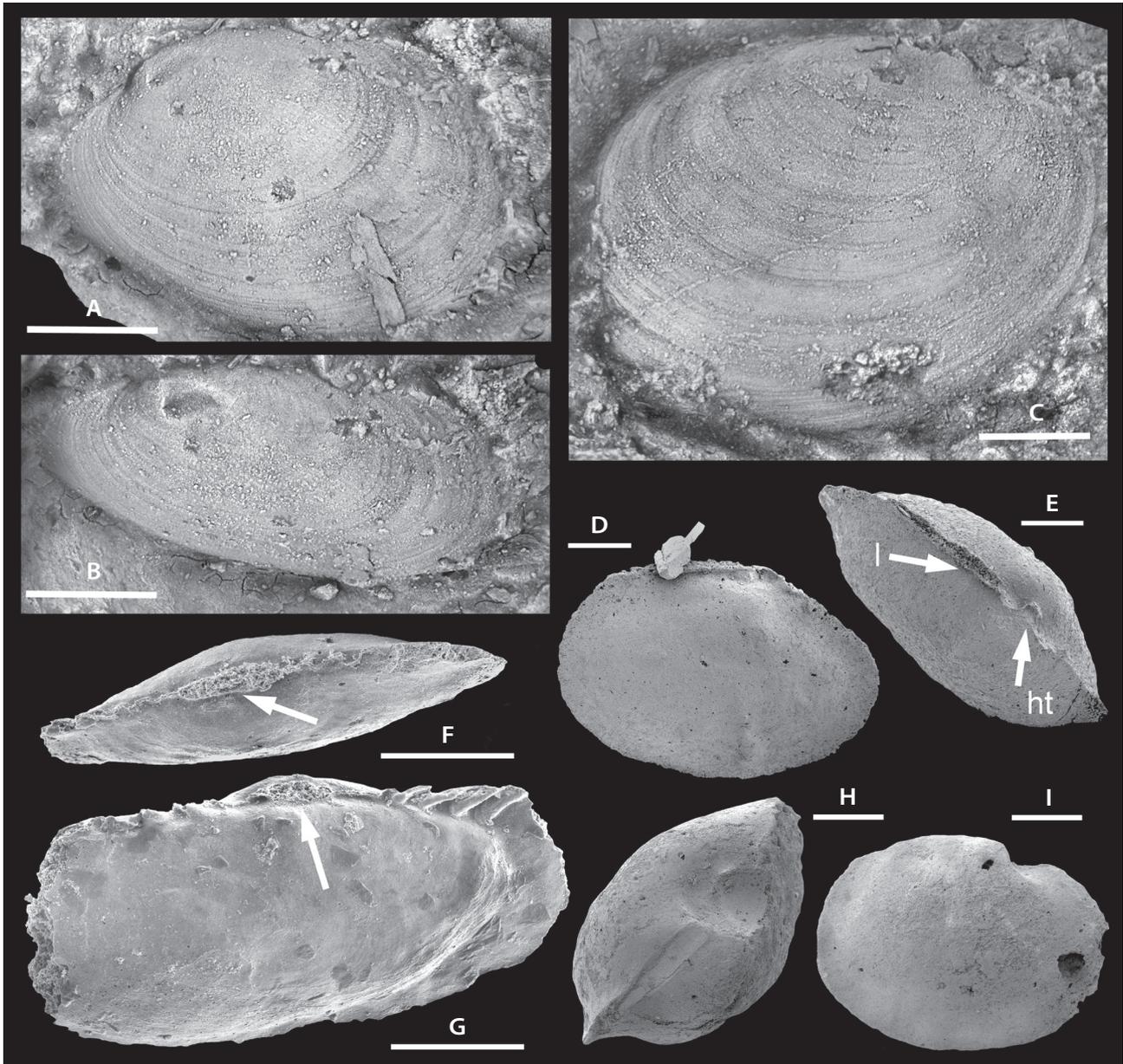


Figure 1. Bivalved Cambrian molluscs. • A–C – *Fordilla troyensis* Barrande, 1881, topotype specimens from Troy, New York State, U.S.A. (Cambrian Series 2). A, B – SMNH Mo 115043.1, left valve in lateral (A) and oblique dorso-lateral (B) views. C – SMNH Mo 115043.2 right valve. • D, E – *Pojetaia runnegari* Jell, 1980, internal moulds, Aftenstjernesø Formation (Cambrian Series 2, Stage 4), Navarana Fjord, North Greenland (Fig. 2A). D – PMU 36935, lateral view, right side. E – PMU 36934, oblique dorsal view showing ligament (arrow l) on supra-apical surface and hinge teeth (arrow ht) on sub-apical surface. • F, G – *Tuarangia gravgaerdensis* Berg-Madsen, 1987, Andrarum Limestone, Bornholm, Denmark (Cambrian, Miaolingian Series, Guzhangian Stage). Images: Vivianne Berg-Madsen. F – MGUH 17542, dorsal view showing hinge line with teeth located anterior and posterior of the median ligament (arrow). G – MGUH 17541, lateral view of right valve with median ligament arrowed. • H, I – *Pojetaia robsonae* Peel & Skovsted, 2021, internal moulds, (Cambrian Series 2), Judge Daly Promontory, Ellesmere Island, Nunavut, Canada. H – GSC 141603, antero-dorsal view, with ligament and large hinge tooth. I – GSC 141602, lateral view of right valve. Scale bars: 1 mm (A–C); 200 μ m (D–G); 500 μ m (H, I).

by Hinz-Schallreuter (1995) were correct, but he was uncertain if this was the case. Ordovician to Recent groups traditionally placed within Bivalvia were assigned by Carter *et al.* (2011) to the Clade Eubivalvia Carter, 2011 in Carter *et al.* (2011). *Fordilla* was considered to be a crown group bivalve by Sharma *et al.* (2013) and Bieler *et al.* (2014), but Ponder *et al.* (2020) retained Fordillida in

Euprotobranchia, while placing *Tuarangia* in Eubivalvia. The placing of Tuarangiida in Eubivalvia and Fordillida in Euprotobranchia by Ponder *et al.* (2020, p. 552) recalls the opinion of Yochelson (1981) that *Fordilla* is bivalved, but not Bivalvia (= Pelecypoda).

The laterally compressed early Cambrian univalve *Watsonella* Grabau, 1900 and the more strongly coiled

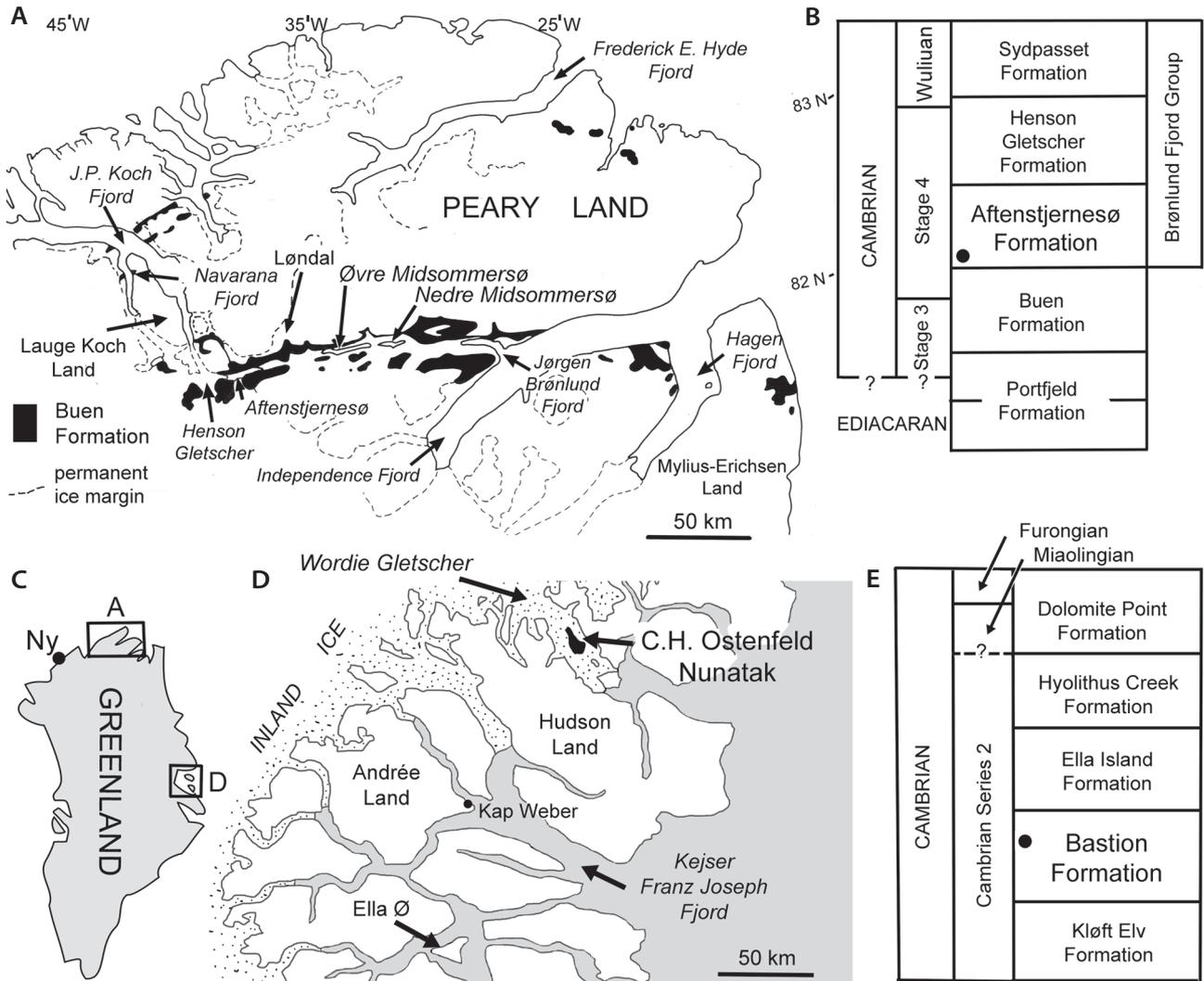


Figure 2. Geographical and geological information. • A – Peary Land region. Johannes C. Troelsen collection 57 was made from talus on the steep valley side north side of Øvre Midsommersø. The map shows the regional outcrop of the Buen Formation, which is overlain by the thin Aftenstjernesø Formation from Henson Gletscher eastward to the Jørgen Brønlund Fjord area. • B – Cambrian stratigraphy in south-western Peary Land showing derivation of J.C. Troelsen collection 57 (black dot) from the basal Aftenstjernesø Formation. • C – Greenland, showing position of Fig. 2A, D and location of Nyboe Land (Ny). • D – North-East Greenland, GGU samples 314918 and 314919 with *Fordilla troyensis* (Skovsted 2004) were collected from the Bastion Formation at the northern tip of C.H. Ostenfeld Nunatak. Material described by Poulsen (1932) was collected from the Bastion Formation just west of Kap Weber. • E – Cambrian stratigraphy of North-East Greenland showing derivation (black dot) of *Fordilla troyensis* from the upper Bastion Formation (Cambrian Series 2, Stage 4).

Anabarella Vostokova, 1962 are widely regarded as ancestors of *Fordilla* (Carter *et al.* 2006) due to the presence of longitudinal ridges on the dorsum of the supra-apical surface that suggest an incipient hinge zone (Kouchinsky 1999, Devaere *et al.* 2013, Guo *et al.* 2021). This relationship was also supported by similarity in shell microstructure between *Watsonella* and *Fordilla* described by Runnegar & Pojeta (1992) and Vendrasco *et al.* (2011). Hinge teeth and an opisthodontic ligament, characteristic features of Bivalvia, are well-developed in *Pojetaia* (Jell 1980, Runnegar & Bentley 1983, Runnegar & Pojeta 1992, Elicki & Gürsu 2009, Vendrasco *et al.* 2010, Peel &

Skovsted 2021), while hinge teeth are seemingly absent in the type species of *Fordilla*, *Fordilla troyensis* Barrande, 1881, but present in *Fordilla sibirica* Krasilova, 1977 and *Fordilla germanica* Elicki, 1994.

