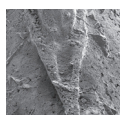


Pseudomyona from the Cambrian of North Greenland (Laurentia) and the early evolution of bivalved molluscs

JOHN S. PEEL



The laterally compressed, univalve, Cambrian (Miaolingian Series, Drumian Stage) mollusc *Pseudomyona* is recorded for the first time from Laurentia. Distinctive internal moulds of the type species *Pseudomyona queenslandica*, a species otherwise known from Australia and northern Siberia, are described from the Ekspedition Bræ Formation of southern Lauge Koch Land, North Greenland. A new species, *Pseudomyona groenlandica*, characterised by a proliferation of hinge teeth on the supra-apical surface, is described from the overlying Fimbuldal Formation of south-east Freuchen Land. The increase in hinge teeth supports the hypothesis that the bivalved *Tuarangia* from the Miaolingian Series (Guzhangian Stage) of New Zealand and Bornholm, Denmark, evolved from *Pseudomyona*. Although bivalved, *Tuarangia* is not interpreted as Class Bivalvia, but as the most derived member of an early clade in the evolution of Class Rostroconchia. The emended Order Tuarangiida, containing *Tuarangia* and *Pseudomyona*, forms a sister group to ribeirioids and later rostroconchs • Key words: Mollusca, Rostroconchia, Bivalvia, Cambrian (Miaolingian), Greenland, Laurentia.

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There is broad agreement from genomic and morphological studies of present day bivalves that the Ordovician–Recent members of the Class Bivalvia Linnaeus, 1758 form a monophyletic group, although some relationships within the group remain unresolved (Schneider 2001; Giribet 2008; Plazzi *et al.* 2011; Sharma *et al.* 2012, 2013; Bieler *et al.* 2014; González *et al.* 2015; Lemer *et al.* 2019). However, the derivation of Bivalvia from ancestral univalved molluscs and its stem group evolution in the Cambrian remains the subject of speculation (Cope 1997, 2000; Carter *et al.* 2000, 2011; Fang & Sánchez 2012; Cope & Kříž 2013; Ponder *et al.* 2020). Two Cambrian bivalved groups are recognised as potential ancestors of Bivalvia but their morphological dissimilarity, together with the general absence of material from the late Cambrian (Furongian), obscures the evolutionary pathway. The Order Fordillida Pojeta, 1975 includes *Fordilla* Barrande, 1881 (Fig. 1L, N) and *Pojetaia* Jell, 1980 (Fig. 1M) and its oldest members appeared in the Terreneuvian. The Order Tuarangiida MacKinnon, 1982 contains *Tuarangia* MacKinnon, 1982 (Fig. 1K) and is described from the late Miaolingian Series (Guzhangian Stage), about 20 Ma later. *Tuarangia* and the youngest

specimens of *Pojetaia* occur together in the Guzhangian of Denmark (Hinz-Schallreuter 2000).

Carter *et al.* (2011) rationalised the dilemma concerning origin(s) by recognising two major divisions of Class Bivalvia. A Grade Euprotobranchia Nevesskaja, 2009 embraced the two orders Fordillida and Tuarangiida, which were considered in some way likely to be ancestral to crown group bivalves, but together did not comprise a monophyletic entity. The grade recognises the dichotomy as stem group bivalves between *Fordilla* and *Pojetaia*, and *Pseudomyona* Runnegar 1983 and *Tuarangia*, discussed by Runnegar & Pojeta (1992), as a result of which *Pseudomyona* and *Tuarangia* were not considered to be Bivalvia. Carter *et al.* (2006) had considered *Tuarangia*, *Pseudomyona*, *Watsonella* Grabau, 1900 (Fig. 1J) and *Anabarella* Vostokova, 1962 to form a sister group to *Pojetaia* and *Fordilla* and post-Cambrian Bivalvia.

A Clade Eubivalvia Carter in Carter *et al.* (2011) included the post-Cambrian groups traditionally regarded as Bivalvia, but Sharma *et al.* (2013), Bieler *et al.* (2014) and others considered *Fordilla* to be a crown group bivalve. Conversely, Ponder *et al.* (2020, p. 552) placed

just Tuarangiida within Eubivalvia, citing Carter *et al.* (2000), and left Fordillida within Euprotobranchia.

Numerous claims of Cambrian bivalves have been evaluated by Runnegar & Pojeta (1992), Pojeta (2000), Geyer & Streng (1998) and Elicki & Gürsu (2009) but just three well known genera (*Fordilla*, Fig. 1L, N; *Pojetaia*, Fig. 1M; *Tuarangia*, Fig. 1K) and two less well known taxa (*Camya* Hinz-Schallreuter, 1995; *Anhouria* Geyer & Streng, 1998) have been maintained. However, it should be recalled that members of the Class Stenothecoida Yochelson, 1969 are possibly the most common bivalves in the Cambrian in which the two valves, as in Bivalvia, are disposed around a plane of symmetry lying between the valves. In Greenland, stenothecoid shells range from Cambrian Series 2 to Miaolingian Series, Guzhangian Stage (Peel 1988). While interpreted as molluscs by Yochelson (1969), or as brachiopods or molluscs by subsequent workers, the internal structures of stenothecoids (Koneva 1976, 1979) show no similarity to other members of the Mollusca, and the relationships of the group are obscure (Ponder *et al.* 2020).

A number of univalved molluscs referred to the Class Rostroconchia Pojeta *et al.*, 1972 and the Class Helcionelloida Peel, 1991a resemble bivalves in developing laterally compressed shells adapted to a semi-infaunal mode of life (Fig. 1H–J). Gubanov *et al.* (1999) and Gubanov & Peel (2003) considered this adaptation in helcionelloids to be the first major adaptive strategy in Cambrian molluscs, although many specimens lie within a size range (<1000 µm) typical of present day meiofauna (Higgins & Thiel 1988). *Watsonella* has a lateral profile similar to *Fordilla*, although the specimen illustrated herein (Fig. 1J; Cambrian, Terreneuvian Series, basal Stage 2) has a straighter dorsum in lateral perspective than most specimens illustrated by Devaere *et al.* (2013) or Guo *et al.* (2021). *Watsonella* and the strongly coiled, laterally compressed *Anabarella* are widely regarded as ancestral to *Fordilla*, not least on account of the longitudinal ridge complex along the dorsum of the supra-apical surface and convex ventral margin (Kouchinsky 1999; Devaere *et al.* 2013, fig. 14) suggestive of an incipient hinge zone. Runnegar & Pojeta (1992) and Vendrasco *et al.* (2011a) noted that similarity in shell microstructure between *Watsonella* and *Fordilla* supports this evolutionary relationship. *Pojetaia* (Fig. 1M) has a small number of well-developed hinge teeth, usually absent in *Fordilla*, and an opisthodontic ligament, but it is placed within the same Family Fordillidae (Ponder *et al.* 2020). *Pojetaia* is widely distributed in Terreneuvian–Miaolingian strata (Elicki & Gürsu 2009, Hinz-Schallreuter 2000).

Although bivalved, *Tuarangia*, from the late Miaolingian (Guzhangian Stage) of New Zealand and Denmark (MacKinnon 1982, 1985; Berg-Madsen 1987; Hinz-Schallreuter 1995, 2000) is morphologically quite

distinct from the fordillids, with numerous hinge teeth distributed on either side of the median, amphidetic, ligament in lateral view (Fig. 1K), and a different shell microstructure (Runnegar & Pojeta 1992; Vendrasco *et al.* 2011a, b). Runnegar & Pojeta (1992) concluded that *Tuarangia* did not share a common bivalved ancestry with *Fordilla* and *Pojetaia* but formed a separate clade together with *Pseudomyona* (Fig. 1A). *Pseudomyona*, however, is clearly univalved in contrast to the bivalved *Tuarangia*, which prompted Hinz-Schallreuter (2000) to accept *Tuarangia* as a member of Class Bivalvia, recalling the opinions of MacKinnon (1982, 1985) and Berg-Madsen (1987), but to exclude *Pseudomyona*. Runnegar & Pojeta (1992) noted that Class Bivalvia would not be monophyletic if *Tuarangia*, *Fordilla* and *Pojetaia* were all interpreted as true bivalves, and concluded that *Tuarangia* was not a true bivalve, an opinion endorsed by Vendrasco (2012). The assignment of Tuarangiida to Eubivalvia by Ponder *et al.* (2020, p. 552) and placement of fordillids away from the crown group of Bivalvia is a decision that echoes the widely denigrated opinion of Yochelson (1981) concerning *Fordilla*, but is contrary to the crown group status of fordillids interpreted by Sharma *et al.* (2013), Bieler *et al.* (2014) and others.

The present paper explores the relationship between *Pseudomyona* and *Tuarangia* in describing internal moulds of two species of *Pseudomyona* from the Miaolingian Series (Drumian Stage) of North Greenland. Together, these species represent the first record of the genus from Laurentia. *Pseudomyona groenlandica* sp. nov. is characterised by the proliferation of hinge teeth along the dorsal margin when compared to the type species *Pseudomyona queenslandica* (Runnegar & Jell, 1976), which was first described from the Drumian of Australia (Runnegar & Jell 1976). This evolution in hinge structure confirms the relationship between *Pseudomyona* and *Tuarangia*, and supports their interpretation as members of a clade within Rostroconchia.

Materials and methods

Specimens of *Pseudomyona* from Greenland are derived from Cambrian (Miaolingian Series) carbonates within a belt of Lower Palaeozoic strata that crops out across North Greenland as part of the southern shelf succession of the transarctic Franklinian Basin (Higgins *et al.* 1991a, b). Cambrian stratigraphy in the Freuchen Land to Peary Land region was described by Ineson *et al.* (1994) and Ineson & Peel (1997, 2011; Fig. 2B). The described specimens are preserved as internal moulds, which are compared with silica replicas of entire shells from the Kuonamka Formation (Miaolingian Series) of northern Siberia (Gubanov *et al.* 2004).

