A new helcionelloid mollusc from the Cambrian of Greenland and Idaho (Laurentia)

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Ressericonella gen. nov., a new genus of helcionelloid mollusc, characterized by a narrow shell with a shallowly convex dorsal surface and flat to shallowly concave lateral areas, is described from the Cambrian of Greenland and Idaho. The type species is *Helcionella aequa* Resser, 1939 from the Langston Formation (Naomi Peak Limestone Member) of early middle Cambrian age (Miaolingian Series, Wuliuan Stage, *Albertella* Biozone). *Ressericonella pipalukae* gen. et sp. nov. occurs in the latest early Cambrian (Cambrian Series 2, Stage 4, *Bonnia–Pagetides elegans* Biozone) of southern Freuchen Land, North Greenland. Silicified specimens of *Ressericonella pipalukae* from North Greenland preserve two-layered shell structure in which an inner layer with a transverse fibrous pattern similar to lamello-fibrillar structure is overlain by an outer layer with fine threads radiating from the apex.

Keywords: Mollusca, Helcionelloida, Cambrian, Idaho, North Greenland.

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Helcionelloids are diverse and widespread during the Cambrian and dominate mollusc assemblages. Their bilaterally symmetrical, slightly coiled, calcareous shells occur from the earliest Cambrian to the Early Ordovician (Gubanov & Peel 2001). Historically, most helcionelloids described before the middle of the last century were based on millimetre-sized hand specimens and assigned to one of three widely-drawn genera: Helcionella Grabau & Shimer, 1909, Scenella Billings, 1872 or Metoptoma Phillips, 1836, although the last-mentioned was originally defined as a Carboniferous gastropod (Phillips 1836). However, researchers subsequently started to describe diverse assemblages from microscopic residues of limestones treated with weak acetic acid, which promoted an explosive increase in helcionelloid taxonomy (Rozanov & Missarzhevsky 1966; Rozanov et al. 1969; Yu 1979; Zhou & Xiao 1984; Geyer 1986; Missarzhevsky 1989; Bengtson et al. 1990; Parkhaev 2001; Vendrasco et al. 2010, 2011; Li et al. 2021; Peel & Kouchinsky 2022). Most of this material has been diagenetically phosphatised but significant assemblages of silicified material have also been documented (Runnegar & Jell 1976; Gubanov *et al.* 2004; Jacquet & Brock 2016).

In a Greenland context, embracive descriptions of early Cambrian helcionelloid assemblages from North-East Greenland were given by Skovsted (2004, 2006), while Peel & Kouchinsky (2022) monographed an extensive middle Cambrian (Miaolingian Series, Wuliuan Stage) fauna. Other accounts include Peel (1988, 1989, 1991a,b, 1994, 2021, 2023), Atkins & Peel (2004, 2008), Peel & Skovsted (2005), Peel *et al.* (2016) and Oh *et al.* (2024).

A distinctive helcionelloid species identified during our ongoing studies of the latest early Cambrian of southern Freuchen Land, North Greenland (Fig. 1A, C), compares closely to *Helcionella aequa* Resser, 1939 from the earliest middle Cambrian (Miaolingian Series, Wuliuan Stage) Naomi Park Limestone of Idaho (Fig. 1A) and we establish a new genus, *Ressericonella* gen. nov., to accommodate these two species. The genus is named for Charles Elmer Resser (1889–1943), an American palaeontologist who was a prolific contributor to the taxonomy of Laurentian Cambrian invertebrates, although his profligacy in introducing new taxonomic names for trilobites is legendary (Sundberg 2007).

Material

Specimens of *Helcionella aequa* Resser, 1939 were collected on the north side of Two Mile Canyon, near its mouth, two miles south-east of Malad, northern Wasatch Mountains, southern Idaho, USA (Fig. 1A). According to Resser (1939, p. 8), the specimens were derived from collections made at locality 54s by F. B. Meek and C. D. Walcott in 1898, and C.D. Walcott and L. D. Burling in 1906. In the collection of the Natural History Museum, Smithsonian Institution, Washington DC, the holotype, USNM 98487, is associated

with two additional specimens. *Helcionella aequa* was assigned by Resser (1939) to the "Langston" limestone. Maxey (1958) referred to this limestone as the Naomi Peak Limestone Member of the Langston Formation, which he referred to an *Albertella–Kochaspis* subzone, now the *Albertella* Biozone (Kimmig *et al.* 2019, fig. 1c).

Samples from southern Freuchen Land, North Greenland, were collected from dark thin limestone lenses located 1–2 m above the base of the upper member of the Henson Gletscher Formation (Fig. 2) on the south-western corner of a nunatak (Fig. 1C; 82°09'N, 42°25'W) that was illustrated by Geyer & Peel (2011, fig. 2B). This is locality 1 of Blaker & Peel (1997, figs 8A, 10) and Geyer & Peel (2011, figs 1D, 2B), see also Streng *et al.* (2016, fig. 1E) and represents the reference section (thickness 112 m) of the Henson Gletscher Formation described by Ineson & Peel (1997, figs 21, 32, 33). The limestone samples were collected by J.S.



