Molluscs are one of the most diverse of extant invertebrate phyla with an extensive geological record reaching back to the Precambrian–Cambrian boundary (Budd & Jensen 2007, Maloof et al. 2010, Wanninger & Wollesen 2019). Most extant molluscan classes are traditionally recognised from around the late Cambrian (Furongian)–Early Ordovician boundary or later (Runnegar & Pojeta 1974, Yochelson 1978, Budd & Jensen 2007, Vinther et al. 2012a, Vinther 2015) but older Cambrian strata yield a variety of extinct and often poorly understood groups that usually rest uncomfortably in phylogenetic schemes (Pojeta & Runnegar 1976; Runnegar & Pojeta 1985; Yu 1987; Missarzhevsky 1989; Qian & Bengtson 1989; Peel 1991a; Gravestock et al. 2001; Steiner et al. 2007; Parkhaev 2008, 2019; Maloof et al. 2010; Parkhaev & Demidenko 2010; Rozanov et al. 2010; Hou et al. 2017).

Spectacular rare finds from Lower Palaeozoic lagerstätten have generated considerable excitement amongst students of molluscan evolution on account of unexpected morphological features and exceptional preservation (Conway Morris & Peel 1995; Sutton et al. 2001, 2012; Caron et al. 2006; Conway Morris & Caron 2007; Vinther et al. 2017). Foremost amongst these is the slug-like Halkieria evangelista Conway Morris & Peel, 1995 from the early Cambrian (Cambrian Series 2, Stage 4) of North Greenland (Laurentia) with its chain mail armour of small pointed sclerites and much larger anterior and posterior plates (Conway Morris & Peel 1995). To abuse a well-known English idiomatic expression, famously paraphrased by the English journalist Fonblanque (1837, p. 342), Halkieria is “a smooth round peg, in a sharp-cornered square hole” that can slip effortlessly into a variety of phylogenetic settings. Evolutionists disagree about its affinities despite this morphological facility and Halkieria has been placed in (and variously rejected from) the stem groups of molluscs, stem group aculiferans and polymorphs within the aculiferan crown group. Head and intermediate plates are described from the Aftensternesø Formation and placed within a new taxon proposed as Qaleruaqia sodermanorum gen. et sp. nov. • Key words: Mollusca, Aculifera, palaeoloricate, Cambrian Series 2, North Greenland, Laurentia.

In the Aculifera–Conchifera model of molluscan evolution, spiculate aplacophorans and polyplacophorans with a dorsal series of shell plates are recognised as sister groups within the clade Aculifera, itself a sister group of the clade Conchifera that contains all other mollusces. While aculiferans and conchiferans had their common origin near the Precambrian–Cambrian boundary, the crown groups of most major molluscan classes are seen traditionally to have emerged in the latest Cambrian (Furongian)–Early Ordovician. Matthevia Walcott, 1885, from the latest Furongian–Early Ordovician of Laurentia, has been regarded almost universally as the oldest undoubted fossil chiton, a palaeoloricate. Palaeoloricates, however, are paraphyletic and Matthevia is variously interpreted as a time indicator for the origin of crown group Aculifera, within either the stem or crown groups of Aplacophora or Polyplacophora. The discovery of rare disarticulated plates from the early Cambrian (Cambrian Series 2, Stage 4) of North Greenland (Laurentia) extends the geological record of palaeoloricates by about 25 Ma. In bridging the gap between lower stem group aculiferans and the occurrence of Matthevia, the new finds offer the potential for a corresponding earlier origin of both aplacophorans and polyplacophorans within the aculiferan crown group. Head and intermediate plates are described from the Aftensternesø Formation and placed within a new taxon proposed as Qaleruaqia sodermanorum gen. et sp. nov. • Key words: Mollusca, Aculifera, palaeoloricate, Cambrian Series 2, North Greenland, Laurentia.
Most recent discussions of molluscan evolution have concentrated on the Aculifera–Conchifera model (Fig. 1A) in which Aculifera (aplacophorans and polyplacophorans) form a sister group to other, conchiferan, molluscs (Sigwart & Sutton 2007; Sutton & Sigwart 2012; Sutton et al. 2012; Vinther et al. 2012a, b, 2017; Scherholz et al. 2013; Kocot et al. 2019, 2020; Wanninger & Wollesen 2019). Vinther (2014) summarised the gradual integration of evidence from developmental biology and classical palaeontology that brought forward the hypothesis that aplacophorans and polyplacophorans shared a common ancestry. He credited Ivanov (1996) as the first to explicitly propose that aplacophorans may have evolved from a chiton-like mollusc with shell plates serially arranged along the dorsum (Scheltema & Ivanov 2002, Scherholz et al. 2013). Descriptions of Ordovician and Silurian specimens by Sutton et al. (2001, 2004, 2012), Cherns (1998a, b, 2004) and Sigwart & Sutton (2007) have added remarkable support from the fossil record. Sigwart & Sutton (2007) proposed that some Ordovician palaeoloricates, usually interpreted as primitive polyplacophorans (Smith 1960, Hoare & Pojeta 2006, Pojeta et al. 2010), were probably stem group aplacophorans and this theme was strengthened with the description of the remarkable 7-plated Kulindroplax perissokomos Sutton, Briggs, Siveter, Siveter, & Sigwart, 2012 from the Silurian of England.

Based on molecular phylogenetic analysis, Vinther et al. (2012a) concluded that crown group aculiferans (aplacophorans and polyplacophorans) arose during the Early Ordovician, although Kocot et al. (2020) suggested a slightly earlier separation, in the Furongian. Vinther et al. (2012a) suggested that late Cambrian (Furongian) palaeoloricates such as Matthevia Walcott, 1885 (Walcott 1885, 1886; Yochelson 1966; English 2002; Vendrasco & Runnegar 2004) were upper stem group aculiferans derived from lower stem group aculiferans that include Halkieria. Sutton et al. (2012) placed Matthevia within the aplacophoran crown group and Halkieria as a stem group mollusc.

Following the discovery of the exceptionally preserved Calvapiloosa kroegeri Vinther, Parry, Briggs & Van Roy, 2017 from the Fezouata Formation Lagerstätte (Early Ordovician) of Morocco, Vinther et al. (2017, fig. 4) placed Matthevia within the evolving aplacophoran line as a crown group or upper stem group aculiferan, at a higher level than the lower sachitids, including Halkieria and Calvapiloosa, which they placed within the aculiferan stem rather than the stem group of Mollusca. While accepting Calvapiloosa as an aculiferan, Zhao et al. (2017) were sceptical about accepting Halkieria as a mollusc.