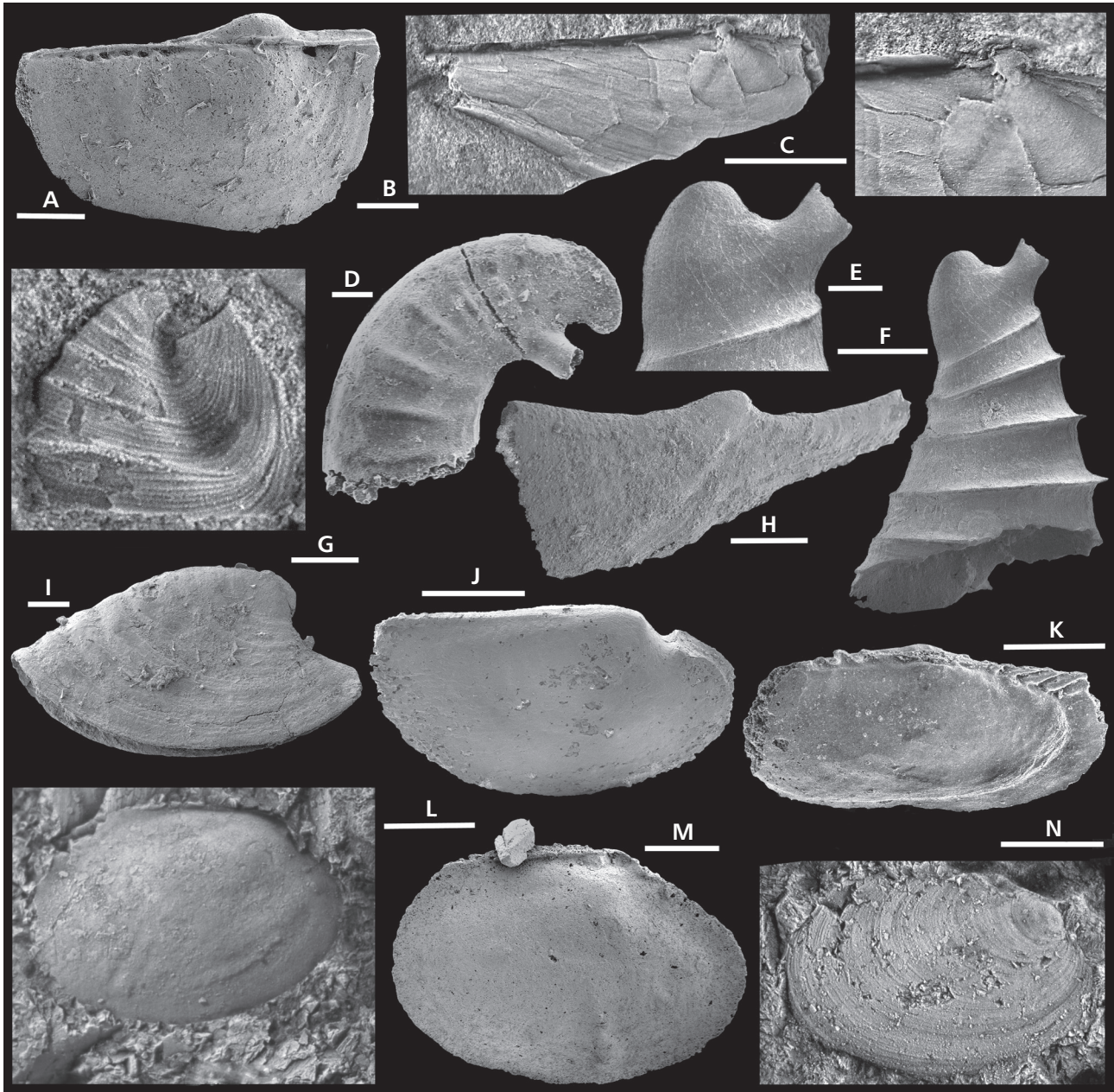


Figure 1. Cambrian and Ordovician molluscs. All specimens oriented with sub-apical surface to the right. • A – *Pseudomyona groenlandica* sp. nov., Fimbuldal Formation, Miaolingian, Drumian Stage, lateral view of internal mould, PMU 377511 from GGU sample 315006, Freuchen Land, North Greenland. • B, C – *Pinnocaris lapworthi* Etheridge, 1878, Ordovician, Girvan, southern Scotland, lateral view of partially crushed specimen showing the coiled early growth stage (C), NHM In 20400. • D – *Runnegarella americana* (Runnegar & Pojeta, 1980), Forteau Formation, Cambrian Series 2, Stage 4, western Newfoundland, lateral view of internal mould, PMU 25031. • E, F – *Yochelcionella ostentata* Runnegar & Jell, 1976, Kuonamka Formation, Cambrian Series 2, Stage 4, northern Siberia, lateral views of silica replica, SMNH 160579, with detail of apex (E) showing radial ornamentation (images Alexander Gubanov). • G – *Eotebenna arctica* Peel, 1989, Henson Gletscher Formation, Cambrian Series 2, Stage 4, south-west Freuchen Land, North Greenland, lateral view, MGUH 18.701 from GGU sample 315109, mirrored illustration. • H – *Eotebenna viviannae* Peel, 1991b, Kuonamka Formation, Cambrian Series 2, Stage 4, northern Siberia, lateral view of silica replica, SMNH Mo 160588 (image Alexander Gubanov). • I – *Mellopegma* sp., Fimbuldal Formation, Miaolingian, Drumian Stage, southern Lauge Koch Land, lateral view (mirrored), PMU 37506 from GGU sample 315006. • J – *Watsonella crosbyi* Grabau, 1900, Cambrian, Terreneuvian Series, Hérault Limestone, Montagne Noire, France, lateral view (mirrored) of internal mould (USTL 1226/10; image Léa Devaere). • K – *Tuarangia gravgaardensis* Berg-Madsen, 1987, Andrarum Limestone, Miaolingian, Bornholm, Denmark, dorso-lateral view (mirrored) of internal mould (MGUH 17.451; image Vivianne Berg-Madsen). • L, N – *Fordilla troyensis* Barrande, 1881, Aftenstjernesø Formation, Cambrian Series 2, Stage 4, southern Peary Land, lateral views of internal mould with muscle scar traces (L – MGUH 33533) and external surface showing comarginal ornamentation (N – MGUH 33534). • M – *Pojetaia runnegari* Jell, 1980, Aftenstjernesø Formation, Cambrian Series 2, Stage 4, northern Lauge Koch Land, internal mould in lateral view (M – PMU 36935 from GGU sample 315045). Scale bars: 100 µm (A, I); 200 µm (D, E, H, I, K, M); 500 µm (F, J); 1 mm (G, L, N); 3 mm (B, C).

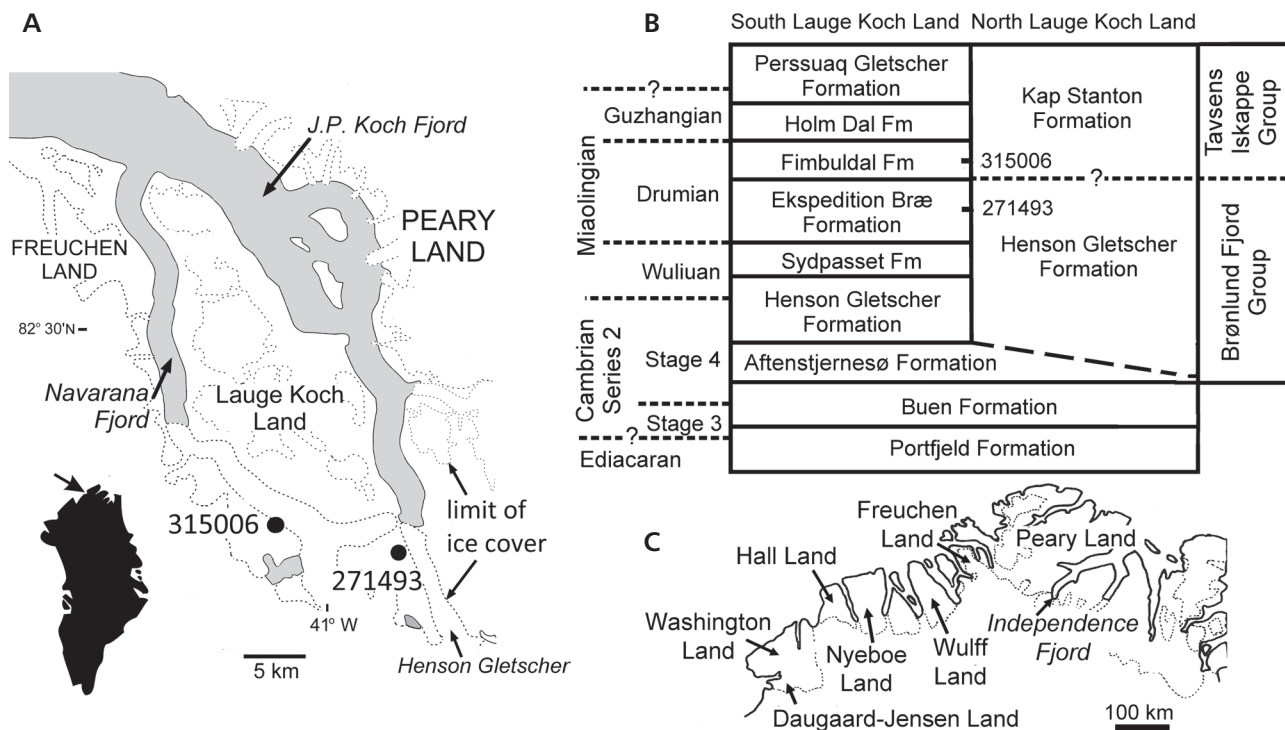


Figure 2. Occurrence of *Pseudomyona* in North Greenland. • A – GGU sample sites in south-east Freuchen Land and southern Lauge Koch Land, with inset map of Greenland locating J.P. Koch Fjord (arrow). • B – stratigraphic nomenclature with location of GGU samples. • C – land areas in North Greenland.

Pseudomyona queenslandica occurs in the Ekspedition Bræ Formation. GGU sample 271493 was collected by J.S. Peel on 26th June 1978 from about 35 m above the base of the formation in its type section (Ineson & Peel 1997, fig. 41) in southern Lauge Koch Land (82° 10' N, 40° 24' W; Fig. 2A); Miaolingian Series, Drumian Stage, *Ptychagnostus atavus* Biozone (Robison 1984). Trilobites from the Ekspedition Bræ Formation were described by Geyer & Peel (2017, 2020).

Pseudomyona groenlandica sp. nov. is described from the Fimbuldal Formation, with GGU sample 315006 collected by J.S. Peel on 2nd July 1984 from the recessive interval in the middle of the Fimbuldal Formation on the south-west side of the glacier draining into Navarana Fjord, eastern Freuchen Land (82° 17' N, 41° 22' W; Fig. 2A); Miaolingian Series, Drumian Stage, *Ptychagnostus punctuosus* Biozone (Robison 1984).

The limestone samples were dissolved in 10% acetic acid to release phosphatic microfossils. Selected specimens were coated with gold prior to stereoscan microscopy, and images were assembled subsequently in Adobe Photoshop CS4.

Terminology is illustrated in Figure 3, in which the straight hinge zone is interpreted as dorsal and the curved margin as ventral. The term half-pegma is introduced for one of a pair of prominent opposing teeth located one

on each sub-apical lateral surface, at the dorsum. Unlike a full pegma, which extends from one lateral area to the other across the median plane (Pojeta & Runnegar 1976), opposing half-pegmas seemingly only come into contact with each other when the ventral margin of the univalved shell is closed.

Institutional abbreviations. – ANU – Australian National University, Canberra; GGU – Grønlands Geologiske Undersøgelse, the Geological Survey of Greenland, now part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen; MGUH – Natural History Museum of Denmark, Copenhagen; NHM, Natural History Museum, London; PMU – Palaeontological type collection of the Museum of Evolution, Uppsala University; SMNH – Swedish Museum of Natural History, Stockholm; USTL – Université des Sciences et Technologies de Lille, France.

Systematic Palaeontology

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Phylum Mollusca Linnaeus, 1758

Class Rostroconchia Pojeta, Runnegar, Morris & Newell, 1972

Discussion. – *Watsonella* (Cambrian, Terreneuvian Series) was considered to be the oldest rostroconch by Pojeta & Runnegar (1976) on the basis of the interpreted presence of a pegma on the sub-apical surface, but restudy by MacKinnon (1985), Li *et al.* (2011), Devaere *et al.* (2013), Kouchinsky *et al.* (2017) and Guo *et al.* (2021) has rejected this interpretation. The status of several Miaolingian taxa as possible rostroconchs was discussed by Wagner (1997), Vendrasco *et al.* (2010; 2011a, b) and Vendrasco (2012). Herein, Order Tuarangiida is considered to form the oldest group of rostroconchs, with *Pseudomyona* appearing in the early Drumian. Additionally, Rostroconchia includes the orders Ribeirioida Kobayashi, 1933, Conocardioida Neumayr, 1891 and Anetshelloida Mazaev, 2012, although the relationships between ribeirioids, conocardioids and their descendent scaphopods have been questioned (Engeser & Riedel 1996; Peel 2004, 2006; Mazaev 2012; Vendrasco 2012)

Order Tuarangiida MacKinnon, 1982

Diagnosis (emended). – Pseudo-bivalved (univalve) or bivalved laterally compressed D-shaped shells with a long straight dorsal hinge zone and convex ventral margin. Hinge zone in pseudo-bivalved forms is flexible with a prominent, raised, undivided early growth stage along the median plane of symmetry and a variable numbers of hinge teeth. Bivalved forms are equivalve, with taxodont dentition consisting of a number of oblique, subparallel, bar-like teeth forming two elements on each valve that are separated by a narrow, erect, amphidetic ligament. Inner shell surface formed of foliated calcite.