Fig. 1. Stratigraphy and derivation of samples. **A:** location of Freuchen Land (North Greenland) and Malad (Idaho). **B:** Cambrian stratigraphy of southern Freuchen Land showing sample horizon (black dot). **C:** map of Freuchen Land–Peary Land region, North Greenland, showing location of fossil locality (black dot). **D:** simplified stratigraphy of the Malad region in Idaho showing members of the Langston Formation (after Kimmig *et al.* 2019).

Peel and M.R. Blaker on 6th July 1985 (GGU sample 298550) and August 17th 1985 (GGU sample 301346). They were digested in 10% acetic acid and selected silicified specimens were imaged using a Zeiss Supra 35VP scanning electron microscope. All images were assembled using Adobe Photoshop CS4.

Faunas from the Henson Gletscher Formation in southern Freuchen Land, Lauge Koch Land and western Peary Land (Fig. 1C) range in age from early Cambrian (Cambrian Series 2, Stage 4) to middle Cambrian (Miaolingian Series, Wuliuan Stage; *Ptychagnostus gibbus* Biozone), but Drumian Stage strata occur in



Aftenstjernesø Formation

Fig. 2. Stratigraphic section of the Henson Gletscher Formation at the fossil locality in southern Freuchen Land (Fig. 1C) showing derivation of GGU samples. Section measured by J.R. Ineson (after Ineson & Peel 1997, fig. 32).

the Henson Gletscher Formation further to the west, along the northern coast of North Greenland (Higgins *et al.* 1991; Robison 1994; Blaker & Peel 1997; Ineson & Peel 1997; Geyer & Peel 2011).

Fossils from the upper member of the Henson Gletscher Formation in southern Freuchen Land (Figs 1C, 2) comprise the Bonnia-Pagetides elegans Biozone of Gever & Peel (2011) and Sundberg et al. (2016, 2022), which is the youngest biozone of Cambrian Stage 4 recognized in the Henson Gletscher Formation in North Greenland. The Bonnia-Pagetides elegans Biozone overlies strata referred to the Eoagnostus roddyi-Oryctocarella duyunensis Biozone by Sundberg et al. (2016, 2022). Note that an inadvertent error in Sundberg et al. (2022, fig. 4) places Oryctocarella duyunensis within the Bonnia-Pagetides elegans Biozone instead of the older eponymous biozone. This stratigraphic position in the figure should be assigned to Pagetides elegans. Unfortunately, both Oryctocarella duyunensis and Pagetides elegans are thereby omitted from their respective biozones in the Greenland column.

Systematic palaeontology

Institutional abbreviations and repositories. GGU prefix indicates a sample collected during field work by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now part of the Geological Survey of Denmark and Greenland, Copenhagen, Denmark (GEUS). Specimen repositories: palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden (PMU prefix); palaeontological collection of the Natural History Museum, Smithsonian Institution, Washington DC, USA (USNM prefix).

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Phylum Mollusca Cuvier, 1797 Class Helcionelloida Peel, 1991a Family Helcionellidae Wenz, 1938

Genus Ressericonella gen. nov.

Type species. Helcionella aequa Resser, 1939 from the Naomi Peak Limestone, the lowest member of the Langston Formation, Malad, southern Idaho; Cambrian, Miaolingian Series, Wuliuan Stage, *Albertella* Biozone. Here designated.

Derivation of name. Ressericonella is named for Charles Elmer Resser (1889–1943), American palaeontologist, combined with conella (Latin), meaning little cone, in the form of *Helcionella*, the eponymous genus of the class and family. Gender is feminine.

Diagnosis. Laterally compressed helcionelloid curved through about three quarters of a whorl such that the tightly coiled apex overhangs the sub-apical margin. Lateral surfaces are shallowly concave to shallowly convex, passing abruptly onto the shallowly convex supra-apical surface. Aperture sub-rectangular. Sub-apical surface arched into an apertural sinus. Ornamentation of numerous spiral cords crossed by comarginal growth lines, sometimes with weak rugae.

Discussion. Ressericonella gen. nov. is based on two species: the type species *Ressericonella aequa* (Resser, 1939) from southern Idaho, USA, and a new species, *Ressericonella pipalukae* sp. nov., from southern Freuchen Land, North Greenland. The former species occurs in the Naomi Peak Limestone Member (Miaolingian Series, Wuliuan Stage, *Albertella* Biozone) of the Langston Formation (Resser 1939; Maxey 1958; Kimmig *et al.* 2019). The latter species occurs in slightly older strata of the Henson Gletscher Formation (latest Cambrian Series 2, Stage 4, *Bonnia–Pagetides elegans* Biozone) in southern Freuchen Land (Geyer & Peel 2011).

In dorsal view, the rate of lateral expansion of *Ressericonella* decreases after the initial growth stage, resulting in an unusually narrow shell with sub-parallel lateral surfaces (Figs. 3B, 4C, F, J). In lateral view, the rate of shell expansion decreases with growth, causing smaller specimens (Figs. 3E, 4G) to exhibit a proportionately longer aperture where the apex is less strongly overhanging. Conversely, the large holotype of *Ressericonella aequa* has a relatively shorter aperture with a more pronounced overhang of the apex (Fig. 3A, C).

