A NEW FAMILY OF CAMBRIAN RHYNCHONELLIFORMEAN BRACHIOPODS (ORDER NAUKATIDA) WITH AN ABERRANT CORAL-LIKE MORPHOLOGY

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Abstract: Tomteluva perturbata gen. et sp. nov. and Nasakia thulensis gen. et sp. nov., two new rhynchonelliformean brachiopod taxa, are described from carbonate beds from the lower middle Cambrian (Series 3, Stage 5) basinal Stephen Formation, Canada, and the upper lower Cambrian (Series 2, Stage 4) Henson Gletscher Formation, North Greenland, respectively. The two taxa are characterized by an unusual coral-like morphology typified by a high conical ventral valve with an anteriorly curved umbo and a tube-like structure inside the ventral valve, interpreted as pedicle tube. Both resemble the problematic late middle Cambrian (Drumian) species Anomalocalyx cawoodi Brock from Australia, whose systematic affiliation is controversial. Together, the three genera are interpreted as representatives of a new family of rhynchonelliformean brachiopods, the Tomteluidae fam. nov., which is interpreted as an aberrant or derived taxon within the Order Naukatida. Convergence between the Tomteluidae and the coralla of small solitary Cambrian coralimorphs, as well as the late Palaeozoic reef-building richthofenioid brachiopods, might indicate adaptation to a similar life habits and environments. However, their small size (length 4 mm), well-developed pedicle and perfect morphological symmetry make it more likely that tomteluvids lived attached to frondose algae or sponges, above the seafloor, in a similar fashion to the acrotretoid brachiopods with which they show a high degree of morphological convergence. Morphological features of the pedicle tube of N. thulensis suggest that the tomteluvid pedicle is homologous to that in modern rhynchonellate brachiopods. This is the first evidence of the pedicle type within the Naukatida and represents the oldest confirmation of a rhynchonellate pedicle.

Key words: Tomteluidae fam. nov., Naukatida, Cambrian, pedicle preservation, convergence, tomography.

The middle Cambrian Stephen Formation in the Canadian Rocky Mountains is best known for including the celebated Burgess Shale (and equivalent deposits) hosting exceptionally preserved soft-bodied fossils within siliciclastic mudstone sediments (Collins et al. 1983; Briggs et al. 1994; Caron et al. 2010, 2014). These fossils are renowned for their exquisite preservation and diversity, but many of them are also notoriously problematic as regards their systematic placement and phylogenetic interpretation. Although some can be interpreted as stem-group representatives of well-established higher taxa (Ramskold and Hou 1991; Smith and Ortega-Hernández 2014), many remain enigmatic despite exquisite levels of preservation (e.g. Siphusauctum, see O’Brien and Caron 2012). Furthermore, certain taxa appear to combine characters of rather different phyla and their systematic placement remains debated (e.g. Echmatocrinus; see Sprinkle and Collins 2011 vs Ausich and Babcock 2000).

Problematic fossils are not confined to just the shale intervals of the Stephen Formation as demonstrated by Tomteluva perturbata gen. et sp. nov. described herein. The new taxon originates from carbonate layers within the formation, and the unusual morphology of its bivalved calcareous shell complicates interpretation. Despite confident interpretation as a brachiopod, systematic placement of T. perturbata within this phylum is not
straightforward. The taxon is characterized by an aberrant morphology that combines brachiopod characters with features reminiscent of coeval stem-cnidarians, such as Cothonion (Jell and Jell 1976; Peel 2011) or Cambroctoconus (Park et al. 2011; Geyer et al. 2014).

In this paper, Tomteluva perturbata is compared with two similar forms and the three taxa are placed together in the new family Tomtelulidae. Anomalocalyx cawoodi was described by Brock (1999) from the middle Cambrian of Australia, and Nasakia thulensis gen. et sp. nov. is described herein from the uppermost lower Cambrian of North Greenland. The geological record of tomtelulids thus extends from the lower Cambrian to the middle Cambrian (Series 2, Stage 4 to Drumian), with a distribution encompassing both Gondwana and Laurentia.

Lower to middle Cambrian rhynchonelliformean brachiopods have a high morphological disparity, resulting in a rather large number of high-rank taxa, all of which accommodate low numbers of genera. These genera belong to the orders Chileida, Obolellida, Kutorginida, Naukatida and Protorthida, all of which are essentially restricted to the lower and middle Cambrian and comprise the oldest known brachiopods with a calcium carbonate shell. Whereas the Protorthida commonly is interpreted as ancestral to sister group to the Orthida and other strophic forms (Williams et al. 1996, 2000a; Carlson 2007), the phylogenetic positions and relationships of the other orders are problematic and currently unresolved. Their resemblance to certain linguliform taxa, that is taxa with an organophosphatic shell, further complicates their interpretation. Indeed, it questions the current classification of brachiopods into three subphyla, a scheme that is largely based on shell mineralogy (Williams et al. 2000b). Similarities of shell morphology and ultrastructure caused Holmer et al. (2009) to propose a close relationship of the organophosphatic Salanygolina Ushatinskaya, 1987 and the Chileida. Similar morphological relationships, but different shell mineralogies, exist between the Linguloida and Obolellida, as well as between the Paterinida and Protorthida.

Elucidation of the interrelationships of the described early and middle Cambrian brachiopod families currently classified into rhynchonelliformean and linguliformean taxa would provide a key to understanding the early phylogeny and diversification of brachiopods during the Cambrian explosion. The possibility of different shell mineralogies within individual brachiopod lineages suggested by Holmer et al. (2009), as well as the discovery of bimineralic shells within the Linguliformea (Balthasar 2007), provides novel possibilities for the interpretation of early brachiopod interrelationships. Such interpretations are also relevant to current efforts in reconstructing the brachiopod stem (Skovsted et al. 2009, 2011; Murdock et al. 2014; Zhang et al. 2014). These typically focus on the organophilic tommotiids, while largely ignoring potential stem-group members with a calcium carbonate shell, e.g. Apistoconcha Conway Morris, 1990 and Aroonia Bengtson, 1990 (both in Bengtson et al. 1990).

In order to shed new light onto early brachiopod phylogeny, additional information is required from well-preserved taxa, particularly rhynchonelliformes, from the early and middle Cambrian. These will clarify the currently poorly resolved interrelationships among the oldest rhynchonelliformean and linguliformean orders. The new genera described herein are referred to the Order Naukatida and contribute to this debate by displaying a previously unreported set of characters, many of which recall yet another linguliformean taxon, the Acrotretida.

**MATERIAL**

The new material studied in the present account originates from two areas of Laurentia, one in British Columbia, Canada, containing Tomteluva perturbata gen. et sp. nov. and one in North Greenland, yielding Nasakia thulensis gen. et sp. nov. (Fig. 1).