Discussion. – MacKinnon (1982) proposed the Order Tuarangiida to contain the single species *Tuarangia paparua* MacKinnon, 1982 from the Miaolingian of New Zealand, interpreted as a pteriomorph(?) bivalve; he later acknowledged that it might be phylogenetically related to *Pseudomyona* (MacKinnon 1985). The univalved *Pseudomyona* was placed together with *Tuarangia* within the Family Tuarangiidae MacKinnon, 1982, and regarded as a ‘quasiroostroconch’ or bivalved monoplacophoran by Runnegar (1983, p. 133). Hinz-Schallreuter (2000) established the Order Pseudomyonida and Family Pseudomyonidae for *Pseudomyona*. She stated that there was no indication of the pegma characteristic of rostroconchs in the pseudo-bivalved shell of *Pseudomyona*, an observation contradicted herein. Parkhaev (2019) placed *Pseudomyona* as Bivalvia, family *incertae sedis*.

In contrast to Order Pseudomyonida, there is wide usage of Order Tuarangiida in the literature on account of its relevance to discussions concerning the origin of Bivalvia (MacKinnon 1982, 1985; Berg-Madsen 1987; Carter *et al.* 2000, 2011; Elicki & Gürsu 2009; Fang & Sánchez 2012; Ponder *et al.* 2020). For this reason, and its historical priority, Order Tuarangiida is retained here, although with significant emendation from the concept of the original author (MacKinnon 1982).

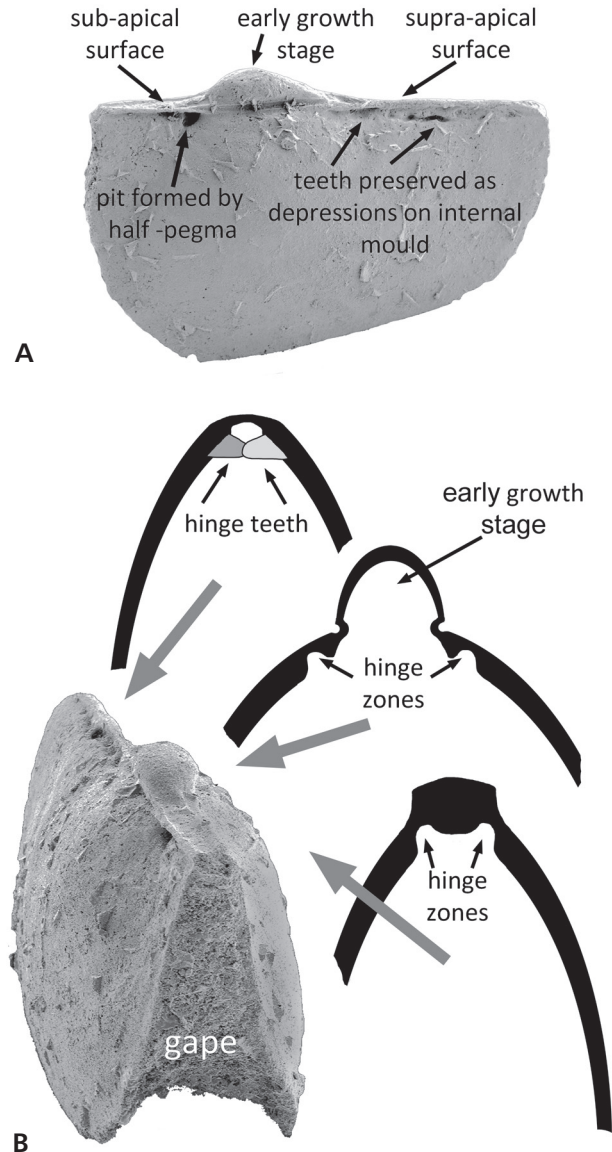


Figure 3. Morphological terminology of *Pseudomyona groenlandica* sp. nov. • A – internal mould in lateral view showing principal morphological terms. • B – internal mould in oblique dorsal view showing sub-apical surface and gape between lateral surfaces. Schematic cross-sections show relationship between features of the internal mould and shell (black). Ridges on the internal mould correspond to grooves on the shell interior representing hinge zones.

Family Tuarangiidae MacKinnon, 1982

Diagnosis. – Small elongate, subquadrate to trapezoidal bivalves with long straight hinge line and very subdued umbones near lateral midline. Dentition taxodont consisting of a number of oblique, subparallel bar-like teeth forming two elements on each valve that are separated by a narrow, erect, amphidetic ligament (slightly re-phrased from MacKinnon 1982).

Family Pseudomyonidae Hinz-Schallreuter, 2000

Diagnosis (emended). – Pseudo-bivalved, laterally compressed with prominent early growth stage raised above the straight, flexible, hinge zone; comarginal growth lines continuous across the dorsal line. Few to many hinge teeth developed mainly along the supra-apical surface, with more prominent teeth adjacent to the terminations of the early growth stage interpreted as half-pegmas.

Genus *Pseudomyona* Runnegar, 1983

1976 *Myona?* Runnegar & Jell, p. 135.

1983 *Pseudomyona* Runnegar, p. 140.

Type species. – *Myona? queenslandica* Runnegar & Jell, 1976 from the Currant Bush Limestone (Gowers Formation), Miaolingian Series, Drumian Stage, Thornton, Georgina Basin, Queensland, Australia.

Diagnosis (emended). – Pseudo-bivalved, with comarginal ornamentation continuous across the dorsum; bilaterally symmetrical, with dorsal plane of symmetry separating the lateral surfaces. D-shaped in lateral view with the straight dorsal hinge line interrupted by a swollen early growth stage located at about one third of the distance from the sub-apical margin to the supra-apical margin. Inner surface with prominent grooves (ridges on the internal mould) on the dorsal area extending from alongside the early growth stage to each extremity. Teeth on the dorsal margin of each lateral surface forms pits on the internal mould; sub-apically, usually a single deep pit (half-pegma), but supra-apically a single pit or series of up to 10 pits representing interdigitating teeth.

Discussion. – The early growth stage in *Pseudomyona* forms a distinctive elevation above the general level of the dorsum and is located closer to the sub-apical margin; the supra-apical surface is extended, tapering towards the supra-apical margin (Fig. 3A). The greatest height and width (thickness) are beneath the early growth stage (Figs 1A, 3A). A similar arrangement is seen in the Late Ordovician, pegma-bearing, *Pinnocaris lapworthi* Etheridge, 1878 where the coiling of the elevated early

whorls is clearly visible, and the supra-apical surface is much more extended (Peel 2004; Fig. 1B, C). In contrast, *Eotebenna viviannae* Peel, 1991b, which occurs together with *Pseudomyona queenslandica* in Siberia (Gubanov *et al.* 2004), tapers towards the sub-apical margin and expands towards the supra-apical margin (Fig. 1H). Internal moulds of the latter, however, show none of the features of a dorsal hinge present in *Pseudomyona* (Peel 1991a, b). Although laterally compressed, *Eotebenna arctica* Peel, 1989 displays an upright form with a planar aperture (Fig. 1G), unlike the curved lateral ventral margins of *Pseudomyona*, although the aperture continues into a deep sub-apical sinus. *Yochelcionella ostentata* Runnegar & Jell, 1976 and *Runnegarella americana* (Runnegar & Pojeta, 1980) develop tall shells with the characteristic snorkel located high above, and separate from, the plane of the aperture (Fig. 1D–F).

The Terreneuvian *Watsonella* (Fig. 1J) and some specimens of the contemporaneous *Anabarella plana* (Gubanov & Peel 2003) have a similar elongate form to *Pseudomyona* but lack the prominent, protruding early growth stage of the latter. Furthermore, they show no evidence of teeth along the dorsal surface of the internal mould (Fig. 1J). Most specimens of *Watsonella* have a convex dorsal profile in lateral view, unlike the straight dorsum of *Pseudomyona*, while typical *Anabarella* are coiled through almost one whorl (Gubanov & Peel 2003). Ridges and grooves along the dorsal crest of *Watsonella* and *Anabarella* (Li *et al.* 2011, Devaere *et al.* 2013, Guo *et al.* 2021) suggest the presence of a functional dorsal hinge, as in *Pseudomyona*. *Mellopegma* (Cambrian Series 2–Mialongian Series) differs from *Pseudomyona* in its convex supra-apical surface in lateral view, with a slightly overhanging apex (Fig. 1I), whereas the dorsal surface in *Pseudomyona* is straight, with an upright early growth stage. *Mellopegma*, and the morphologically similar *Eurekapegma* MacKinnon, 1985 from the Miaolingian of New Zealand (MacKinnon 1985, Runnegar 1996), lack structures indicating a flexible hinge zone.

Two species of *Pseudomyona* are recognised and described below, distinguished from each other by the development of a long series of interdigitating hinge teeth along the supra-apical surface in *Pseudomyona groenlandica* sp. nov.

***Pseudomyona queenslandica* (Runnegar & Jell, 1976)**

Figures 4, 5

1976 *Myona? queenslandica* Runnegar & Jell; p. 135, fig. 8d, 4–9.

1978 *Myona?* – Runnegar, pl. 2, figs 26, 27.

1983 *Pseudomyona queenslandica*. – Runnegar, p. 140, figs 6, 7.

- 1992 *Pseudomyona queenslandica*. – Runnegar & Pojeta, fig. 3a, c–d, f–g.
 1995 *Pseudomyona queenslandica*. – Hinz-Schallreuter, p. 82, fig. 7.1–7.3.
 2000 *Pseudomyona queenslandica*. – Hinz-Schallreuter, p. 239, fig. 9s.
 2004 *Pseudomyona queenslandica*. – Gubanov *et al.*, p. 12, fig. 9a–s.
 2011 *Pseudomyona*. – Vendrasco *et al.*, p. 844.

Holotype. – ANU 29071, Currant Bush Limestone (Gowers Formation), Thornton, Georgina Basin, Queensland, Australia; Miaolingian Series, Drumian Stage (Floran local stage).

Type horizon and locality. – Currant Bush Limestone (Gowers Formation), Thornton, Georgina Basin, Queensland, Australia; Miaolingian Series, Drumian Stage (Floran local stage).

Material. – PMU 37507–37510 from GGU sample 271493, south-east Lauge Koch Land, North Greenland (Fig. 2A), type section of the Ekspedition Bræ Formation. SMNH 160598, 160599, 160600, 160602 and one associated specimen (Fig. 4J), from a total of 27 specimens from locality 8/32, Kuonamka Formation, Bol'shaya Kuonamka River, northern Siberia, section 8 of Gubanov *et al.* (2004, figs 1, 2) and Kouchinsky *et al.* (2011, figs 1, 2), Miaolingian Series, Drumian Stage, *Tomagnostus fissus*–*Paradoxides sacheri* Zone.

Runnegar & Jell (1976) described three phosphatised internal moulds from the Currant Bush Limestone (Gowers Formation) of Queensland, Australia (Miaolingian Series, Drumian Stage), with additional specimens described by Runnegar (1983). Hinz-Schallreuter (1995) noted 13 internal moulds also from the Currant Bush Limestone (Gowers Formation) of Thornton, Queensland.

Diagnosis (emended). – Type species of *Pseudomyona* in which each lateral surface carries a single tooth on the sub-apical area, interpreted as a half-pegma, and one or two teeth on the supra-apical surfaces adjacent to the dorsal hinge zone, the latter may be elongated and both may be divided. The teeth are represented by pits on the internal mould.

Description. – The shell exterior of *Pseudomyona queenslandica* was described by Gubanov *et al.* (2004) on the basis of silicified specimens from the Kuonamka Formation (Fig. 4). The shell exterior is not known in available material from Australia and Greenland. The shell is bilaterally symmetrical along the dorsal line, pseudo-bivalved, D-shaped in lateral view with the straight dorsal hinge line interrupted by a swollen early growth stage

located at about one third of the distance from the sub-apical margin to the supra-apical margin (Fig. 4A, B, J). The ventral margin varies from almost hemispherical (Fig. 4J) to asymmetric with tapering towards the supra-apical margin and with the greatest height developed below the early growth stage (Fig. 4A).