The coiled shell with flattened lateral surfaces and sub-rectangular aperture of *Ressericonella* gen. nov. recall several Cambrian helcionelloid genera mainly from Cambrian Stage 4 to Wuliuan Stage: *Coreospira* Saito, 1936, *Hampilina* Kobayashi, 1958, *Wakayella* Kruse, 1998, *Eocyrtolites* Yu, 1986, and *Tichkaella* Geyer, 1986. *Coreospira* differs from the cyrtoconic *Ressericonella* in having the lateral margins of the supra-apical (dorsal) surface forming a broad rounded ridge that overhangs the lateral areas, which display prominent rugae. In the type species, *Coreospira rugosa* Saito, 1936, and *Coreospira walcotti* Knight, 1947, the shell is tightly coiled through more than one whorl in the adult shell (Saito 1936; Knight 1947; Oh *et al.* 2021) but *Coreospira* carinata (Rasetti, 1957) has a cyrtoconic form. Gever (2014) noted the similarity between Helcionella aequa [= Ressericonella aequa] and Tichkaella Geyer, 1986 in terms of the presence of radial ornamentation and laterally compressed shell. But Ressericonella differs from Tichkaella in the absence of prevailing paired radial ornamentation on dorsum (Geyer, 1986, pl. 4, 52b) and flattened sub-apical surface (Geyer, 1986, pl. 4, 51a). Ressericonella has a more strongly coiled shell than *Hampilina* or *Wakayella* but their prominent comarginal rugae are absent or only weakly developed (Kruse 1998; Oh et al. 2021). Ressericonella also differs from Eocyrtolites in having a much narrower subapical width relative to the supra-apical width (Yu 1986). Although classified into different genera, the cyrtoconic shells with sub-parallel lateral surfaces observed in Ressericonella and other related genera may indicate a close relationship. Their unique morphology distinguishes them from other helcionelloid species, and their occurrences in nearly coeval strata further support this connection. (Cambrian Series 2, Stage 4 to Miaolingian Series, Wuliuan Stage; Kruse, 1986; Yu, 1986, 1996; Oh et al., 2021).

A few species of *Dorispira* Parkhaev in Parkhaev & Demidenko, 2010, such as *Dorispira tavsenensis* Peel & Kouchinsky, 2022 and *Dorispira tippik* Peel & Kouchinsky, 2022 from the Henson Gletscher Formation (Wuliuan Stage of North Greenland), also have a sub-rectangular aperture, but *Dorispira* is readily distinguished from *Ressericonella* by its sharp comarginal rugae that cross over the dorsal surface (Parkhaev & Demidenko 2010).

Ressericonella aequa (Resser, 1939)

Fig. 3

1939 *Helcionella aequa* Resser, p. 24, pl. 1, figs 45–47. 1957 *Helcionella aequa* Rasetti, p. 970, 971. 2014 *Helcionella aequa* Geyer *et al.*, p. 380.

Figured material. USNM 98487, holotype (Fig. 3A–C) and two additional specimens, USNM98487b and USNM 98487c, in the same museum tray as the holotype (Fig. 3D, E–H). Naomi Peak Limestone Member of the Langston Formation, near Malad, Idaho (Resser 1939; Maxey 1958). Cambrian, Miaolingian Series, Wuliuan Stage (*Albertella* Biozone).

Description. Laterally compressed cyrtoconic shell with bilateral symmetry. Shell width much narrower than length. Adult shell coiled through about threequarters of a whorl (holotype; Fig. 3A–C). Apex recurved, overhanging the sub-apical surface. Aperture sub-rectangular to trapezoidal, with apertural sinus at the sub-apical margin mainly evident in juvenile shells. Supra-apical surface shallowly convex; lateral surfaces flat to slightly concave; junction between the supra-apical surface and lateral surfaces relatively prominent, slightly angular. Densely spaced fine spiral cords and comarginal growth lines overprint very shallow rugae mainly developed on lateral surfaces.

Discussion. Resser (1939) illustrated only the holotype, but two additional specimens present in the same box as the holotype are likely conspecific and are also figured (Fig. 3D–H). The lateral surfaces of the holotype are exfoliated such that ornamentation is poorly preserved, except on the supra-apical surface (Fig. 3B), where the finely developed spiral ornamentation and comarginal growth lines are clearly visible, as is also the case in the two accompanying specimens (Fig. 3D, F).

Ressericonella pipalukae gen. et sp. nov.

v?2016 *Coreospira* sp. Peel *et al.* p. 264, fig. 14N, O. 2024 Helcionelloid indet. Oh *et al.* p. 8, fig. 5D, E.

Figs. 4, 5A, B

Holotype. PMU 18380 from GGU sample 301346, upper member of the Henson Gletscher Formation, southern Freuchen Land. Cambrian Series 2, Stage 4, *Bonnia– Pagetides elegans* Biozone.