Matthevia was originally described from the Furongian of New York (Walcott 1885, 1886; English 2002) but later recorded also from the Ordovician (Pojeta et al. 2005). As the hitherto oldest palaeoloricate, it holds a key position in discussions concerning the time of emergence of total group aplacophorans and polyplacophorans (Vendrasco & Runnegar 2004, Pojeta et al. 2010). Thus, Vinther et al. (2012a) cited the absence of polyplacophorans and aplacophorans from the early and middle Cambrian as a problem for hypotheses that placed aplacophorans as a sister group to all other molluscs, the so-called Testaria hypothesis (Haszprunar 1996, 2000; Salvini-Plawen 2006; Fig. 1B), an absence that supports the notion that aplacophorans evolved from Early Ordovician palaeoloricates (stem group aculiferans). Following a somewhat chequered history of interpretation (Walcott 1885, 1886; Yochelson 1966; English 2002; Vendrasco & Runnegar 2004), and despite being known only from disarticulated plates, a generally accepted picture has emerged of the nature of this serially plated mollusc. An excellent reconstruction as an 8-plated form by Brian Roach was presented by Vinther (2014, fig. 2) and Vinther et al. (2012a, fig. 4), although the question of eight plates, as in polyplacophorans, as conventionally assumed, or seven plates as in Kulindroplax is unresolved.

This paper describes Qaleruaqia sodermanorum gen. et sp. nov. on the basis of rare isolated plates from the Aftenstjernesø Formation (Cambrian Series 2, Stage 4) in North Greenland (Fig. 2). The rare specimens of Qaleruaqia sodermanorum gen. et sp. nov. are compared to the unique articulated specimens of Halkieria evangelista that were collected only about 12 km to the north-east (Fig. 2). Head and intermediate plates are recognised in Qaleruaqia following comparison with Matthevia and other serially plated fossils. Qaleruaqia is interpreted as lying close to the basal node of the crown group Aculifera in the model of Vinther et al. (2017), as an upper stem group aculiferan or as an early member of either the stem group Aplacopora or the stem group Polyplacophora. Thus, Matthevia is no longer the oldest palaeoloricate and
the early–middle Cambrian gap in the record of potential aculiferan fossils noted by Vinther et al. (2017) is closed. The geological record of palaeoloricates is extended back by some 20 m.y., from the late Furongian to Cambrian Stage 4, potentially offering an earlier origin for crown group aculiferans than current models suggest (Vinther et al. 2017, Kocot et al. 2020).

The problematic fossil taxa discussed herein extend over 100 Ma from the Cambrian (Terreneuvian) to the Silurian (Wenlock; Fig. 3). Crown group chitons (Order Chitonida) are known from the Carboniferous onwards, while multiplacophorans range from Silurian to Permian (Vinther et al. 2012b); extant aplacophorans have no fossil record.

**Geological background**

All described specimens are derived from the Aftenstjerneø Formation in Lauge Koch Land, North Greenland (Fig. 2). The Aftenstjerneø Formation is the lowest formation in the carbonate-dominated Bronlund Fjord and Tavsens Iskappe groups that prograded northwards into the deep water trough of the transarctic Franklinian Basin (Higgins et al. 1991, Ineson et al. 1994, Ineson & Peel 1997). In southern Lauge Koch Land, the groups consist of an alternation of cliff-forming prograding coarse, cross-bedded dolomitic grainstones with frequent debris flows, deposited during highstands of sea level, and recessive mudstone–limestone–dolomite units representing lowstand conditions (Higgins et al. 1991, Ineson & Peel 1997; Fig. 2B). The alternation of highstand and lowstand deposition permits a lithostratigraphic subdivision that is not applied in northern Lauge Koch Land, where dark outer shelf mudstones and carbonates of the Henson Gletscher and Kap Stanton formations dominate the succession (Ineson et al. 1994) beyond the offshore limit of the prograding units (Fig. 2B).

The Aftenstjerneø Formation is mainly composed of dolostone grainstones, but a debris flow characteristically occurs at the top of the formation throughout the area. In southern Lauge Koch Land it attains a thickness of about 62 m (Ineson & Peel 1997) but this is reduced to about 18 m at the collection locality in northern Lauge Koch Land (Fig. 2A). The formation represents the first establishment of carbonate deposition following sandstones and recessive mudstones of the Buen Formation. The latter formation crops out extensively across eastern areas of North Greenland and yields rich faunas indicative of Cambrian Stages 3 and 4 (Peel & Willman 2018). The Sirius Passet Lagerstätte of northwestern Peary Land is located within basal strata of the Buen Formation transitional to a deep water trough siliciclastic succession to the north (Conway Morris et al. 1987; Ineson & Peel 2011; Peel & Ineson 2011a, b; Harper et al. 2019; Fig. 2). Fossils from the Aftenstjerneø Formation indicate Cambrian Stage 4 and are confined to the basal few metres of dolomitic grainstones that are rich in glauconite, phosphorite bioclasts, pyrite and phosphatised hardgrounds (Frykman 1980, Peel 2017). This distinctive horizon can be traced from southern to northern Lauge Koch Land and in outcrops across Peary Land to the east.
Material and methods

Grønlands Geologiske Undersøgelse (GGU) sample 315045 was collected by J.S. Peel on 7th of July 1984 from the basal beds of the Aftenstjernesø Formation in Lauge Koch Land, North Greenland (Fig. 2). The locality lies on the east side of Navarana Fjord, on the northern limb of a prominent east–west trending anticline, at an altitude of about 260 m a.s.l. (82° 36´ N, 42° 18´ W). The sample was collected from about 60 cm above the base of Aftenstjernesø Formation, from within a bluish-black weathering, bioclastic dolostone, 40 cm thick, with abundant pyrite and an irregular, phosphatized, upper surface.

The dolostone sample was dissolved in 10% acetic acid. Selected specimens were coated with gold prior to stereoscan microscopy, and images were assembled subsequently in Adobe Photoshop CS4.

Institutional abbreviations. – GGU – Grønlands Geologiske Undersøgelse, the Geological Survey of Greenland, now part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark; MGUH – Geological Museum, Copenhagen, now part of the Natural History Museum of Denmark; PMU – the palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden; SM – Sedgwick Museum, University of Cambridge, U.K.