Peel (2021a) concluded that *Tuarangia* was the most derived member yet known of an early clade, together with the pseudo-bivalved *Pseudomyona* Runnegar, 1983, within Class Rostroconchia Pojeta, Runnegar, Morris & Newell, 1972, after documenting the evolution of *Pseudomyona* in the Miaolingian of North Greenland. Peel (2021a) emended the Order Tuarangiida accordingly, although this action does not exclude *Tuarangia* from

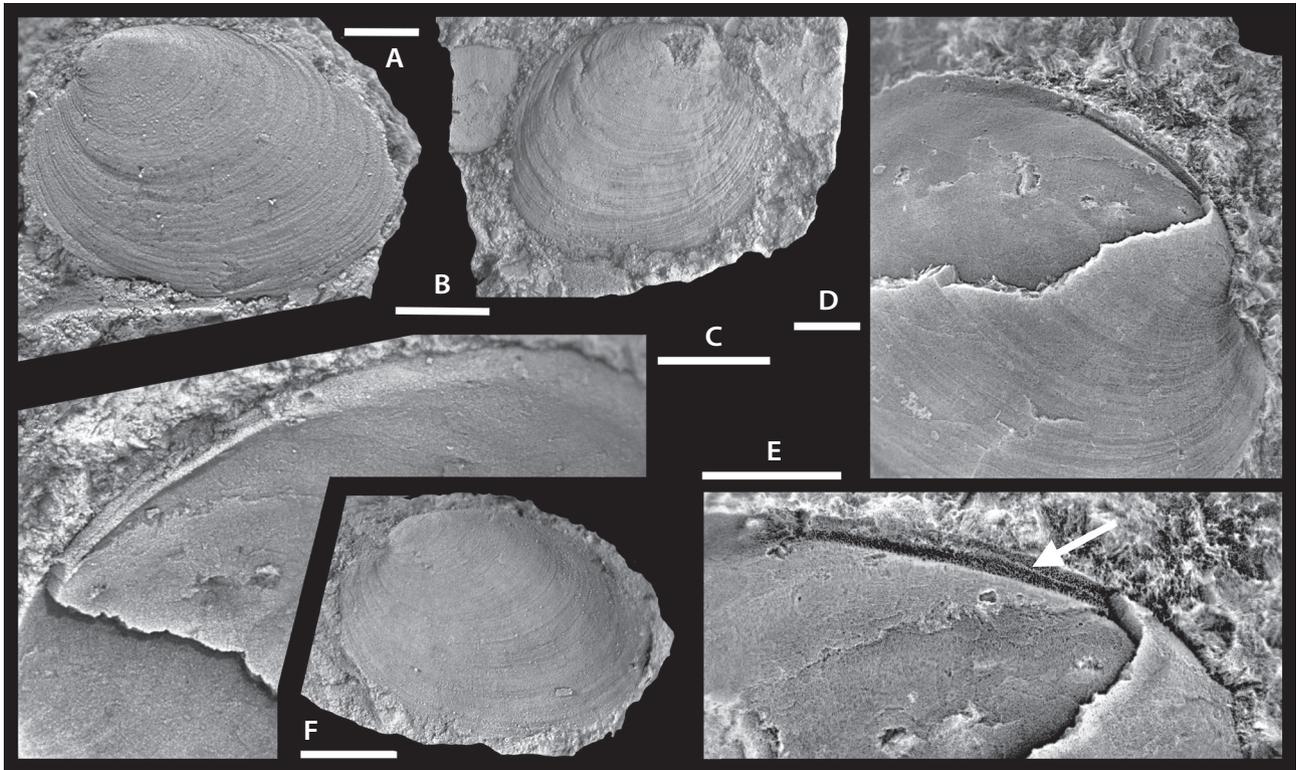


Figure 3. *Fordilla troyensis* Barrande, 1881, Bastion Formation, Cambrian Series 2 (Stage 4), Kap Weber, North-East Greenland. A – MMH (MGUH) 3516, left valve. B – MMH (MGUH) 3514, right valve. C–E – MGUH 34307, detail of ligament area on interior of right valve (C), shown as inverted digital image (D, E). Arrow in E indicates median ridge. F – MMH (MGUH) 3515, left valve. Scale bars: 500 µm (A, C, D, E); 1 mm (B, F).

being ancestral to Class Bivalvia, or some of the bivalved groups currently placed therein. However, differences in the number and distribution of hinge teeth, shell structure and the age of first appearance indicate a separate origin of *Pseudomyona* and *Tuarangia* from that of *Fordilla* and *Pojetaia* (Runnegar & Pojeta 1992, Vendrasco *et al.* 2011, Vendrasco 2012, Peel 2021a).

Following revision of Tuarangiida (Peel 2021a), this paper examines the nominate genus of the other euprobranch order of Carter *et al.* (2011), the Order Fordillida, with a focus on material of *Fordilla* from the lower Cambrian (Cambrian Series 2, Stage 4) of Greenland. New information concerning the musculature and shell microstructure of *Fordilla* is presented in describing well-preserved specimens from the Aftenstjernesø Formation of North Greenland and the Bastion Formation of North-East Greenland, expanding earlier reports by Runnegar & Pojeta (1992), Skovsted (2004) and Vendrasco *et al.* (2011). Exceptionally preserved shell microstructure is replicated in a thin phosphatized layer on the valve interior, and includes exquisite details of the attachment surfaces of shell musculature.

Fordilla has an unusual history. The type suite was acquired by Silas W. Ford from the lower Cambrian (Cambrian Series 2, Stage 4) at Troy in New York State. Ford was a contemporary of Charles D. Walcott and

made significant contributions to the palaeontology of the Cambrian of easternmost New York State (Hernick 1999). Ford (1873, p. 139) gave a full description of a “Bivalve of uncertain class, gen. nov.?” but did not provide illustrations. He noted that isolated valves were frequently found together on the same hand specimen in limestone from Troy and this relative abundance of specimens on outcrop was later noted by Yochelson (1981). Ford sent five specimens to the Czech palaeontologist Joachim Barrande in Prague who formally proposed *Fordilla troyensis* (Barrande 1881, description of plate 361 in *Système Silurien du centre de la Bohême, Volume 6*). Barrande (1881) illustrated not only the five specimens sent to him, but also the package as he received it from Ford, concurring in the identification as Bivalvia. Some of Barrande’s (1881) illustrated specimens were re-illustrated by Pojeta *et al.* (1973). Pojeta (1975, p. 369; pl. 4, figs 1,2) designated as lectotype the specimen in the collections of the National Museum, Prague, that was illustrated by Barrande (1881, pl. 361, fig. 1) and by Pojeta *et al.* (1973, fig. 1b). Yochelson (1981, text-fig. 1) also illustrated material from the type lot, in addition to additional specimens from Troy.

Ford (1873) referred his material to the lower Potsdam, but Walcott (1886, p. 125), in restating Barrande’s (1881) discussion, proposed a middle Cambrian age. Specimens

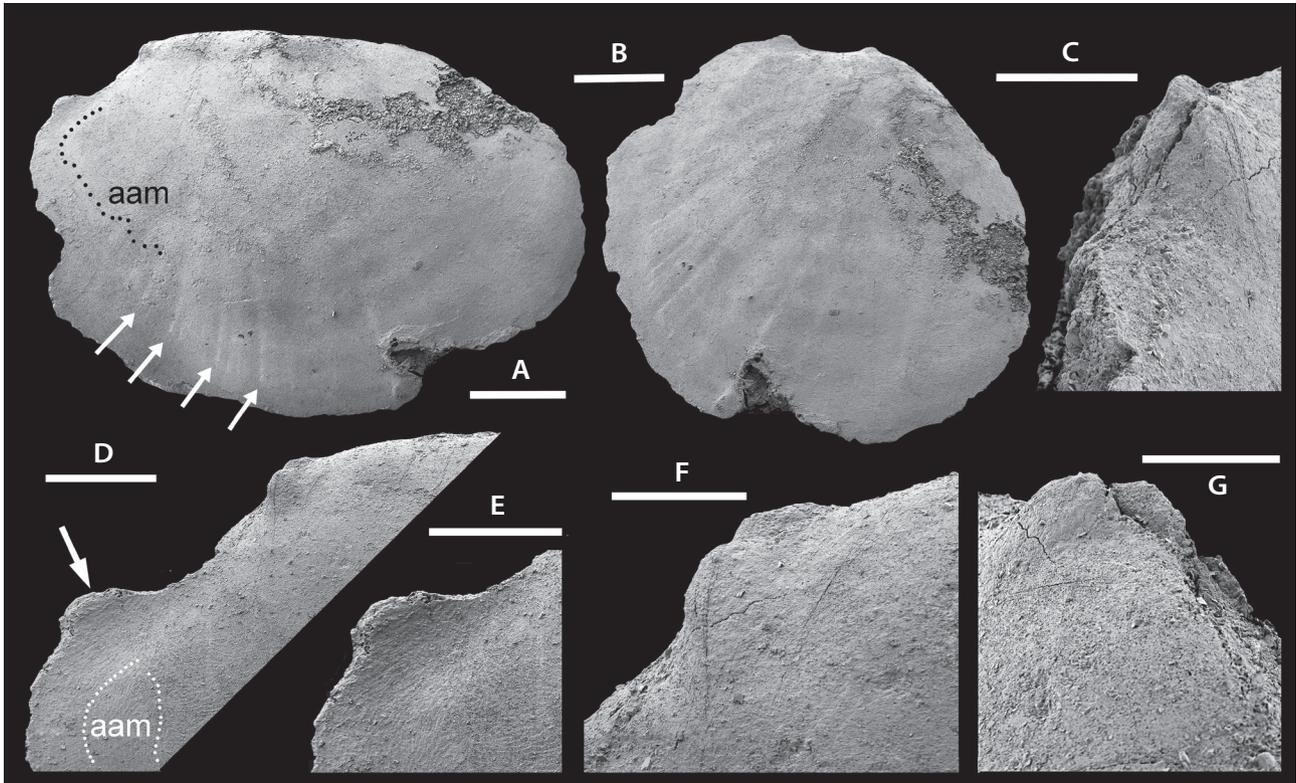


Figure 4. *Fordilla troyensis* Barrande, 1881, Bastion Formation, Cambrian Series 2 (Stage 4), C.H. Ostenfeld Nunatak, North-East Greenland. A–G – MGUH 27104 from GGU sample 314919, internal mould, left valve in lateral (A) and oblique lateral (B) views showing shallow radial furrows on antero-lateral surface (arrows in A) and detail of umbones (C, F, G). Margin of anterior adductor muscle scar indicated by dotted line (D), with detail of shell microstructure (E). Anterior thickening of internal mould indicated by arrow in D. SEM images courtesy of Christian B. Skovsted. Scale bars: 100 µm (C, F, G), 200 µm (D, E), 500 µm (A, B).

were probably collected from the Holcomville Member of the Browns Pond Formation (Cambrian Series 2, Stage 4, Dyeran Laurentian Regional Stage; Landing *et al.* in press) that underlies the Granville Formation. The collection has been referred to as a “Schodack” faunule and as an early Cambrian *Elliptocephala* faunule (Lochman 1956). Kouchinsky *et al.* (2022) commented that *Fordilla troyensis* was derived from the upper *Elliptocephala asaphoides* assemblage, Cambrian Series 2, upper Stage 3 or 4, from a continental slope debris flow of the Middle Granville Formation, in the Taconian allochthon of eastern New York State, U.S.A.

***Fordilla* from Greenland**

Fordilla was first described from Greenland by Poulsen (1932) from the Bastion Formation (Cambrian Series 2, Stage 4) of Hyolithus Creek, 3 km north-west of Kap Weber, Andrée Land, North-East Greenland (Figs 2D, E; 3). Poulsen (1932) reported ten specimens with recrystallised calcareous shell that were interpreted as Lamellibranchiata (= Bivalvia), although Ulrich & Bassler (1931) and others summarised by Pojeta (1975) had con-

sidered *Fordilla troyensis* to be a conchostracan crustacean.