Additional figured material. PMU 18378 from GGU sample 298550, PMU 18379, PMU 18382 and PMU 18381 from GGU sample 301346 from the same locality and horizon as the holotype.

Derivation of name. For Pipaluk Jette Tukuminguaq Kasaluk Palika Häger Freuchen (1918–1999), Greenlandborn daughter of Danish Explorer Peter Freuchen and his wife Navarana, whose names are commemorated in Freuchen Land and Navarana Fjord (Fig. 1).

Diagnosis. Species of *Ressericonella* with smooth transition between the supra-apical surface and the lateral surfaces, and fine spiral (radial) and comarginal ornamentation without rugae.

Description. Moderately expanding, laterally compressed shell coiled through half to twothirds of a whorl. Aperture sub-rectangular, shell length about twice to three times shell width (Fig. 4F, G) with the apertural sinus at the sub-apical margin mainly



Fig. 3. *Ressericonella aequa* (Resser, 1939), Two Mile Canyon, Wasatch Mountains, Idaho. Langston Formation (Naomi Peak Limestone Member). Cambrian, Miaolingian Series, Wuliuan Stage, *Albertella* Biozone. **A–C:** USNM 98487, holotype, lateral (A,C) and dorsal (B) views. **D:**USNM 98487b, specimen in same museum tray as the holotype, fragment with dorsal ornamentation. **E–H:** USNM 98487c, specimen with broken apex in the same museum tray as the holotype, lateral (E) and oblique lateral (F–H) views. Scale bars: 1 mm.

evident in juvenile shells (Fig. 4C, D). The degree of expansion at the earliest growth stage is relatively rapid, but slower at the later growth stage, so that the width of the shell becomes constant in the adults (Fig. 4I, F, J). Apex pointed, recurved, overhanging the subapical surface; sometimes with shallow constrictions that possibly delimit the protoconch (Fig. 4C, H, I). Supra-apical surface transversely shallowly convex, becoming flattened in later growth stages (Fig. 4I, L); transition from the supra-apical surface to the lateral surfaces initially smooth (Fig. 4A, C), becoming more abruptly rounded in later growth stage (Fig. 4I, L); sub-apical surface strongly concave, with variable curvature. The shell surface smooth, without comarginal rugae; ornamented by comarginal growth lines and extremely finely spaced spiral cords (Fig. 4B, D). Shell seemingly composed of two shell layers, with an outer

spirally (radially) ornamented layer overlying an inner layer with transverse fibrous structure (Figs. 4G, K, 5).

Discussion. Ressericonella pipalukae gen. et sp. nov. is variable in form, particularly with regard to the degree of curvature in the early growth stages of preserved shells. This is partly an ontogenetic effect, but may be affected by lateral crushing of the silicified shells, also seen in the holotype (Fig. 4H, L). *Ressericonella pipalukae* lacks the comarginal rugae seen on the lateral areas of *Ressericonella aequa*, from which it differs in the more rounded transition from the dorsum to the lateral areas.

In lateral view (Fig. 4G), *Ressericonella pipalukae* appears much more rapidly expanding than the holotype of *Ressericonella aequa*, but the latter is a larger specimen that markedly reduces the rate of expansion as it



Fig. 4. *Ressericonella pipalukae* gen. et sp. nov. from the upper Henson Gletscher Formation, southern Freuchen Land. Cambrian Series 2, Stage 4, *Bonnia–Pagetides elegans* Biozone. GGU sample 301346 unless stated. **A:** PMU 18378 from GGU sample 298550, sub-apical view. **B–E:** PMU 18379, sub-apical view (C) with detail of apertural emargination showing fine spiral ribs (D) and oblique lateral view (B) with repaired injury in apertural margin (E, arrow in B). **F–H, K, L:** PMU 18380, holotype, dorsal (supra-apical, F), lateral (G) and oblique lateral (H, L) views with surface detail (K, arrow in G). **I, J:** PMU 18381, oblique dorsal (I) and apical (J) views, with broken sub-apical margin. Scale bars: 200 μm (D, E, K); 300 μm (A–C, G–J, L); 400 μm (F).

gets larger. Lateral expansion is reduced with growth in both species such that dorsum almost stops increasing in width (Figs. 3B, 4F).

The silicified holotype of *Ressericonella pipalukae* preserves two-layered shell structure on the dorsolateral area (Fig. 4G, H, K) with an outer spirally (radially) ribbed layer overlying an inner fibrous layer. In detail (Fig. 4K), the fibres appear to lie on imbricated laminae that step down towards the dorsum. In this view, the spiral (radial) cords are narrow and often paired, but their appearance is clearly affected by imperfect silicification during diagenesis. Oh *et al.* (2024) interpreted radial threads on a variety of silicified shells from the Cambrian, inclusive the same samples in southern Freuchen Land, as fossilized periostracal structures.

One fragmented helcionelloid with radial ornaments, previously referred to as Helcionelloid indet. by Oh *et al.* (2024, fig. 5D, E; PMU 21541 from GGU sample 301347), is assigned herein to *Ressericonella pipalukae*. This assignment is justified based on the similar outline of the umbonal region and the same shell structure (see below).