The Canadian specimens were collected during two expeditions led by the Royal Ontario Museum (ROM) in 2010 and 2012. They originate from a section located on the south-eastern slope of Odaray Mountain, ca. 10.3 km south-east of Field, British Columbia. Here, a complete, ca. 150-m-thick succession of the basinal expression of the middle Cambrian Stephen Formation (‘thick’ Stephen Formation; Fig. 2A) is exposed along the western side of a roughly south striking gully. The gully follows a NW–SE striking normal fault which, in the area of Odaray Mountain, is associated with the Cathedral escarpment (Fig. 1; Collins et al. 1983). All specimens of Tomteluva perturbata come from two levels within a ca. 0.6-m-thick packstone bed, which appears to be an amalgamation of several slumping events (R. Gaines pers. comm. 2012). The first level is at the base of the bed (sample ROM63412) and the second 0.4 m above (sample ROM63413). The bed occurs ca. 13 m above the base of the formation (51°20’21.1” N, 116°22’23.1” W) and forms the lowest level of a ca. 24-m-thick carbonate unit consisting predominantly of thin-bedded wackestones. It sits atop a 1-m-thick shale interval yielding exceptionally preserved fossils (locality 12 of Collins et al. 1983; ROM ‘ORU’ locality).

The stratigraphic position in the lowest part of the Stephen Formation would suggest a Glossopleura Biozone age for the investigated packstone bed. This is analogous to other sections of the Stephen Formation where the boundary between the Glossopleura and the following Ehmaniella biozones can be found in the lowest part of the formation (Rasetti 1951; Fletcher and Collins 1998).
However, trilobites are known from various levels throughout the Odaray Mountain section, and Rasetti (1951) reported a faunule with *Ehmaniella* and *Soleno-pleurella* near the base of the formation. Additionally, Collins et al. (1983) mentioned specimens of *Olenoides* in the lowest part of the section (confirmed by the most recent ROM field work activities) and *Ehmaniella burgessensis* in the ‘upper part of the section’. Several ptychopariid and corynexochid trilobites, including juveniles of *Kootenia* sp. and *Bathyuriscus adaeus* Walcott, 1916, occur in association with *Tomteluva perturbata*. This suggests an *Ehmaniella* Biozone age for the entire thick Stephen Formation at Odaray Mountain, confirming Rasetti’s conclusion that the base of the Stephen Formation at Odaray Mountain is younger than elsewhere (Rasetti 1951). Besides trilobites, *T. perturbata* is associated with other rhychonelliformean brachiopods (*Diraphora* Bell, 1941 and *Nisusia* Walcott, 1905), linguliformean brachiopods (obolids, acrotretids, cera-
tretids and paterinids), two species of helcionellid molluscs, common bivalved specimens of *Stenothecoides* Resser, 1938, echinoderm ossicles, *Hyolithellus* Billings, 1871, siliceous sponge spicules and rare bradoriid arthropods.

Most specimens of *Nasakia thulensis* gen. et sp. nov. were collected from the Henson Gletscher Formation on a nunatak in southern Freuchen Land, North Greenland (82°09′ N, 42°25′ W; Fig. 1). This is locality 1 of Blaker and Peel (1997, figs 8A, 10) and Geyer and Peel (2011, figs 1D, 2B, 4). The locality is a reference section for the formation described by Ineson and Peel (1997, figs 21, 32, 33) in which three members can be recognized: a lower member of dark carbonates (thickness 27 m); a middle member of unfossiliferous, pale weathering sandstones (78 m); and an upper member of cherty carbonates (about 7 m) from which the specimens of *N. thulensis* were recovered. Samples were collected by John S. Peel and Mark R. Blaker in 1985. GGU samples

**FIG. 1.** Sample localities. A, overview of North America with working areas indicated. B, map of border area between British Columbia and Alberta in the Canadian Rocky Mountains. C, detail of B, with sample locality of *Tomteluva perturbata* gen. et sp. nov. southeast of Odaray Mountain indicated by a star. D, location of the Freuchen Land to Henson Gletscher region in North Greenland. E, detail of D, showing sample localities (stars) of *Nasakia thulensis* gen. et sp. nov. in southern Freuchen Land and adjacent to Henson Gletscher in south-west Peary Land.
298550, 301346 and 301347 were collected about 1 m above the base of the upper member, and GGU sample 301350 about 2 m higher. The specimens are associated with linguliformean brachiopods, helcionellid molluscs, sponge spicules, sclerites of Microdictyon robisoni Bengtson et al., 1986 and Hyolithellus. The upper member yields abundant trilobites of the Ovatoryctocara granulata assemblage, a key association of trilobites in discussions concerning the as yet unresolved placement of the boundary between Cambrian series 2 and 3, and Cambrian stages 4 and 5 (Geyer and Peel 2011). In addition to Ovatoryctocara granulata Chernysheva, 1962, Geyer and Peel (2011) recorded O. yaxiensis Yuan et al., 2009, Protoryctocephalus arcticus Geyer and Peel, 2011, Lancastria cf. plana (Tomashpolskaya in Khalflin 1960), Pagetides elegans Rasetti, 1945, Zacanthopsis blakeri Geyer and Peel, 2011, Bonnia brennus (Walcott, 1916), Onchocephalus freuceni Geyer and Peel, 2011 and Fritzolenellus cf. truemani (Walcott, 1913).

A single specimen of Nasakia thulensis was collected from near the base of the upper member of the Henson Gletscher Formation (GGU sample 218583, collected by Jon R. Ineson in 1979) at the head of Henson Gletscher in south-west Peary Land (82°10'N, 39°40'W; Fig. 1E). The acid residue also contains hyoliths, helcionellid molluscs, chancelloriids, sponge spicules, echinoderm plates, Hyolithellus, Microdictyon and linguliformean brachiopods, while the associated trilobite assemblage includes Fritzolenellus cf. truemani, Pagetides elegans, Bonnia brennus, Kootenia sp. and ptychoparioids (Geyer and Peel 2011).

METHODS

All studied specimens are silicified and have been obtained by the dissolution of the carbonate host rock in 10% formic (Canadian specimens) or 10% acetic acid (Greenland material) and by subsequent picking under a stereoscopic microscope. Selected specimens were mounted on stubs and coated with a gold–palladium alloy and imaged using a field emission scanning electron microscope (Zeiss Supra 35VP) at the Evolutionary Biology Centre, Uppsala University. The Canadian material is deposited in the collections of the Royal Ontario Museum (ROM) in Toronto, Canada. Specimens from Greenland are deposited in the palaeontological collections (PMU) of the Museum of Evolution, Uppsala University, Sweden. Samples with GGU prefix indicate material collected during field campaigns of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), Copenhagen, Denmark.

Two articulated shells of Tomteluva perturbata gen. et sp. nov. (ROM63413.11) and ROM63413.12) were studied using microtomography. The specimens were mounted on florist’s foam and scanned in a Nikon Metris 225-kV X-ray CT system in a customized bay at the Manchester X-Ray Imaging Facility, School of Materials, University of Manchester. All scans were conducted with a tungsten reflection target, and 3142 projections were collected on a 2000×2000 Perkin Elmer 1621-16-bit amorphous silicon flat-panel detector, with no filtration, and a gain of 32. Specimens were scanned at a 50 kV and 200 μA, the reconstructed volumes having 3.4 and 4.9 μm voxels, respectively. One of the two specimens (ROM63413.11) was subsequently mounted on an SEM stub with nail polish and also scanned on the TOMCAT beamline at the Swiss Light Source, Paul Scherrer Institut, Villigen, Switzerland (Stampanoni et al. 2006; Murdock et al. 2012, 2014). Measurements were taken using a 2× objective, with an exposure time of 1 s, energy of 37 keV.
1001 projections over 180°, with a 350-mm sample to detector distance, and a LAG:Ce 100-µm scintillator. To image the entire specimen, four stacked scans were collected, which were reconstructed to create 1.625-µm voxel data sets. These were subsequently manually concatenated using the Fiji software package.