Systematic palaeontology

This published work and the nomenclatural acts it contains have been registered in ZooBank database (International Commission on Zoological Nomenclature): http://zoobank.org/References/2C80D14F-6260-4A65-9E43-AE8460A129EC

Phylum Mollusca Linnaeus, 1758
Subphylum Aculifera Hatschek, 1891
Palaeoloricata Bergenhayn, 1955
Family Mattheviidae Walcott, 1886

Discussion. – Palaeoloricata was recognised as a subclass of Class Polyplacophora de Blainville, 1816 by Cherns (1998a, b) and Hoare & Pojeta (2006) in their studies of Ordovician and Silurian polyplacophorans, although Runnegar et al. (1979), Vendrasco & Runnegar (2004) and Pojeta et al. (2010) considered it to be an order. Palaeoloricata are a paraphyletic group including aplacophorans, chitons and stem group aculiferans (Sigwart & Sutton 2007, Pojeta et al. 2010, Vinther 2015) and the name is used here informally. The original spelling Matthevidae of Walcott (1886, see also Yochelson 1966) was modified to Mattheviidae by Runnegar et al. (1979), Smith & Hoare (1987) and later authors.

Pojeta et al. (2010) described three families in their revision of palaeoloricata from Furongian strata in Missouri, USA, giving a detailed review of earlier proposals. Mattheviids were characterised as having one or two deep lacunae and large apical areas on the intermediate valves. It is with members of this family that plates of Qaleruaqia gen. nov. are tentatively compared. Aulochitonids lack lacunae and have a small apical area, whereas dycheidiids, only questionably regarded as polyplacophorans by Pojeta et al. (2010), have shallow median lacunae, gaping intermediate plates but no apical area.

Questions of plate orientation and directional terminology in Matthevia and other palaeoloricata were discussed by Pojeta et al. (2010). As most material is disarticulated, the precise attitude of plates in life is unknown, particularly as regards the inclination of more elongate plates and the degree of overlap: various restorations have been presented (Vendrasco & Runnegar 2004, Vinther 2014). Posterior and anterior in Qaleruaqia

Figure 3. Geological record of aculiferan taxa mentioned in the text. Abbreviations: Llandovery, Prid. – Pridoli.
are used here in accordance with the overall direction of growth in intermediate plates, but their degree of inclination is not known (Fig. 4A).

Genus *Qaleruaqia* gen. nov.

**LSID.** – lsid:zoobank.org:act:44F403B6­EAF3­4276­9463­2A5FD410115A

**Type species.** – *Qaleruaqia sodermanorum* gen. et sp. nov., from the lower Aftenstjernesø Formation, Navarana Fjord, Lauge Koch Land, North Greenland, Cambrian Series 2, Stage 4, by monotypy.

**Etymology.** – From ‘Qaleruaq’, Greenlandic, meaning shell; feminine.

**Diagnosis** – Intermediate plate oval, with sub-parallel sides in dorsal perspective (Fig. 5B), saddle-shaped in lateral view with convex antero-lateral margins (Fig. 5C). Postero-lateral marginal areas shallowly concave in dorsal view, forming wing-like structures adjacent to the convex middorsal area. Apical area about as long as broad, with broad transverse ribs fading laterally; lacuna very shallow. Shell growth mixoperipheral with dorsal ornamentation of comarginal ridges. Outer shell layer formed by imbricating lamellae which slope towards the antero-lateral margins, with each lamella overlying the previous lamella. Inner shell layer with radial fibrous structure.

Head plate oval, width about two thirds of length, with a short, convex supra-apical surface and a long, concave sub-apical surface. Early growth stage bulbous, located nearer to the slightly pointed, supra-apical margin. Concave sub-apical train with sub-quadrangular and slightly arched margin. Holoperipheral growth, with ornamentation of comarginal cords that is traversed by broad radial folds on the sub-apical surface near the margin.

**Discussion** – *Qaleruaqia* is known from isolated sclerites of the type species *Qaleruaqia sodermanorum* gen. et sp. nov. that are considered to represent head and intermediate plates (Figs 4–6). The presence on the ventral surface of the apical area and shallow lacuna supports interpretation of the intermediate plates of *Qaleruaqia* gen. nov. as the intermediate plates of a mattheviid palaeoloricate similar to *Chelodes* Davidson & King, 1874 (Cherns 1998a, b). The sclerite interpreted as the head plate resembles the head plate of *Matthevia variablis* Walcott, 1885 (Runnegar et al. 1979) and *Matthevia wahwahensis* Vendrasco & Runnegar, 2004 from the Furongian of USA. However, the intermediate plates of *Matthevia* are heavily calcified with one or more deep lacunae.

Both plate morphotypes of *Qaleruaqia* occur together in GGU sample 315045 from the basal Aftenstjernesø Formation of Navarana Fjord, Lauge Koch Land (Fig. 2). It is not known how many intermediate plates, and possibly a discrete tail plate, are present within the scleritome. The available sample, however, is very small, with only three known specimens of the intermediate plate of *Qaleruaqia sodermanorum* and two head plates.

**Other species.** – Known only from the type species at the type locality.

*Qaleruaqia sodermanorum* sp. nov.

**Figures 4–6**

**LSID.** – lsid:zoobank.org:act:6CEE7CDE­4C86­412D­B5C7­AEA12E103150

**Types.** – Holotype: PMU 36057 from GGU sample 315045, Aftenstjernesø Formation, Navarana Fjord, Cambrian Series 2, Stage 4.

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**Figure 4.** Interpretative sketches of *Qaleruaqia sodermanorum* gen. et sp. nov. • A – intermediate plate in lateral view and longitudinal section showing the disposition of the apical area and the shallow lacuna. • B – longitudinal section of shell near anterior margin of intermediate plate showing the overlapping comarginal lamellae in the outer layer downstepping towards the posterior and radial fibrous structure of the inner layer. • C, D – reconstructions of anterior end in lateral view (anterior to left), with overlapping (C) and sequential (D) intermediate plates.
Paratypes: Intermediate plates PMU 36058 and PMU 36059, and head plate PMU 36060, from the same sample and locality as the holotype.

Type horizon and locality. – Lower Aftenstjerneos Formation (Brønlund Fjord Group; Fig. 2B), eastern side of Navarana Fjord, Lauge Koch Land, North Greenland; Cambrian Series 2, Stage 4.

Material. – Known only from the four illustrated specimens (Figs 5, 6) and one additional head plate, all from GGU sample 315045. All specimens are secondarily phosphatised, originally calcareous.

Etymology. – For Gudrun and Einar Söderman (Uppsala).

Diagnosis. – As for genus.

Description. – In dorsal external view, the bilaterally symmetrical intermediate plate appears to be oval in shape, with parallel or sub-parallel sides and uniformly rounded terminations (Fig. 5B). In lateral view, however, its form is seen to be saddle-shaped, with the lateral areas forming convex shields which meet their maximum height of half the length at about two thirds of the distance from the presumed posterior margin (uppermost in Fig. 5B) to the anterior margin (Fig. 5C). The plate is flat along the median plane from posterior to anterior. At the posterior, the median dorsal area is initially convex, but becomes rounded terminations (Fig. 5B). In lateral view, growth is holoperipheral, with comarginal cords and interspersed fine growth lines; down-stepping of growth lamellae is towards the plate margin. Three or four weakly defined, broad radial folds traverse the sub-apical surface near the margin (Fig. 6F).