A specimen referred to as *Coreospira* sp. in Peel *et al.* (2016, fig. 14N, O) from the *Ovatoryctocara granulata*

assemblage of the Henson Gletscher Formation in the Løndal area (PMU 28970 from GGU sample 218681) is tentatively assigned to *Ressericonella pipalukae*, mainly based on the sub-rectangular aperture and fine radial and comarginal ornamentation, but further study is required based on more complete samples.

A small repaired shell injury (Fig. 4B, E) is likely of non-biogenic origin.

Ressericonella sp.

Fig. 5C-E

Figured material. PMU 18383 from GGU sample 301346, upper member of the Henson Gletscher Formation, southern Freuchen Land. Cambrian Series 2, Stage 4, *Bonnia–Pagetides elegans* Biozone.

Discussion. A single specimen (Fig. 5C–E) is tentatively assigned to *Ressericonella* sp. because it has a much more tightly coiled (rapidly expanded shell), represented by a narrower umbilicus and a more laterally compressed shell profile (compare 4G and 5C), although similar shell structure (see below).



Fig. 5. Shell structures of *Ressericonella* from the upper Henson Gletscher Formation, southern Freuchen Land. Cambrian Series 2, Stage 4, *Bonnia–Pagetides elegans* Biozone. GGU sample 301346. **A, B:** *Ressericonella pipalukae* sp. nov. PMU 18382, lateral view (A) and magnified view showing the outer layer (OL) and the inner layer (IL) (B). **C–E:** *Ressericonella* sp. PMU 18383, lateral view (C), oblique lateral view (D) and magnified view (E) showing the outer layer (OL) and the inner layer (IL) (E). The box in A and D indicates the magnified area in B and E respectively. Dashed lines denote the boundary between the outer and inner layers. Scale bars: 100 μm (B); 200 μm (A, D, E); 300 μm (C).

Remarks on shell structure

Several samples preserve shell structure consisting of outer and inner layers ('OL' and 'IL' in Fig. 5B, E). The outer layer is characterized by radially arranged lineations ('radial threads') originating from the umbonal region, covering the shell surface (Figs. 4B, C, D, G, K, 5C, D). Similar features have been reported in other helcionelloid species with silicified or phosphatized forms, described as 'radial threads' (Runnegar & Jell 1976), 'radial striation' (Gubanov et al. 2004), and 'radiating ridges' (Vendrasco et al. 2011). According to a recent study (Oh et al. 2024), these features possibly represent the molluscan periostracum. The structure observed in a specimen (Fig. 4B-D) reveals closely spaced radial threads resembling fine spiral ribbing, indicating potential variations in periostracal morphology. The outer layer with radial threads may correspond to a thin encrustation on the shell surface, while the original shell, composed of calcareous material (e.g., aragonite), could have been lost during diagenesis or the acid etching process used to obtain the samples.

The underlying inner layer shows a fibrous pattern arranged transversely, perpendicular to the radial threads on the outer layer. This fibrous pattern is similar to lamello-fibrillae, although it has been replaced by coarse silica (Fig. 5B). While the lamello-fibrillar microstructure is uncommon in modern molluscs, it appears to have been common in Cambrian forms [e.g., *Pelagiella deltoides* Runnegar & Jell, 1976, in Vendrasco *et al.* 2010; *Ilsanella* cf. *orectes* (Jiang in Luo *et al.*, 1982) in Feng & Sun 2003]. The lamello-fibrillar microstructure of *Pelagiella* is known from the outermost shell layer (Li *et al.* 2017), but it also occurs in the internal mould of *P. deltoides*, representing the innermost surface of the shell (Vendrasco *et al.* 2010).

The recognition of the multi-layered shell structure of Ressericonella pipalukae sp. nov. (Fig. 5) can be compared to other Cambrian helcionelloids. Vendrasco & Checa (2015) suggested that Mackinnonia davidi (Runnegar in Bengtson et al., 1990) [= Davidonia rostrata (Zhou & Xiao, 1984)] from the Parara Limestone of South Australia has a two-layered shell consisting of a prismatic outer layer and a calcitic semi-nacre inner layer. They noted the similarity of the shell microstructure of Davidonia rostrata with other Cambrian molluscan taxa such as *Mellopegma* Runnegar and Jell, 1976 (a stenothecid helcionelloid), suggesting a possible phylogenetic relationship between them. Ebbestad *et al.* (2024) reported Davidonia puppis (Høyberget, Ebbestad, Funke & Nakrem, 2015) from the Gislöv Formation (Cambrian Series 2, Stage 4) in southern Sweden. At least two layers of shell were identified, consisting of the relatively thick, fibrous inner layer and thin outer layer shaping the smooth cap shaped outline enveloping the strongly undulated internal mould (Ebbestad *et al.* 2024, fig. 14I, J).

Li *et al.* (2017) documented five types of shell microstructures in the Cambrian helcionelloid *Pelagiella madianensis*, indicating an aragonitic composition organised into a hierarchical structure with four orders. Their findings included specimens with preserved internal moulds and outermost layers (termed 'acidetched shell residue') that are similar to the specimens examined here (Li *et al.* 2017, fig. 1A, b; Fig. 5), however it is uncertain whether *Ressericonella* also has the same complex hierarchical shell morphology.

