The periostracum, a non-calcified organic layer that envelops the mineralized shell layer ('ostracum') of molluscs, acts as an initial framework for the calcified 'ostracum'. Despite its significance in biomineralization in molluscs, fossil examples of the periostracum are limited in the geological record, especially from the Palaeozoic era, due to its susceptibility to post-mortem decay. In this study, we describe radial threads found on the outer surface of Cambrian molluscs, including helcionelloids and rostroconchs, which we interpret as fossilized periostracal structures. These radial threads are observed in 13 species from five valid genera, exhibiting a widespread palaeogeographical distribution encompassing Gondwana (Australia), Siberia, western Laurentia (Utah), and eastern Laurentia (Greenland), and spanning Cambrian Stage 4–Drumian deposits. These radial threads always cover the outermost surface of shells, dividing it into regular intervals, and develop through incremental growth. They originate from the apical area of helcionelloids or the umbo of rostroconchs. Detailed examination has revealed that the radial threads initiate at the apical region, but may be absent from the protoconch (embryonic shell). The radial threads are most likely preserved by mineral encrustation on the periostracum. Similar, but not homologous, radial threads are found in other fossil and modern molluscan taxa, such as the adhesive radial lines of anomalodesmatan bivalves or the periostracal ridges of viviparid gastropods.

**Periostracum, radial thread, helcionelloids, Cambrian molluscs**

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Preservation, material and methods

Preservational modes in Cambrian micromolluscs

The lower and middle Cambrian molluscs described herein are from various localities including North Greenland, Australia, Siberia, and USA (Fig. 2; see Supplementary data for detailed information regarding geological background). They are preserved as mineral-replaced shell and/or moulds composed of silicate or phosphate minerals. Silicification and phosphatization are some of the main taphonomic processes involved in the conservation of organisms, replicating skeletal and non-biomineralized structures. The pathways are similar, both involving the nucleation and precipitation of authigenic silicate or phosphate minerals on organic templates, which are encrusted and replicated (Muscente et al. 2015; 2017).

Phosphatization of early to middle Cambrian (Cambrian Stage 4–Miaolingian) micromolluscs most commonly involved preservation as internal moulds (Creveling et al. 2014; Peel & Kouchinsky 2022) with diageneric phosphate, filling the internal cavity to produce phosphatic internal moulds (Fig. 1A, D) that
Phosphatization may have replaced the original calcareous shell but usually encrusted its outer surface with a thin skin of mineral growth that permits recognition of fine details of underlying ornamentation (e.g. Peel & Kouchinsky 2022, fig. 4F, I). Following etching of calcareous shells during sample preparation, phosphatic encrustations may also reveal moulds of the shell exterior.

In contrast to phosphatization, silicification in Cambrian Small Shelly Fossils usually entirely replaced the calcareous shells of Cambrian micro-molluscs (Runnegar & Jell 1976; Gubanov et al. 2004). Silicification may also preserve exquisite details of the shell exterior by encrustation (i.e. precipitation on
the external surface) of silica, mimicking the external morphology, as an ‘external coating’ (Figs 1B, C, E–K, 3, 4; Butts 2014). Fine-scaled replication of the internal shell structure, however, of the type well documented on phosphatic internal moulds (Vendrasco et al. 2010, 2011a) is not known in silicification.

Present day molluscan specimens for comparison

Periostracal ridges were examined in the freshwater viviparid snail Cipangopaludina chinensis malleata (Reeve, 1863). These snails were collected from Republic of Korea and cultured in a water tank at room temperature at Korea Polar Research Institute (KOPRI). One-week-old juveniles of the cultured animals were fixed using formalin, dehydrated through a serial series to absolute ethanol, and dried using hexamethyldisilazane (HMDS), after the soft parts were eliminated. Shells were gold-coated in a Cressington 108 Auto Sputter Coater, and examined with a Field Emission SEM JEOL JSM-7200F at KOPRI (Fig. 5).

Adhesive radial lines and calcified periostracal structure in extant anomalodesmatan bivalves were studied in Lyonsia norwegica (Gmelin, 1791) and Lyonsia arenosa (Møller, 1842). The dried specimens without soft parts are housed in the Museum of Evolution, Uppsala University, Sweden (UPSMZC 190031, 190033, 190035, and 190040); they were coated with ammonium chloride sublimate prior to photography (Fig. 6).