Ventrally, the apical area of the plate is developed as a prominent shelf extending anteriorly into the interior from the posterior, and with a slight overhang at its anterior margin delimiting a shallow lacuna (Fig. 5L). The anterior margin of the apical area is excavated medially and its surface is marked by a series of W-shaped low, rounded, transverse ridges and intervening channels which increase in amplitude from posterior to anterior (Fig. 5E, L). About seven ridges are present, fading away laterally. The surface is generally smooth, but a patch of cellular structure, with a network of depressed ridges around raised centres, is preserved just antero-lateral of the ridges (Fig. 5K, arrows). Details of the internal surface at the anterior of the plate are not known.

Plate growth is mixoperipheral. The dorsal surface of the intermediate plate is marked by a uniform series of comarginal ridges spaced at about 5 or 6 per 100 µm near the anterior margin (Fig. 5G). The ridges are asymmetric in cross-section, steepened on the side facing the posterior (Fig. 5A, arrow cml), forming an imbricate stack of comarginal laminae in which the latest deposited lamella lies uppermost and slopes towards the antero-lateral margins (Fig. 6B-D). The lamellae are thus down-stepping towards the posterior (Figs 5A, 6C). The comarginal ridges fade at the transition to the postero-lateral wing-like areas (Fig. 5B). In the holotype, this distal termination of the ridges is related to the loss of the thin outer shell layer which carries the ridges. A broken margin (arrows in Fig. 5A; Fig. 6B) separates this ridge-bearing outer layer from an underlying layer characterised by a faint radial fibrous structure. The same fibrous layer is evident at the broken anterior margin of the sclerite (Fig. 5D; Fig. 6A, arrows).

The bilaterally symmetrical head plate is oval with width about two thirds of length (Fig. 6E). A bulbous initial growth stage lies nearer to the slightly pointed supra-apical margin, interpreted as anterior (Fig. 6C, D). The supra-apical surface is convex whereas the longer sub-apical surface is concave (Fig. 6G), with a sub-rectangular margin, in dorsal view. Growth is holoperipheral, with comarginal cords and interspersed fine growth lines; down-stepping of growth lamellae is towards the plate margin. Three or four weakly defined, broad radial folds traverse the sub-apical surface near the margin (Fig. 6F).

Discussion. – The outer surface of the holotype of Qaleruaqia sodermanorum is pierced by numerous small holes, the irregular form, size and distribution of which usually reflect imperfect phosphatisation (Figs 5F, 6A). However, many holes with a more regular circular cross-section and diameter of 20–30 µm (Fig. 6I) appear to have a biogenic origin. Their scattered nature may suggest microborings (Stockfors & Peel 2005a, b) but sensory pores (aesthetes) are a character of the outer shell layer of polyplacophorans (Schwabe 2010) and can be highly variable in form (Vendrasco et al. 2009); they are reported also from Palaeozoic material (Hoare 2000, 2009; Vendrasco & Runnegar 2004). Pojeta et al. (2010) reported a series of horizontal canals interpreted as aesthetes within the dorsal area of intermediate plates of Hemithecella eminensis Stinchcomb & Darrough, 1995 with diameters ranging from 110–280 µm, significantly larger than the vertical holes observed here in Qaleruaqia sodermanorum that are of similar size to the aesthetes of most modern chitons (Vendrasco et al. 2009). No vertical canals were observed in Hemithecella eminensis by Pojeta et al. (2010).

Intermediate plates of most described mattheviid taxa differ from Qaleruaqia sodermanorum in being posteriorly acuminate, with a long, narrow apical area (Cherns 1998a, b; Vendrasco & Runnegar 2004; Hoare & Pojeta 2006; Pojeta et al. 2010). The posterior is more bluntly rounded in Qaleruaqia sodermanorum. Growth lines at the broken posterior termination are divergent rather than convergent on an apex (Fig. 5G, J), suggesting that the transition from the dorsal surface to the apical area probably was a short transverse fold. The apical area is short, almost an equiangular triangle in preserved
specimens (Fig. 5L). The anterior margin is uniformly convex in dorsal view, lacking the median sinus seen in the intermediate plates of most other genera (Cherns 1998a, b; Hoare & Pojeta 2006; Pojeta et al. 2010). Intermediate plates of the Furongian–Early Ordovician *Matthevia* Walcott, 1885 are narrow and strongly tapering towards the posterior, with a deep median dorsal sinus and an apical area that is often more than half of the total length (Yochelson 1966, Vendrasco & Runnegar 2004, Pojeta et al. 2005). Plates of *Matthevia* are massively thickened with one or two deep lacunae, in contrast to the relatively thin-shelled *Qaleruaqia sodermanorum*, which has only a single shallow lacuna (Fig. 4A; Fig. 5L, lac).

*Hemithecella* Ulrich & Bridge, 1941 (Furongian–Early Ordovician) has triangular intermediate plates that are often extremely long and narrow in contrast to the oval form of *Qaleruaqia sodermanorum*. The apical area extends to more than half the plate length above an almost

**Figure 5.** *Qaleruaqia sodermanorum* gen. et sp. nov., intermediate plates, Afensjermeso Formation, Navarana Fjord, Cambrian Series 2, Stage 4. All specimens from GGU sample 315045. A–D, F – PMU 36057, holotype, A – detail of postero-lateral margin showing comarginal lamellae (cml), with arrows indicating boundary between outer lamellar shell layer and inner radial fibrous layer, B – dorsal view with posterior at top, C – oblique lateral view, D – detail of anterior margin showing radial fibrous layer (arrows), F – postero-dorsal view with anterior at top; E, K, L – PMU 36058, apical area with growth lamellae, E – oblique posterior view, K – detail of wrinkled structure (arrows), L – plan view of apical area and shallow lacuna (lac); G–J – PMU 36059, dorsal surface with comarginal lamellar ornamentation, G – dorsal view, H – oblique postero-lateral view, I – oblique lateral view, J – detail of posterior (damaged) showing divergent comarginal ornamentation. Scale bars: 100 µm.
cylindrical lacuna (Stinchcomb & Darrough 1995, Pojeta et al. 2010) that is much longer than the shallow lacuna of Qaleruaqia sodermanorum (Figs 4A, 5L).