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References

- Atkins, C.J. & Peel, J.S. 2004: New species of *Yochelcionella* (Mollusca; Helcionelloida) from the Lower Cambrian of North Greenland. Bulletin of the Geological Society of Denmark 51, 1–9. https://doi.org/10.37570/bgsd-2004-51-01
- Atkins, C.J. & Peel, J.S. 2008: Yochelcionella (Mollusca, Helcionelloida) from the lower Cambrian of North America. Bulletin of Geosciences 83, 23–38. https://doi.org/10.3140/ bull.geosci.2008.01.023
- Bengtson, S., Conway Morris, S., Cooper, B.J., Jell, P.A. & Runnegar, B.N. 1990: Early Cambrian fossils from South Australia. Memoirs of the Australasian Association of Palaeontologists 9, 1–364.
- Billings, E. 1872: On some new species of Palaeozoic fossils. The Canadian Naturalist 6, 213–222.
- Blaker, M.R. & Peel, J.S. 1997: Lower Cambrian trilobites from North Greenland. Meddelelser om Grønland, Geoscience 35, 1–145. https://doi.org/10.1017/s0016756898258432
- Cuvier, G. 1797: Tableau Élementaire de l'historie Naturelle des Animaux, 710 pp. Paris: Baudouin.

- Ebbestad, J.O.R., Cederström, P. & Peel, J.S. 2024. Helcionelloid molluscs from the lower Cambrian (Series 2, Stage 4) of southern Sweden. Historical Biology 36, 1854–1882.
- Feng, W.M. & Sun, W.G. 2003: Phosphate replicated and replaced microstructure of molluscan shells from the earliest Cambrian of China. Acta Palaeontologica Polonica 48, 21–30.
- Geyer, G. 1986: Mittelkambrische Mollusken aus Marokko und Spanien. Senckenbergiana lethaea 67, 55–118.
- Geyer, G., Peel, J.S., Streng, M., Voigt, S., Fischer, J. & PREUßE, M. 2014: A remarkable Amgan (Middle Cambrian, Stage 5) fauna from the Sauk Tanga, Madygen region, Kyrgyzstan. Bulletin of Geosciences 89, 375–400.
- Geyer, G. & Peel, J.S. 2011: The Henson Gletscher Formation, North Greenland, and its bearing on the global Cambrian Series 2–Series 3 boundary. Bulletin of Geosciences 86, 465–534. https:// doi.org/10.3140/bull.geosci.1252
- Grabau, A.W. & Shimer, H.W. 1909: North American index fossils, invertebrates, Volume 1, 853 pp. New York: A.G. Seiler & Company. https://doi.org/10.5962/bhl.title.52120
- Gubanov, A.P. & Peel, J.S. 2001: Latest helcionelloid molluscs from the Lower Ordovician of Kazakhstan. Palaeontology 44, 681–694. https://doi.org/10.1111/1475-4983.00198
- Gubanov, A., Kouchinsky, A., Peel, J.S. & Bengtson, S. 2004: Middle Cambrian molluscs of 'Australian' aspect from northern Siberia. Alcheringa 28, 1–20. https://doi.org/10.1080/03115510408619272
- Higgins, A.K., Ineson, J.R., Peel, J.S., Surlyk, F. & Sønderholm, M.1991: Lower Palaeozoic Franklinian Basin of North Greenland.Bulletin Grønlands Geologiske Undersøgelse 160, 71–139.
- Høyberget, M., Ebbestad, J.O.R., Funke, B. & Nakrem, H.A. 2015. The shelly fauna and biostratigraphy of the lower Cambrian (provisional Series 2, Stage 4) Evjevik Member, Ringstrand Formation in the Mjøsa area, Norway. Norwegian Journal of Geology 95, 23–56.
- Ineson, J.R. & Peel, J.S. 1997: Cambrian shelf stratigraphy of North Greenland. Geology of Greenland Survey Bulletin 173, 1–120. https://doi.org/10.34194/ggub.v173.5024
- Jacquet, S.M. & Brock, G.A. 2016: Lower Cambrian helcionelloid macromolluscs from South Australia. Gondwana Research 36, 333–358. https://doi.org/10.1016/j.gr.2015.06.012
- Kimmig, J., Strotz, L.C., Kimmig, S.R., Egenhoff, S.O. & Lieberman, B.S. 2019: The Spence Shale Lagerstätte: an important window into Cambrian biodiversity. Journal of the Geological Society 176, 609–619. https://doi.org/10.1144/jgs2018-195
- Knight, J.B. 1947: Some new Cambrian bellerophont gastropods. Smithsonian Miscellaneous Collections 106, 1–11.
- Kobayashi, T. 1958: On some Cambrian gastropods from Korea. Japanese Journal of Geology and Geography 29, 111–118.
- Kruse, P.D. 1998: Cambrian palaeontology of the eastern Wiso and western Georgina Basins. Northern Territory Geological Survey Report 9, 68 pp.
- Luo, H., Jiang, Z., Wu, X., Song, X. & Ouyang, L. et al. 1982: The Sinian-Cambrian boundary in eastern Yunnan, China, 285 pp. Kunming: P.R. China. (Chinese with English abstract)
- Li, L., Zhang, X., Yun, H. & Li, G. 2017: Complex hierarchical microstructures of Cambrian mollusk *Pelagiella*: insight into

early biomineralization and evolution. Scientific Reports 7, 1935. https://doi.org/10.1038/s41598-017-02235-9