The early growth stage is elongate, tapering towards the supra-apical margin (Fig. 4F, H, K). It is asymmetric in lateral profile (Fig. 4D) with a more shallowly sloping supra-apical surface and a steeper sub-apical surface that may be concave (Fig. 4I, J). It is strongly convex in transverse profile such that it overhangs the adjacent lateral shell surfaces (Fig. 4E), the junction being marked by a pronounced groove that may continue around the supra-apical termination. The sub-apical surface of the dorsum is marked by a prominent carina of the same transverse width as the early growth stage, into which it grades abruptly (Fig. 4G, H). The carina is the locus of a gape in the sub-apical margin (Fig. 4F) that is parallel-sided close to the dorsum (Fig. 4F) and is traversed by fine, continuous, comarginal growth lines (Fig. 4G). On the supra-apical surface, the dorsum is angulated without apparent interruption of the crossing growth lines; a narrow gape may be present at the junction with the ventral surface. Preservation of this region is poor, however, and the crest of the angulation is often disrupted by diagenetic fractures (Fig. 4B). Ornamentation consists of comarginal growth lines that may be slightly rugose. Partially exfoliated specimens show widely spaced radial ribs traversing the growth lines, the ribs becoming more abundant and more closely spaced near the margins (Fig. 4A, C).

As with the Australian material described by Runnegar & Jell (1976), Runnegar (1983), Runnegar & Pojeta (1992) and Hinz-Schallreuter (1995, 2000), all specimens from North Greenland are internal moulds. Their length:width ratio is about 1.6 (Fig. 5). In contrast to the smooth exterior of the supra-apical surface of the Kuonamka material (Fig. 4), this surface of the internal mould carries two prominent ridges that originate one on each side of the early growth stage below the groove that forms the junction between the early growth stage and the lateral areas of the shell (Fig. 5A–C). These ridges delimit a concave area along the median line of the dorsum immediately adjacent to the early growth stage before coalescing into a single ridge at about half the distance to the supra-apical margin. On the sub-apical surface the angular margins of the upper surface of the carina pass into ridges on the lateral areas of the early growth stage that lie above the groove at the junction between the early growth stage and the lateral areas of the shell (Fig. 5B, C). In apical view (Fig. 5B, C) the transverse profile of the supra-apical surface is seen to be narrow and acute, whereas the carina on the sub-apical surface is broad, with a flattened upper surface.

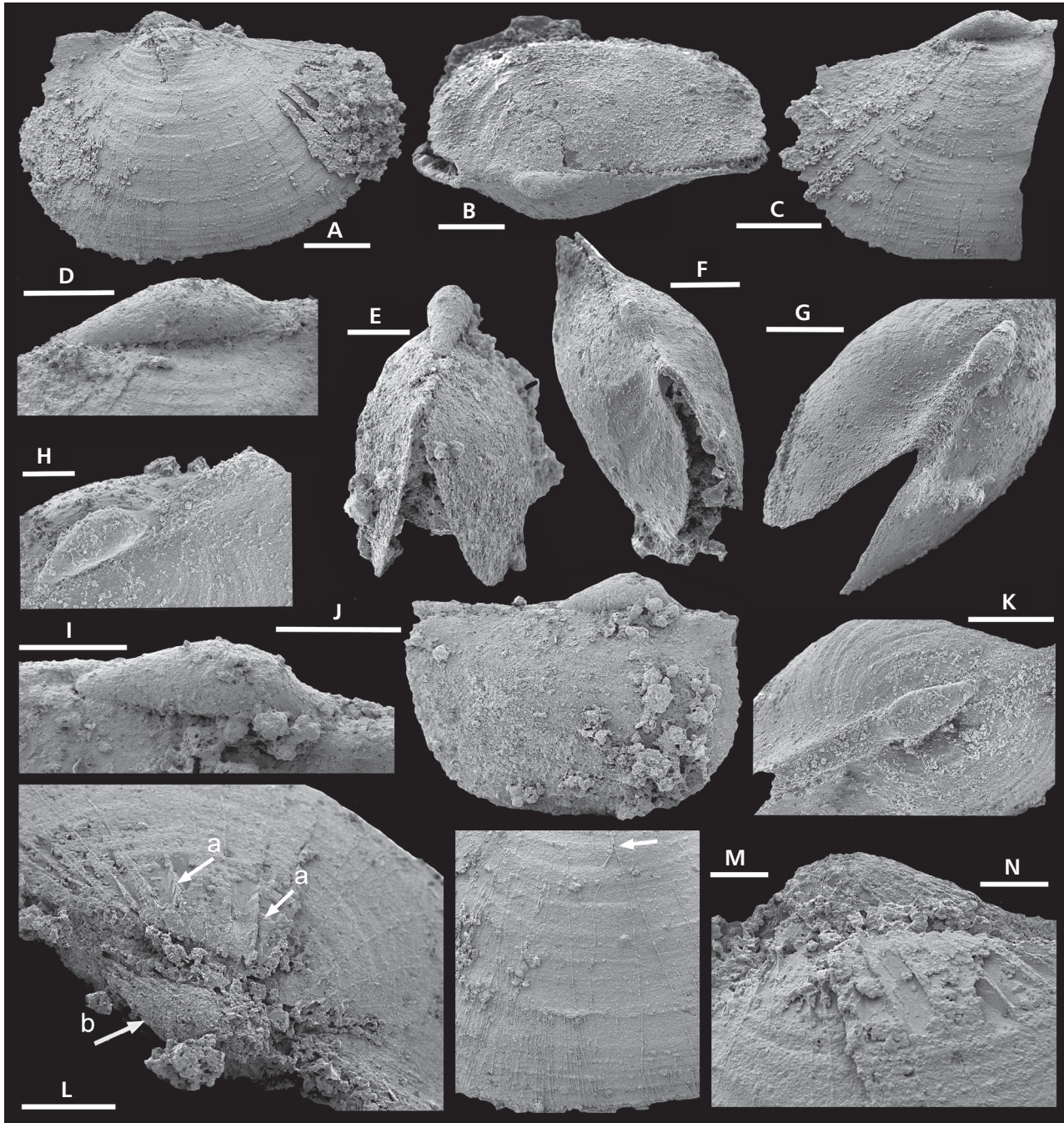


Figure 4. Silicified specimens of *Pseudomyona queenslandica* (Runnegar & Jell, 1976) from the Kuonamka Formation of northern Siberia; Miaolingian Series, Drumian Stage. A, L–N – SMNH 160599 showing radial ridges crossing comarginal growth lines; A, N – lateral view, with detail of apex (N); L – apico-lateral view showing stacked arrow-head crystals culminating at the ridges (arrow a) and fine ridges (arrow b) on the early growth stage; M – detail of ventral margin showing bifurcating ridge (arrow). B, F – SMNH 160602, apico-lateral view (B) showing diagenetic fracture along dorsal area; sub-apical view (F) showing gape. C, D – SMNH 160600, lateral view (C) with detail of early growth stage (D). E, I, J – specimen associated with SMNH 160598–160600, supra-apical surface (E), lateral view (J) with detail of early growth stage (I). G, H, K – SMNH 160598, sub-apical surface and gape (G) with growth lines crossing carina (G); early growth stage and carina on sub-apical surface (H, K). Scale bars: 50 μm (N); 100 μm (D, E, H, I, L, M); 200 μm (A–C, F, G, J, K). Images: Alexander Gubanov.

At the junction between the early growth stage and the sub-apical surface, in lateral view, a deep pit is present on each lateral surface below the carina (Fig. 5A, C, E, I, arrows a). The pits correspond to teeth on the shell interior

and are variable in shape within available material. In a similar perspective, paired pits are also present on the lateral surfaces of the shell at the point where the ridges on the supra-apical surface coalesce (Fig. 5C, E, arrows b).

The pits are elongated subparallel to the crest of the dorsum and may be divided (Fig. 5E–H, J).

Discussion. – Specimens of *Pseudomyona queenslandica* from North Greenland and Australia show variation in the form of the pits on the internal mould. Those on the sub-apical surface are usually deeper in the Greenland material and are interpreted as representing half-pegmas, elements of a pegma that are not continuous across the median plane from one lateral surface to the other (Fig. 4A, E). Pits on the supra-apical surface form an elongated depression of variable form, which extends up to about half of the distance from the early growth stage to the margin.

Details of shell structure of the shell interior or muscle scars described by Runnegar (1983) and Runnegar & Pojeta (1992) are not preserved on the internal moulds from the Ekspedition Bræ Formation. Preservation of the shell surface is discussed below.

Occurrence. – Miaolingian Series, Drumian Stage, of Queensland, northern Siberia and North Greenland.

***Pseudomyona groenlandica* sp. nov.**

Figures 6–8

Holotype. – PMU 37511 from GGU sample 315006 (Fig. 6A–H), south-west side of glacier feeding into the head of Navarana Fjord, south-east Freuchen Land, North Greenland (Fig. 2A).

Paratypes. – PMU 37512–37515 from the same sample and locality as the holotype.

Type horizon and locality. – Fimbuldal Formation (Fig. 2B), south-west side of glacier feeding into the head of Navarana Fjord, south-east Freuchen Land, North Greenland (Fig. 2A). Cambrian, Miaolingian Series, Drumian Stage.