Chelodes Davidson & King, 1874 is best known through the detailed monograph of Silurian type material from Gotland, Sweden, by Cherns (1998a), although Runnegar et al. (1979) and Pojeta et al. (2010) assigned Furongian and Early Ordovician material to the genus. Intermediate plates are sub-triangular, almost as wide as long in the Gotland material, but Ordovician material assigned to the genus by Runnegar et al. (1979) and Pojeta et al. (2010) has elongate triangular plates. A shallow median dorsal sinus is usually present in the anterior margin of intermediate plates. However, the head plate of Chelodes actinis Cherns, 1998a from Gotland has an elongate shape in dorsal perspective similar to that of the intermediate plates of Qaleruaqia. The Greenland species differs from Chelodes actinis in its greater height in lateral perspective (Fig. 4C) and in having a more prominent apical area.

Many Cambrian and Ordovician specimens figured by Hoare & Pojeta (2006) and Pojeta et al. (2010) are relatively poorly preserved and details of ornamentation are obscure. Hemithecella eminensis Stinchcomb & Darrough, 1995 and Hemithecella expansa Ulrich & Bridge, 1941, illustrated by Pojeta et al. (2010) from the Furongian of Missouri, display comarginal growth lines which display periodic rugae in the anterior part of the plate. A median dorsal sinus is present, in contrast to the uniformly convex anterior margin of Qaleruaqia sodermanorum, the latter also differing in the slope of growth lamellae towards the anterior, with the lamellar stack down-stepping to the posterior (Figs 5A, 6B).

The head plate of Qaleruaqia sodermanorum closely resembles the head shield of Matthevia in its low form, oval shape and inflated early growth stage (Fig. 6C–H). The head plate of Matthevia variabilis was illustrated by Walcott (1885, fig. 3; 1886, pl. 32, fig. 4) and the illustration was reproduced by Yochelson (1966, pl. 1, fig. 18) who commented that the specimen was missing. Runnegar et al. (1979, pl. 1, fig. 23) illustrated a specimen from the Furongian Hoyt Limestone of New York, which appears to be the original figured specimen of Walcott (1885, 1886). Walcott (1885, 1886) considered the plate to be an operculum, but Yochelson (1966) doubted this interpretation, but he did not include it in his reconstruction of Matthevia. English (2002) described collections from the type locality of Matthevia variabilis at Skidmore Quarry, near Saratoga Springs, New York, but did not locate the head shield in his studied material. He restored Matthevia with a conical head plate but noted that the flat plate occurred in samples from a separate horizon. The head plate of Qaleruaqia sodermanorum differs from that of Matthevia variabilis and Matthevia wahwahensis Vendrasco & Runnegar, 2004 in having a more swollen apex and being slightly pointed at the supra-apical margin, whereas in Matthevia variabilis it is equally rounded at both extremities.

Runnegar et al. (1979) considered that the swollen apex of Matthevia lay closer to the posterior margin but a reconstruction of Matthevia wahwahensis by Vendrasco & Runnegar (2004, fig. 4.3) placed it closer to the anterior margin, see also Vinther et al. (2012a, fig. 4C). This interpretation, with the convex supra-apical surface located anteriorly, is favoured here in Qaleruaqia sodermanorum on account of the shallow arching of the sub-apical margin and the slightly pointed supra-apical margin (Figs 4C, D; 6E–H).

Shell formation in Qaleruaqia

The imbrication of comarginal growth lamellae of intermediate plates shows down-stepping of individual lamellae towards the posterior (Figs 4B, 5A, 6C), indicating that shell growth in the mixoperipheral intermediate plates of Qaleruaqia sodermanorum was accomplished in similar fashion to that described in present day chitons by Beedham & Trueman (1967) and Checa et al. (2017). In extant chitons, and also in Qaleruaqia, calcareous skeletal elements are anchored firmly in the mantle tissues and the secreting edge embraces the outer margin. In contrast, the body in conchiferan molluscs moves separately from the periostracum and shell, a development that enables the animal to withdraw or extend its soft parts, and shell growth takes places on the inner surface beneath previous layers. Withdrawing into its shell provides enhanced safety while the chiton’s defensive solution is to armour its exposed girdle with a myriad of small calcareous spicules in the tissues surrounding the shells and to clamp or enrol (Todt et al. 2008, Schwabe 2010, Sigwart et al. 2019).

Comarginal holoperipheral growth ornamentation on the head plate of Qaleruaqia does not show comparable down-stepping to that seen in the intermediate plates, but rather a down-stepping pattern towards the margin similar to that seen in Halkieria and other molluscs.

Surprisingly, the distinctive imbricate style of shell growth seen in the intermediate plates of Qaleruaqia has not been reported in other palaeoloricates, although most of the material from Laurentia described by Hoare & Pojeta (2006) and Pojeta et al. (2010) is internal moulds lacking details of ornamentation. Excellently preserved Silurian specimens of Chelodes clearly show downstepping of growth lamellae on the intermediate plates towards the anterior margin (Cherns 1998a, pl. 3) whereas down-stepping in Qaleruaqia is towards the posterior (Figs 5A, 6C). It is likely that the posterior down-stepping in intermediate plates of Qaleruaqia represents an unusually high degree of marginal overlap.
of the dorsal surface by the mantle. Anterior downstepping in the head plate and in plates of other palaeoloricates may have resulted from the mantle embracing the inner shell layer (fibrous in *Qaleruaqia*; Fig. 6A) but having edge-to-edge contact with just the outer edge of the overlying outer lamellar layer (Beedham & Trueman 1967, fig. 4a; Checa et al. 2017, fig. 8a).

Down-stepping of growth lamellae towards earlier growth stages is seen in several Cambrian mollusc-like taxa where the outer shell layer is scaly, including *Yunnanopleura* Yu, 1987, discussed below (Qian & Bengston 1989, Kouchinsky et al. 2015). A similar imbrication of growth lamellae resulting from accretion on the outer surface of a sclerite embedded in tissue was described by Peel (2019) in the paraconodont *Tarimspira artemi* Peel, 2019 from the lower Cambrian (Cambrian Series 2, Stage 4) of North Greenland.

**Qaleruaqia and micropolyplacophorans**

Vendrasco et al. (2009) revived interpretation of the *Ocruranus–Eohalobia* group as possible stem group chitons in accordance with the micropolyplacophoran hypothesis of Yu (1987, 2001, 2014) concerning mainly Chinese material from Cambrian Series 1. Thus, *Eohalobia* Jiang, 1980, interpreted as the head plate, was placed in synonymy with *Ocruranus* Liu, 1979 interpreted as the tail plate with the scleritome completed by an intermediate valve assigned to *?Gotlandochiton*. Vendrasco et al. (2009) acknowledged that the first undisputed chitons (i.e. at that time the palaeoloricate *Matthevia*) occurred in the Furongian (Runnegar et al. 1979, Pojeta et al. 2010; Fig. 3), although *Matthevia* was placed within the aplacophoran line by Sutton et al. (2012) and Vinther et al. (2017). This first appearance of a palaeoloricate is revised
The appearance of the aculiferans. While the Ocruranus filling the gap between the earliest conchiferans and alicates Chinese fossils as probable stem group sachitids forms, but articulated specimens are not known. Arrangements have been suggested in these early Cambrian. Thus, at least three different plate arrangements have been suggested in these early Cambrian forms, but articulated specimens are not known.