The obtained microtomography data sets were visualized using a range of techniques introduced by Sutton et al. (2014). Data sets were volume-rendered in the open source software Drishti (Limaye 2012) by loading the data from tiff-stacks via the Drishti importer, applying a range of transfer functions in the 2D histogram, modifying colour and transparency settings and adding clipping planes to best demonstrate the gross morphology and microstructure of the fossils. Figures and movies were rendered within the Drishti package.

GENERAL DESCRIPTION OF TOMTELUVIDS

The three species Tomteluva perturbata gen. et sp. nov. (Figs 3–6) from the lower middle Cambrian of Canada, Nasakia thulensis gen. et sp. nov. from the upper lower Cambrian of North Greenland (Figs 7, 8) and Anomalocalyx cawoodi Brock, 1999 from the upper middle Cambrian of Australia are considered to represent a new rhynchonelliformean family, Tomteluvidae fam. nov., based on their unique morphology and a character combination that is unmatched among known brachiopods. Tomteluvid taxa all have a strongly ventribiconvex, astrophic shell with a unisulcate commissure (Figs 3C, 7A), and their high conical ventral valve with an anteriorly curved umbo makes them easily recognizable and distinct (e.g. Figs 3I, L, 7H). The ventral posterior shell slope is convex catacline to procline in lateral profile, long and divided medi ally by an approximately parallel-sided, convex ridge (Figs 3D, M, 7K, M). A circular to irregular hole at the beak constitutes the only potential pedicle opening. This hole forms one end of an internal mineralized tube-like structure which widens dorsally and extends from the beak along the inner posterior valve slope for at least half the height of the ventral valve. A small, longitudinal canal inside the posterior wall of the tube-like structure has been observed in CT data of T. perturbata (Fig. 6F–I). This canal runs dorsoventrally and appears to merge with the tube-like structure close to the beak (Fig. 6E). A similar configuration is preserved in N. thulensis where a phosphatized internal mould of the tube-like structure is present in one specimen (Fig. 7B–C). Here, the distal part of the mould shows a short rod-like extension (Fig. 8I) that is distinctly smaller in diameter than the remainder of the mould. A pair of longitudinal grooves along both posterolateral surfaces of the proximal part of the mould might arise from the fusion of the rod-like extension with the larger tube-like structure (Figs 7C, 8G, J). Thus, the rod-like extension in N. thulensis could be homologous to the small tube-like structure seen in T. perturbata. Brock (1999) described a single U-shaped groove on the anterolateral surface of the tube-like structure of A. cawoodi. How this groove might relate to the smaller tubes observed in T. perturbata and N. thulensis is unclear.

Dorsal valves are only known from T. perturbata and A. cawoodi. In both taxa, the dorsal valve is sulcate and shows paired anteriorly pointing shell thickenings, or plates, on the interior posterior shell margin. Furthermore, a set of catacline plates is present along the posterior margin of T. perturbata, that is a median high plate bordered laterally by lower plates that extend laterally (see also Remarks on genus Anomalocalyx Brock, 1999 emend. below).

No endogenous shell substance of tomteluvid taxa is preserved. Whereas Brock (1999) reported that specimens of A. cawoodi were preserved as epitaxial coatings of epi dote, the shells of T. perturbata and N. thulensis are replaced by silica. This has been confirmed by EDX analyses of the shells, but is also suggested by the acid resistance of the specimens and occasionally observed beekite rings (Fig. 7C). In contrast to N. thulensis, the silicification process in T. perturbata often incorporated clay minerals on the inner and outer surface of the shell (Fig. 5D), shown in the EDX analysis by the presence of aluminium and potassium. Brock (1999) argued that the shell of A. cawoodi was originally made of calcium carbonate because associated taxa with a known calcareous shell, such as rhynchonelliformean brachiopods and molluscs, are preserved in the same way. A similar scenario is evident for T. perturbata and N. thulensis, both of which are associated with similarly preserved shells of rhynchonelliformean brachiopods and helcionellid molluscs (see Method above). Furthermore, the possibility of T. perturbata and N. thulensis having an organophosphatic shell can be excluded as samples yielding the two species also contain linguliformean brachiopods with their original organophosphatic shells present.

HOMOLOGY AND ANALOGY

Assessment of the systematic affinity of the Tomteluvidae requires critical evaluation of the observed features and their potential homology with well-established characters of other crown brachiopods. This applies particularly to the external median ridge, the umbonal opening and interior tube-like structure of the ventral valve, as well as the ridges and plate along the posterior margin and the paired plates on the inner posterior slope of the dorsal valve.
The convex median ridge dividing the ventral external posterior slope of all tomteluvid taxa is bordered laterally by two subtriangular areas separated from the lateral shell surface by a variably distinct flexure. In *T. perturbata* and *A. cawoodi*, the median ridge and the subtriangular area also have an ornamentation that differs from the remainder of the shell, that is they lack the radial ornament of costae. A faint suture dividing the ridge along its entire length has been observed on the crest of the median ridge in *N. thulensis* (Figs 7K, M, 8A–B, D) and in some specimens of *T. perturbata* (e.g. Fig. 3E, M). The ridge is undivided into *A. cawoodi* and the remaining studied specimens of *T. perturbata* (Fig. 3A, D). Concentric ornamentation, as present in *N. thulensis* and *A. cawoodi*, crosses the subtriangular areas and the median ridge, but is interrupted at the median suture, if the latter is present (Fig. 8A–B). Brock (1999) interpreted the ventral posterior slope of *A. cawoodi* as an interarea with a convex pseudo-deltidium in the light of its median ridge. A similar interpretation is likely for *T. perturbata* and *N. thulensis*, but the presence of a median suture in these taxa suggests that their median ridge represents a deltidium (or symphytium) rather than a pseudo-deltidium. The presence of a suture in some, but not all, specimens of *T. perturbata* suggests that the absence of a suture might represent an artefact of preservation resulting from the silicification process, rather than a true character. The preservation of *A. cawoodi* by coatings of epidote might also have obscured delicate structures such as a suture. Hence, it may be reasonable to assume that all tomteluvid taxa originally had a deltidium.