Skovsted (2004) illustrated an internal mould of *Fordilla troyensis* from acid residues of the Bastion Formation on C.H. Ostenfeld Nunatak, North-East Greenland (Fig. 2D) and a specimen from this locality is also described herein (Fig. 4). Fragments of phosphatic internal moulds with preserved shell microstructure from the Aftenstjernesø Formation of northern Nyeboe Land (Fig. 2C) were tentatively assigned to *Fordilla troyensis* by Peel & Skovsted (2021, fig. 3u).

In 1949, the Danish geologist Johannes C. Troelsen (1913–1992) collected small slabs of richly fossiliferous bioclastic dolostone from talus on the valley side north of Øvre Midsommersø (‘Upper Midsummer Lake’) in southern Peary Land (Fig. 2A). An undated hand written note accompanying the collection indicates that specimens, including *Fordilla troyensis*, were identified subsequently by Christian Poulsen (Copenhagen). Troelsen (1956) noted the occurrence of the fauna containing fragments of olenellid trilobites at the base of the Brønlund Fjord dolomite, currently recognised as the Aftenstjernesø Formation of the Brønlund Fjord Group (Ineson & Peel 1997; Fig. 2B), but the collection was seemingly

overlooked until relocated by Peel *et al.* (1974). The material contains numerous specimens of *Fordilla troyensis* preserved as isolated valves with recrystallised shell and as their internal moulds (Fig. 5).

On account of the widespread interest at that time in *Fordilla* as the oldest bivalve (Pojeta & Runnegar 1976; Pojeta 1978, 2000), I submitted the specimens from Øvre Midsommersø to John Pojeta Jr (U.S. Geological Survey, Washington DC). Runnegar & Pojeta (1992, fig. 1a, b) published details of the shell microstructure of one internal mould of a right valve, unfortunately without details of its derivation and curatorial status. Vendrasco *et al.* (2011, text-fig. 2) illustrated shell microstructure from the same specimen on the basis of SEM images supplied to him by Bruce Runnegar (University of California, Los Angeles), noting its derivation from the Aftenstjernesø Formation (Peel *in* Vendrasco *et al.* 2011, p. 828). Troelsen's material from Øvre Midsommersø is described herein, including the specimen with microstructure (MGUH 34316) illustrated by Runnegar & Pojeta (1992) and Vendrasco *et al.* (2011), and a partially exfoliated left valve (MGUH 34312) illustrated by Pojeta (2000, fig. 1d).

Geological background. – Currently described specimens of *Fordilla* from Greenland are derived from the Aftenstjernesø Formation at Øvre Midsommersø in North Greenland, and the upper Bastion Formation at Kap Weber and C.H. Ostenfeld Nunatak, North-East Greenland. (Fig. 2). The Aftenstjernesø Formation is the lowest formation in the carbonate-dominated Brønlund Fjord Group, a sedimentary complex that progrades across the platform margin and shelf northwards into the deepwater trough succession of the transarctic Franklinian Basin (Higgins *et al.* 1991, Ineson *et al.* 1994, Ineson & Peel 1997). North of the lakes Øvre Midsommersø and Nedre Midsommersø ('Upper and Lower Midsummer lakes'; Fig. 2A), pale, cliff-forming strata comprising the lower part of the Brønlund Fjord Group typically form the sky line above mainly recessive slopes formed by dark siliciclastic sediments of the underlying Buen Formation (Cambrian Stages 3–4; Peel & Willman 2018). These siliciclastic sediments overlie a dolostone-dominated unit, the Portfeld Formation, of Ediacaran–Cambrian age (Willman *et al.* 2020).

Dolostones of the Aftenstjernesø Formation vary in thickness from 30 m to 130 m in outcrops from Lauge Koch Land and southern Peary Land (Ineson & Peel 1997; Fig. 2A). Fossils are confined to the basal few metres of dolomitic grainstones that form a distinctive, sediment-starved, outer ramp sequence rich in glauconite, phosphorite bioclasts, pyrite, and phosphatised stylolites and hardgrounds (Frykman 1980, Ineson & Peel 1997, Peel 2017). The horizon can be traced from Independence

Fjord westward to Navarana Fjord (Fig. 2A). Fossils are often abundant in these basal strata, although difficult to extract and mainly studied from residues after treatment in weak acetic acid (Peel 2020, 2021b; Peel *et al.* 2021).

A diverse assemblage from the basal Aftenstjernesø Formation at northern Navarana Fjord includes numerous hyoliths, helcionelloids, the oldest described palaeoloricates and other molluscs, *Chancelloria*, brachiopods and the trilobites *Serrodiscus* and *Ekvipagetia* (Peel 2020, 2021b; Peel *et al.* 2021). The bivalve *Pojetaia* is common at this locality, but *Fordilla* has not been recorded. This contrasts with the samples collected by J.C. Troelsen from Øvre Midsommersø, which contain abundant *Fordilla* but not *Pojetaia*. To a large extent, this apparent exclusivity reflects preservation and preparation. Usually, the large specimens of *Fordilla*, preserved as isolated valves (length 2–3 mm) are not phosphatised, and therefore not recovered from acetic acid residues, as is also the case with other calcareous shelly fossils such as trilobites in that size range or larger. However, the smaller specimens of *Pojetaia* (1 mm) are usually preserved as phosphatised internal moulds of articulated specimens and therefore occur commonly in acetic acid residues. *Pojetaia* and *Fordilla* both occur in northern Nyeboe Land (Peel & Skovsted 2021) and in the Bastion Formation of North-East Greenland (Skovsted 2004, 2006). The material of *Fordilla* from Øvre Midsommersø is unusual in that a thin layer of brown phosphate occurs on some of the available internal moulds, preserving in detail an impression of shell microstructures on the inner surface of the isolated valves.

Trilobites from the basal Aftenstjernesø Formation in North Greenland described by Blaker & Peel (1997) are characteristic of the *Elliptocephala asaphoides* assemblage of the Taconic allochthon in New York State and this formation was correlated with the Middle Granville Formation by Landing *et al.* (in press).

The Bastion Formation of North-Greenland crops out from Ella Ø in the south to C.H. Ostenfeld Nunatak in the north (Fig. 2D) and was assigned to the Vibeke Elv Group (originally inadvertently named as Vibeke Elr Group by Stouge *et al.* 2012, see Watt 2019) of the lower Cambrian to Middle Ordovician carbonate Kong Oscar Fjord Supergroup (Smith *et al.* 2004, Stouge *et al.* 2012). Following older descriptions listed by Watt (2019), the Bastion Formation was redefined by Cowie & Adams (1957), with a lower sandstone member overlain by shales and siltstones with beds and lenses of limestone. Rich faunas from the upper member of Cambrian Series 2 (Stage 4) age were described by Poulsen (1932), Skovsted & Peel (2001), Skovsted & Holmer (2003, 2005), Skovsted (2003, 2004, 2006), Malinky & Skovsted (2004), Skovsted *et al.* (2004), Peel & Skovsted (2005) and Stein (2008).

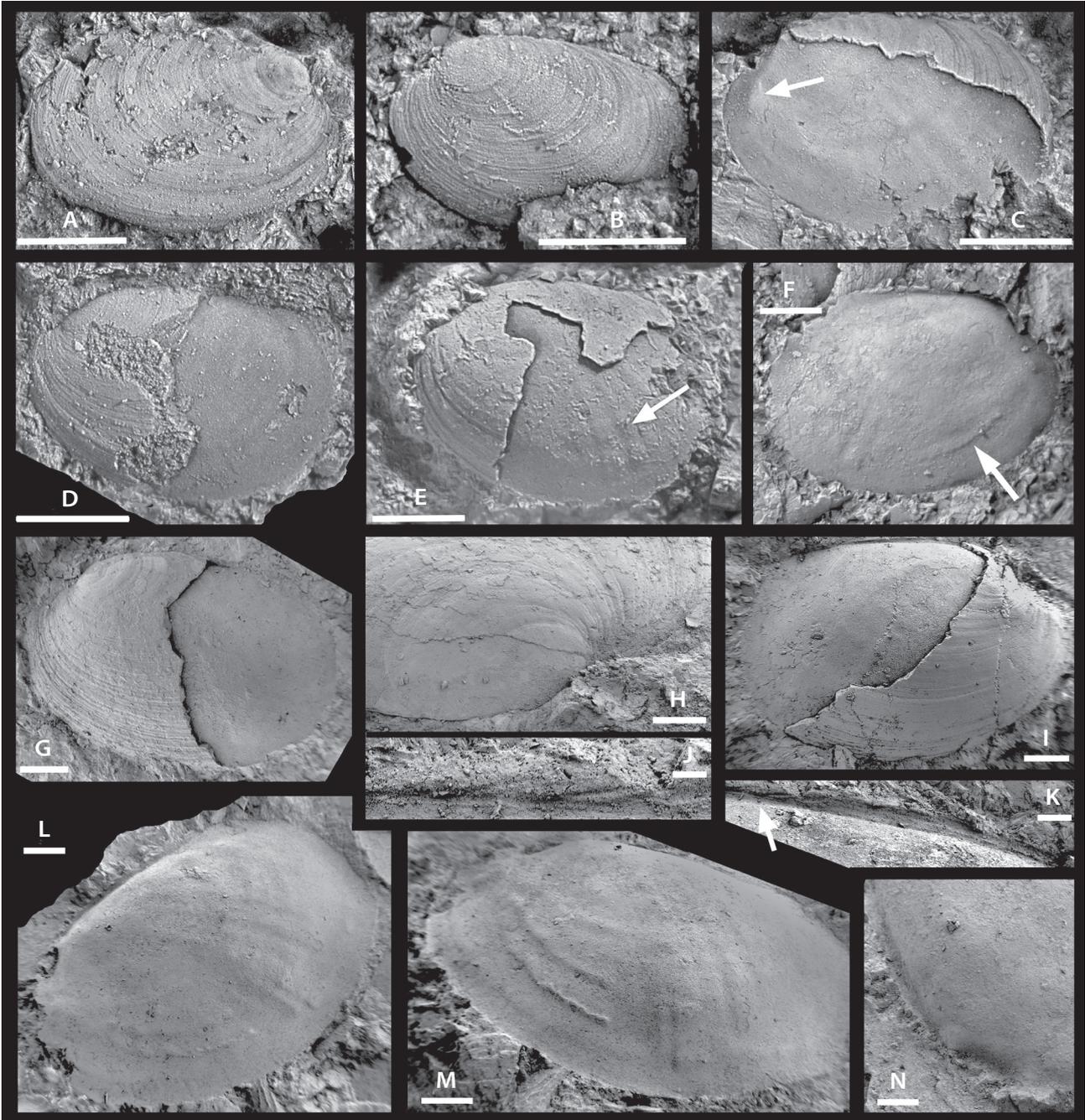


Figure 5. *Fordilla troyensis* Barrande, 1881, Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), J.C. Troelsen collection 57, Øvre Midsommersø, southern Peary Land, North Greenland. A – MGUH 33534, right valve. B – MGUH 34308, left valve. C – MGUH 34309, partly exfoliated left valve showing anterior adductor muscle scar on internal mould (arrow). D – MGUH 34310, partly exfoliated left valve. E – MGUH 34311, partly exfoliated left valve showing radial tracks of subsidiary muscles (arrow). F – MGUH 33533, internal mould, right valve, with pallial structure (arrow). G, H – MGUH 34312, partly exfoliated left valve, with detail of umbo (H). This specimen was illustrated by Pojeta (2000, fig. 1d). I–K – MGUH 34313, partly exfoliated right valve, with detail of ligament area (K), arrow locating enlarged area (J). L–N – MGUH 34314, internal mould of left valve with radial and commarginal muscle scar tracks (L, M) and detail of apical area (N). Scale bars: 50 µm (J); 100 µm (K); 200 µm (H, N); 500 µm (F, G, I, L, M); 1 mm (A–E).