Abbreviations and specimen repositories

GGU indicates a sample collected under the auspices of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark. Two bulk limestone samples (C3392 and C3393) from the First Discovery Limestone are registered with Geological Survey of New South Wales, and seven illustrated specimens with the prefix MMMC (MMMC05959–MMMC05965 inclusive) are deposited in the Micropaleontology Collection of the Geological Survey of New South Wales in Sydney. MGUH indicates a specimen deposited in the invertebrate palaeontology collection of the Natural History Museum of Denmark, Copenhagen, Denmark. PMU and UPSMZC indicate specimens deposited in the palaeontological and zoological collections, respectively, of the Museum of Evolution, Uppsala University, Sweden. SMNH Mo indicates a specimen deposited in the fossil mollusc collection of the Swedish Museum of Natural History, Stockholm, Sweden.

Results

Preservational variation in Yochelcionella

Observed morphological features in specimens of Yochelcionella Runnegar & Pojeta, 1974 from Australia, North Greenland, and Siberia vary depending on the mode of preservation (see Figs 1, 3). Specimens of Yochelcionella gracilis Atkins & Peel, 2004 from the Henson Gletscher Formation (Cambrian Stage 4) in the Løndal area, North Greenland are found as phosphatized internal moulds (Fig. 1A, D) or silicified ‘external coating’ of shell (Fig. 1B, C; Peel et al., 2016). In the latter case, the thin silicified layer with concentric growth lines represents the outer shell layer. When the silicified ‘external coating’ is preserved, the margins of the comarginal plications are more acute and protuberant than on the internal moulds (compare Fig. 1A with Fig. 1C). Five to seven growth lines are placed per 100 μm of shell length (Fig. 1B). Beneath the ‘external coating’, a narrow gap is visible at the crest of the comarginal plications (black arrow in Fig. 1B).

This outer shell layer with fine growth lines is also found in other samples of Y. gracilis from the Henson Gletscher Formation (Cambrian Stage 4) in Freuchen Land, North Greenland (Fig. 3). The spacing and thickness of each growth line correspond to that in the Løndal materials (see Fig. 3D for Freuchen Land material and Fig. 1B for Løndal material). Additional to the growth lines, radial threads are found covering the outer shell layer of the well-preserved Freuchen Land materials (Fig. 3). The radial threads cross the comarginal plications and growth lines, as in other fossil mollusc specimens figured herein (Fig. 4). Internal moulds of Yochelcionella observed from partly exfoliated silicified specimen show that the radial threads are confined to the outer surface of the shell (Fig. 3E, F).