Only Yunnanopleura of the numerous shells described by Yu (1987), Qian & Bengtson (1989) and Parkhaev & Demidenko (2010) develops a prominent apical area. On this basis it was interpreted by Yu (1987, 2014) as an intermediate plate comparable to Chelodes. The elongate shell is about twice as long as wide and has a pointed apex (‘posterior’) that overhangs the sub-apical margin. The apical area is about one fifth of the total length of about 2 mm and may show conspicuous lamellae that down-step towards the supra-apical margin as in Qaleruaqia (Qian & Bengtson 1989, fig. 62). The interpretation of these prominent growth lamellae on the apical area as dentition by Parkhaev & Demidenko (2010) is rejected. Thus, growth is mixoperipheral in the Chinese material, as in Qaleruaqia. Down-stepping of growth lamellae towards the mid-dorsum is seen on the apico-lateral margins in specimens assigned to Yunnanopleura (Kouchinsky et al. 2017, fig. 36b) and possibly Yu (2014, fig. 1.3), but most of the dorsal ornamentation of comarginal growth lines in the material from the Anabar Uplift of Siberia, and in specimens illustrated by Yu (1987, 2014) from Meisuchun, shows down-stepping of lamellae towards the margin.

The restoration proposed by Kouchinsky et al. (2017) regarded Yunnanopleura as the tail plate, Purella as the head plate and (presumably) a thorax covered with pointed siphogonuchitid sclerites, in similar fashion to Halkieria (Fig. 7E). Their comparison to the posterior plate of Halkieria implies that the apex of Yunnanopleura was located anteriorly and not posteriorly as suggested by Yu (1987), which is inconsistent with the presence of an apical area in the Chinese material (Yu 1987). An apical area is lacking in plates of Halkieria and not visible in illustrations of the Siberian material attributed to Yunnanopleura by Kouchinsky et al. (2017).

Yunnanopleura differs from intermediate plates of Qaleruaqia in its pointed posterior and its coplanar margin. In Qaleruaqia the intermediate plate is saddle-shaped in lateral perspective (Fig. 5B). However, similarity in the development of an apical area and corresponding mixoperipheral growth in Yunnanopleura from the Terreneuvian (Meisuchunian) of China suggests a possible link to younger palaearolicates such as Qaleruaqia, Matthevia and Chelodes.

Restoring Qaleruaqia as a palaearolicate

Complete specimens of multisclerite molluscs are rare in the Palaeozoic and restorations based on isolated sclerites are usually rooted in their predetermined taxonomic position. Pojeta et al. (2010) noted that no articulated chiton scleritomes were known from the Cambrian. Matthevia (Furongian–Early Ordovician) has been considered to be the oldest palaearolicate chiton, with the status of the micropolyplacophorans of Yu (1987) being equivocal (Qian & Bengtson 1989, Vendrasco et al. 2009, Pojeta et al. 2010, Vinther 2015).

Walcott (1885, 1886) considered Matthevia to be a pteropod with two skeletal elements, subsequently interpreted as the head plate (interpreted as an operculum by Walcott 1885, 1886) and intermediate plates (Runnegar et al. 1979, Vendrasco & Runnegar 2004). Yochelson (1966) restored Matthevia with two plates, excluding the head plate, in his novel reconstruction that formed the basis for Class Matthevia Yochelson. 1966. Runnegar & Pojeta (1974, fig. 5) considered the scleritome of Matthevia to include seven or eight plates, with their reconstruction showing seven, and this figure was cited also by Runnegar et al. (1979). English (2002, fig. 4) proposed eight plates (but excluding a flat head plate). Eight plates including the flat head plate were retained in reconstructions made by Vendrasco & Runnegar (2004, fig. 4), Vinther (2014, fig. 2) and Vinther et al. (2012a, fig. 4c). However, the actual number of plates in the scleritome of Matthevia is not known. There are eight plates in the unusual chiton Echinaochiton Pojeta, Eernisse, Hoare & Henderson, 2003 from the Middle Ordovician of Wisconsin (Pojeta et al. 2003, Pojeta & DuFoe 2008; Fig. 3) and in the Late Ordovician Septemchiton Bergenhayn, 1955 (Rolfe 1981; Fig. 3). However, Sutton et al. (2012) considered Septemchiton to be a crown group aplacophoran, placing the genus together with the 7-plated Acaenoplax Sutton, Briggs, Siveter & Siveter, 2004 and Kulindroplax from the Silurian (Sutton et al. 2004, 2012). Cherns (2004) proposed a Family Heloplacidae for several forms from the Silurian of Gotland, Sweden, related to Acaenoplax (Fig. 3).
Conventional restoration of *Qaleruaqia* as a palaeoloricate chiton suggests a head plate followed by six intermediate plates and a tail plate, which may be closely similar morphologically to the intermediate plates, as has been proposed in *Matthevia*. This is more plates than available specimens in the current small sample of *Qaleruaqia sodermanorum*, where a posterior plate is not known. The partial restorations (Fig. 4C, D) portray just the anterior part of the animal and the inclination and degree of overlap of the intermediate plates is arbitrary. The uniformly convex anterior margin of the intermediate plates may suggest no overlap of plates (Fig. 4D) as an anterior sinus is usually present in overlapping plates (Cherns 1998a, b; Hoare & Pojeta 2006). Alternatively, the height and convex form of the plate in lateral view (Fig. 5C) and the development of an apical area may be an indication of overlap (Fig. 4C), although the relative shortness (posterior–anterior) of the apical area suggests that the plates were not so steeply inclined as in *Matthevia* or *Hemithecella*.