Material. – Described specimens of *Fordilla* from North Greenland were collected by J.C. Troelsen while a member of the Danish Expedition to Peary Land, 1947–1950 (Dansk Pearyland Ekspedition, 1947–1950). Troelsen collection 57 (6th April 1949) consisted of small

loose blocks of the Aftenstjernesø Formation (Brønlund Fjord Dolomite of Troelsen 1949, Ineson & Peel 1997) picked from talus slopes on the northern side of Øvre Midsommersø, at an altitude of 696 m above lake level (approximate position 82° 12' N, 35° 25' W; Peel *et al.*

1974; Fig. 2A). There is no doubt that the talus material is derived from the basal member of the Aftenstjernesø Formation (Fig. 2B), as noted by Troelsen (1956). Troelsen's collection contains about 15 specimens of *Fordilla* in addition to the specimens illustrated herein.

Material of *Fordilla* from the Bastion Formation (Cambrian Series 2, Stage 4) of North-East Greenland studied by Poulsen (1932; Fig. 3) was collected by Christian Poulsen, Alfred Rosenkrantz and Sigurd Hansen during the Danish East Greenland Expedition of 1929 at Hyolithus Creek, Kap Weber, Andrée Land (73° 30' N, 24° 42' W; Fig. 2D, E). In addition to figured specimens (MMH (MGUH) 3514–3516), four additional specimens were examined from collection GM 1936.125 in the collections of the former Geological Museum, now integrated into the Natural History Museum of Denmark, Copenhagen. One of these specimens is illustrated here (Fig. 3C–E).

GGU sample 314919 (containing MGUH 27104; Fig. 4) was collected in 1988 by J.S. Peel and M.P. Smith from about 125 m above the base of the Bastion Formation, at the northern tip of C.H. Ostenfeld Nunatak, North-East Greenland (74° 22.5' N, 23° 07' W; Skovsted 2004, 2006; Fig. 2D).

Institutional abbreviations. – GGU – Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark. MGUH – Geological Museum, Copenhagen (formerly the Mineralogical Museum – MMH), now part of the Natural History Museum of Denmark. PMU – Palaeontological collection of the Museum of Evolution, Uppsala University, Uppsala, Sweden. SMNH – Swedish Museum of Natural History, Stockholm, Sweden, USNM – Natural History Museum, Smithsonian Institution, Washington DC, U.S.A.

***Fordilla troyensis* from North Greenland**

Available specimens of *Fordilla troyensis* from New York State (Fig. 1A–C) attain a length of 4.5 mm, which is about 50% larger than the largest specimens from North Greenland (Fig. 5). In lateral view, specimens from the Aftenstjernesø Formation in North Greenland vary in shape from oval (Fig. 5E) to elongate (Fig. 5A). The apex is located at about 20% of the distance from the sub-apical (anterior) to the supra-apical (posterior) margin, compared to about 35% in *Fordilla sibirica* and *Fordilla germanica*, and 30% in *Fordilla* sp. from Turkey (Elicki & Gürsu 2009, table 3). Ornamentation consists of commarginal growth lines, which are periodically more strongly expressed (Figs 1A–C, 5B). A weak radial striation is seen in some specimens from New York State (Fig. 1A).

In several specimens from the Aftenstjernesø Formation, a slightly elevated, smooth early growth stage

about 400 µm in length is delimited from the later shell (maximum length about 2 mm) by an increase in prominence of the commarginal ornamentation, although weak growth lines are visible within this early stage. (Fig. 5A, B, H). Runnegar & Bentley (1983) recognised prodissoconchs 1 and 2 in *Pojetaia runnegari* but Runnegar (2007, fig. 1) concluded that only a single prodissoconch was present in *Pojetaia runnegari*, as also seems to be the case in *Fordilla troyensis* from North Greenland. The umbones are close together, as seen in the articulated specimen from North-East Greenland (Fig. 4) and also a specimen from Bornholm, Denmark, originally described by Poulsen (1967; Fig. 6), suggesting limited opening of the valves (Savazzi 1987, Ubukata 2000).

Internal moulds of *Fordilla troyensis* from New York generally display prominent swellings representing muscle scars deeply impressed into the thick shell (Pojeta 1975, Yochelson 1981) but such structures are much less strongly expressed in material from the Aftenstjernesø Formation. Three or four radial grooves and intervening broad, rounded ridges on the supra-apical flanks culminate in muscle scars (Fig. 5E, F, L). Periodic commarginal ridges can be traced across the lateral areas but may be prominent, with a beaded structure, on the sub-apical flanks (Fig. 5F, L, M).

Ligament

Internal moulds of *Fordilla sibirica* illustrated by Krasilova (1977) and Pojeta (1978, 1987, 2000) display a prominent dorsal ridge formed along the hinge line by the opisthodetic ligament (Fig. 7). Such a strongly defined ridge is not recognised in *Fordilla troyensis* from Greenland on the illustrated internal mould of an articulated specimen from the Bastion Formation (Fig. 4), but an acute ridge is seen in the articulated specimen illustrated by Poulsen (1967) from the Norretorp Member ('Green Shales') of the Læså Formation of Bornholm, Denmark (Fig. 6).

Specimens from the Bastion Formation at Kap Weber (Poulsen 1932; Fig. 3) and from the Aftenstjernesø Formation (Fig. 5) are disarticulated but the dorsal margin lacks deep impression of a ligament in the hinge. However, the extent of the opisthodetic ligament in the valve margin is seen (Fig. 3C–E) where a median ridge within the shell thickness extends about half way from the apex to the supra-apical (posterior) margin (arrow in Fig. 3E). In a second specimen, a series of parallel striations terminates posteriorly in oblique grooves (Fig. 5I–K). It is uncertain if the various striations primarily reflect layered shell structure in cross-section or layering within the attached ligament, although the structures correspond to the surface between the two. The fine lamination

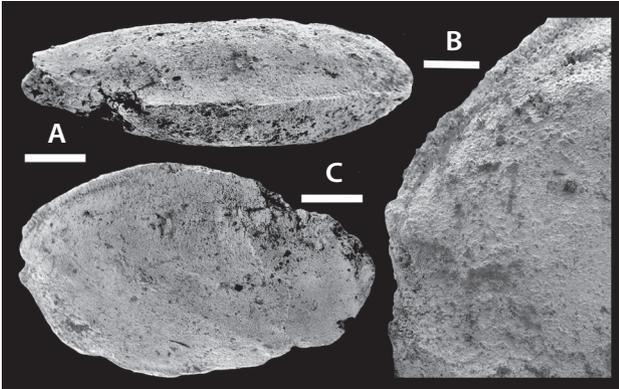


Figure 6. *Fordilla troyensis* Barrande, 1881, MMH (MGUH) 10544, internal mould of conjoined valves, Cambrian Series 2 (Stage 3), Norretorp Member ('Green Shales') of the Læså Formation (Poulsen 1967, Nielsen & Schovsbo 2007); locality 139 (Grødbyå) of Poulsen (1967), south coast of Bornholm, Denmark. A – dorsal view, anterior to right. B – detail of early growth stage showing umbones separated by hinge line and ligament. C – oblique lateral view (anterior to left) showing ligament. Scale bars: 200 µm (B); 500µm (A, C).

illustrated by Vendrasco *et al.* (2011, pl. 1, figs 7, 8) in the ligament of *Pojetaia runnegari* has not been observed in the Greenland material, where the coarsely laminated ligament has a granular texture, although fine incipient fibres are developed perpendicular to the surface of the internal mould (Fig. 3E, arrow). The ligament may be described as planivincular: simple, slightly arched and attached to unmodified valve margins. Textural differentiation into an inner granular layer and an outer laminar layer within ligaments of this type described by Waller (1990) and Ubukata (2000) is not recognised and the relatively coarse layering seems to have been developed throughout. However, an outermost layer corresponding to the periostracum may have degraded diagenetically together with this organic outer layer. Jermak (1988) described in detail the two-layer ligament structure of *Fordilla sibirica*, allowing interpretation of an inner compressional ligament and an outer laminated ligament representing a continuation of the periostracum.

Hinge line

The description of the genus *Fordilla* given by Pojeta (1975, p. 367), based on *Fordilla troyensis* from the type area around Troy in New York State, noted the lack of anterior and posterior dentition. In proposing *Fordilla sibirica*, Krasilova (1977, fig. 4a; pl. 2, figs 5–7) illustrated a sigmoidal deflection of the hinge line on the sub-apical (anterior) surface of the internal mould, also clearly visible in an internal mould illustrated by Pojeta (1978, pl. 1, figs 4–6; Fig. 7) of a specimen from the early Cambrian of the Lena River, Siberia, as *Fordilla cf. troyensis*. Pojeta (1987, fig. 14.112e) and Pojeta (2000, fig. 1b) later referred this

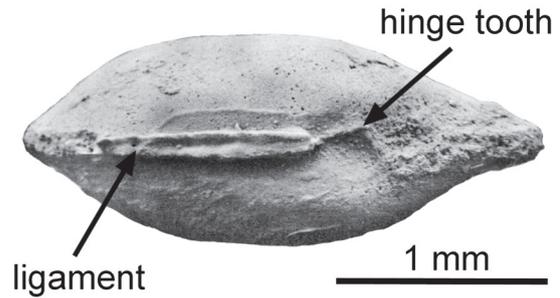


Figure 7. *Fordilla sibirica* Krassilova, 1977, USNM 247821, internal mould in dorsal view showing hinge tooth on sub-apical surface, anterior to right. Cambrian Series 2, Khara-Ulach, Chekurovka, Lena River, Siberia. Image courtesy of John Pojeta Jr.

specimen to *Fordilla sibirica*. However, *Fordilla sibirica* was interpreted as a junior synonym of *Fordilla troyensis* by Jermak (1986), who also illustrated the sigmoidal bend in the anterior hinge line (Jermak 1986, pl. 15, fig. 4). Jermak (1988) gave a well-illustrated description of the hinge of this material attributed to *Fordilla* based on specimens from the Tyuser Formation, northern Siberia. He proposed that the sigmoidal bend did not represent deflections (hinge teeth) of the hinge line, as supposed by Krasilova (1977), but was produced by internal chondrophores, indicating the presence of a ligament on the sub-apical anterior surface (Jermak 1988, p. 182), a feature also discussed by Yochelson (1981). Locking of the sub-apical anterior hinge was thus considered to result from ligament action between the valves from interlocking chondrophores rather than the interdigitation of hinge teeth on the shell margin.

This interpretation does not appear to have been taken up by other workers and the structure was interpreted by Pojeta (1978, 1987, 2000) and Kouchinsky *et al.* (2022) to represent the interaction of a single cardinal tooth in each valve, as also reported by Elicki & Gürsu (2009) in *Fordilla germanica* Elicki, 1994 from the Charlottenhof Formation (Cambrian Stage 4) of the Görlitz Synclinorium of Germany (Elicki 1994, fig. 11) and *Fordilla* sp. from the Çal Tepe Formation of Turkey (Elicki & Gürsu 2009, pl. 2g). Dentition along the supra-apical (posterior) hinge line has not been reported.

The tooth-bearing *Fordilla sibirica*, known from the Tuysler Formation (Cambrian Stage 3, Atdabanian Regional Stage) of Siberia (Kouchinsky *et al.* 2022) seems to be the oldest recognised species of *Fordilla*. *Fordilla troyensis*, in which hinge teeth are lacking, is characteristic of Cambrian Stage 4. The development of an anterior hinge tooth in *Fordilla sibirica* may reflect the more posterior position of the apex when compared to *Fordilla troyensis* and a need for stabilisation of the anterior part of the hinge line.