Specimens of Yochelcionella ostentata Runnegar & Jell, 1976 from the First Discovery Limestone Member, Coonigan Formation (Miaolingian), New South Wales, Australia also show both the outer shell layer with fine growth lines and distinct radial threads (Fig. 1E–I). Although affected by recrystallization during diagenesis, close observation of an Australian specimen indicates that the radial threads appear to have formed by the aggregation of successive growth stages (Fig. 5A–C) in which each newly-formed comarginal increment grows outward from beneath the previous one with the radial threads formed by the imbricated edges (Fig. 5C). Comarginal increments are laterally extended from each edge of radial threads (Fig. 5C), and neighboring comarginal increments are
Fig. 3. Radial threads of *Yochelcionella gracilis* Atkins & Peel, 2004 from the Henson Gletscher Formation, Cambrian Stage 4, southern Freuchen Land, North Greenland. A–D, PMU 21538 from GGU sample 301347. The white arrow in (D) indicates the silica-replaced shell with only concentric growth lines exposed where the radial thread-bearing outermost layer has been removed. E–G, PMU 21539 from GGU sample 301347. Black arrows in (F) indicate a gap between the radial thread-bearing ‘external coating’ layer and the internal mould. H–J, PMU 21540 from GGU sample 301347. Black arrows in (J) identify the crests of the comarginal plications where the radial threads are incompletely preserved. Scale bar: 500 µm (A, E, J), 300 µm (D & I), 200 µm (B, C, F), 100 µm (G & H).
Fig. 4. Cambrian molluscs with radial threads. A–C, *Pseudomyona queenslandica* (Runnegar & Jell, 1976), SMNH 160599 from the Kuonamka Formation, Miaolingian, northern Siberia. White arrow in (C) indicates the radial threads developed on the rostroconch shell in the early juvenile stage. D, *Pseudomyona queenslandica* (Runnegar & Jell, 1976), SMNH 160600, lateral view from the Kuonamka Formation, Miaolingian, northern Siberia. E, F, *Dorispira accordionata* (Runnegar & Jell, 1976), MMMC05961 from sample (KOPRI CO2-1) from the First Discovery Limestone Member, Coonigan Formation, Miaolingian, New South Wales, Australia. G, H, *Dorispira accordionata* (Runnegar & Jell, 1976), MMMC05962 from sample (KOPRI CO2-10) from the First Discovery Limestone Member, Coonigan Formation, Miaolingian, New South Wales, Australia. I, J, *Dorispira accordionata* (Runnegar & Jell, 1976), MMMC05963 from sample (KOPRI CO1-14) from the First Discovery Limestone Member, Coonigan Formation, Miaolingian, New South Wales, Australia. K, L, Helcionelloida indet. PMU 21542 from the Marjum Formation, Miaolingian, Utah, USA. M, N, Helcionelloida indet. MMMC05964 from sample (KOPRI CO2-2) from the First Discovery Limestone Member, Coonigan Formation, Miaolingian, New South Wales, Australia. White arrow in N indicates fibrous microstructure. O, *'Stenotheca' pojetai* (Runnegar & Jell, 1976), MMMC05965 from sample (KOPRI CO3-12) from the First Discovery Limestone Member, Coonigan Formation, Miaolingian, New South Wales, Australia. Scale bar: 400 µm (M), 300 µm (K), 200 µm (A, D, E, G, H, L, O), 100 µm (B, C, F, I, J, N).
Fig. 5. Detailed morphology related to radial thread structures. A–C, *Yochelcionella ostentata* Runnegar & Jell, 1976, from the Coonigan Formation, Miaolingian, New South Wales, Australia (KOPRI CO2-19 from sample MMMC05959, silicified specimen; same specimen with Fig. 1E–G). White arrows in A indicate comarginal increments between radial threads. Magnified view in (C) shows that the newly formed units consist of the upturned edge (i.e. radial thread) and the comarginal increments that are extended from each edge. D, E, Helcionelloid indet. from the Henson Gletscher Formation, Cambrian Stage 4, Freuchen Land, North Greenland (PMU 21541 from GGU sample 301347, silicified specimen). Black arrow in (D) indicates the apical tip where the radial threads are absent, possibly corresponding to the protoconch. The lateral side in (E) is partially exfoliated, therefore the thin internal mould beneath the radial thread-bearing layer is exposed. Note that the fibrous microstructure (white dotted lines) of the internal mould. Black dotted lines indicate the distribution of the radial threads, which is perpendicular to the white dotted lines. White arrows indicate a gap between the radial thread-bearing layer and the internal mould, possibly reflecting the true thickness of the original shell. F, *Yochelcionella gracilis* Atkins & Peel, 2004 from the Henson Gletscher Formation, Cambrian Stage 4, southern Freuchen Land (PMU 21540 from GGU sample 301347, silicified specimen; same specimen as Fig. 3H–J). White arrow indicates merging radial threads. Scale bar: 10 µm (A & C), 30 µm (D), 50 µm (B & F), 200 µm (E).
also laterally associated with each other (white arrows in Fig. 5A).

The presence of the radial threads is also confirmed in the silicified material of *Y. ostentata* from Siberia, which seemingly have a smooth surface between the comarginal plications (Fig. 1J, K; Gubanov et al. 2004). The radial threads and fine growth lines in the Siberian specimens (Fig. 1J, K) are not as distinct as in the materials from Australia and North Greenland.

**Radial threads in Cambrian molluscs**

In addition to *Yochelcionella*, radial threads have been confirmed on the outermost surface of phosphatized and silicified specimens from five molluscan genera, *Pseudomyona* Runnegar, 1983, *Anabarocoma* Gubanov, Kouchinsky, Peel & Bengtson, 2004, *Mellopegma* Runnegar & Jell, 1976, and *Dorispira* Parkhaev in Parkhaev & Demidenko, 2010, belonging to the classes Rostroconchia and Helcionelloida. Accordingly, seven species including two species of *Yochelcionella* are illustrated herein (Table 1; Figs 1, 3, 4, 5), which occurred on various palaeocontinents (Fig. 2; Supplementary data): Gondwana (First Discovery Limestone Member, Coonian Formation, Miaolingian, New South Wales, Australia), Siberia (Kuonamka Formation, Miaolingian, northern Siberia), and Laurentia (Henson Gletscher Formation, Cambrian Stage 4, North Greenland in present day eastern Laurentia; the Marjum Formation, Miaolingian, USA of western Laurentia).