A circular opening at the tip of the ventral valve is another character considered to be characteristic for the new family Tomteluidae despite the incomplete preservation of the ventral umbo of almost all studied specimens. The beak of *T. perturbata*, *N. thulensis* and *A. cawoodi* is typically broken (Figs 3A, C, E, J, 7A, E; Brock 1999, fig. 4B, H, K), suggesting that the observed irregular apical openings might represent holes due to breakage, rather than primary features. However, a few specimens of *T. perturbata* and *N. thulensis* have a beak preserved (Figs 3I, L, 7H, 8F), and all of these show an opening at the tip. Furthermore, the preservation of specimens of *T. perturbata* with conjoined valves indicates that no additional shell opening was present between the valves (Figs 3A, E, 6C); the opening at the ventral beak therefore provides the only possible region from which a pedicle may emerge. Accordingly, these openings are interpreted as pedicle foramina and represent the only shell openings in tomteluvid taxa. The open notothyrium described for *A. cawoodi* by Brock (1999) is here considered to be a preservational artefact (see Remarks on genus *Anomalocalyx* Brock, 1999 emend. below).

The tube-like structure of tomteluvids appears to be unique among brachiopods. Brock (1999) considered the tube of *A. cawoodi* to represent a spondylial platform, by analogy to the configuration described by Grant (1993) for the aberrant richthofenoid * Cyndalia* Grant, 1993. A spondylium forms by the coalescence of anteriorly extending dental plates (Williams et al. 1997a) and is primarily a half tube. In combination with a convex pseudo-deltidium, a spondylium can form a tube-like structure as present in *Cyndalia* and, for example, in many clitambonids such as *Vellamo* Opik, 1930. In the case of tomteluvids, this would mean that their convex deltidium should represent the posterior wall of the tube-like structure. However, microtomography of conjoined specimens of *T. perturbata*, as well as the examination of etched specimens of *N. thulensis* and *T. perturbata*, indicates that the tube-like structure is distinct from the deltidium. Thus, the posterior wall of the tube-like structure is not the deltidium but a separate shell layer (Figs 4I, J, 6E–H, 7G). The same might in fact be true for *A. cawoodi* (see Brock 1999, fig. 4F). Furthermore, the posterior wall of the tube-like structure bears a median longitudinal canal in *T. perturbata* and a homologous structure appears to be present in *N. thulensis*. Such features have not been observed in any spondylium. In contrast, the tube-like structures of *T. perturbata* and *N. thulensis* are supported in the umbonal cavity by symmetrically arranged septa, resembling configurations described as spondylium tripexus (Williams et al. 1997a). Popov and Tikonov (1990) described a structure situated anteriorly to the interarea of the naukatid genus *Oinia* Popov and Tikonov, 1990, as an indicative for initial formation of the posable spondylium.

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**FIG. 3.** *Tomteluva perturbata* gen. et sp. nov., exterior views. A–B, D, conjoined shell, paratype, ROM63413.2; A, posterior view showing dorsal apex and laterally poorly defined ventral interarea divided by convex deltidium; B, dorsal view of dorsal valve with distinct sulcus and multisulcule ornamentalation; D, oblique lateral view showing the transition between smooth interarea and costellate exterior surface of ventral valve. C, F, conjoined shell, paratype, ROM63413.3; C, anterior view illustrating unisulcate anterior commissure with sulcus in dorsal valve but the lack of distinct complementary fold in ventral valve; F, ventral view showing ventral umbo with pedicle foramen and seemingly bilobed outline of ventral valve. E, conjoined shell, holotype, ROM63413.1; incompletely preserved ventral interarea reveals articulation between dorsal and ventral valves by overlap of interareas (see also Fig. 5F). G, juvenile conjoined shell in dorsal view with bilobed outline and multisulcule ornamentalation of dorsal valve, paratype, ROM63412.1. H, L, incomplete ventral valve showing pedicle tube and filled umbonal cavity, paratype, ROM63412.2. I, M, lateral view and posterior view of conjoined juvenile shell, paratype, ROM63412.3; note faint suture on deltidium in M. J, ventral valve with remnants of dorsal valve attached in lateral view, paratype, ROM63413.4. K, lateral view of incomplete ventral valve, paratype, ROM63413.5. Scale bar represents 1 mm.
which they termed the anteris (= anterise of Popov et al. 1997; Bassett et al. 2001). The anteris in *Oina* is an arcuate plate that, according to Popov and Tikonov (1990), bears hinge teeth. *Oina* is further characterized by an elevated visceral platform resembling a spondylium which is situated anteroventrally to the anteris and has been interpreted as a surface for muscle attachment (Bassett et al. 2001). A ventral extension of the anteris, as well as its lateral fusion with the visceral platform, might be able to produce the tube-like structure seen in the Tomteluidae. In fact, such a fusion seems to be realized in the naukatid *Pelmanella* Popov et al., 1997, in which the
*Tomtehuva perturbata* gen. et sp. nov., interior views. A–C, dorsal valve in ventral (A), oblique anterior (B) and oblique lateral view (C) showing paired cardinalia interpreted as muscle platforms and anterior surface of interarea with ventrally elongated chilidium (see also Fig. 5G), paratype, ROM63413.6. D–E, fragmentary dorsal valve with interarea and cardinalia incompletely preserved, paratype, ROM63413.7. F, coarsely recrystallized dorsal valve with cardinalia still discernible, paratype, ROM63413.8. G–H, K, two ventral valves showing ventral interior void of muscle scars or mantle canal patterns and poorly preserved pedicle tube; G, same specimen as in Figure 3J (ROM63413.4); H, K, paratype, ROM63413.9. I–J, L, ventral interiors of umbonal parts of incompletely preserved ventral valves in dorsal view showing pedicle tube along posterior valve slope in various preservation states; note potential canal in posterior wall of pedicle tube in J (arrow); paratypes, ROM63412.2 (same as Fig. 3H, L), ROM63412.4 (J) and ROM63412.5 (L). Scale bar represents 1 mm.
anteris and visceral platform enclose a short anteriorly directed tube (compare Popov et al. 1997, fig. 4P). The homologous nature of the anteris and posterior wall of the tube-like structure could also explain the teeth seen in A. cawoodi. Despite the uncertainties surrounding the tube-like structure of the Tomteluvidae and its origin, the structure’s direct connection to the presumed pedicle foramen makes a function as a pedicle tube appear logical.

The posterior margin of the dorsal valve of T. perturbata is characterized by a pair of transversely elongate catacline ridges that are connected medially by a higher semicircular plate that is also catacline. The posteriorly facing surfaces of the plate and ridges are seemingly free of ornamentation and separated from the ornamented exterior shell surface by a distinct flexure (Fig. 5F–G). Such a configuration resembles the dorsal interareas of many other rhychonelliformean brachiopods, that is an interarea divided medially by a chilidium. Unlike other rhychonelliformean brachiopods, however, the propareas and chilidium of T. perturbata are not visible in conjoined valves. Rather, they overlap with the dorsal margin of the ventral interarea (Figs 3A, E, 5F, 6C), suggesting an articulatory function.