**Qaleruaqia and halkieriids**

*Halkieria evangelista* Conway Morris & Peel, 1995 is undoubtedly the most cited Cambrian fossil yet described from North Greenland and continues to form a central element in discussions of lophotrochozoan evolution (Conway Morris & Peel 1995, Vinther & Nielsen 2005, Conway Morris & Caron 2007, Vinther et al. 2017, Zhao et al. 2017, Han et al. 2019) The up to 8 cm long fossil was a slug-like animal in which the dorsal surface is covered by a chain mail of many hundred small pointed sclerites, with prominent plates at the anterior and posterior (Fig. 7E, F). Comparison of the plates of *Qaleruaqia sodermanorum* with these anterior and posterior plates is apposite, not only on account of morphological similarity, but also due to the occurrence together with *Qaleruaqia sodermanorum* in GGU sample 315045 of disarticulated halkieriid sclerites assigned to *Hippopharangites* Bengtson in Bengtson et al., 1990 (Fig. 7A–D).
Fully articulated specimens of *Halkieria evangelista* are a key element in the diverse fauna of the Sirius Passet Lagerstätte (Conway Morris *et al.* 1987; Conway Morris & Peel 1995; Ineson & Peel 2011; Peel & Ineson 2011a, b; Harper *et al.* 2019). The single locality with exceptionally preserved fossils (Fig. 2A) lies in strata assigned to Cambrian Stage 3 (Montezuman Stage of Laurentian usage) in the lower part of the Buen Formation (Babcock & Peel 2007, Hollingsworth 2011).

Intermediate plates of *Qaleruaqia sodermanorum* viewed in dorsal perspective display a superficial resemblance to the posterior plate of *Halkieria evangelista* (Fig. 7E, F) but are considered to be oriented differently. Thus, the narrower end of the intermediate plate in *Qaleruaqia* (uppermost in Fig. 5B) is interpreted as posterior, whereas the apex of the posterior plate in *Halkieria* is anterior (Fig. 7E, F). The posterior plate in *Halkieria* has holoperipheral growth, whereas growth in intermediate plates of *Qaleruaqia* is mixoperipheral. In contrast to *Qaleruaqia*, there is no indication of an apical area in *Halkieria*. The well developed, sub-marginal, anterior apex of *Halkieria* is not seen in *Qaleruaqia* where growth lamellae diverge slightly at the margin, suggesting a transverse fold, rather than converge on a single point (Fig. 5J). The shell margins are coplanar in *Halkieria* whereas *Qaleruaqia* is strongly saddle-shaped in lateral view (Fig. 5C, I).

The anterior plate in *Halkieria* is oriented with its apex overhanging the posterior margin, as is the case also with the earliest growth area in *Qaleruaqia*, but *Halkieria* is wider than long, and convex along the median dorsal margin. It is not known if *Halkieria* had spiculate girdles that can be compared to the dense thatch of *Cavapilosa*. However, spicules are characteristic of the Late Ordovician and Silurian aplacophorans *Phthipodochiton* Sutton & Sigwart, 2012, *Acaenoplax* Sutton, Briggs, Siveter & Siveter, 2001 and *Kulindroplax* Sutton & Sigwart, 2012, *Matthevia* is conventionally restored with eight plates (Vendrasco *et al.* 2009) compared to the single plate of *Cavapilosa*, although the exact number of plates is not known. *Qaleruaqia* developed anterior and intermediate plates (a posterior plate is not known) and probably had a similar number of plates to *Matthevia*.

Comarginal ornamentation in intermediate valves of *Qaleruaqia* differs profoundly from the anterior and posterior plates of *Halkieria* in that shell lamellae in *Qaleruaqia* are deposited externally on top of preceding shell layers at the growing edge, down-stepping towards the posterior (Figs 5B, C, E; 6C, D). Successive shell layers appear to have been added internally, underneath earlier growth lamellae in *Halkieria* (Fig. 7F). However, this latter form of accretional growth is seen in the head plate of *Qaleruaqia*, intermediate valves of palaeoloricates, and most other molluscs. *Halkieria* plates may show a sub-radial ornamentation consisting of fans of fine lines which do not originate at the apex (Fig. 7G). They may be a reflection of shell structure and, as such, can be compared to the radially fibrous inner shell layer of *Qaleruaqia* (Figs 5C, D; 6A). Similar fibrous structure is known from other Cambrian molluscs, including *Ocruranus* and pelagiellids (Vendrasco *et al.* 2009).

Conway Morris & Peel (1995) described three types of small sclerites occurring in articulated specimens of *Halkieria evangelista* (Fig. 7E) of which the cultrate sclerites most closely resemble the sclerites of *Hippophrangites* that occur together with *Qaleruaqia* in GGU sample 310345 (Fig. 7A–D). These *Hippophrangites* sclerites display the characteristic scale-like tubercles on their convex surface described by Bengtson *et al.* (1990), whereas the cultrates of *Halkieria evangelista* are longitudinally ribbed.

### *Qaleruaqia* and *Calvapilosa*

*Calvapilosa kroegeri* Vinther, Parry, Briggs & Van Roy, 2017 from the Fezouata Formation Lagerstätte (Ordovician, Tremadocian) of Morocco is characterised by an elongate mantle with a dense covering of hair-like spicules; a single oval anterior plate, about one quarter of the total length, occurs within the spicule mass (Vinther *et al.* 2017). In the holotype (Vinther *et al.* 2017, fig. 1) the anterior plate has a length of 5 mm, compared to a length of about 1.2 mm in intermediate plates of the holotype of *Qaleruaqia sodermanorum* (Fig. 5B, C). The posterior plate in *Halkieria evangelista* (Fig. 7E, F) may exceed 12 mm in length, about one fifth of the overall length, but the anterior plate is only about two thirds of this (Conway Morris & Peel 1995).

The single plate in *Calvapilosa* is closely similar to the head plates of *Matthevia* and *Qaleruaqia* with regard to its oval form, the anterior location of its apex and the tendency to develop a concave posterior train. Its shallow posterior sinus parallels the slight arching of the posterior margin seen in the two Cambrian forms. The plates of all three genera differ from the anterior plate of *Halkieria*, where the apex overhangs the posterior margin. It is not known if *Matthevia* and *Qaleruaqia* had spiculate girdles that can be compared to the dense thatch of *Cavapilosa*. However, spicules are characteristic of the Late Ordovician and Silurian aplacophorans *Phthipodochiton* Sutton & Sigwart, 2012, *Acaenoplax* Sutton, Briggs, Siveter & Siveter, 2001 and *Kulindroplax*. *Matthevia* is conventionally restored with eight plates (Vendrasco *et al.* 2009) compared to the single plate of *Cavapilosa*, although the exact number of plates is not known. *Qaleruaqia* developed anterior and intermediate plates (a posterior plate is not known) and probably had a similar number of plates to *Matthevia*.

Interpretation of *Calvapilosa* as an early aplacophoran would entail a significant loss of the series of dorsal plates usually located posterior to the head plate in palaeoloricates. Such a loss would stand in stark contrast to the interpretation of the single plate as a plesiomorphic character within aculiferans (Vinther *et al.* 2017), although...
other contenders for this role in the earliest Cambrian (Yu 1987, Qian & Bengtson 1989, Parkhaev & Demidenko 2010) might be better placed than the Ordovician Calvapilosa. Absence of plates is a character of living aplacophorans, but the Ordovician and Silurian forms placed within Aplacophora by Sutton et al. (2012) retain seven or eight plates.