Despite the variations in geographic occurrence, age, and degrees of fidelity, the morphology of the radial threads is seemingly consistent. They are always observable on the outermost surface of the fossils, and absent from the interior (Figs 3C, 4H). The thickness of the threads in the silicified samples ranges from approximately 3 to 7 μm depending on preservation, and at most 14 per 100 μm of shell width. They always originate from the apical region of the shell, forming a star-shaped structure in dorsal view, and continue towards the apertural margin (Figs 1G, K, 3H, 4F, K, 5A, D). This suggests that the structures reflect the original shell rather than being a taphonomic overprinting. The radial threads are sometimes exfoliated at the margins of rugae/plications in the specimens where comarginal structures are strongly developed (black arrows in Fig. 3J). Shell microstructures, such as prismatic or laminar patterns are not recognized in detail on the shell underlying the radial threads in silicified specimens, but a few specimens preserve a fibrous texture where the radial threads are exfoliated (white arrow in Fig. 4N and white dashed lines in Fig. 5E).

Helcionelloid indet. from Freuchen Land, North Greenland (Fig. 5D, E) reveals that the radial threads originate from the apical area, similar to *Yochelcionella ostentata* (Fig. 5A), but not precisely from the apical tip (Fig. 5D). The region without the radial threads at the apex is about 30 μm in diameter and could reflect the protoconch (embryonic shell), potentially suggesting that radial threads in this specimen did not develop at the embryonic stage.

Radial threads on the illustrated rostroconch mollusc *Pseudomyona queenslandica* from the Kuonamka Formation, northern Siberia (Fig. 4A–D), are especially well preserved near the commissure margin and wing, covering the growth lines. Most threads are linear, although instances of bifurcating, merging and irregular threads are present (white arrow in Fig. 4B). Merging of two neighbouring threads is also observed in other helcionelloid taxa (white arrow in Fig. 5F). A single rostroconch shell reflecting the early juvenile stages in ontogeny also has radial threads (white arrow in Fig. 4C), but these are finer than those in the subsequent pseudo-bivalved shell and arranged in a different pattern. However, it is unclear how the radial threads originate in *P. queenslandica* within the juvenile shell.

**Comparison to modern specimens**

Molluscan periostracum often displays various microstructures, not just the simple thin layered form (see Carter & Aller 1975; Bottjer & Carter 1980 for the classification of periostracal structures). We have examined several periostracal features of modern molluscan specimens to morphologically compare to the Cambrian radial threads. The compared modern periostracal features include projecting periostracum, adhesive radial lines secreted on the periostracum, and intra-periostracal calcification.

Projecting periostracum refers to regularly formed, projecting, non-calcified structures of the periostracum. The organic structures secreted over the exterior of the true periostracum includes shingles, hairs, thorns and hairlets (Bottjer & Carter 1980). Where and how these structures originate is still unknown (Allgaier 2011). Especially, the projecting periostracal structure of the Family Viviparidae (fresh-water snail) resemble the radial thread structure of Cambrian molluscs. The viviparids have radially (i.e. spirally in the tightly coiled shell) arranged periostracal ridges which start forming during embryonic to juvenile developmental stages (Jokinen 1984). The viviparid gastropod *Cipangopaludina chinensis malleata* (Reeve, 1863) shows well-developed periostracal ridges (Fig. 6). The periostracum of *C. chinensis malleata* is about 3–5 μm thick, and sometimes peeled off from the underlying mineralized shell layer at the
margin (Fig. 6E, F). The periostracal ridges in the juvenile shells of *C. chinensis malleata* consist of simple ridges (Fig. 6D), short-hooked hairs (Fig. 6E), and long-hooked hairs (Fig. 6C). The ridges and hairs are confined to the outermost layer of the periostracum (Fig. 6E). Each row of ridges (or hairs) is regularly distributed at intervals of 20–25 µm, and the interspaces between them are wrinkled (Fig. 6D). These wrinkles extend laterally from the ridges (or hairs), and are not observed on the inner surface of the periostracum (Fig. 6E).