Internally, the dorsal valves of T. perturbata and A. cawoodi are characterized by a pair of small plates emerging from the posterior valve slope (Figs 4B, F, 6I; Brock 1999, fig. 4O). Brock (1999, p. 184) described the plates of A. cawoodi as ‘small, simple, divergent and shallow socket-like plates excavated into the posterior valve wall’, which he suggested accommodated the putative teeth of the ventral valve. Enlarged anteriorly projecting plates have been considered of secondary origin due to multiple epitaxial coatings (Brock 1999). However, it is likely that such plates better reflect the original condition of A. cawoodi. In T. perturbata, the plates project anteriorly to form distinct platforms, the ventral surfaces of which are inclined towards the valve’s midline (Fig. 4B, F). Structures similar in shape and position to the paired plates of T. perturbata and A. cawoodi are known from many rhychonelliformean suprageneric taxa, where they are summarized under the term cardinalia. These enable articulation, provide lophophore support and serve as muscle attachment surfaces (Williams et al. 1997a). As the paired plates in tomteluvids have a position equivalent to the cardinalia of rhychonelliformean brachiopods and serve an equivalent purpose (i.e. presumably for muscle attachment), the term cardinalia is also applied to describe dorsal valves of the Tomteluvidae. However, the use of the same term does not necessarily imply homology of the two structures, in particular as the shape and
FIG. 6. *Tomteluva perturbata* gen. et sp. nov., microtomography of specimen ROM63413.11. A–C, tomographic reconstruction of specimen in anterior and posterior view (A, C), and in longitudinal section (B) showing three partitions of shell interior into pedicle tube (t), umbonal cavity (u) and ‘mantle cavity’ (m); position of tomograms seen in D–L indicated in C. D–L, tomograms of specimen representing cross-sections at different heights of the shell; D–I, hand-coloured to highlight the distinction between shell wall and septa (brown) and preserved parts of the pedicle tube (yellow); D–G, umbonal tomograms showing pedicle tube (t) surrounded anterolaterally by umbonal cavity (u) with radial septa; note the development of thin canal in posterior wall of pedicle tube (arrows) from indistinct depression (D), to distinct groove (E), to being embedded within wall (F–G). H–I, postumbonal tomograms showing sudden increase in shell diameter and absence of septa; posterior wall of pedicle tube still present. J–L, tomograms showing the transition between ventral and dorsal valve; J, unusual thickness of shell posteromedially probably due to the overlap of deltidium and chilidium (compare with Fig. 5F); K, posterior shell wall appears double layered with outer layer representing shell of ventral valve and inner layer interarea of dorsal valve; L, tomogram of dorsal valve showing anteriorly projecting cardinalia (arrows); e, empty space; s, shell; si, blocky silica crystals; p, pyrite crystal. Upper scale bar represents 1 mm (A, C) and 600 μm (B); lower scale bar represents 1 mm (D–L).
the ultrastructure of the tomteluvid cardinalia are not readily comparable to those of other rhychoconelliforms. Cardinalia of the latter are made of secondary shell, a character that currently cannot be demonstrated in the Tomteluvidae due to their recrystallized shells. Nevertheless, based on the equivalent position and function, we consider a homologous origin for both types of cardinalia as likely.

**AFFINITY OF TOMTELUVIDAE**

The Tomteluvidae, with their unique shell morphology exemplified by the characteristic conical, anteriorly curved ventral valve with a typically procline interarea and a sulcate dorsal valve with plate-like cardinalia, are best interpreted as an aberrant or specially adapted taxon within the Naukatoidea. Characters such as an astrophic shell, an apical foramen and a covered delthyrium support this affiliation. The interpretation that the tube-like structure represents the lateral fusion of anteris and visceral platform sustains the naukatid affinity of the Tomteluvidae. The general morphology of tomteluvids is closest to the naukatid family Pelmanellidae with its two genera Pelmanella and Bynguanoia Roberts in Roberts and Jell, 1990. The pelamanellid ventral interior with elevated visceral platform and anteris is probably homologous to the internal tube-like structure of tomteluvids. Furthermore, the dorsal interior of pelmanellids shows paired platforms at the posterior margin which can be interpreted as homologues of the cardinalia seen in *T. perturbata* and *A. cawoodi*.

Tomteluvids are reminiscent of certain kutorginid taxa, such as *Agyrekia* Konova, 1979 or *Nisisia*, which also have a high conical procline ventral valve with an apical foramen. In addition, the catacline ridges (propareas) lateral to the chilidium in the dorsal valve of *T. perturbata* could be interpreted as homologous to the paired plates kutorginids use for articulation. Brock (1999) compared these paired plates with the ‘socket plates’ of *A. cawoodi*. However, the ventral valves of tomteluvids lack the complementing grooves on the ventral valve to accommodate the ridges for articulation. Also, kutorginids have a strophic shell and are characterized by a large posterior opening between the valves (see also discussion by Brock 1999).

The unusual morphology of the tomteluid taxod could also have been derived from another brachiopod order. Brock (1999) compared the morphology of *Anomalocalyx* with late Palaeozoic aberrant strophomenates, that is the richthofenioids. Like tomteluvids, richthofenioids are characterized by a high conical ventral valve and are astrophic. Richthofenioids are derived from a strophic ancestor (Wardlaw et al. 2000), and a similar derived origin might be the case in the tomteluvids. Thus, tomteluvids recall certain clitambonitoid taxa, such as *Vellamo*.

In this genus, a high conical ventral valve with a catacline interarea is characterized by a well-developed deltium which, together with the spondylium, forms a tube-like structure along the posterior valve slope. The deltium and notothyrium are closed, except for an apical pedicle foramen which opens into the tube-like structure. The spondylium is supported by a septum which connects it to the internal anterior valve slope. The dorsal valve has a well-developed chilidium bordered laterally by propareas. Overall, the configuration is very similar to that seen in *T. perturbata*. However, typical clitambonitoids like *Vel-lamo* first occur in the early Ordovician, and it is therefore more likely that naukatids (including tomteluvids) were ancestral to clitambonids rather than the alternative scenario of tomteluvids being aberrant clitambonids. In addition, tomteluvids lack articulation by means of teeth and sockets and their tube-like structure, as discussed above, is not readily comparable to a spondylium.

**ARTICULATION OF TOMTELUVIDAE**

When Popov and Tikonov (1990) introduced the Order Naukatida, they placed it within the Class Articulata, based on the observation of ventral denticles interlocking with dorsal sockets: a configuration they termed protodontic. This type of articulation is essentially only seen in *Oina*, although Popov and Tikonov (1990) also described it for *Naukat Popov and Tikonov, 1990. Popov et al. (1997) described the new genus *Pelmanella* from the lower Cambrian of Greenland which they assigned to the Naukatida. Due to the absence of denticles on the anteris, a new family, the Pelmanellidae, was proposed to also include *Bynguanoia*. Tomteluvids, like pelmanellids, also lack articulation structures such as teeth and sockets, despite their original description in *A. cawoodi* (see Remarks on genus *Anomalocalyx* Brock, 1999 emend. below). Nevertheless, *T. perturbata* displays a type of articulation that might be representative for the whole family. In *T. perturbata*, the dorsal interarea, with its catacline propareas and chilidium, interlocks with the inside of the ventral interarea (Figs 3E, 5F). In combination with a deep unisulcate commissure and the dorsal beak interlocking with the notch in the deltium, this provides a firm articulation between the valves in a closed state. A similar way of interlocking dorsal and ventral valves is common in the Acrotretida (see below).