In agreement with the description of *Fordilla troyensis* by Pojeta (1975), hinge teeth are not recorded here on the

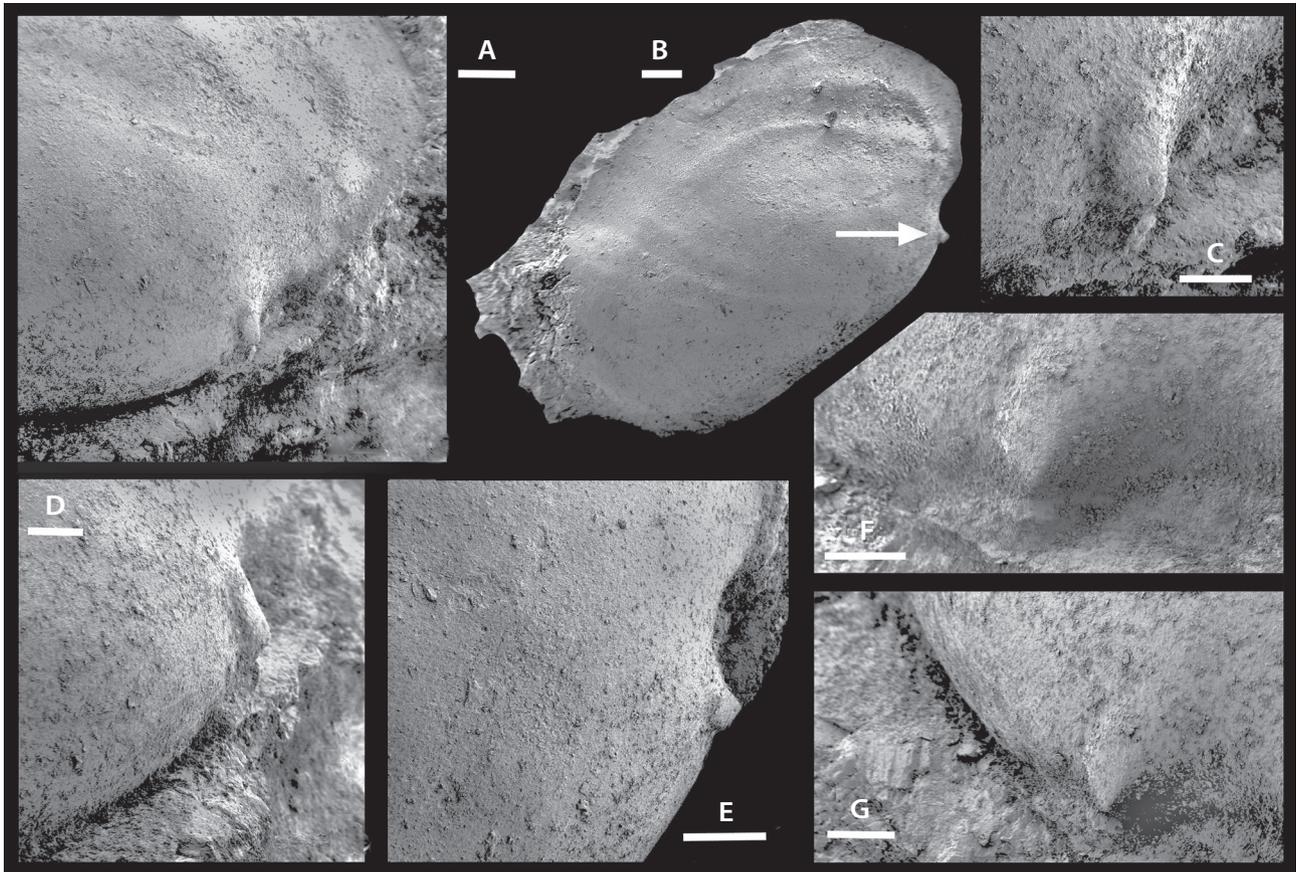


Figure 8. *Fordilla troyensis* Barrande, 1881, MGUH 34315, Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), J.C. Troelsen collection 57, Øvre Midsommerso, southern Peary Land, North Greenland. A, C–G – details of apical spike on internal mould (arrow in B). B – internal mould of left valve with prominent commarginal ridges on sub-apical surface, oriented with hinge line at bottom right, and with apical spike marked by arrow. Scale bars: 100 µm (C, D, F, G); 200 µm (A, E), 400 µm (B).

sub-apical surface of an internal mould with conjoined valves described by Skovsted (2004, fig. 9a–c not d–f) from the Bastion Formation of North-East Greenland (Fig. 4). This part of the hinge is often not well exposed in disarticulated specimens from the Aftenstjernesø Formation in Peary Land, but where visible, it is straight, without teeth or any deflection (Figs 5N; 8A, F).

In internal moulds of *Pojetaia runnegari* Jell, 1980 illustrated by Runnegar & Bentley (1983, fig. 7f, g), two teeth are present on the sub-apical hinge line in one valve (the left or the right) located either side of a single tooth in the opposing valve. A similar situation is seen on internal moulds of *Pojetaia runnegari* from Cambrian Stage 4 in Greenland (Skovsted 2004, fig. 8q; Peel 2021b, figs 9.14, 9.16; Figs 1D, E; 9). A rather different pattern of teeth, reminiscent of *Fordilla sibirica*, is seen on a globose internal mould described as *Pojetaia robsonae* by Peel & Skovsted (2021) from the Kane Basin Formation of similar age in eastern Nunavut, Arctic Canada (Fig. 1H).

Gaps or sinuses between the left and right valves have not been observed in *Fordilla troyensis*. A small swelling of the internal mould at the anterior end of the hinge line

of one specimen (Fig. 4D, E, arrow) might suggest the presence of a small sinus or gape, but this is not confirmed. Pojeta & Runnegar (1976, fig. 12) discussed water flow through the mantle cavity of *Fordilla*, considering it most likely that inhalant and exhalant currents were posterior, as in most bivalves, although anterior to posterior water flow occurs in present day arcids (Allen 1985). The small size of the structure in the specimen from North-East Greenland and its location adjacent to the hinge likely preclude its interpretation as the site of an inhalant stream. However, commarginal shell microstructure in the small sail-like extension of the sub-apical surface at this point on internal moulds of *Fordilla* from North Greenland seems to support the presence of a small gape, albeit of uncertain function (Fig. 10E).

Shell microstructure

Shell microstructure is preserved on some phosphatised internal moulds of *Fordilla troyensis* as an impression of the inner surface of the valve and as such represents

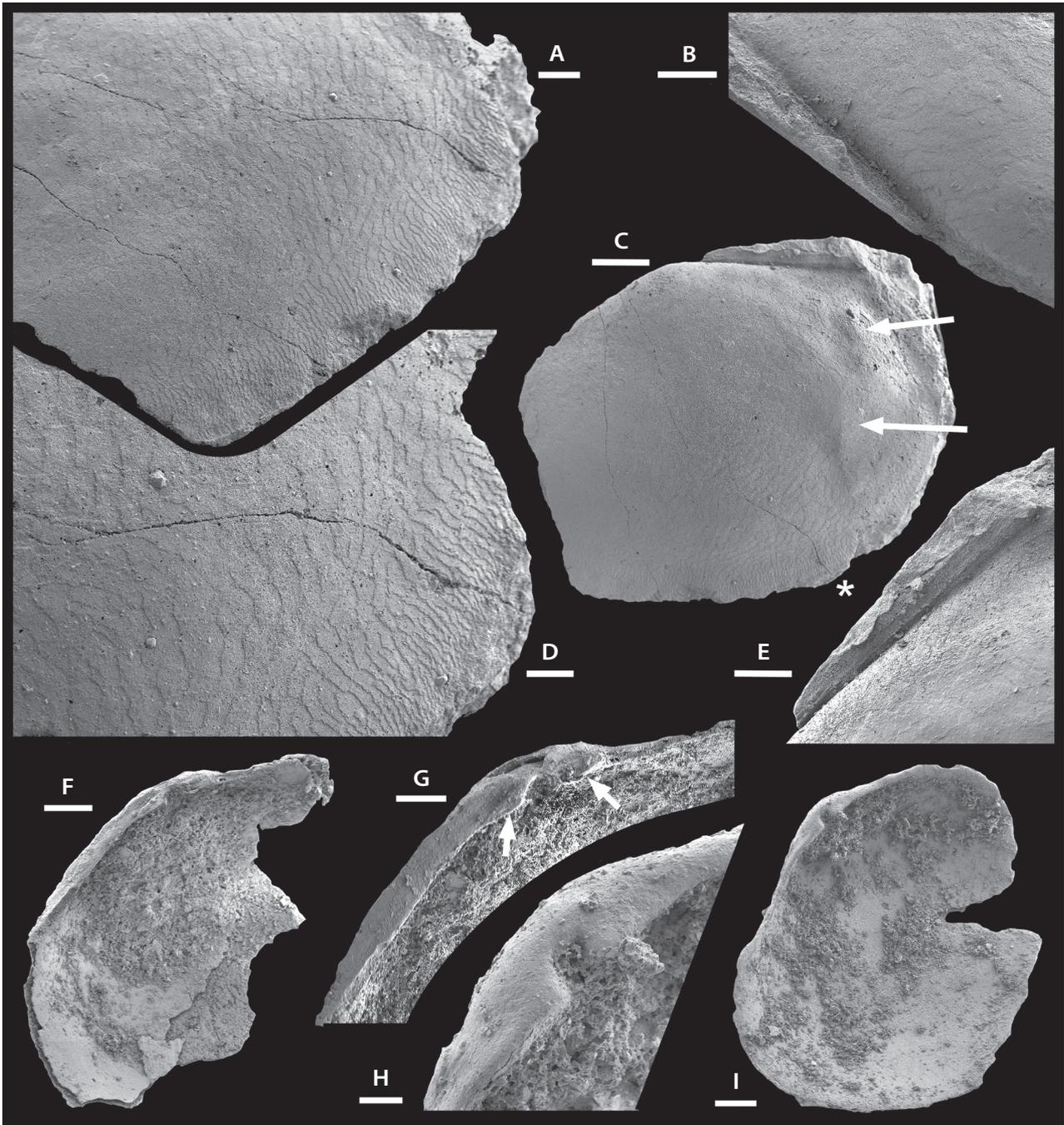


Figure 9. *Pojetaia runnegari* Jell, 1980. Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), Løndal, southern Peary Land, North Greenland. • A–E, PMU 21535 from GGU sample 255530, internal mould collected by P. Frykman (14th July 1979) from about 1.4 m above the base of the Aftenstjernesø Formation in Løndal (Fig. 2A; 82° 17.5' N, 37° 03' W). A, D – detail of impression of shell microstructure at ventral margin, located by asterisk in C. B – detail of shell microstructure adjacent to ligament, rotated relative to C. C – lateral view, arrows indicate posterior adductor muscle scar. Asterisk locates A and B. E – impression of ligament attachment zone on valve margin. • F–I – specimens from GGU 255513, collected by P. Frykman (12th July 1979) from about 1.5 m above the base of the Aftenstjernesø Formation in Løndal (Fig. 2A; 82° 16' N, 37° 03' W). F, G – PMU 21536, phosphate encrusted left valve showing hinge teeth (arrowed in G) on either side of median socket. H, I – PMU 21537, phosphate encrustation of right valve with socket of tooth from left valve. Scale bars: 50 µm (D, H); 100 µm (A, B, E, G); 200 µm (C, F, I).

a mirror image of that surface (Fig. 11, located by asterisk in Fig. 12A). In the following description structures are described as they are preserved on an internal mould representing the internal surface of a well-preserved right

valve (Figs 10A, 12A). This is the same specimen illustrated by Runnegar & Pojeta (1992, fig. 1a).