**Discussion**

Vendrasco et al. (2009) interpreted Ocruranus as a possible stem group chiton while acknowledging that the first undisputed chitons (i.e. Matthevia) occurred in the Furongian (Runnegar et al. 1979, Pojeta et al. 2010), although Sutton et al. (2012, fig. 2) placed Matthevia high in their Aplacophora clade. This oldest date is revised to Cambrian Series 2, Stage 4 following the description of Qaleruaqia sodermanorum. However, agreement is expressed with Vinther et al. (2012a) that the precise affinities of individual taxa as stem aculiferans, stem chitons or stem aplacophorans within the paraphyletic palaeoloricates are far from resolved. Molecular clock evidence cited by Vinther et al. (2012a) for the origin of aculiferans yielded a date of 488 Ma (credibility interval 517–453 Ma). Kocot et al. (2020) suggested a slightly older date for aculiferan diversification (499 Ma) with a credibility interval of 479–520 Ma). Qaleruaqia sodermanorum dates from about 512 Ma and the oldest Matthevia from about 490 Ma.

The micropolyplacophorans of Yu (1987) were regarded as probable stem group sachitids filling a gap between the earliest conchiferans and the appearance of the aculiferans by Vinther (2015), although Aculifera and Conchifera are regarded as sister groups by Vinther et al. (2017). Vinther et al. (2012a) noted that the absence of suitable intermediaries from Cambrian Series 1–3 was a problem for hypotheses that placed aplacophorans as a sister group to other molluscs (Haszprunar 1996, 2000; Salvini-Plawen 2006; Fig. 1B), although it may be countered that some members of the Ocruranus–Eohalobia group could fill this gap. The absence of stem group chitons and aplacophorans before the Furongian supported their thesis that aplacophorans evolved from palaeoloricates in the Ordovician (Vinther et al. 2012a; Fig. 8B) but this aspect is weakened by the current...
description of *Qaleruaqia sodermanorum* from Cambrian Series 2 as regards its timing. Furthermore, the similarity between Chinese specimens of *Yunnanopleura* and intermediate plates of *Qaleruaqia* indicates an alternative (Fig. 8A) to the evolutionary pathway via *Halkieria* proposed by Vinther *et al.* (2012a, 2017).

Vinther *et al.* (2017) presented an analysis of ancestral molluscs that naturally focused on their accompanying description of the exceptionally preserved *Calvapilosa kroegeri* from the Early Ordovician of Morocco as a lower stem group aculiferan. In this model (Fig. 8B), the upper stem group aculiferan *Halkieria* is the sister group to Aculifera (Aplacophora and Polyplacophora, the latter including multiplacophorans). Their time tree, based on Bayesian total evidence analysis (Vinther *et al.* 2017, fig. 4), needs only slight modification following the description of *Qaleruaqia sodermanorum*. *Matthevia* was placed within the aplacophoran branch (Vinther *et al.* 2017, fig. 4), being regarded as an early crown or higher stem group aculiferan. *Qaleruaqia sodermanorum* could occupy a similar place to *Matthevia*, with the basal node of their clade Aplacophora thereafter being revised downwards from the Cambrian–Ordovician boundary interval to Cambrian Series 2. On account of its greater age and geological association with halkieriids (*Hippopharangites*), the description of *Qaleruaqia sodermanorum* strengthens the postulated derivation of aculiferans from a sachtid (*Halkieria*) root. There is, however, no convincing analysis of the distribution of most described palaeoloricate taxa between the aculiferan stem or the aplacophoran and polyplacophoran clades of Aculifera. Referral of *Matthevia* to the aplacophoran clade, as distinct from its traditional location in the polyplacophoran clade, is arbitrary. Pending such an analysis, *Matthevia* and *Qaleruaqia* are placed in the upper stem group (Fig. 9).

Given the focus of their study, it is perhaps not surprising that Vinther *et al.* (2017) placed the single plated *Calvapilosa* closer to the Aculifera–Conchifera basal node than *Halkieria*, although *Calvapilosa* occurs 30 Ma later in the geological record at a time when palaeoloricates are diversifying. The single shell of *Calvapilosa* more closely resembles the head plate of *Matthevia* and *Qaleruaqia* than that of *Halkieria*, suggesting that it might be placed together with these, with significant shell loss, rather than in the lower aculiferan stem (Fig. 9).

Zhao *et al.* (2017) placed *Calvapilosa* as an aculiferan but doubted its relationship to *Halkieria*, which they located together with tommotiids outside of Mollusca. They cited the lack of a radula in *Halkieria* as support for its supposed non-molluscan nature (Zhao *et al.* 2017), and presumably for its separation from *Calvapilosa* where a radula is clearly preserved (Vinther *et al.* 2017). Zhao *et al.* (2017) argued that a radula was not present in *Halkieria* because one is not preserved in material from the Sirius Passet Lagerstätte, while a radula is preserved in *Wiwaxia* from the Burgess Shale Lagerstätte and *Calvapilosa* from Fezouata Lagerstätte. This argumentation is rejected and seems to demonstrate a lack of awareness of both the complexity and variable nature of preservation at Sirius Passet (Strang *et al.* 2016a, b; Peel & Ineson 2011a; Peel 2017; Hammarlund *et al.* 2019; Harper *et al.* 2019) where exceptional preservation was not afforded equally to all members of the biota. Individual taxa followed their own post mortem preservational pathways, some with preserved soft parts and some without. Shell-bearing Sirius Passet forms such as *Halkieria evangelista*, hyoliths and trilobites retain little information other than their articulated shells (Babcock & Peel 2007, Peel 2010). The abundant trilobites almost never show traces of limbs, but often retain mineralised digestive glands (Babcock & Peel 2007).

It is unfortunate that the elegant scheme of Vinther *et al.* (2017) lacks discussion of the *Ocuranus–Eohalobia* group of Vendrasco *et al.* (2009) as these earliest Cambrian problematic fossils may offer other pathways to and through the Aculifera (Fig. 8A). Also the problematic Cambrian Series 2 scleritome of *Trachyplax* Larsson, Peel & Högström, 2009 is not mentioned despite several similarities with Silurian and younger multiplacophorans that are considered to be a branch of polyplacophorans (Vinther *et al.* 2017, fig. 4). While current restorations of its scleritome were not satisfying either to its authors (Larsson *et al.* 2009) or reviewers (Vinther *et al.* 2012b), the occurrence of *Trachyplax* in North Greenland in strata of the same age as *Qaleruaqia* urges circumspection.

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