**TOMTELUVIDS AND CAMBRIAN CORALIMORPHS**

The high, conical ventral valve of the Tomteluvidae with its curved umbo recalls the corallum of coeval solitary
stem-group cnidarians of similar size, such as Treto-
cylichne Engelbretsen, 1993 from the Drumian of Aus-
tralia (Engelbretsen 1993); Cambroctoconus Park et al.,
2011 from the Drumian of China (Park et al. 2011) and
Cambrian Stage 5 of Kyrgyzstan (Geyer et al. 2014);
and in particular, the operculate Cothonion Jell and Jell,
1976 reported from the late early Cambrian of Australia
(Jell and Jell 1976) and North Greenland (Peel 2011).
However, the presence of distinct brachiopod features in
the Tomteluvidae, such as bilateral symmetry, an inter-
area with deltidium and the presence of cardinalia, as
well as the distinct lack of cnidarian characters such as
numerous, symmetrically arranged septae, clearly distin-
guishes them from these early coral-like organisms. The
similarity in overall morphology, however, may indicate
an adaptation to a similar environment and ecospace.
Tomteluvids not only resemble coeval stem-group cor-
als, but ecologically also may be comparable to
younger cnidarians, such as the upper Ordovician coral
Talfania Peel and McDermott, 2014, and many solitary
rugose corals.

During life, coralla of CATHONION, TRETOCYlichne AND
Cambroctoconus were cemented to hard substrates, such as frag-
ments of brachiopods and trilobites, by means of a variably
developed holdfast or attachment disc (Jell and Jell 1976;
Park et al. 2011; Peel 2011). The shapes of their coralla are
not constant within a species or even within individuals
within a sample, but range from straight to bent cones.
Bent early growth stages of these taxa can be explained as
an attempt of the organism to control growth direction, in
response to either an original settlement of the larva on
an inclined or irregular surface or to a postsettlement
movement of the substrate. A reaction to budding from the
outside of the parental corallite may also have promoted
curvature of the juvenile growth stage of Cambroctoconus,
while competition for space with adjacent individuals also
influenced the shape of coralla (Park et al. 2011).

The curved to coiled early growth stages seen in many
 coralla of Talfania described by Peel and McDermott
(2014) resulted from circumferential attachment to cri-
noid stems or disarticulated columnals. However, as with
the Cambrian stem-group corals, the shape of the
individual coralla varied depending on the substrate and
substrate stability, in combination with an inferred prefer-
ence for upward growth as indicated by a component of
translation along the stems (Peel and McDermott 2014).
In contrast, the curvature in rugose corals is commonly
the result of the larva settling on a shelf fragment and an
initial vertical growth. However, with increasing size and
weight, the corallum breaks away from the attachment
and becomes free lying; liberosessile in the terminology of
Neuman (1988). Such free-lying corals may approach
bilateral symmetry, as seen to perfection in the early
Devonian species Calceola sandalina (Linné, 1771) which,
in addition, developed a broad, flattened lower side to the
corallum.

In contrast to these cnidarians, the degree of curvature
and bilateral symmetry of early growth stages of tom tel-
vids appears to be uniform during ontogeny and distinct
for the individual species. A strongly curved umbo is
characteristic for T. perturbata, whereas the curvature in
N. thulensis is moderate and even minor in A. cawoodi.
As the curvature of the umbo also invariably lies within
the plane of symmetry, environmentally induced reasons
for the curvature as seen in Cambrian coralimorphs and
other cnidarians can be excluded. Tomteluvids may have
been attached as juveniles, and then become free lying as
adults, by analogy to liberosessile rugose corals (Neuman
1988) or as is also typical for strophomenate brachiopods.
As a consequence, the foramen in strophomenates
becomes sealed in adult individuals, but sealed foramina
have not been observed in any tomteluvid specimen. Fur-
thermore, the complexity of the tube-like structure of the
tomteluvid ventral valve, interpreted to represent a pedi-
cle tube, suggests that it retained its function in adults.
While the interarea is somewhat flattened in T. perturbata
and A. cawoodi and may have provided a resting surface,
the absence of a flattened interarea in N. thulensis makes
a free-lying life habit unlikely. This interpretation is sup-
ported by the small size (maximum 4 mm) of Tomteluvi-
dae. In contrast, the elaborate pedicle tube strongly
suggests that the pedicle played a pivotal role in the life
habit of Tomteluvidae. Hence, these species were most
likely attached throughout their life, although the strong
curvature of the ventral valve seems to rule out simple
upwards growth from a flat substrate.

**FIG. 7.** Nasakia thulensis gen. et sp. nov., ventral valves. A, D, paratype in oblique anterior and lateral view showing sulcate commis-
sure (PMU28784 from GGU sample 301347). B–C, coarsely silicified valve with preserved phosphatized mould of pedicle tube in ante-
rior and posteralateral view (note beekite rosette with six rings in C) (paratype, PMU28785 from GGU sample 301347). E, I,
incompletely preserved valve showing valve interior with pedicle tube along posterior valve slope supported anteriorly by pair of septa
(paratype, PMU28786 from GGU sample 301350). F–H, K–L, holotype in anterior, oblique dorsal, lateral, posterior and oblique poste-
rior view (PMU28783 from GGU sample 301346); F, note median fold in juvenile shell, which becomes indistinct in the adult growth
stage; G, pedicle tube supported by paired septa; K, interarea divided medially by narrow deltidium; note that concentric growth lines
continue onto ridge, but deflect ventrally and end at suture. J, M–N, paratype, PMU28787 from GGU sample 301347; J, dorsal view
showing septa in umbonal cavity; M, interarea with umbo partly exfoliated exposing internal pedicle tube; N, lateral view showing flex-
ure in concentric fila indicating lateral border of interarea. Scale bar represents 1 mm (A–D, F–H, J–N); 2 mm (E, I).
FIG. 8. *Nasakia thulensis* gen. et sp. nov., close-ups of ventral valves. A, interarea at umbo showing narrow deltidium; note that regular concentric fila deflect ventrally on deltidium; detail of Figure 7K (holotype, PMU28783). B–C, details of interarea of specimen in Figure 7M showing deltidium (B) and exfoliated umbo revealing internal pedicle tube (C); note smooth surface of tube (PMU28787). D, umbonal tip of incompletely silicified specimen in posterior view showing faint median suture (PMU28788 from GGU sample 301350). E–F, details of holotype showing median fold of anterior umbonal surface (E) terminating in apical foramen (F) (PMU28783). G–J, details of internal mould of pedicle tube showing distinct longitudinal groove crossed by faint transverse annulations (G) and fine longitudinal striation (H); I, dorsal tip of internal mould; might be homologous to canal in *Tomteluva perturbata*; J, detail of G showing deflection in annulation when crossing longitudinal groove (PMU28785). K–L, holotype; interior with potential remnants of a shell layer sealing off umbonal cavity (K) and concentric fila near valve margin (L); (PMU28783). All scale bars represent 100 μm.
TOMTELUVIDS AND ACROTRETOID BRACHIOPODS

Many of the features of the new family Tomteluvidae are reminiscent of coeval phosphatic-shelled acrotretoid brachiopods (Acrotretidae and Ceratretidae) rather than other rhynchonelliformean taxa, illustrating the myriad difficulties in unravelling early brachiopod relationships. Similarities include size, valve shape, pedicle opening, configuration of interareas and internal features, as well as the mode of articulation of the valves. The largest recovered tomteluvid measures 4.0 mm in width, that is – in relative terms – rather small for an adult rhynchonelliform brachiopod. In general, nauktids are also small, but may reach widths of up to 8 mm (Popov et al. 1997; Roberts and Jell 1990). Although typical early and middle Cambrian acrotretoids rarely exceed a width of 3 mm (Popov and Holmer 1994; Streng and Holmer 2006), specimens up to 5 mm wide have been described (Rowell 1980), placing tomteluvids and acrotretoids in the same size category.