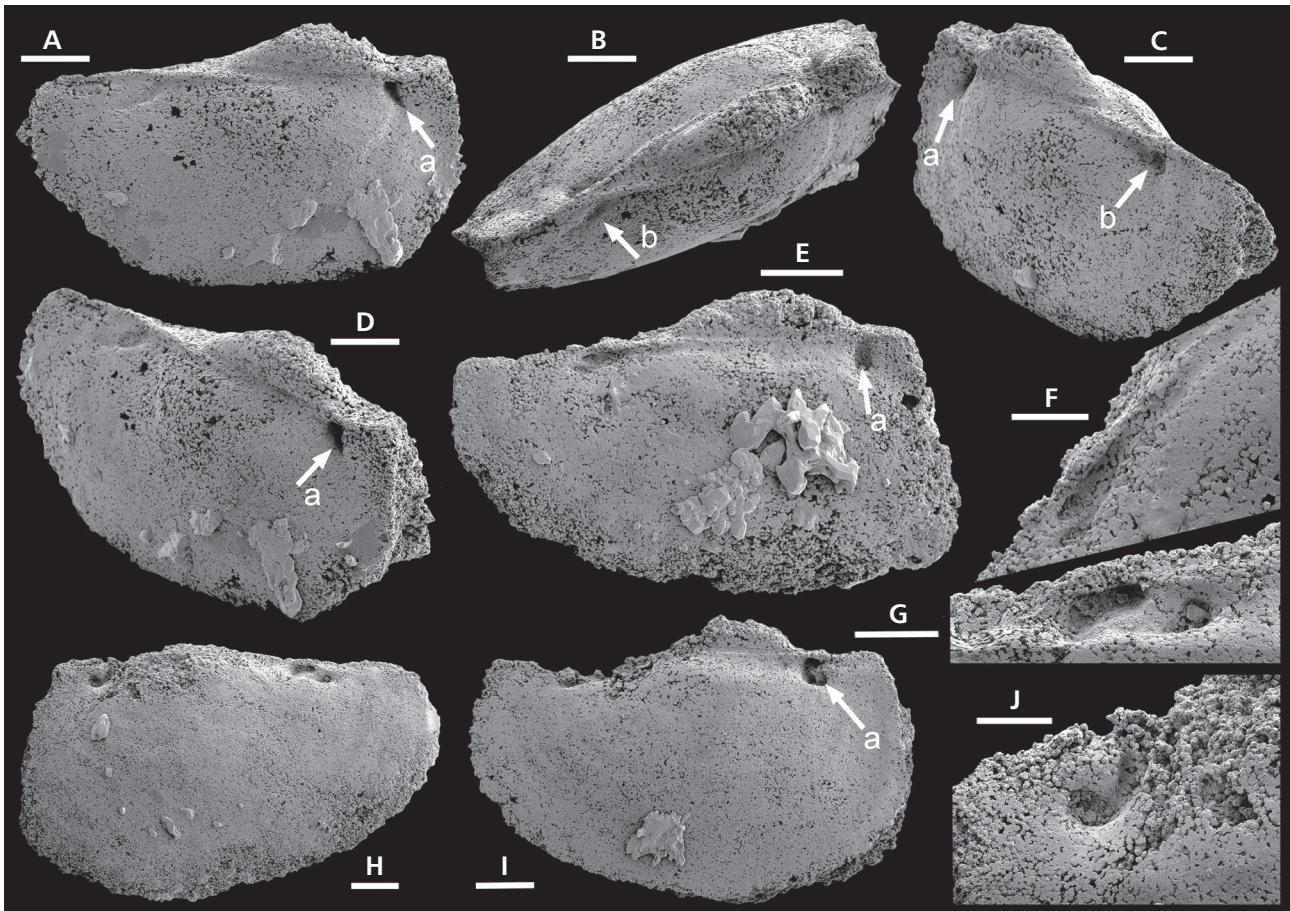


Figure 5. *Pseudomyona queenslandica* (Runnegar & Jell, 1976), internal moulds from GGU sample 271493, Ekspedition Bræ Formation, Lauge Koch Land, North Greenland, Miaolingian Series, Drumian Stage. A–D – PMU 37507, lateral view (A); dorsal view (B); dorso-lateral view (C); dorso-lateral view (D). E, F – PMU 37508, lateral view (E) with detail of bifurcating supra-apical pit (F). G, H, J – PMU 37509, lateral view (H) with detail of supra-apical (G) and sub-apical (J) pits. I – PMU 37510, lateral view. Symbols: arrow a – prominent sub-apical pits; arrow b – supra-apical pits. Scale bars: 50 µm (F, G, J); 100 µm (A–E, H, I).

Material. – In addition to the illustrated specimens, a few fragments also from GGU sample 315006.

Etymology. – From Greenland (Danish, Grønland).

Diagnosis. – Species of *Pseudomyona* in which the dorsal hinge zone carries a dominant peg-like tooth on each side of the sub-apical surface (half-pegma) and a series of interdigitating peg-like hinge teeth extending along the length of the supra-apical surface. The teeth are represented by pits on the internal mould.

Description. – All specimens from North Greenland are internal moulds, which form the basis of the following description. Length:width ratio is about 1.5. In lateral view the specimens are wedge-shaped, tapering towards the supra-apical margin (Fig. 6B, D), with a straight hinge zone developed on either side of the swollen early growth stage; the highest point of this earliest growth stage is located at about one third of the distance from the sub-apical to the supra-apical margin. The sub-apical ventral margin is shallowly concave immediately below the hinge zone but quickly becomes convex such that the shell attains maximum height below the early growth stage. Thereafter, the margin is straight before increasing in curvature towards the supra-apical margin (Fig. 6B, D). A broad gape is present in the sub-apical area, narrowing along the ventral margin towards the supra-apical margin. The lateral surfaces of the internal mould are marked by subdued comarginal corrugations.

The supra-apical surface of the internal mould carries a prominent ridge on each side of the early growth stage below the groove that forms the junction between the early growth stage and the lateral areas of the shell exterior (Fig. 6A–C). A concave area is formed between the ridges along the median line of the dorsum immediately adjacent to the early growth stage before they join together into a single ridge at about half the distance to the supra-apical margin. This single ridge becomes less prominent towards the margin in some specimens (Fig. 8). The sub-apical surface carries two ridges at the junction between the dorsum and the lateral areas of the early growth stage that mainly lie above the groove at the junction between the early growth stage and the lateral areas of the shell (Fig. 6A, I). In apical view (Fig. 6E), the transverse profile of the supra-apical surface is narrow and acute compared to the sub-apical surface, which is broad, with a flattened upper surface (Figs 6E, 7A).

In lateral view (Fig. 6A, B, D), a deep pit is present on each lateral surface at the junction between the early growth stage and the sub-apical surface, below the carina. The pits were produced by prominent tooth-like structures on the shell interior and may be accompanied by a second, smaller, pit (Fig. 8D). A row of pits is also present on the

lateral surfaces of the shell from the early growth stage to the supra-apical margin. As many as 11 pits produced from teeth on each lateral surface of internal moulds have been observed (Fig. 8A, E), interdigitating with those on the opposite lateral surface (Fig. 6E, H).

Discussion. – *Pseudomyona groenlandica* is distinguished from *Pseudomyona queenslandica* by the proliferation of hinge teeth along the supra-apical surface. Only a few teeth are present in the latter, close to the early growth stage (Fig. 5H), whereas a row of teeth extends from the early growth stage to the supra-apical margin in *Pseudomyona groenlandica* (Fig. 8E).

Occurrence. – Known only from the type locality in Freuchen Land, North Greenland (Fig. 2A).

Morphology and function

Contrasting styles of preservation in specimens from Australia, Greenland and Siberia establish a clear picture of the morphology of *Pseudomyona*. Silicified specimens from the Kuonamka Formation of northern Siberia (Gubanov *et al.* 2004) illustrate the ornamented outer surface and also details of the periostracum (Fig. 4). Phosphatic internal moulds from Australia and Greenland provide a detailed picture of the morphology of the internal surface of the shell and its hinge structures (Figs 5–8). Australian material also replicates details of shell microstructure (Runnegar 1983; Vendrasco *et al.* 2010, 2011a, b) not preserved in Greenland specimens.

Periostracum in *Pseudomyona queenslandica*

A combination of possible exfoliation, recrystallisation and partial silicification seems to be responsible for the preservation of the radial ribs present on the outer surface of some of the specimens of *Pseudomyona queenslandica* from the Kuonamka Formation of Siberia. Comarginal growth ornamentation in most available specimens is subdued, but the growth lines are preserved in fine detail in two illustrated specimens that have clearly been partially exfoliated prior to silicification, or differentially silicified (Fig. 4A, C, M). In SMNH 160599, the outermost shell layer is lacking, represented by a gap beneath the outer encrustation of the shell (Fig. 4A, right side). Radial ribs overlie and traverse the comarginal growth lines on the preserved surface. The ribs are narrow and widely spaced in SMNH 160599 (Fig. 4A), but become closely spaced near the ventral margin and along the sub-apical carina (Fig. 4A, C, M). Rarely, two adjacent ribs coalesce (Fig. 4M, arrow).

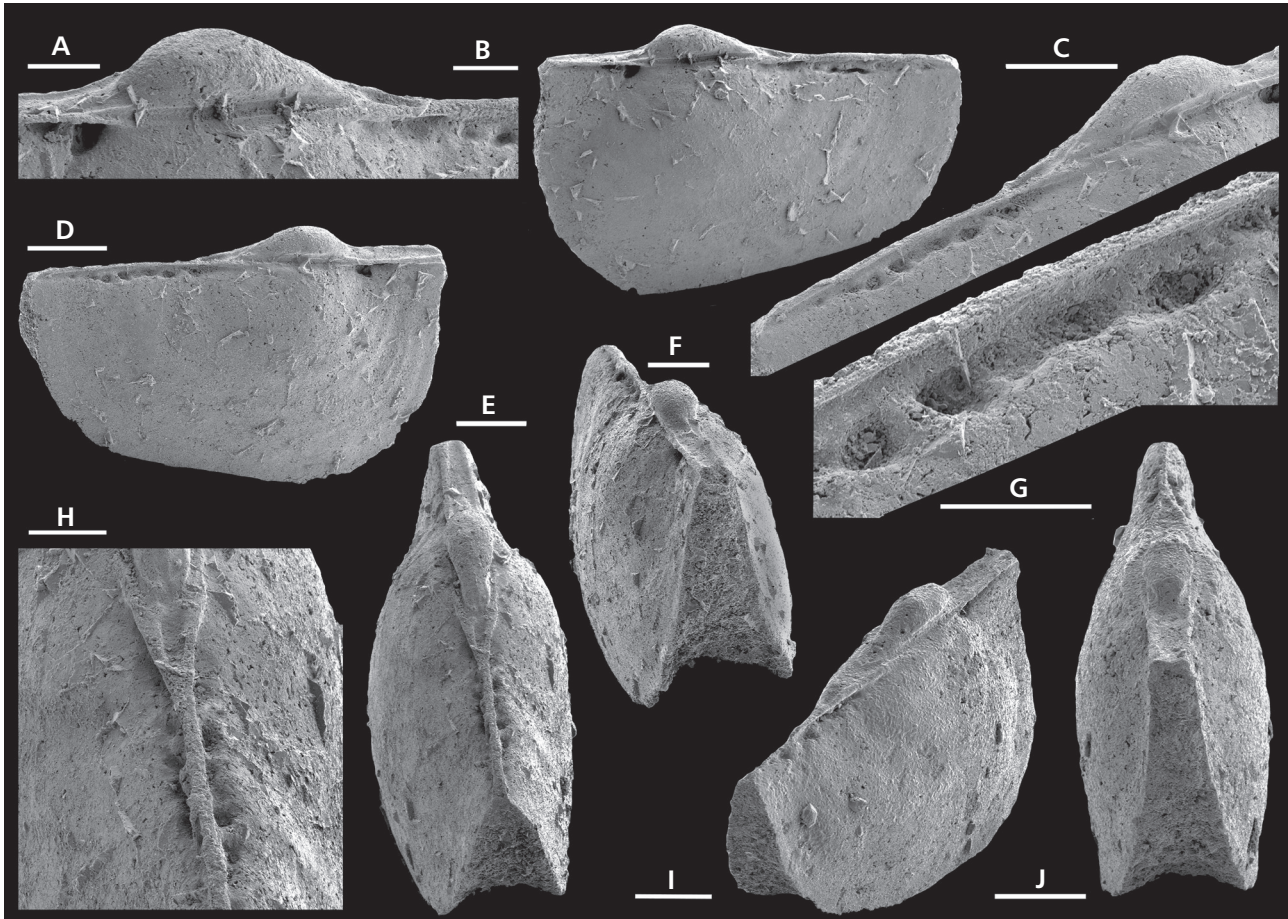


Figure 6. *Pseudomyona groenlandica* sp. nov., internal moulds from GGU sample 315006, Fimbuldal Formation, Freuchen Land, North Greenland, Miaolingian Series, Drumian Stage. A–H – PMU 37511, holotype, lateral view (B) with detail of early growth stage (A); lateral view (D) with detail of pits on supra-apical surface (C, G); oblique dorsal view (E) with interdigitating pits on supra-apical surface (detail in H); sub-apical surface (F). I, J – PMU 37512, oblique dorso-lateral view (I); oblique dorsal view of sub-apical carina (J). Scale bars: 50 µm (A, C, G, H); 100 µm (B, D–F, I, J).

In the apical region of SMNH 160599 (Fig. 4A), the ribs are seen to represent the crest of rows of steeply inclined, imbricated, arrow-head crystals deeper in the shell (Fig. 4L, arrows a). Fine ridges are also present on the early growth stage (Fig. 4L, arrow b). Similar structures are present in silicified specimens of *Anabaroconus sibiricus* Gubanov, Kouchinsky, Peel & Bengtson, 2004 from the same sample from the Kuonamka Formation (Gubanov *et al.* 2004, fig. 5n, u) and were also described by Vendrasco *et al.* (2011b, fig. 5.18) in *Mellopegma georginense* Runnegar & Jell, 1976 from the Miaolingian of Australia. They are also illustrated herein in the apical area of *Yochelcionella ostentata* Runnegar & Jell, 1976 from the basal Kuonamka Formation, Cambrian Series 2, Stage 4, of northern Siberia (Gubanov *et al.* 2004; Fig. 1E, F).