- Li, L., Zhang, X., Skovsted, C.B., Yun, H., Pan, B. & Li, G. 2021: Revisiting the molluscan fauna from the Cambrian (Series 2, stages 3–4) Xinji Formation of North China. Papers in Palaeontology 7, 521–564. https://doi.org/10.1002/spp2.1289
- Maxey, G. B. 1958: Lower and Middle Cambrian stratigraphy in northern Utah and southeastern Idaho. Geological Society of America Bulletin 69, 647–688.
- Missarzhevsky, V.V. 1989: Drevneyshie skeletnye okamenelosti i stratigrafiya ogranichnykh tolshch dokembriya i kembriya. Trudy Geologicheskogo Instituta, Akademiya Nauk SSSR 443, 1–237.
- Oh, Y., Lee, D.-C., Lee, D.-J., & Lee, J.-G. 2021: Cambrian helcionelloids (univalved molluscs) from the Korean Peninsula: systematic revision and biostratigraphy. Alcheringa 45, 127–139. https://doi. org/10.1080/03115518.2021.1929479
- Oh, Y., Peel, J.S., Zhen, Y.Y., Smith, P.M., Lee, M. & Park, T.-Y.S. 2024: Periostracum in Cambrian helcionelloid and rostroconch molluscs: comparison to modern taxa. Lethaia 57, 1–17 https:// doi.org/10.18261/let.57.1.6
- Parkhaev, P.Yu. 2001: Molluscs and siphonoconchs, 133–210. In: Alexander, E.M., Jago, J.B., Rozanov, A.Yu. & Zhuravlev, A.Yu. (eds): The Cambrian biostratigraphy of the Stansbury Basin, South Australia. Transactions of the Palaeontological Institute, Russian Academy of Sciences 282.
- Parkhaev, P.Yu. & Demidenko, Yu. 2010: Zooproblematica and Mollusca from the lower Cambrian Meishucun section (Yunnan, China) and taxonomy and systematics of the Cambrian small shelly fossils of China. Paleontological Journal 44, 883–1161. https://doi. org/10.1134/S0031030110080010
- Peel, J.S. 1988: Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddelelser om Grønland, Geoscience 20, 145–168.
- Peel, J.S. 1989: A Lower Cambrian *Eotebenna* (Molluscs) from Arctic North America. Canadian Journal of Earth Sciences 26, 1501–1503.
- Peel, J.S. 1991a: Functional morphology of the Class Helcionelloida nov., and the early evolution of the Mollusca. In: Simonetta, A. & Conway Morris, S. (eds): The early evolution of Metazoa and the significance of problematic taxa, 157–177. Cambridge: Cambridge University Press. https://doi.org/10.1093/sysbio/42.1.106
- Peel, J.S. 1991b: The classes Tergomya and Helcionelloidea, and early molluscan evolution. Bulletin Grønlands Geologiske Undersøgelse 161, 11–65. https://doi.org/10.34194/bullggu.v161.6717
- Peel, J.S. 1994: An enigmatic cap-shaped fossil from the Middle Cambrian of North Greenland. Bulletin Grønlands geologiske Undersøgelse 169, 149–155. https://doi.org/10.34194/bullggu. v169.6729
- Peel, J.S. 2021: An outer shelf shelly fauna from Cambrian Series 2 (Stage 4) of North Greenland (Laurentia). Journal of Paleontology 95, Memoir 83, 1–41. https://doi.org/10.1017/jpa.2020.112
- Peel, J.S, 2023: Muscle scars in Miaolingian helcionelloids from Laurentia and the diversity of muscle scar patterns in Cambrian univalve molluscs. Alcheringa 47, 221–233. https://doi.org/10.10 80/03115518.2023.2243501