A ventriciconvex shell with a high, procline to catacline conical ventral valve with an apical pedicle foramen is characteristic for many Cambrian acrotretoids, such as Prototreta Bell, 1938 or Dactylotreta Rowell and Henderson, 1978. An anteriorly curved apex, however, as extreme as that developed in Tomteluva, has not been observed in the acrotretoid brachiopods. Nevertheless, slightly anteriorly curved beaks reminiscent of Anomalocalyx, with a ventrally rather than a commonly posteriorly directed pedicle foramen, have been observed in the late Cambrian acrotretid taxa Tapuritreta reclinata Streng, Mellbin, Landing and Keppie, 2011 and Ottenbyella? sp. B (see Streng et al. 2011), in addition to the middle Cambrian cera-tretid Erbrotreta singularis Holmer and Ushatinskaya, 1994. In terms of ontogeny, an acrotretid from the lower Ordovician of Sweden, described as ’gen. et sp. nov. a’ (Popov and Holmer 1994), is extremely similar to Tomteluva in having a narrow juvenile ventral valve followed by a distinct increase in diameter during adult growth stages.

The pseudointerarea of acrotretoid genera is characterized by subtriangular propareas which are typically separated by either a median furrow, the intertough, or a median ridge, termed the interridge. In acrotretoid taxa bearing an interridge, such as Tapuritreta reclinata, pseudointerareas resemble the interarea of tomteluvids with their ridge-like deltidium, although a median suture has not been observed in any acrotretoid genus. Furthermore, when crossing the interridge, concentric ornamentation commonly deflects dorsally in acrotretoids, indicative of a potential tooth-like extension at the posterior margin (Ushatinskaya 1998; Streng 1999, and references therein). In tomteluvids, concentric fila and growth lamellae invariably bend ventrally at the deltidium, thereby leaving a median notch at the posterior margin.

Like tomteluvids, acrotretoids lack an opening between the valves, that is an apical foramen provides the only possibility for a pedicle to emerge. The external apical foramen is connected to the internal foramen by a pedicle tube, the length of which is dependent on the development of the apical process. Thus, acrotretoid taxa with a strongly elevated apical process, or with processes that occlude the entire apical cavity, have a comparatively long pedicle tube. Acrotretoid taxa in which the apical process occludes the apex, such as Dactylotreta, Prototreta or Vandalotreta (Streng 1999, fig. 12; Streng and Holmer 2006, fig. 7.7), resemble the configuration seen in the umbo of tomteluvids. The similarity becomes even stronger if the presence of a shell layer sealing off the umbonal cavity, as potentially present in N. thulensis (Fig. 8K), can be confirmed for all tomteluvids.

As mentioned above, the general means of articulation in tomteluvids is very similar to that of the Acrotretoidea. As in tomteluvids, many acrotretoids have steep anadine dorsal propareas that overlap with the ventral pseudointerarea. This overlap, in combination with a non-planar commissure, provides the basic articulation of acrotretoid valves. In addition, certain taxa developed a tooth-like extension of the ventral pseudointerarea which interlocks with the median groove of the dorsal valve (e.g. Ushatinskaya 1998; Streng 1999, and references therein; Streng and Holmer 2006). This latter feature contrasts with tomteluvids, where the ventral interarea has a notch which appears to interlock with the dorsal beak (Figs 3A, 6C).

Despite the impressive number of similarities between Tomteluvidae and Acrotretoidea, most of these must be considered as convergent characters due to their comparable size and a potentially similar ecology. Differences in the dorsal and ventral interareas are too substantial to suggest a relationship between the two taxa. These include in particular the presence of a deltidium and chilidium in the Tomteluvidae, for which no direct counterparts exist in the Acrotretoidea. The same applies to the cardinalia seen in the Tomteluvidae – a structure unknown in acrotretoid brachiopods. Differences in the pedicle tube and the inferred pedicle type are also significant. Whereas acrotretoids have a smooth pedicle tube and a presumed simple pedicle representing an extension of the coelomic cavity (Williams et al. 2000b), the preserved internal mould of the tube-like structure of N. thulensis suggests a longitudinally structured, fibrous pedicle similar to that of modern rhynchonelliform brachiopods (see also Pedicle of Tomteluvidae below).

Evidence on the ecology of acrotretoid brachiopods during the Cambrian is scarce. Attachment to fronds of algae-like organisms has been described for an early
Cambrian acrotretoid brachiopod (Wang et al. 2012) and may prove to have been a lifestyle common among members of this order. None of the available tomteluid collections preserve remains of frondose organisms, but their presence in Cambrian ecosystems is well documented. Selections preserve remains of frondose organisms, but their presence in Cambrian ecosystems is well documented. (Wang et al. 2004; Hu 2005), the Burgess Shale (Walcott 1919; Briggs et al. 1994) and Kaili (Yang 2006; Wu et al. 2011). However, there is also evidence that acrotretoids, as well as rhynchonelliformean brachiopods, lived attached to sponges and chancelloroids (see Holmer et al. 2005, and references therein; Bengtson and Collins 2015; Topper et al. 2015). Samples with T. perturbata yielded significant amounts of silicious sponge spicules, and the same is true for samples containing A. cawoodi (Brock 1998a) and N. thulensis. Hence, it is plausible to consider that tomteluid may have been attached to sponges. Evaluation of the attachment strategies observed in the exceptionally preserved brachiopods from the mudrocks of the Stephen Formation suggests that brachiopods had a certain degree of control when selecting a substrate (Topper et al. 2015). The aberrant shape of tomteluid might represent an adaption to a distinct substrate, a substrate the brachiopod larva was able to select. In modern environments, loosely and irregular coiled vermetid and siliquariid gastropods provide a classical example of organisms with an aberrant shape living in association with sponges (e.g. Bieler 2004). Species of the latter group are obligatory sponge commensals living a sessile mode of life, embedded inside a sponge host (Bieler 2004). However, the shape of adult siliquariid shells is highly irregular and not comparable to the regular and symmetrical curved ventral valve of tomteluid. Nevertheless, a similar life strategy seems plausible. Juvenile siliquariid gastropods settle on a sponge and become subsequently passively embedded by the growth of the host (Savazzi 1996). Analogously, the tomteluid larva could settle on a suitable sponge and become at least partly (i.e. the umbonal part) embedded into the tissue of the sponge. This could also explain the commonly missing apical tip of the ventral valves, although taphonomy might explain the absence as well. However, partial embedding can only work if the sponge does not put any constraints on the regular growth of the brachiopod.