Vendrasco *et al.* (2011b) suggested that the radial ridges represent mineralised traces of the periostracum, the outermost, proteinaceous layer in the mollusc shell, which forms the template for crystallisation of the underlying calcium carbonate. This interpretation

is supported here, not least on account of the pristine comarginal ornamentation preserved on the underlying shell surface (Fig. 4A, C, M). Harper (1997) noted that the periostracum in present day Bivalvia varies greatly in thickness; while often very thin, it may exceed 100 µm. While its under surface is a precise template for the growing shell, the outer surface is often smoother, with a subdued reflection of growth lines. This difference is visible here when comparing the sub-periostracal shell surface with the outer preserved surface in silicified specimens from Kuonamka (Fig. 4). However, it is premature to suggest that the smoothed outer surface (Fig. 4B, J, K) is silicified periostracum since this outer proteinaceous layer is often quickly lost in present day molluscs; corrosion or weathering of the outer shell layer may also subdue expression of the growth lines.

The function and original composition of the radial ridges are not known, although some compositional difference from the overlying (and missing in Fig. 4A, C, M) proteinaceous layer is implied by their preservation.

Calcium carbonate is often disseminated within the periostracum of recent bivalves as small spicules (Carter & Aller 1975, Harper 1997, Checa *et al.* 2014) but ridges or canals of the type preserved here have not been recorded. Near the margin, the ridges become more numerous and closely packed, with new ridges introduced at slightly more prominent comarginal growth lines (Fig. 4M). In addition to the comarginal growth lines, the underlying surface preserves a finely dimpled pattern also seen on some internal moulds from the Greenland samples (Fig. 7E).

Close study of the dorsal area of SMNH 160599 (Fig. 4L, N) indicates that a variety of diagenetic processes has occurred. Due to incomplete silicification, the radial ridges are seen to represent the locus of the acute tips of stacked, arrow-head crystals oriented with their axes perpendicular to the shell surface but within the preserved shell layer, *i.e.* below the supposed periostracum, which is not preserved by material other than the radial ridges. The spar crystals seemingly indicate recrystallisation of the calcareous shell prior to silicification, but why these crystals are closely associated with the radial ridges is not known. The same structure is evident in illustrations of co-occurring specimens of the cap-shaped helcionelloid *Anabaroconus sibiricus* Gubanov, Kouchinsky, Peel & Bengtson, 2004 from the upper Kuonamka Formation (Gubanov *et al.* 2004, fig. 5n, u).

Hinge teeth and half-pegmas

Pits along the dorsal margin are characteristic of internal moulds of *Pseudomyona*. In *Pseudomyona groenlandica*, the development of a series of pits along the supra-apical surface of each lateral area (Figs 6C, E, G, H; 8A, E) is a clear indication of interlocking hinge teeth comparable to those seen in *Tuarangia* (Fig. 9) and many recent bivalves (Ponder *et al.* 2020). A series of hinge teeth of this kind is not developed in *Pseudomyona queenslandica* where a shallow pit or pits is present just beyond its supra-apical end (Fig. 5C, E, arrows with bar).

A deep pit is present on each lateral surface at the sub-apical end of the early growth stage of *Pseudomyona queenslandica* (Fig. 5C, E, I, arrows a) and in *Pseudomyona groenlandica* (Figs 6A, 8D). These pits were formed by teeth that do not interlock across the median line but are juxtaposed against each other (Fig. 5B). As such, they do not serve to prevent translation of the lateral areas against each other, as do the interlocking teeth, but may function as paired buttresses to prevent the compaction of the lateral areas of the shell with contraction of adductor muscles. Together, these opposing sub-apical teeth, termed half-pegmas (Fig. 3A), function as a pegma, the diagnostic character of Class Rostroconchia (Pojeta & Runnegar 1976, Wagner 1997).

When in contact, the separate half-pegmas together form an anvil against which adductor muscles can bend the elastic lateral areas of the shell (Runnegar 1983) when closing the ventral margin. On relaxation of the muscles, the same elasticity and possible hydrostatic adjustment from the adductor muscles opens the ventral margin. This is also the case with a transversely complete pegma, as in rostroconchs (Pojeta & Runnegar 1976), but the latter also inhibits the degree of flexing of the shell along the hinge that is possible in *Pseudomyona*.

Most rostroconch pegmas are continuous transverse structures between the two lateral surfaces that provide increased stability, but they must be physically reformed to permit growth of the shell when opposing ventral margins come in contact. Pojeta & Runnegar (1976) describe frequent shearing and fracturing in the hinge zone as the lateral areas add new shell material at the ventral margin. The half-pegmas in *Pseudomyona* do not form a continuous structure from one lateral surface to the other, but occur as opposing, separate, teeth. Contraction of the adductor musculature brings the half-pegmas of each pair into contact. Their separation on muscle relaxation in the present material better allows the shell to grow without the cleavage and fracturing reported by Pojeta & Runnegar (1976), although the present half-pegmas may become conjoined in larger shells.

The half-pegmas of *Pseudomyona* are viewed as an independent (or incipient) stage in pegma development. It may seem more logical to regard half-pegmas as a degradation of the full pegma condition of ribeirioid and other rostroconch groups, resulting from increased dorsal hinge development. Thus, they are not present in *Tuarangia*, which is considered to be a descendant of *Pseudomyona*, where they would serve no purpose in the bivalved form. At the present time, however, suitable pegma-bearing ancestors to *Pseudomyona* are not known from older Cambrian strata.

The presence of a pegma is the defining character of the Rostroconchia. Thus, the opposing half-pegmas of *Pseudomyona*, if interpreted as an incipient pegma, may suggest that *Pseudomyona* is the earliest rostroconch. However, the mechanical stabilisation of the sub-apical area by a transverse structure can take several forms, depending upon shell morphology, such that the acquisition of a pegma or pegma-like structures probably represents analogous rather than homologous developments. *Enigmaconus* MacKinnon, 1985 from the Guzhangian Tasman Formation of New Zealand and *Nyeboeconus* Peel, 1994 from the Drumian Henson Gletscher Formation of North Greenland have wider, relatively tall, cap-shaped, shells in which the transverse pegma is located low on the sub-apical surface (MacKinnon 1985, Peel 1994). *Eurekapegma* MacKinnon, 1985, also from the Tasman Formation, has a strongly

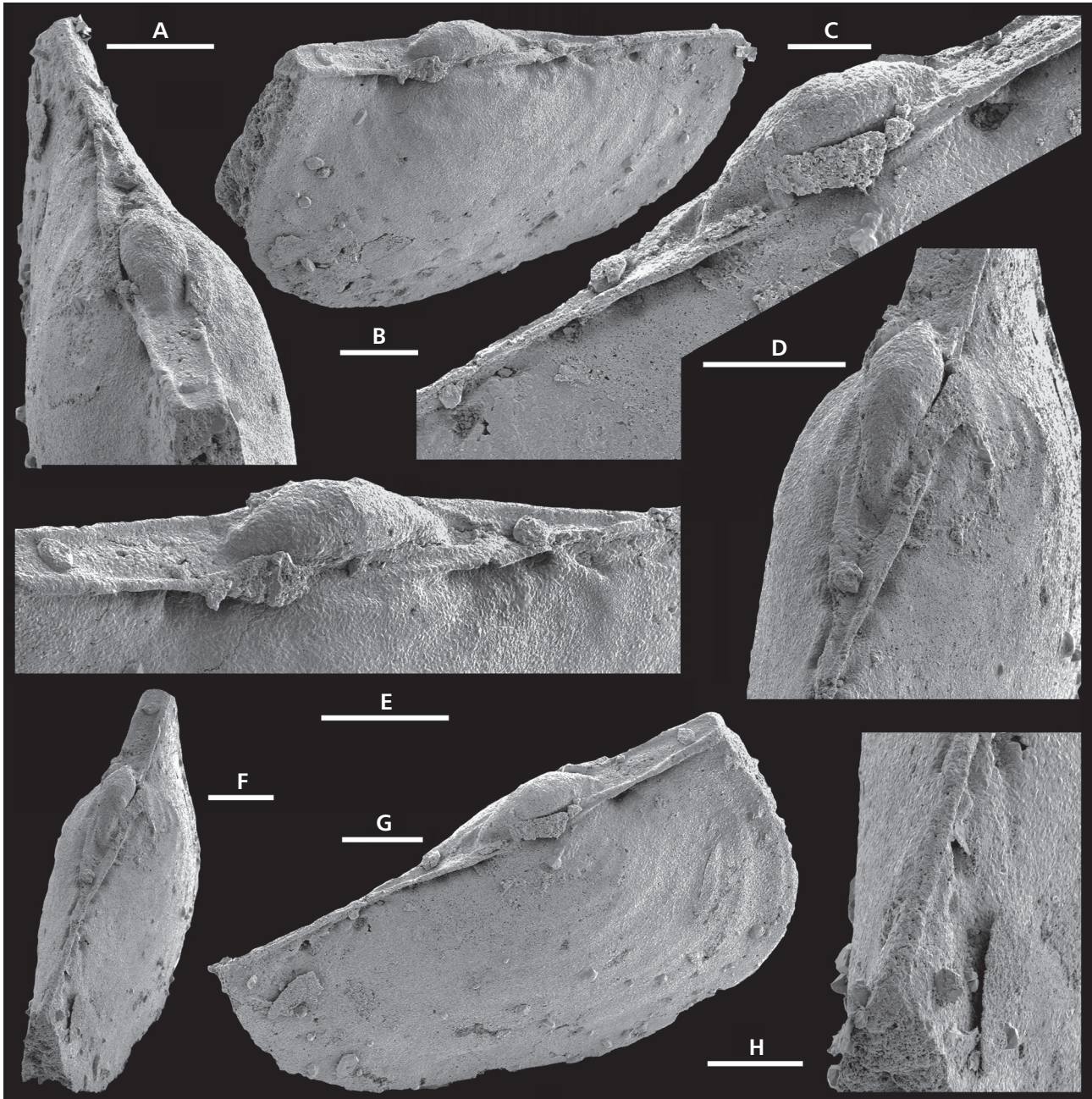


Figure 7. *Pseudomyona groenlandica* sp. nov., internal moulds from GGU sample 315006, Fimbuldal Formation, Freuchen Land, North Greenland, Miaolingian Series, Drumian Stage. A–H – PMU 37513, oblique dorsal views (A, F) with detail of supra-apical termination (H); oblique dorso-lateral views (B, G), early growth stage (C–E). Scale bars: 100 µm (A, B, D–G), 50 µm (C, H).

laterally compressed shell closely similar in shape to *Mellopegma*, although some specimens (Fig. 10) show considerable allometry in their growth style reminiscent of the yochelcionellid *Eotebenna viviannae* (Fig. 1H). *Eurekapegma* develops a prominent, internal, transverse plate, termed the zygon by MacKinnon (1985), extending almost to the ventral margin, but not present immediately below the dorsal crest (MacKinnon 1985, fig. 7), as is also the case in *Pinnocaris lapworthi* Etheridge, 1878

from the Ordovician of Scotland (Peel 2004; Fig. 1B, C). MacKinnon (1985) and Vendrasco *et al.* (2011b) considered *Eurekapegma* to be a possible descendant of *Mellopegma*.

A pegma was stated to be present in *Watsonella* by Pojeta & Runnegar (1976) as the oldest rostroconchs, but studies by MacKinnon (1985), Li *et al.* (2011), Devaere *et al.* (2013), Kouchinsky *et al.* (2017) and Guo *et al.* (2021) have rejected this interpretation. However, the

rapid change of direction between the supra-apical and sub-apical surfaces, in lateral view (Fig. 1J), in this and other laterally compressed Cambrian univalves may perform a similar strengthening function as a separate pegma. Other taxa, such as *Anabarella australis* Runnegar in Bengtson *et al.* (1990), develop a deep cleft on the sub-apical surface at the transition to the sub-apical fold (Bengtson *et al.* 1990, Peel 1991a, Parkhaev 2001).