Adhesive radial lines secreted from the arenophilic gland on the outermost periostracum surface occur in some anomalodesmatan bivalves (Sartori & Harper 2009; Pimenta & Oliveira 2013; Oliveira & Sartori 2014). The subclass Anomalodesmata is a marine

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**Table 1. List of Cambrian molluscs with radial thread structures. Asterisks (*) in species names indicate taxa illustrated in this study.**

<table>
<thead>
<tr>
<th>Class</th>
<th>Species name</th>
<th>Stratigraphy (Age)</th>
<th>Locality</th>
<th>Region</th>
<th>Preservation</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rostroconchia</td>
<td><em>Pseudomyona queenslandica</em></td>
<td>Kuonamka Fm. (Miaolingian)</td>
<td>Bol’shaya Kuonamka River, northern Siberia</td>
<td>Siberia</td>
<td>Silicified</td>
<td>Gubanov et al., 2004; Peel, 2021</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Anabaroconus sibiricus</em></td>
<td>Kuonamka Fm. (Miaolingian)</td>
<td>Bol’shaya Kuonamka River, northern Siberia</td>
<td>Siberia</td>
<td>Silicified</td>
<td>Gubanov et al., 2004</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Yochelcionella ostentata</em></td>
<td>Kuonamka Fm. (Miaolingian)</td>
<td>Bol’shaya Kuonamka River, northern Siberia</td>
<td>Siberia</td>
<td>Silicified</td>
<td>Gubanov et al., 2004</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td>&quot;Stenotheca&quot; pojetai (Runnegar &amp; Jell, 1976)*</td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>Runnegar and Jell, 1976</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Anabaroconus penecyrano</em></td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>Runnegar and Jell, 1976</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Dorispira accordionata</em></td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>Runnegar and Jell, 1976</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Yochelcionella cyrano</em> Runnegar &amp; Pojeta, 1974</td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>Runnegar and Jell, 1976</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Yochelcionella daleki</em> Runnegar &amp; Jell, 1976</td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>Runnegar and Jell, 1976</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Yochelcionella ostentata</em></td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>Runnegar and Jell, 1976</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td>Helcionelloida indet.1*</td>
<td>First Discovery Limestone Member, Coonigan Fm. (Series 2, Stage 4)</td>
<td>Cymbric Vale Station, New South Wales, Australia</td>
<td>Gondwana</td>
<td>Silicified</td>
<td>This study (Fig. 4M, N)</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Mallotegma georginensis</em></td>
<td>The middle Cambrian</td>
<td>Australia</td>
<td>Gondwana</td>
<td>Phosphatized</td>
<td>Vendrasco et al., 2011b</td>
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<tr>
<td>Helcionelloida</td>
<td><em>Dorispira arguta</em> (Resser, 1939)</td>
<td>Marjum Formation (Miaolingian)</td>
<td>Utah, USA</td>
<td>Laurentia (west)</td>
<td>Silicified</td>
<td>Robison, 1964b</td>
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<tr>
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<td>Helcionelloida indet.2*</td>
<td>Marjum Formation (Miaolingian)</td>
<td>Utah, USA</td>
<td>Laurentia (west)</td>
<td>Silicified</td>
<td>This study (Fig. 4K, L)</td>
</tr>
<tr>
<td>Helcionelloida</td>
<td><em>Yochelcionella gracilis</em> Atkins &amp; Peel, 2004*</td>
<td>Henson Gletscher Formation (Series 2, Stage 4 –Miaolingian)</td>
<td>Freuchen Land, North Greenland</td>
<td>Laurentia (east)</td>
<td>Silicified</td>
<td>This study (Fig. 3)</td>
</tr>
</tbody>
</table>
Fig. 6. SEM images of the present day viviparid gastropod *Cipangopaludina chinensis malleata* (Reeve, 1863) from South Korea showing projecting periostracum on the juvenile shell surface. A, oblique lateral view showing the periostracum with two types of hairs (long and short) and the raised ridges. B, oblique anterior view showing the smooth surface of the shell interior (SI) which is exposed below the fracture. C, magnified view of the periostracal surface showing the long-hooked hairs and raised ridges. D, raised ridges with wrinkled comarginal ornamentation between the ridges on the periostracal surface. E, fractured section showing the partially peeled-back periostracum (P) and the underlying mineralized shell (MS). The short hairs and the wrinkled comarginal ornamentation are also shown on the periostracal surface. F, enlarged detail of the shell showing the periostracum (P) and the ostracum (O). Scale bar: 500 µm (A & B), 100 µm (C & D), 50 µm (E), 10 µm (F).