- Peel, J.S. & Kouchinsky, A. 2022: Middle Cambrian (Miaolingian Series, Wuliuan Stage) molluscs and mollusc-like microfossils from North Greenland (Laurentia). Bulletin of the Geological Society of Denmark 70, 69–104. https://doi.org/10.37570/bgsd-2022-70-06
- Peel, J.S. & Skovsted, C.B. 2005: Problematic cap-shaped fossils from the Lower Cambrian of North-East Greenland. Paläontologische Zeitschrift 79, 461–470.
- Peel, J.S., Streng, M., Geyer, G., Kouchinsky, A. & Skovsted, C.B. 2016: Ovatoryctocara granulata assemblage (Cambrian Series 2–Series 3 boundary) of Løndal, North Greenland. Australasian Palaeontological Memoirs 49, 241–282.
- Phillips, J. 1836: Illustrations of the Geology of Yorkshire; or a description of the strata and organic remains: accompanied by a geological map, sections and diagrams, and figures of the fossils. Part II. The Mountain Limestone District. John Murray, London, 370 pp.
- Rasetti, F. 1957: Additional fossils from the Middle Cambrian Mt. Whyte Formation of the Canadian Rocky Mountains. Journal of Paleontology 31, 955–972.
- Resser, C.E. 1939: The *Ptarmigania* strata of northern Wasatch Mountains. Smithsonian Miscellaneous Collection 98, 1–72.
- Robison, R.A. 1994: Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. Bulletin Grønlands Geologiske Undersøgelse 169, 25–77. https://doi.org/10.34194/bullggu. v169.6726
- Rozanov, A.Yu. & Missarzhevsky, V.V. 1966: Biostratigrafiya i fauna nizhnikh gorizontov kembriya. Akademiya Nauk SSSR, Trudy Geologicheskaya Instituta 148, 1–125.
- Rozanov A.Yu. *et al.* 1969: Tommotskiy yarus i problema nizhney granitsy kembriya. Akademiya Nauk SSSR, Trudy Geologicheskaya Instituta 206, 1–379.
- Runnegar, B. & Jell, P.A. 1976: Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. Alcheringa 1, 109–138. https://doi.org/10.1080/03115517608619064
- Saito, K. 1936: Older Cambrian Brachiopoda, Gastropoda, etc., from northwestern Korea. Journal of the Faculty of Science, the Imperial University of Tokyo, Section 2, 4, 345–367.
- Skovsted, C.B. 2004: Mollusc fauna of the Early Cambrian Bastion Formation of North–East Greenland. Bulletin of the Geological Society of Denmark 51, 11–37. https://doi. org/10.37570/bgsd-2004-51-02
- Skovsted, C.B. 2006: Small shelly fauna from the upper lower Cambrian Bastion and Ella Island formations, North-East Greenland: Journal of Paleontology 80, 1087–1112.

Streng, M., Butler, A.D., Peel, J.S., Garwood, R.J. & Caron, J.-

B. 2016: A new family of Cambrian rhynchonelliformean brachiopods (Order Naukatida) with aberrant coral-like morphology. Palaeontology 59, 269–293. https://doi: 10.1111/pala.12226

- Sundberg, F.A. 2007: Nightmare on Resser Street dealing with Resser's trilobite taxonomy. In: Mikulic, D.G., Landing, E. & Kluessendorf, J. (eds): Fabulous fossils – 300 years of worldwide research on trilobites, 213–224. New York State Bulletin 507.
- Sundberg, F.A., Geyer, G., Kruse, P.D., McCollum, L.B., Pegel', T.V., Żylińska, A. & Zhuravlev, A.Yu. 2016: International correlation of the Cambrian Series 2-3, Stages 4-5 boundary interval. Australasian Palaeontological Memoirs 49, 83–124.
- Sundberg, F.A., Webster, M. & Geyer, G. 2022: Biostratigraphical significance of a new trilobite fauna from the Harkless Formation (upper Stage 4, Series 2, Cambrian), Nevada, USA. Lethaia 55, 1–12. https://doi.org/10.18261/let.55.3.8
- Vendrasco, M.J. & Checa, A.G. 2015: Shell microstructure and its inheritance in the calcitic helcionellid *Mackinnonia*. Estonian Journal of Earth Sciences 64, 99–104. http://hdl.handle. net/10481/35706
- Vendrasco, M.J., Porter, S.M., Kouchinsky, A., Li, G. & Fernandez, C.Z. 2010: New data on molluscs and their shell microstructures from the Middle Cambrian Gowers Formation, Australia. Palaeontology 53, 97–135. https://doi. org/10.1111/j.1475-4983.2009.00922.x
- Vendrasco, M.J., Kouchinsky, A.V., Porter, S.M. & Fernandez, C.Z. 2011: Phylogeny and escalation in *Mellopegma* and other Cambrian molluscs. Palaeontologia Electronica 14: 1–44. palaeo-electronica.org/2011_2/221/index.html
- Wenz, W. 1938: Gastropoda. Allgemeiner Teil und Prosobranchia. In: Schindewolf, O.H. (ed.), Handbuch der Paläozoologie 6, 1–240. Berlin: Gebrüder Bornträger.
- Yu, W. 1979: Earliest Cambrian monoplacophorans and gastropods from western Hubei with their biostratigraphical significance. Acta Palaeontologica Sinica 18, 233–270 [Chinese with English abstract].
- Yu, W. 1986. Lower Cambrian univalved molluscs from Kuruktag, Xinjiang. Acta Palaeontologica Sinica 25, 10–16. [Chinese with English abstract].
- Yu, W. 1996. Early Cambrian stenothecoid molluscs from China. Records of the Western Australia Museum 18, 209–218.
- Zhou, B. & Xiao, L. 1984: Early Cambrian monoplacophorans and gastropods from Hainan and Huoqiu Counties, Anhui Province. Professional Papers of Stratigraphy and Palaeontology 13, 125–140 [Chinese with English abstract]