The flexible hinge of *Pseudomyona*

The longitudinal ridges along the dorsum of internal moulds of *Pseudomyona* are not seen on the outer surface, although their position on the sub-apical surface is indicated by the angular edges of the carina (Figs 3B; 6E, F; 7A, B). The ridges are not continuous along the entire length of the dorsal surface but form separate sub-apical and supra-apical systems that overlap on the lateral areas of the early growth stage (Figs 5A–C, 6A–D), clearly an accommodation of the presence of this growth stage to the overall hinge function along the dorsal surface. Adjacent to the early growth stage and on the sub-apical surface, the ridges represent channels on the shell interior and are often parallel-sided with a sharp, right-angled junction with the flattened upper surface (Figs 5B, 6E, 7D). Distally, on the supra-apical surface, the ridges coalesce to a single median ridge or angulation (Figs 6H, 7H, 8E).

The width of the ridges reflects the degree of opening of the individual specimens, as preserved. Ridges are often inconspicuous where the lateral areas of the shell are closed together (Fig. 8) and more prominent, wider, in specimens where the lateral areas show a large anterior gape (Figs 3B; 6E, F). There may be some slight diagenetic influence in both situations, for example where the ridge is maintained between the interdigitating teeth on the supra-apical surface (Fig. 6E, H), although this may just be due to increased gape. There is no direct evidence of the presence of a discrete ligament(s) within the channels on the shell interior. The smooth exterior of silicified specimens (Fig. 4G, K) suggest that an elastic outer shell layer and a thickened periostracum formed the hinge. The groove separating the early growth stage from the lateral areas on the external surface of silicified specimens (Fig. 4D, I) is the only indication of movement in the dorsal area. Its presence reflects the opposite mechanical moment of movement to that experienced across the dorsum, distant from the early growth stage, with opening or closing.

Evolutionary relationships

The lower three series of the Cambrian (Terreneuvian, un-named Cambrian Series 2, and Miaolingian) contain

a morass of small cap-shaped univalve shells that generally exhibit few features useful for their classification. Runnegar & Jell (1976) grouped many of these into an embracive Class Monoplacophora Wenz in Knight, 1952 and Class Rostroconchia was introduced by Pojeta *et al.* (1972) for pseudo-bivalved molluscs (Pojeta & Runnegar 1976). Peel (1991a) avoided using Monoplacophora and proposed a distinction between exogastric tryblidian forms, which he assigned to the Class Tergomya Horný, 1965, and endogastric shells placed within a Class Helcionelloida Peel, 1991b. Both these approaches, most recently reviewed by Guo *et al.* (2021), fail to reflect the complexity of Cambrian mollusc evolution. Parkhaev (2002, 2008, 2017, 2019; Parkhaev in Bouchet *et al.* 2017) developed a different approach but a generally accepted overview of Cambrian groups remains elusive.

Pseudomyona and *Mellopegma*

The origin of *Pseudomyona* is unclear. With regard to the degree of lateral compression and curvature of the ventral margin, *Pseudomyona* is similar to *Mellopegma* (Figs 1I, 10) and Vendrasco *et al.* (2011b) suggested that stenothecids such as *Mellopegma* may have been ancestral to rostroconchs. However, the lateral compression and curved aperture might be expected in any helcionelloid adapting to an infaunal life, as pointed out by Peel (1991a), Waller (1998) and Gubanov *et al.* (1999), while narrowing of the aperture also represents a simple anti-predator defensive strategy in univalved molluscs (Vermeij 1987, Vendrasco *et al.* 2011b). The straight dorsum of *Pseudomyona* (Fig. 1A) contrasts strongly with the longitudinally convex supra-apical dorsum of *Mellopegma* (Fig. 1I), the latter also lacks any indication of a dorsal hinge zone or hinge teeth. The ontogenetic change in coiling and shell expansion in *Pseudomyona*, witnessed by its upright early growth stage, finds no parallel in elongate species of *Mellopegma*, where the initial growth stage is often lower than the crest of the dorsum and overhangs the sub-apical surface (Vendrasco *et al.* 2011b). However, similar profound asymmetry of the logarithmic spiral of the expanding shell is seen in the unrelated elongate yochelcionellid *Eotebenna viviannae* (Fig. 1H) and in some specimens of *Eurekapegma cooperi* MacKinnon, 1985 (Fig. 10) of similar age, both of which are also characterised by strong lateral compression.

In North Greenland, *Mellopegma* is known from the Henson Gletscher Formation to the Fimbuldal Formation (late Stage 4–Drumian; Fig. 2B). It occurs together with *Pseudomyona groenlandica* in GGU sample 315006 where their dissimilar styles of preservation suggest some differences in shell composition. *Mellopegma* is preserved as phosphatic coatings of the shell exterior and

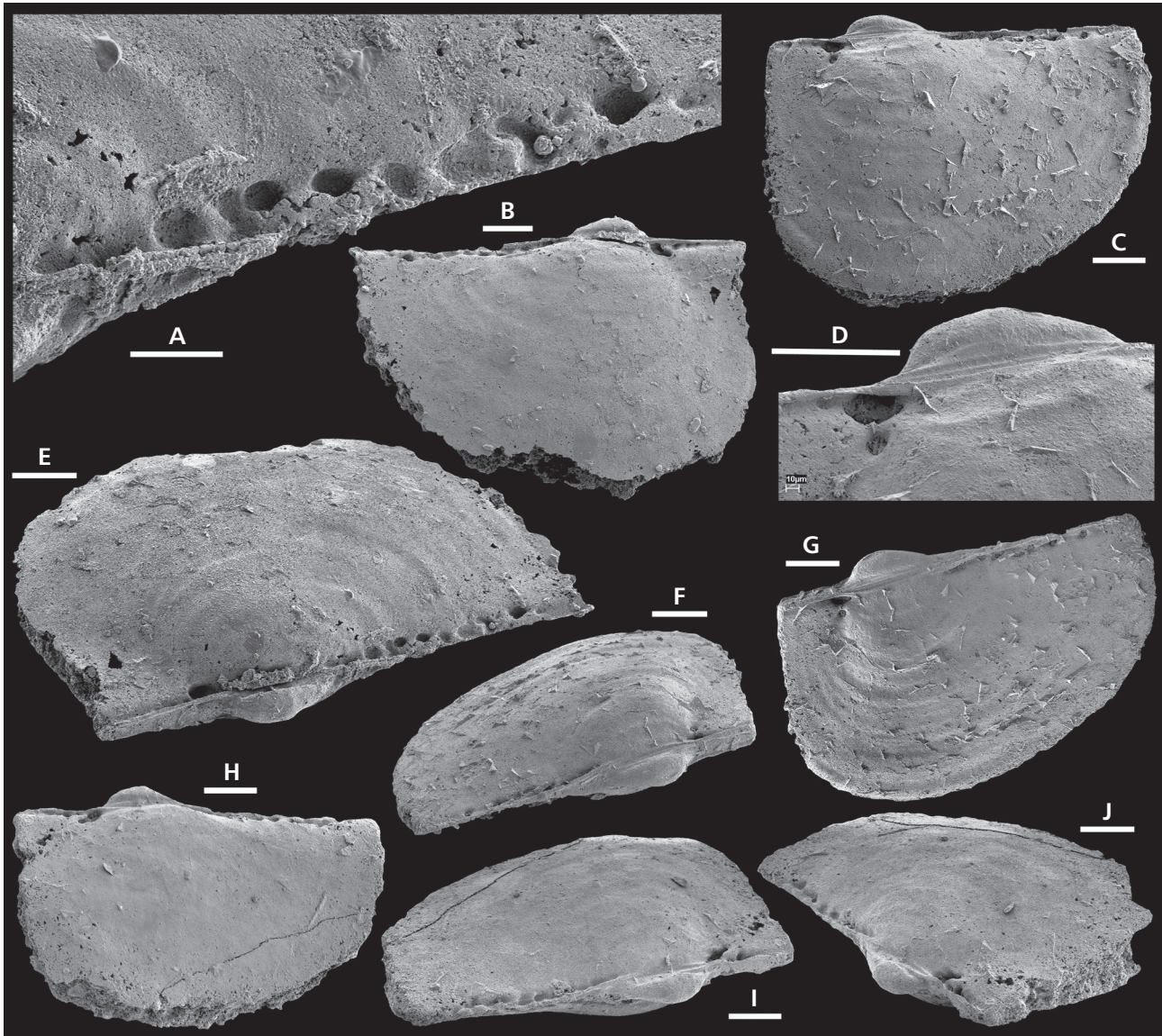


Figure 8. *Pseudomyona groenlandica* sp. nov., internal moulds from GGU sample 315006, Fimbuldal Formation, Freuchen Land, North Greenland, Miaolingian Series, Drumian Stage. A–G – PMU 37514, lateral views (B, C, G) with detail of early growth stage (D); dorso-lateral views (E, F) with detail of hinge teeth pits (A). H–J – PMU 37515, lateral (H) and dorso-lateral (I, J) views. Scale bars: 50 µm (A); 100 µm (B–J).

interior surfaces (Fig. 11) while *Pseudomyona* is known only as internal moulds (Figs 6–8). Internal moulds of *Pseudomyona* show no trace of the small tubercles that occur on internal moulds of *Mellopegma* (Vendrasco *et al.* 2011b).

Pseudomyona and *Tuarangia*

Tuarangia was proposed by MacKinnon (1982), with type species *Tuarangia paparua* MacKinnon, 1982 from the Tasman Formation at Trilobite Rock, Cobb Valley, South Island, New Zealand (Miaolingian Series, Guzhangian Stage, Boomerangian Local Stage, *Ptychagnostus* *cassis*

Biozone). Known from abundant internal moulds, it was classified as Class Bivalvia, Order Tuarangiida nov. by MacKinnon (1982) on account of the bivalved shell and straight hinge line, with numerous teeth disposed either side of a short amphidetic ligament. Runnegar & Bentley (1983) rejected the assignment to Bivalvia, suggesting that *Tuarangia* was a ‘quasiostroconch’ or bivalved monoplacophoran similar to *Pseudomyona queenslandica*. Runnegar (1983) considered the median apical ridge of *Tuarangia* to be the scar of a broken off early growth stage (Fig. 9B, C, E), but this was refuted by MacKinnon (1985) who restated his opinion that the scar was formed by a ligament, and that *Tuarangia* was a bivalve. Additionally, MacKinnon (1985) rejected the notion that