bivalve group which paleontological record dates back to early Ordovician (Pojeta 1971). The function of the adhesive radial lines is currently uncertain, but sand grains adhering to them (Fig. 7H) may increase camouflage. The radial lines may also increase the strength of the organic periostracum. Examination of two anomalodesmatan species *Lyonsia norwegica* (Gmelin, 1791) and *Lyonsia arenosa* (Møller, 1842) clearly show that the adhesive radial lines originate from the apical region (Fig. 7). The distribution of the
adhesive radial lines are confined to the surface of the periostracum and absent on the underlying mineralized shell (Fig. 7F).

*Lyonsia norwegica* (Gmelin, 1791), one of the anomalodesmatan bivalve species that has been examined for adhesive radial lines, well illustrates intra-periostracal calcification in the form of spikes composed of aragonitic prisms (Fig. 7A–E, G, H; Checa & Harper 2010). Intra-periostracal calcification refers to the secretion of calcareous elements within the periostracum before mineralization of the ostracum (Checa & Harper 2010; Glover & Taylor 2010). The spikes of *L. norwegica* with truncated conical form develop radial rows between the adhesive radial lines (Fig. 7C).

**Discussion**

*Periostracum preserved in Cambrian molluscs*

The consistent and regular distribution, the uniform thickness and the pattern of radiation from the apical region, strongly suggest that the presence of the radial threads is a characteristic of the original shell morphology, precluding interpretation of the threads...
as mineralized epibionts or endolith burrow infillings of the type documented in other Cambrian microfossils and clasts (Runnegar 1985b; Li 1997; Stockfors & Peel 2005; Peel 2023b). Supporting this interpretation, other co-occurring similarly-sized fossils such as trilobites, brachiopods, and hyoliths do not bear the radial threads or similar features, even in the same residue. It is noteworthy that the radial threads always cover the external shell ornamentation such as growth lines, and that they are absent inside of the shell. Therefore, the internal mould does not preserve the radial threads (e.g. Fig. 4H). Based on these observations, it can be concluded that radial threads are morphological features that are present only in the outermost shell of some molluscs (except for the protoconch in some specimens), which likely corresponds to periostracum.

Removal of the periostracum in some modern bivalves and gastropods often reveals micro-ornamentation of fine radial lirae which is somewhat similar to Cambrian radial threads (Kamenev 2018; Martins & Simone 2014), although the information regarding the growing mechanism and function is limited. Since the radial lirae of the modern molluscs are developed at the interface between the periostracum and the underlying shell, the structure is likely to be related to the inner surface of the periostracum. The radial lirae could be associated with the initiation of biomineralization, since the interface is the place where the calcium carbonate crystals form as an extrapallial chamber (Ponder et al. 2019). Harper (1997) noted the primary role of the periostracum in the construction of the molluscan shell, not least in the construction of ornament, but that the underside of the bivalve periostracum was generally without internal structures. In Yochelcionella, the thread-bearing layer is not always preserved in otherwise exceptionally preserved specimens (Fig. 4B, C), suggesting that radial thread structure is part of a readily degraded, dominantly organic periostracum.

In terms of preservation, the radial thread-bearing layers in the current material could represent replacement of the periostracum but they probably correspond to a very thin encrustation of minerals (i.e. thin precipitation on the exterior) that reflects the morphology of the periostracum (Butts 2014; Peel & Kouchinsky 2022, fig. 4F, I). This study, therefore, does not necessarily assume direct mineralization of the organic material of the periostracum, which is supported by the presence of the radial thread-bearing ‘external coating’ (see Fig. 8A–D) and underlying mineral-replaced shell. In some Australian material, the radial threads could be viewed as sitting directly on the mineral-replaced shells (e.g. Fig. 4J). Detailed observation, however, reveals that the external coating layer is still recognizable by the presence of comarginal increments associated with each other (white arrows in Fig. 5A).