The internal mould surface of the valve is dominated by a series of shallowly inclined, step-like imbricate

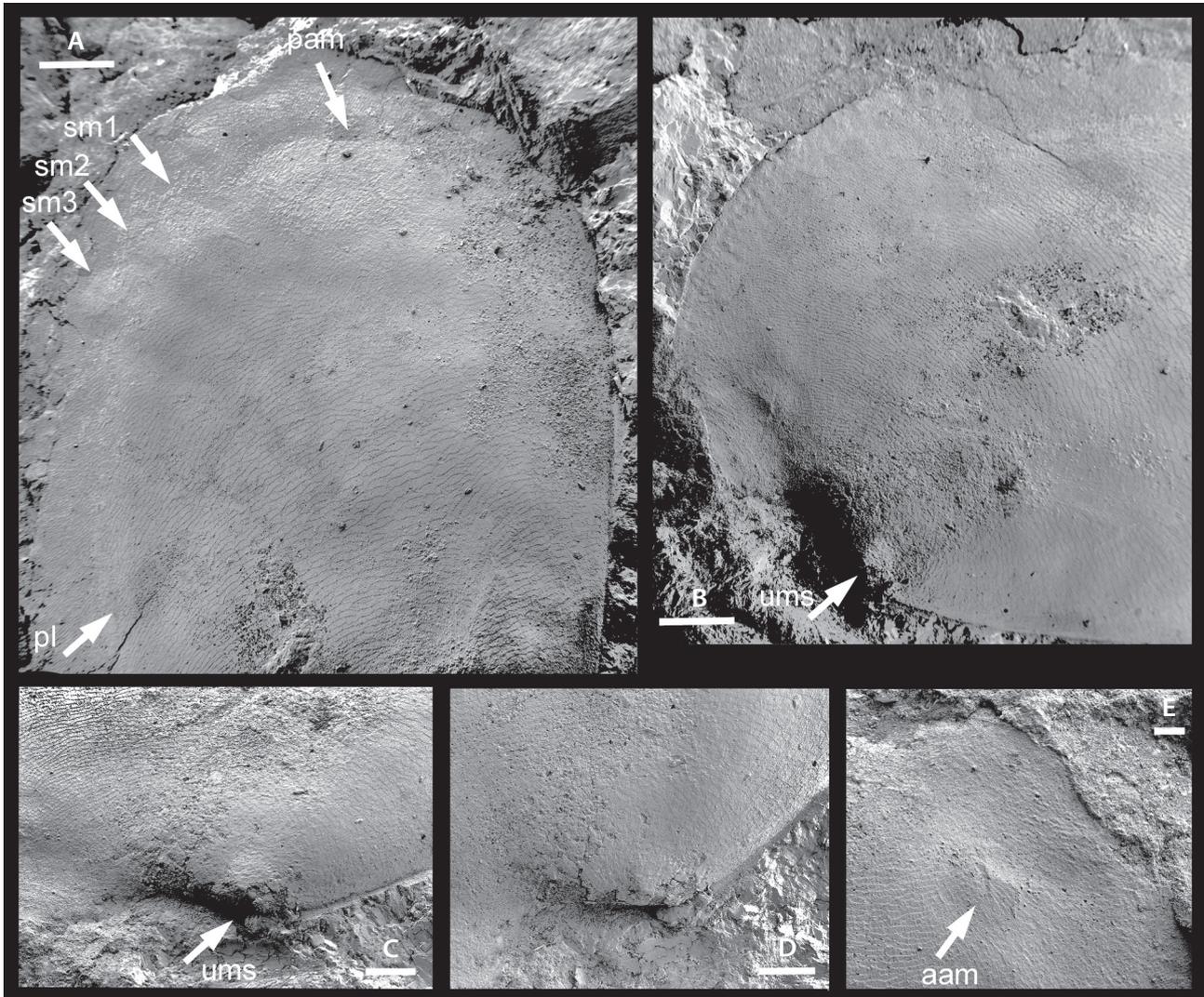


Figure 10. *Fordilla troyensis* Barrande, 1881, MGUH 34316, internal mould, right valve. Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), J.C. Troelsen collection 57, Øvre Midsommersø, southern Peary Land, North Greenland. This specimen was illustrated by Runnegar & Pojeta (1992, fig. 1a, b). A – posterior margin in lateral view (posterior at top) showing posterior adductor muscle complex: pam – principal posterior adductor muscle scar; sm – subsidiary muscle scars; pl – pallial line. B – anterior margin in lateral view (ventral at top) showing umbonal muscle scar (ums) and shell microstructure. C – detail of umbonal area in lateral view (posterior to right) showing umbonal muscle scar (ums) and shell microstructure. Note imbricate lamellae perpendicular to hinge line on supra-apical surface (top right) but largely obscured by commarginal texture on sub-apical surface (bottom left), and showing radial lines on muscle scar. D – detail of umbonal muscle scar with radial ridges, posterior to right. E – junction of sub-apical surface and anterior margin showing anterior adductor muscle scar (aam) and shell microstructure; anterior to right. Scale bars: 50 μm (E); 100 μm (C, D); 200 μm (A, B).

lamellae, the crests of which maintain a high degree of parallelism as they traverse the lateral areas (Figs 10A; 12A, I). The lamellae are dominantly laterally continuous with a width of 10–20 μm between successive crests (Fig. 11). On the internal mould they are stacked such that the lowest lamellae in the imbricate series are closest to the apex, with the series stepping up through progressively higher, overlying, lamellae as the valve margins are approached (Figs 10A, 12I); on the shell interior this stacking order is reversed (compare Fig. 11A, C). Individual lamellae are traversed by closely spaced, irregular ridges producing a fibrous appearance that is

perpendicular to the lamellar crests (Fig. 11A) and 1–2 μm in width; the ridges correspond to grooves on the valve interior (Fig. 11C). The crests of the lamellae are oriented almost perpendicular to the dorsal valve margin but curve smoothly anteriorly across the lateral area to approach the anterior margin also perpendicularly (Figs 10A, B; 12A).

Around the distal edge of the valve, from the posterior to the anterior margin, the imbricate lamellose texture gives way to a narrow commarginal imbricate zone in which the lamellae are more closely spaced, typically less than half the distance between successive crests of that in the dominant central zone (Figs 12I, 13D–F). This

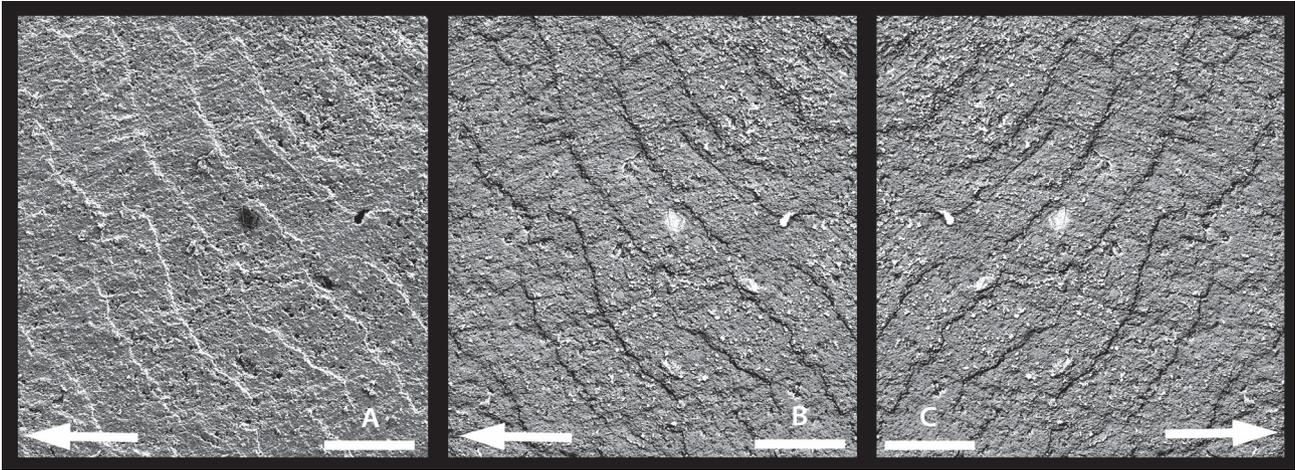


Figure 11. *Fordilla troyensis* Barrande, 1881, MGUH 34316, internal mould, right valve, Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), J.C. Troelsen collection 57, Øvre Midsommersø, southern Peary Land, North Greenland. Detail of imbricate lamellar microstructure on internal mould (A), digitally inverted with the conversion of dark tones to light to create a correct sense of relief on the shell interior (B) and mirrored to create a correct view of inner shell surface (C); located by asterisk in Fig. 9A; arrows indicate posterior. Scale bars: 20 μm .

feature is also seen in *Fordilla troyensis* from the Bastion Formation (Fig. 4A, D). Crests of lamellae in this marginal zone are perpendicular to the shell margin (Fig. 13B, D). At the posterior margin, they are also perpendicular to the crest orientation in the coarser lamellar pattern characteristic of the central area (Fig. 10A), but the orientation of the two patterns coincides at the anterior margin (Fig. 10B). Below the hinge line, on the sub-apical surface, a texture of commarginal discontinuous ridges, which also affects the ad-dorsal end of the anterior adductor muscle complex, is imposed on the imbricate lamellar patterns (Figs 10E; 12F, I). In general, the two lamellar patterns are separated by a commarginal belt of muscle attachment scars and pallial structures (Figs 5F, 12A, 13D), although the transition marked by the introduction of narrower lamellae and more numerous crests may occur closer to the ventral margin (Fig. 13D). Textures associated with the muscle attachment scars are discussed below.

The microstructure of *Fordilla troyensis* is generally similar to that of *Pojetaia runnegari* (Fig. 9A–C). Vendrasco *et al.* (2011) and Kouchinsky *et al.* (2022) noted that the central area of the valve in *Pojetaia runnegari* developed a polygonal pattern instead of the laterally continuous lamellae seen in *Fordilla troyensis*. This distinction is less clear in examined Greenland specimens of *Pojetaia*, although the lateral continuity is disturbed (Fig. 9A, left side). However, an internal mould from the Xinji Formation of China illustrated by Li *et al.* (2019, fig. 27a) shows similar lateral continuity of the lamellae in the central area of the valve to *Fordilla troyensis* from the Aftenstjernesø Formation (Figs 10A, 12A).

Similarity in shell microstructure between *Anabarella* and *Watsonella* from Siberia was noted by Kouchinsky (1999) who suggested a link to the earliest bivalves. Li

et al. (2021) recognised two shell layers, with an outer prismatic layer and an inner lamello-fibrillar layer showing a conspicuous crossed lamellar texture. In considering earlier descriptions, Li *et al.* (2019) considered the inner shell layer in *Anabarella* from the Xinji Formation of North China to be crossed foliated lamellar microstructure, but this crossed lamellar texture is unlike the low angle, imbricate lamellar microstructure of *Fordilla* and *Pojetaia*. Vendrasco *et al.* (2011) compared the shell microstructure of *Fordilla* and *Pojetaia* to the foliated aragonite of modern tergomyans described by Checa *et al.* (2009).

Muscle attachment scars

Muscle attachment scars described by Pojeta (1975; Fig. 14A) in topotype material of *Fordilla troyensis* consist of prominent elevations on the internal mould. In contrast, clearly elevated scars representing attachment sites embedded into the shell surface are generally absent or only partly developed in specimens from Greenland, and the position of muscles in several specimens is established from changes in the texture of shell microstructure. A notable exception is provided by an internal mould with a pronounced spike on the umbo (Fig. 8). The small size and pointed conical form preclude interpretation of this spine as an internal mould of the prodissoconch, as expressed on the shell exterior, as might otherwise be expected from its location (Fig. 5A, B, H). Not least, the substantial thickening of the shell subsequent to the initial formation of the prodissoconch rules out the suggestion. In some specimens of *Pojetaia* from the Aftenstjernesø Formation, the deep socket formed by the hinge tooth in one valve produces a perforation or notch in the opposing