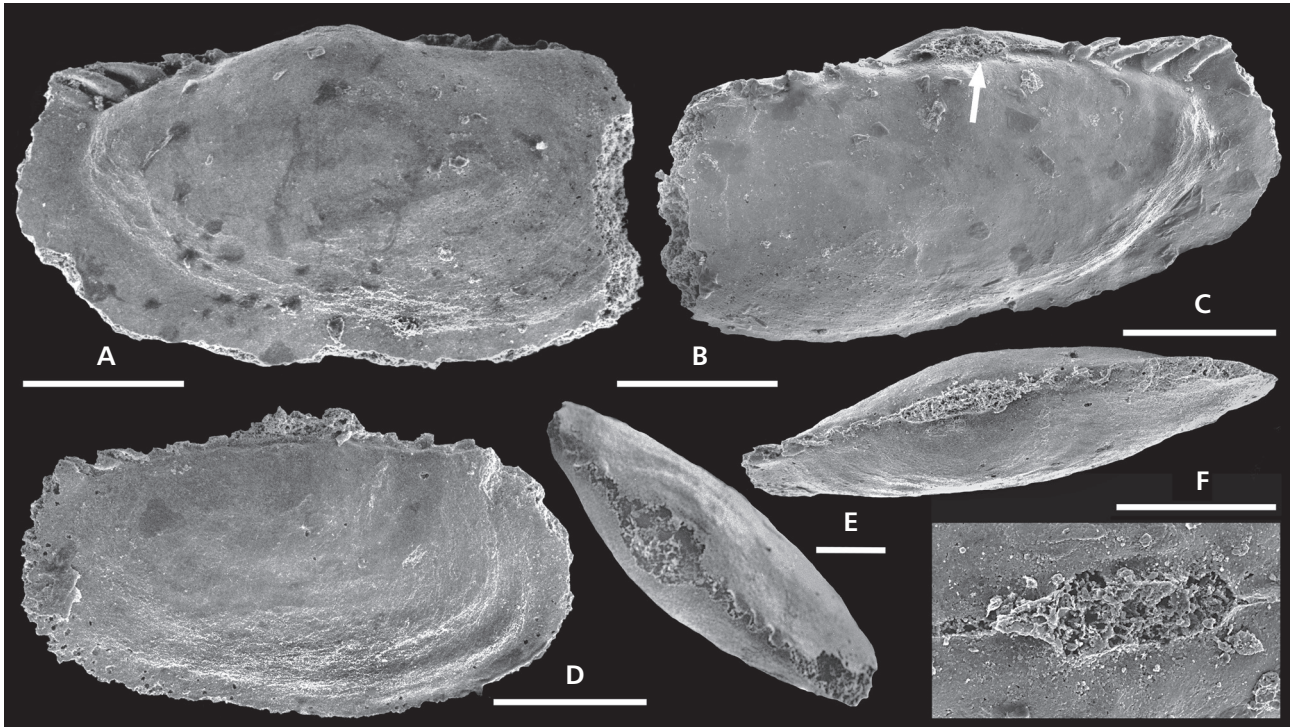


Figure 9. *Tuarangia* from Denmark and Poland • A–D, F – *Tuarangia gravgaerdensis* Berg-Madsen, 1987, internal moulds, Andrarum Limestone, Bornholm, Denmark, Miaolingian Series, Guzhangian Stage; holotype (A, B, F), MGUH 17.451, lateral view of left valve (A), dorso-lateral view of right valve with arrow locating ligament scar (B) and scar of ligament (F); paratype (C, D), MGUH 17.452, dorsal view showing ligament scar and interdigitating hinge teeth (C) and lateral view of left valve (D) • E – *Tuarangia* sp., glacial erratic, northern Poland, Collections of Zakład Paleobiologii, PAN, Warszawa, Poland. Scale bars: 200 µm (A–E), 80 µm (F). Images: Jerzy Dzik (E), otherwise Vivianne Berg-Madsen.

bivalves were descended from rostroconchs, suggesting that they were derived directly from monoplacophorans. *Tuarangia*, however, was considered to be probably closely related to *Pseudomyona* (MacKinnon 1985).

In proposing a second species, *Tuarangia gravgaerdensis*, based on internal moulds from the Andrarum Limestone bed (Alum Shale Formation) of Bornholm, Denmark (Guzhangian Stage, *Solenopleura brachymetopa* Biozone, placed within the global *Lejopyge laevigata* agnostoid Biozone by Axheimer *et al.* 2006), Berg-Madsen (1987) maintained the interpretation of *Tuarangia* as a pteriomorph bivalve (Fig. 9). Runnegar & Pojeta (1992) concluded that *Pseudomyona* and *Tuarangia* belonged to the same clade but were not true bivalves.

Hinz-Schallreuter (1995) described *Tuarangia gravgaerdensis tenuiumbonata* from the Exsulans Limestone bed (Alum Shale Formation) of Bornholm, Denmark (Wuliuan Stage, *Ptychagnostus gibbus* Biozone), including internal moulds and specimens with the exterior and inner surfaces preserved. However, Hinz-Schallreuter (2000) subsequently re-interpreted the same material as being derived from the Andrarum [Limestone] Breccia. Thus, *Tuarangia gravgaerdensis tenuiumbonata* and other bivalves that Hinz-Schallreuter (1995, 2000) described from the same samples (*Pojetaia ostseensis* Hinz-

Schallreuter, 1995 and *Camya asy* Hinz-Schallreuter, 1995) are not derived from the Exsulans Limestone (Wuliuan Stage) but are from essentially the same horizon (Andrarum Limestone; Guzhangian Stage) as Berg-Madsen's (1987) material. The records of *Tuarangia* from New Zealand and Bornholm, Denmark are therefore all of Guzhangian age. Berg-Madsen (1987) also described a single internal mould from an erratic boulder in Poland as *Tuarangia* sp. (Fig. 9E), estimated as probably of early Late Cambrian (Furongian) age, although Hinz-Schallreuter (2000) commented that a late Middle Cambrian (Miaolingian) age was possible.

Tuarangia was considered to be a protobranchiate/palaeotaxodont bivalve by Hinz-Schallreuter (2000) who considered *Tuarangia gravgaerdensis* and *Tuarangia gravgaerdensis tenuiumbonata* to be junior synonyms of *Tuarangia paparua*. *Pseudomyona*, placed within a new Order Pseudomyonida and new Family Pseudomyonidae by Hinz-Schallreuter (2000), was interpreted as a ribeirioid rostroconch. Vendrasco *et al.* (2011a) noted that *Tuarangia* and *Pseudomyona* shared similarities, such as a shell consisting of foliated calcite (MacKinnon 1982, Runnegar 1985, Vendrasco *et al.* 2010), which made the separation of *Tuarangia* and *Pseudomyona* proposed by Hinz-Schallreuter improbable.

While *Pseudomyona* and *Tuarangia* are clearly distinct, their close relationship is strengthened by the present description of a series of interdigitating hinge teeth along the supra-apical surface of *Pseudomyona groenlandica*, in which respect it closely resembles *Tuarangia* (Fig. 9C). It is envisaged that the pair of dorsal flexible hinge zones on the sub-apical surface of *Pseudomyona* (Fig. 3B) subsequently coalesce and also acquire interdigitating teeth, likely developed from the half-pegmas, as the early growth stage is superseded by an amphidetic ligament (Fig. 9B, F). However, the teeth of *Tuarangia* are elongate (Fig. 9A, B) whereas those of *Pseudomyona groenlandica* are sub-circular (Fig. 8A). Hinz-Schallreuter (2000) pointed out differences in lateral profile, with the greatest height being near the sub-apical margin in *Pseudomyona* but at the supra-apical

termination in *Tuarangia* but MacKinnon (1982, 1985) described great variation in the lateral profile, and many specimens are close to equilateral (Fig. 9D). The change in profile may reflect the migration of the umbonal region towards mid-length in *Tuarangia*, in connection with the development of the tooth-bearing sub-apical hinge.

In terms of age, specimens of *Pseudomyona groenlandica* are derived from an intermediate stratigraphic position between *Pseudomyona queenslandica*, which lacks the interdigitating tooth series on the supra-apical surface, and the true bivalved *Tuarangia* (Fig. 10). *Pseudomyona* and *Tuarangia* (Order Tuarangiida emend.) are considered to form a sister group to ribeirioids in which the incipient pegma (half-pegmas) was lost as the true bivalved shell of *Tuarangia* with taxodont dentition was developed (Fig. 10).

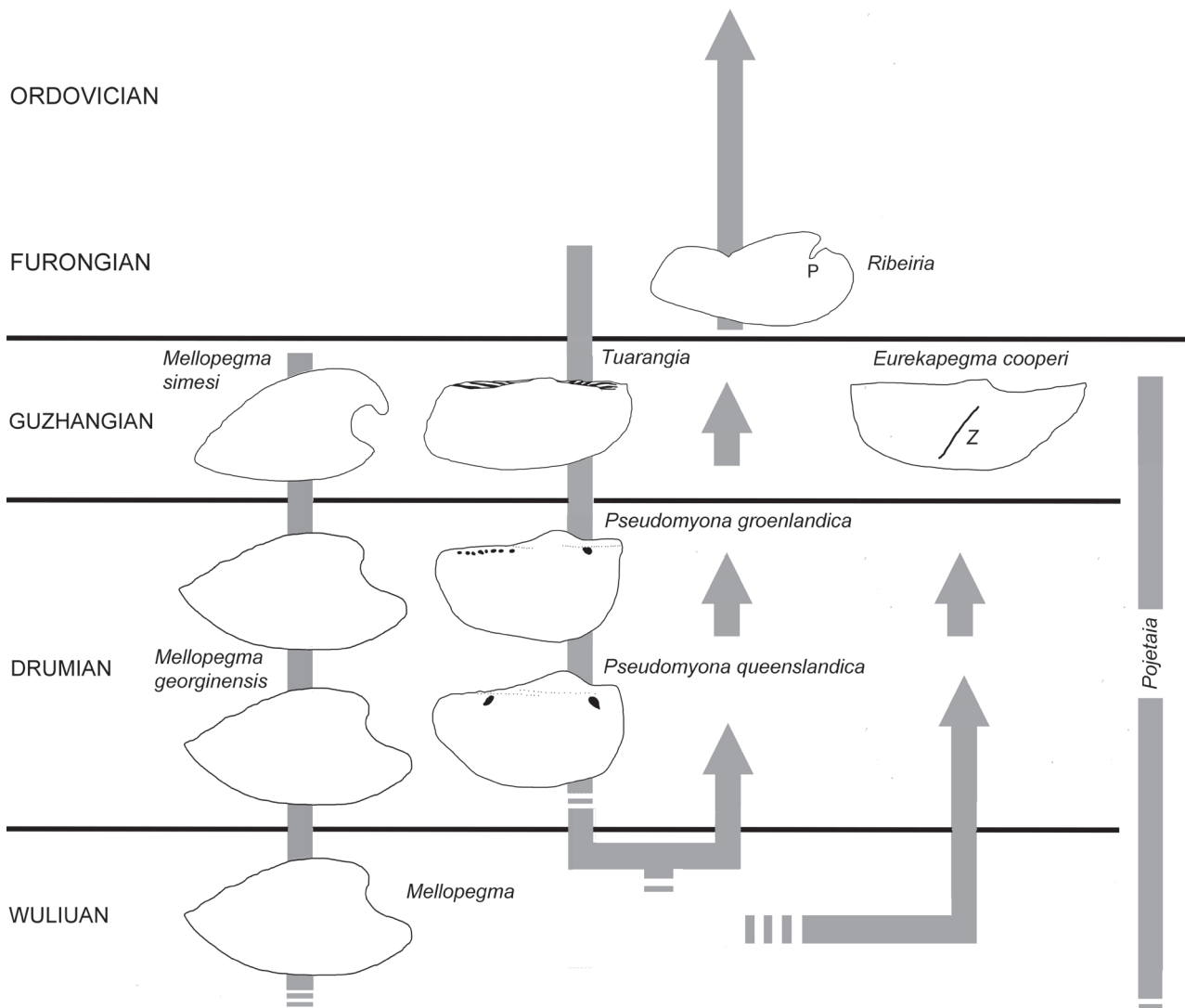


Figure 10. Stratigraphic relationships of Cambrian molluscs represented by their internal moulds. Abbreviations: P – pegma; Z – zygion.

Conclusions

The Cambrian univalve *Pseudomyona* (Miaolingian, Series, Drumian Stage) is recorded for the first time from Laurentia, extending its previously known range from Australia and Siberia. *Pseudomyona queenslandica* (Runnegar & Jell, 1976), the type species, occurs in the Ekspedition Bræ Formation of North Greenland and is followed in the overlying Fimbuldal Formation by *Pseudomyona groenlandica* sp. nov.

The proliferation of interdigitating hinge teeth on the supra-apical surface of *Pseudomyona groenlandica* supports an ancestral relationship with the slightly younger, bivalved, *Tuarangia* (Miaolongian Series, Guzhangian Stage; ?earliest Furongian Series).

Pseudomyona and *Tuarangia* are assigned to an emended Order Tuarangiida, referred to Class Rostroconchia as a sister group to ribeirioids. *Pseudomyona* may be the oldest rostroconch.

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