Several Cambrian shell-bearing problematic groups have been interpreted as having a periostracum. Porter (2004) described the outermost covering within the ‘wall structure’ of the halkieriid sclerites Australohalkieria superstes. This outermost layer showed a similar morphological fabric to typical phosphatized organic material, and subsequently, this layer was compared with a molluscan periostracum. Vendrasco et al. (2017) described hyolith Cupitheca with a phosphatized outer layer. This ‘wavy layer’ was interpreted as a phosphatized periostracum based on its similar microstructure to the outermost organic layer described in Porter (2004) and to the periostracum of the modern bivalve Neotrigonia (Checa et al. 2014). Both cases of apparently preserved periostracum show relatively simple and thin layers, and requires further scrutiny to be compared to the radial threads preserved herein. The described radial thread structure dismisses the simplistic view of the periostracum as a featureless lamellar template for the developing shell.

Are the modern features evolutionarily related to Cambrian radial threads?

The periostracal ridges in the viviparid gastropods can be compared to the radial threads of Cambrian molluscs, whereas the wrinkled layer of the periostracum may also be comparable to the comarginal increments in terms of organized direction and distribution relative to the periostracal ridges (Fig. 6). Fossilized periostracal hairs have been found from cyclophoroidean (land snail) gastropods within Cretaceous amber (Hirano et al. 2019; Neubauer et al. 2019), but no Palaeozoic fossil examples have been recorded yet. The adhesive radial lines are also similar to Cambrian radial threads in terms of morphology such as the developing pattern radiating from the apical region at regular intervals and granular texture. The current description of radial threads from the Cambrian significantly extends the distribution of this morphological feature from the Late Triassic (Sartori & Harper 2009) to the Cambrian, if they are related. Agglutination is well known in other Cambrian organisms, such as foraminifers (Hemleben & Kaminski 1990) and some Cambrian brachiopods (Zhang et al. 2014), but there is no direct evidence that radial threads of Cambrian molluscs have served to adhere grains to the shell surface via arenophilic glands.

The modern features are generally associated with the outermost layer of the periostracum, usually
lacking from protoconchs and prodissoconchs. This observation is consistent to observation in some of our Cambrian material that radial threads originate at the apical area, but not at the precise apical tip (Fig. 5D). Through morphological comparisons with extant molluscs with analogous periostracal structures—rows of ridges and hairs, and adhesive radial lines—these shared features may indicate a plesiomorphic molluscan character, now identifiable in Cambrian molluscs.

**Significance of Cambrian radial threads in the evolution of shell formation mechanism**

Runnegar (1978, p. 328) interpreted the formation of radial threads in *Yochelcionella ostentata* as through 'stockades of calcified spines.' Calcified inclusions are often embedded within the periostracum, reflecting various mechanisms of formation, function and patterns of distribution (Carter & Aller 1975; Checa & Harper 2010; Glover & Taylor 2010). Calcified periostracal structures have been interpreted as a primitive feature of shell formation mechanism of some molluscan group, possibly playing a role in the initial stages of calcification within the broader evolutionary history of Mollusca (Carter & Aller 1975; Runnegar 1978; Schneider & Carter 2001). A radial structure ('radiating granules') was described from the Ordovician anomalodesmatan bivalve *Rhytimya* sp. by Pojeta (1971, pl. 16, fig. 11). Carter & Aller (1975, p. 317) suggested that these 'radiating granules' provided fossil evidence of calcified periostracal processes cemented to the surface of the shell. Bottjer & Carter (1980) considered the 'stockades of calcified spines (Runnegar 1978)' and the 'radiating granules (Pojeta 1971)' as fossil evidence that spicule-like...
calcification is a primitive characteristic in molluscan evolution.

More recent studies, however, do not support the homology of the spicular or spike structures among various bivalve groups or among bivalve, aplacophoran and polyplacophoran molluscs (Checa & Harper 2010; Glover & Taylor 2010). The hypothesis of Runnegar (1978), suggesting that the ‘stockades of spines’ comprising the radial threads in Yochelcionella represented an early spicule stage in the shell development of molluscs, is not supported by our observations (Fig. 5). The present study of Yochelcionella ostentata indicates that the radial threads were formed by the imbrication of successive growing units consisting of an edge and comarginal increments (Fig. 5); they are not spiculate. The calcified spines within the periostracum of Lyonsia norwegica (Gmelin, 1791), a modern anomalodesmatan species (Fig. 7), superficially resemble Cambrian radial threads in their radial arrangement. However, each spine is distributed separately, not forming a ‘thread’, as well as the rows of spikes are much more densely arrayed. Accordingly, the morphology of the Cambrian radial threads fails to support the suggestion that they represent an intermediate stage in the evolution of mollusc shells from spicule-bearing ancestors.

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References


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