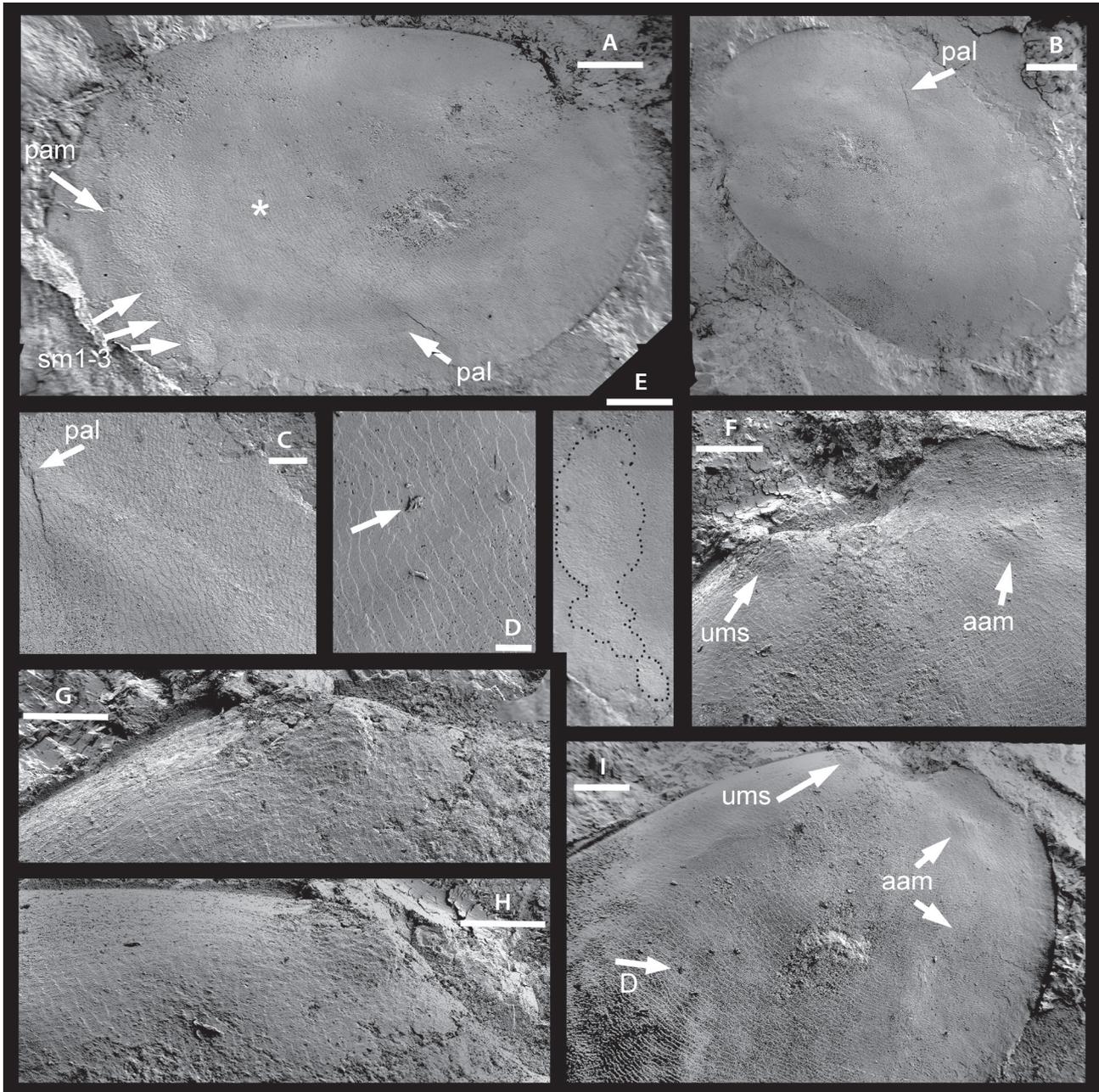


Figure 12. *Fordilla troyensis* Barrande, 1881, MGUH 34316, internal mould, right valve. Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), J.C. Troelsen collection 57, Øvre Midsommersø, southern Peary Land, North Greenland. This specimen was illustrated by Runnegar & Pojeta (1992, fig. 1a, b). A, E – lateral view showing posterior adductor muscle complex (interpretive dotted outline in E): pam – principal posterior adductor muscle scar; sm – subsidiary muscle scars; asterisk locates detail of microstructure in Fig. 11. B, C – lateral view (dorsum down to left) showing pallial line (arrow pal), detail in C. D, F–I – anterior in lateral view (F, I), with umbonal muscle scar (ums) and anterior adductor muscle scar (aam), shown in detail in G, H, and shell microstructure at apex and sub-apical margin. Arrow D in I locates detail of imbricate lamellar shell structure in D; upper arrow aam locates detail of anterior margin microstructure in Figs 10E, 12F. Scale bars: 50 µm (D); 75 µm (C); 100 µm (F, G); 200 µm (I); 300 µm (A, B, E).

valve (Fig. 9H, I) that likely would form a spike on the corresponding internal mould, but the absence of hinge teeth in the *Fordilla* specimen (Fig. 8) excludes this interpretation.

In terms of location, comparison with muscle scars in other specimens (Figs 10B–D, 12G–I) indicates that

the spine should be attributed to an umbonal muscle attachment scar (Fig. 14B, C). While slightly elevated, the scar is clearly delimited from the surrounding impression of the shell surface by its sculpture, which obscures the imbricated lamellae of the surrounding shell surface (Figs 10C–D, 12F–H). Krasilova (1977, fig. 1a, b) identified

such a scar in *Fordilla sibirica* Krasilova, 1977, although it is scarcely visible in her published photographs due to poor reproduction. Similar spines interpreted as pedal elevator muscle scars have been described in *Modiodonta gothlandica* Liljedahl, 1989 and the trigonoid *Silurozodus gotlandicus* Liljedahl, 1992 from the Silurian of Gotland, Sweden (Liljedahl 1989, 1992, 1994). Johnston & Zhang (1998) reviewed spinose pedal scars in *Sinodora cheni* Johnston & Zhang, 1998 from the Devonian of China, and proposed that the development of a single umbonal pedal elevator scar in each valve is an apomorphic feature of trigonioidean bivalves.

Anterior adductor muscle complex

The general form of the anterior adductor muscle scar complex was clearly indicated by Pojeta (1975) in *Fordilla troyensis* from New York State, although fine details of the muscle scar margins and surface texture are not clear (Fig. 14A). A small pedal muscle was identified near the umbo and the anterior adductor continued into a broad pallial line along the ventral margin. Krasilova (1977) recognised an obscure antero-ventral area of mantle muscles in *Fordilla sibirica* and two small pedal muscle scars (Fig. 14B), in addition to the dorso-umbonal scar.

The main area of the anterior adductor muscle scars complex is not clearly recognised on internal moulds of most specimens of *Fordilla troyensis* from the Aftenstjernesø Formation, but the antero-dorsal margin of the scar may be elevated (Figs 5C arrow, 12F) and seemingly represents the pedal muscle scar identified by Pojeta (1975; see Fig. 14A). However, the entire anterior adductor muscle complex in this specimen appears to be divided into a series of closely juxtaposed, equidimensional scars extending along the antero-ventral margin to near the mid-line (Fig. 12I). This series passes posteriorly into a pallial line which forms a much narrower trace in shell microstructure than the ridge indicated by Pojeta *et al.* (1973; Figs 13D, E; 14C).

In several specimens, this extension is marked on the internal model as one or more (Fig. 5L, M) commarginal ridges indicating periodic halts of the growing shell. Interpretation of several closely juxtaposed scars, rather than a single continuous scar, is seemingly confirmed by the presence of radial channels impressed into the surface of the antero-lateral surface of some internal moulds (Fig. 4A, B) that represent ridges on the valve interior. Similar structures are commonly well developed on the postero-lateral surfaces where they also suggest separation of individual closely spaced muscle scars (Figs 5E, 10A). As is the case with the umbonal muscle scar (Fig. 12G, H), the most dorsal scar in this series displays a texture at variance with that of the surface of the lateral areas, most

clearly seen on its posterior margin (Figs 10E aam, 12F aam). Part of the anterior scar margin can be discerned in a specimen from the Bastion Formation (Fig. 4A, D aam).

Posterior muscle complex

Re-study of the internal mould of the right valve illustrated by Runnegar & Pojeta (1992, fig. 1a, b) reveals a complex of muscle scars at the posterior margin (Figs 10A, B; 12A, E; pam and sm) not visible in their published figure. The scars are identified by differences in their microstructure and reflectivity from the surrounding surface. The principle posterior adductor muscle (pam) preserves a dappled texture readily distinguished from the fine radial structure of the valve margin (Fig. 13A–C). A transitional zone of disturbed lamellae occurs between the pam and the prominent laterally continuous lamellae of the valve interior (Fig. 13B). Scars of three subsidiary muscle (sm1–3), loosely delimited from each other by shallow grooves on the internal mould, form a line extending from the ventral margin of the posterior adductor almost to the valve margin (Figs 10A; 12A, E; 13B), with the most distal of these (sm3 in Figs 10A, 12A, 13D) located admarginal of the narrow commarginal line interpreted as the pallial line (pal). The pallial line is indicated by a transitional band between the coarse lamellar structure of the valve centre and the finer, radial microstructure at the valve margin (pal in Fig. 13D) that widens from a point at sm3 across the lateral surface towards the anterior adductor muscle complex.

Discussion

The widespread notion that *Fordilla* was derived from helcionelloids such as *Anabarella* or *Watsonella* (Pojeta 1975, 1978; Pojeta & Runnegar 1976; Kouchinsky 1999; Carter *et al.* 2000, 2006; Vendrasco *et al.* 2011; Vendrasco 2012) largely depends on their contemporary early Cambrian age, similar degree of lateral compression and the location of the apex close to the sub-apical margin. *Watsonella crosbyi* has a similar lateral profile to *Fordilla*, with elongation towards the supra-apical margin, and lateral shields that are strongly convex towards the ventral margin; the apex is also close to the sub-apical margin (Devaere *et al.* 2013). However, the greatest shell height in *Watsonella* tends to be near to the sub-apical margin while it is generally closer to the supra-apical margin in *Fordilla* (Figs 1A, 5D–G). In contrast with *Watsonella*, the ventral margin in *Anabarella plana* is only shallowly convex in lateral perspective and the apex of the more slowly expanding and strongly coiled shell generally overhangs the sub-apical margin (Gubanov & Peel 2003).

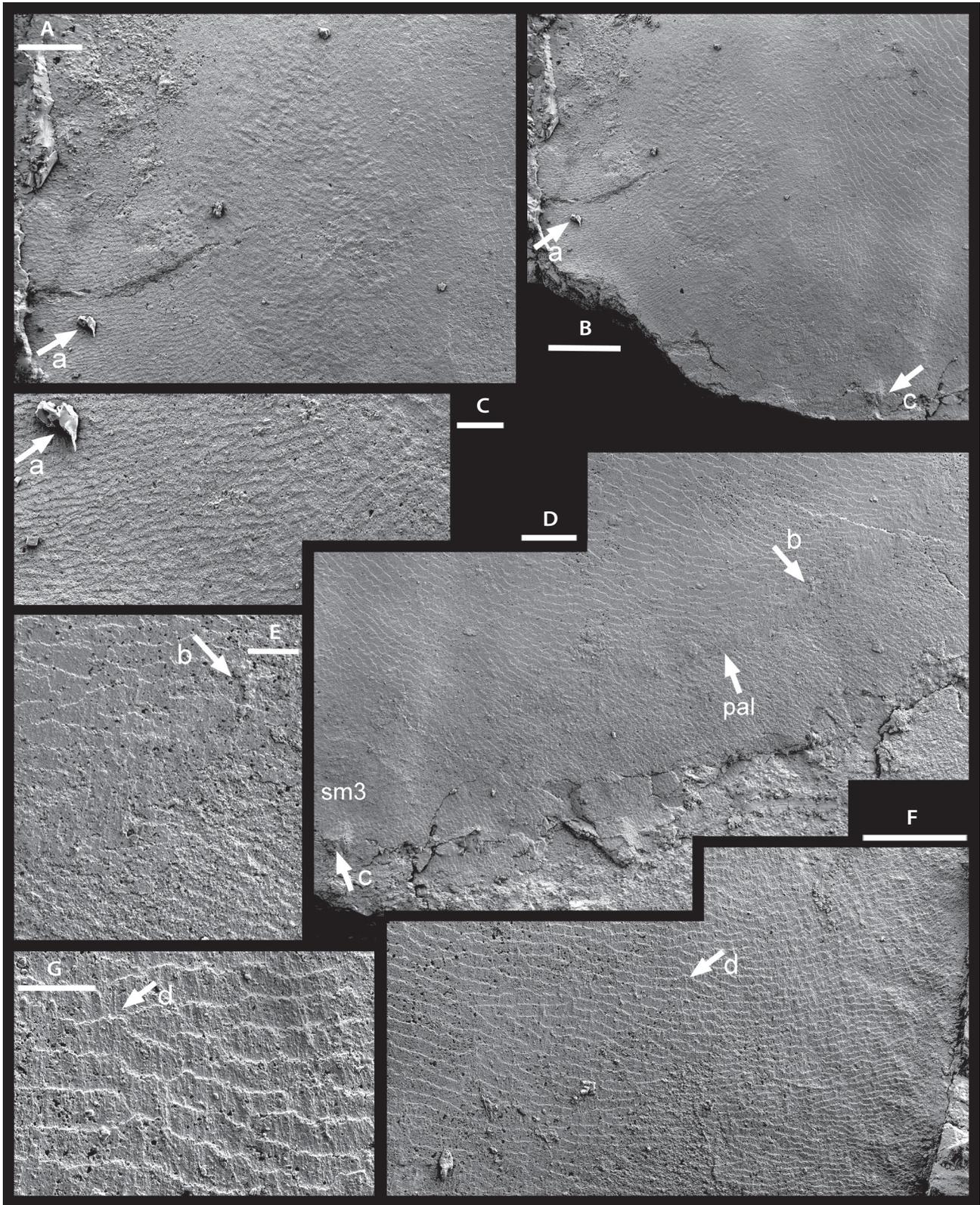


Figure 13. *Fordilla troyensis* Barrande, 1881, MGUH 34316, internal mould, right valve, Aftenstjernesø Formation, Cambrian Series 2 (Stage 4), J.C. Troelsen collection 57, Øvre Midsommersø, southern Peary Land, North Greenland. Arrows a–d locate position of reference points in images. A – posterior adductor muscle, with marginal imbricate lamellar zone (enlarged in C) to lower left. B, C – posterior margin showing principal posterior adductor muscle scar and subsidiary scars with surrounding shell microstructure of imbricated lamellae; detail of closely spaced, radially striking marginal imbricate lamellae (C). D, E – shell microstructure along ventral margin, with closely spaced, radially striking, imbricate lamellae at margin

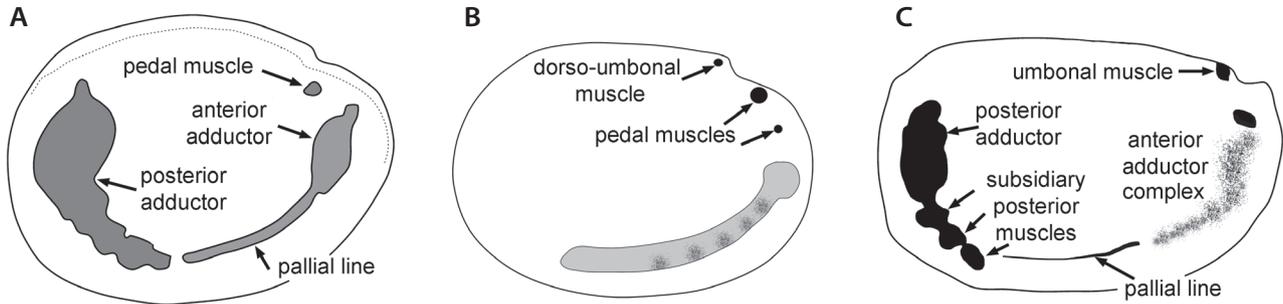


Figure 14. Distribution of muscle attachment scars in *Fordilla*. A – *Fordilla troyensis* from Troy, New York State (based on Pojeta *et al.* 1973). B – *Fordilla sibirica* from Siberia (based on Krasilova 1977). C – *Fordilla troyensis* from the Aftenstjernesø Formation, Peary Land (based on Fig. 12A).

Both helcionelloids have a median dorsal groove or band suggestive of flexibility across the plane of symmetry that can be regarded as a precursor to the hinge line (and bivalved condition) of *Fordilla*, although a similar structure is also present in some rostroconchs, such as *Pseudomyona* (Peel 2021a).

Numerous species referred to *Watsonella*, *Heraultia* Cobbold, 1935 and *Heraultipegma* Pojeta & Runnegar, 1976 were united in *Watsonella crosbyi* by Devaere *et al.* (2013, and references therein) reflecting the great variation in shell form. The holotype of one of these, *Heraultia sibirica* Missarzhevsky, 1974, displays a sharp ridge on the internal mould that appears to pass through a divided apex (Missarzhevsky 1974, pl. 24, fig. 3; Dzik 1994), although this was discounted by Vendrasco (2012) and is not seen in specimens from southern France illustrated by Devaere *et al.* (2013). However, the illustration of a specimen from the Tommotian Stage of Siberia assigned to *Watsonella crosbyi* by Rozanov *et al.* (2010, pl. 33, fig. 6a–c) shows a pronounced median dorsal ridge on the internal mould that appears to divide the shell longitudinally into two halves. The specimen has a strongly curved dorsal surface in lateral view, in contrast to the almost straight dorsal margin of *Fordilla* and *Watsonella*. The issue regarding the extent of the median dorsal ridge in the various specimens rightly or wrongly assigned to *Watsonella* is unresolved. It is evident that flexure can occur across the median plane along the dorsal surface with muscle contraction without separation into left and right valves, as in rostroconchs (Pojeta & Runnegar 1976), but the tight coiling of the sub-apical surface forms an effective lock hindering flexing in that area. In rostroconchs, the transverse sub-apical pegma joining the lateral areas of the shell across the plane of symmetry forms an anvil against which the elasticity of the shell reacts to force separation of the shell margins

after the relaxation of contracting muscles. In contrast, shell opening in a bivalve is effected by the expansion of the internal compressed ligament along the hinge line.

Adductor muscles in *Fordilla* and *Pojetaia* are anisomyarian, with the posterior muscle substantially larger than the anterior muscles (Pojeta 2000, fig. 1; Fig. 14C). A pair of adductor muscle scars and associated subsidiary muscles were also reported in *Tuarangia gravgaardensis* Berg-Madsen, 1987 by Hinz-Schallreuter (1995) and she considered *Tuarangia* to be a bivalve. Pojeta (2000) justifiably questioned the record due to the uncertain clarity of the original illustrations. Both muscle complexes in *Fordilla* extend latero-ventrally in a broad commarginal band, interpreted in part as an unusually broad pallial line by Pojeta & Runnegar (1974; Fig. 14A). However, the extensions are formed of a linear series of closely juxtaposed scars that are delimited by radial grooves on the internal mould, corresponding to ridges on the shell interior (Figs 4A, B; 5E; 10A). In *Pojetaia* a series of discrete subsidiary scars extends posteriorly from the anterior adductor scar (Pojeta 2000, fig. 1e). Three or four, small subsidiary scars occur medio-laterally in *Fordilla* to each large adductor scar in the ventral area, the radial grooves/ridges preserving the migratory tracks of the muscles during growth. These subsidiary muscles can be compared to the numerous closely spaced pedal muscle scars preserved closer to the umbones in some burrowing Palaeozoic bivalves, such as the Early Ordovician *Babinka* Barrande, 1881 (McAlester 1965, Soot-Ryen 1969, Babin 1977, Polechová 2013), the Middle Ordovician *Coxiconchia britannica* (Roualt, 1851), as illustrated by Kříž (1995) and Polechová (2013), and the Devonian *Palaeoneilo muscolosa* (Knod, 1908), discussed by Babin & Farjat (1994), Kříž (1995) and Peel & Berg-Madsen (2023).

separated from more widely spaced, obliquely striking imbricate lamellae by pallial line (pal), detail in E; sm3 – subsidiary muscle 3 (Fig. 12A). F, G – shell microstructure at anterior margin with closely spaced imbricate lamellae at margin continuous with more widely spaced imbricate lamellae in the interior (detail in G). Scale bars: 30 μm (C, E, G); 100 μm (A, D, F); 200 μm (B).

The location of the subsidiary muscles of *Fordilla* close to the shell margin indicates that they had little effect in withdrawing the foot into the shell or controlling its movement. Thus, retention of the pedal muscles in the apical region of crown group bivalves probably represents an adaptation to enhance the ability for withdrawal and better control of the foot, for example in connection with burrowing. As Runnegar & Bentley (1983) commented, it is likely that the subsidiary muscles were not able to cross fuse from one valve to the other to enable shell closure. The marginal position of the subsidiary muscles suggests that their primary function was just attachment of the foot. It seems likely that *Fordilla* and *Pojetaia* were not infaunal burrowers (Fang & Sánchez 2012). In most modern dimyarian bivalves, a small number of minor muscle scars located in the apical region of the shell usually function as pedal retractor muscles (Driscoll 1964, Kříž 1995).

The location and inferred function of the subsidiary muscles in *Fordilla troyensis* invite comparison with the muscle patterns of cap or spoon-shaped Palaeozoic tergomyans and patelliform gastropods such as *Tryblidium* Lindström, 1880 and *Floripatella* Yochelson, 1988. In these, series of muscle attachment scars or continuous muscle bands are distributed around the shell periphery reflecting their function in clamping the shell against the foot and substrate. In contrast, isostrophic bellerophonitiform univalves and anisostrophic gastropods in general, have small numbers of deeply placed muscle scars due to their function in withdrawing the soft parts into the shell (Peel 1991; Harper & Rollins 2000, fig. 4). The peripheral placement of the subsidiary muscles in *Fordilla troyensis* suggests derivation from a clamping univalve, with subsequent retreat of this muscle function in later bivalves to a position closer to the apex in association of the development of the withdrawal and control of a mobile, sometimes burrowing foot.

Unfortunately, muscle scar patterns are poorly known in helcionelloids, with only a few published descriptions (Parkhaev 2001, 2002, 2014; Vendrasco *et al.* 2010; Li *et al.* 2021, 2023; Peel 2023; Peel & Berg-Madsen 2023). They have not been reported in either *Watsonella* or *Anabarella*. Peel & Berg-Madsen (2023, fig. 8) recognised four muscle scar patterns, to which should be added a fifth to contain *Postacanthella* Yue, 1984 in Xing *et al.* (1984) as described by Li *et al.* (2023), that likely confirm that helcionelloids were paraphyletic. These patterns are not closely comparable to the combined adductor and subsidiary muscle pattern seen in *Fordilla*. The *Vendrascoospira–Hensoniconus* group of Peel (2023) and Peel & Berg-Madsen (2023) is based on the Miaolingian genera *Vendrascoospira* Peel & Kouchinsky, 2022 and *Hensoniconus* Peel, 2023 in which two pairs of large scars occurring on the lateral areas of the cap-shaped univalve

shells show a fanciful resemblance to bivalve adductor muscle scars. However, this pattern is not yet recognised in early Cambrian helcionelloids, and other evidence to connect the Miaolingian records to *Fordilla* and the origin of bivalves is lacking.

Conclusions

Phosphatised internal moulds of *Fordilla troyensis* from the Aftenstjernesø Formation (Cambrian Series 2, Stage 4) of North Greenland preserve exquisite impressions of shell microstructure and muscle attachment scars from the inner surface of the shell. The microstructure is dominated by a series of shallowly inclined, step-like imbricate lamellae, closely similar to the pattern described in the contemporary bivalve *Pojetaia runnegari*.

The hinge line in the Greenland material lacks teeth. Striations on the shell interior suggest that the simple ligament had a lamellar structure.

A small umbonal muscle scar is described in addition to well-developed anterior and posterior adductor muscles. Series of commarginal subsidiary muscle scars extending from the anterior and posterior adductor muscles probably controlled the centrally emergent foot, which was capable of only slight withdrawal and manipulation. *Fordilla* was not a burrowing bivalve; it was probably derived from a clamping helcionelloid mollusc with shell musculature distributed around the shell margin.

Acknowledgements

Johannes C. Troelsen generously made his collection available for study in 1974. Christian B. Skovsted (Swedish Museum of Natural History, Stockholm), Arden Roy Bashforth (Natural History Museum of Denmark, Copenhagen) and Vivianne Berg-Madsen (Museum of Evolution, Uppsala) kindly loaned material for study. Olaf Elicki helped with literature. I am grateful to Ed Landing (Albany) for providing information concerning the occurrence of *Fordilla troyensis* around Troy and to Paul A. Johnston (Mount Royal University, Calgary) and Yeongju Oh (Korea Polar Research Institute) for discussions concerning *Fordilla*. Paul A. Johnston and Marika Polechová (Czech Geological Survey, Prague) are acknowledged for reviewing the manuscript, as is the assistance of the journal editors.

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