While an attachment of tomteluid brachiopods to either algae or sponges is conjectural, it is at the moment the most parsimonious solution to explain the aberrant shape. The curvature and slenderess of their umbo might represent a special adaptation to life attached to the sponge or frondose substrate, or at least a growth form unconstrained by the association. Interpreted in this way, tomteluid provide additional evidence of the establishment of tiering patterns in early to middle Cambrian environments (Wang et al. 2012; Topper et al. 2015).

**PEDICLE OF TOMTELUVIDAE**

Within Brachiopoda, two analogous organs of different origin and structure represent what is generally called the pedicle (Williams et al. 1997b). Thus, a pedicle is either an outgrowth of the posterior body wall and has accordingly a coelomic cavity (lingulate type sensu Williams and Carlson 2007) or a more complex organ of connective and muscular tissues surrounded by a pedicle epithelium and an outer cutinose cuticle (rhynchonellate type sensu Williams and Carlson 2007). Whereas modern linguliformeans and rhynchonelliformeans have a lingulate and a rhynchonellate pedicle, respectively, the phylogenetic distribution of pedicle types among the earliest known brachiopods in the Cambrian is poorly resolved. Lagerstätten-deposits such as Chengjiang or the Burgess Shale occasionally preserve pedicles (Jin et al. 1993; Holmer and Caron 2006) and provide unique insight into pedicle morphology and diversity among the earliest brachiopods. However, while pedicle preservation of taxa assigned to the linguliformean subphylum is more common and all taxa show a lingulate-type pedicle, preservation of pedicles of early rhynchonelliformean taxa is rare or these are difficult to study. Zhang et al. (2007, 2011a, b) described the pedicles of a putative kutorginate, stem-chileate and obolellate from the Chengjiang Lagerstätte. The pedicle of the kutorginate taxon appears to have a coelomic cavity and was consequently interpreted as a lingulate pedicle (Zhang et al. 2007). According to Zhang et al. (2011a, b), the pedicle of the stem-chileate and the obolellate, on the other hand, cannot be considered homologous to the lingulate or rhynchonellate type. Instead, a homology with the attachment pad of craniiformeans and strophomenate brachiopods was suggested (Zhang et al. 2011b). Topper et al. (2015) described specimens of the kutorginate Nisusia and the orthid Diraphora still attached to their substrate, but pedicles appear to be short, and no distinct pedicle features can be observed.

One specimen of Nasakia thulensis is preserved with a phosphatized mould of its pedicle tube (Figs 7B, C, 8G–J). In contrast to silification, phosphatization allows delicate details to be replicated, such as the observed faint transverse annulation and delicate longitudinal striation of the mould, which are otherwise not present on silicified surfaces of the same structure (e.g. Fig. 8C). Based on the interpretation of the tube-like structure of tomteluid as a pedicle tube, it can be assumed that the mould reflects characters of the original pedicle. Whereas the replicated annulations show a similar density and disposition to the concentric fila (and most likely reflect growth increments), the fine striation might be the result of longitudinal arrangement of fibres (muscles?) in the proximal part of the pedicle. The preserved thin rod-like extension is considered to be homologous to the longitudinal canal seen in the posterior wall of...
T. perturbata as both are in the same position and of similar sizes. The function of the rod or canal is enigmatic, but might have been related to operating the pedicle. Longitudinal striations are unknown from pedicle tubes of linguliformean brachiopods and are incompatible with an interpretation as a lingulate pedicle; they might reflect the muscular base of a primitive rhynchonellate pedicle. Consequently, the mould represents the first hard evidence for a rhynchonellate pedicle in naukatid brachiopods as well as the oldest evidence for this pedicle type.

CONCLUSIONS

The new family Tomteluvidae represents a distinct group of early and middle Cambrian rhynchonelliformean brachiopods from Laurentia and eastern Gondwana. Their aberrant morphology, with a high, anteriorly curved ventral valve and an interior pedicle tube, is interpreted to represent a modified and specialized habitus most closely comparable to the naukatid brachiopods. The selective pressure driving the aberrant morphology of these taxa remains enigmatic but is here interpreted as an adaption for the attachment to a substrate that did not impose constraints on shell growth. Suggested substrates are sponges or macroalgae, thereby providing additional support for the hypothesis that secondary tiering was already common among the oldest brachiopods. The aberrant morphology further suggests that brachiopods were already highly specialized in both form and ecology in the Cambrian. Convergence between the morphology of tomteluvids in an equivalent position. The term ‘proparea’, normally used to describe the pseudointerarea of linguliform brachiopods, is also applied to describe the interarea of naukatids following previous identical usage of the term (Popov and Tikonov 1990; Brock 1999). The collective term ‘cardinalia’, which includes various structures in the posteromedian region of dorsal valves (e.g. socket ridges or crural plates), is according to Williams et al. (1997a, p. 366) restricted to ‘toothed brachiopods’. Herein, it is also used to describe the structures of tomteluvids in an equivalent position.

Institutional abbreviations. GGU, Geological Survey of Greenland, Copenhagen, Denmark; PMU, Museum of Evolution, Uppsala University, Sweden; ROM, Royal Ontario Museum, Toronto, Canada.

SYSTEMATIC PALAEONTOLOGY

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The brachiopod classification used below generally follows that of Williams et al. (1996), which was based on the Treatise on Invertebrate Paleontology (Kaesler 2000; Selden 2007). However, Anomalocalyx Brock, 1999 is considered to belong to the Naukatida rather than the Kutorginida as suggested by Popov and Williams (2007). The terminology used in the descriptions is that of Williams et al. (1997a) and Williams and Brunton (1997) with two exceptions. The term ‘proparea’, normally used to describe the pseudointerarea of linguliform brachiopods, is also applied to describe the interarea of naukatids following previous identical usage of the term (Popov and Tikonov 1990; Brock 1999). The collective term ‘cardinalia’, which includes various structures in the posteromedian region of dorsal valves (e.g. socket ridges or crural plates), is according to Williams et al. (1997a, p. 366) restricted to ‘toothed brachiopods’. Herein, it is also used to describe the structures of tomteluvids in an equivalent position.
as diagnostic features for the entire order by Popov and Holmer (2000), has been convincingly demonstrated for only a single monospecific genus, namely Oina. The diagnosis for the order is adjusted herein, providing a more general concept. However, considering the scant knowledge of naukatid genera on the one side and their morphological variability on the other side, it is likely that the order in its present configuration might turn out to be polyphyletic.

The superfamily Naukatoidea is divided into two families, the Naukatidae and Pelmanellidae (Popov et al. 1997), but the characters of the new genera Tomteluva and Nasakia require the erection of a new family, the Tomteluidae fam. nov., also accommodating Anomalocalyx Brock, 1999.

Occurrence. Lower and middle Cambrian of central Asia (Aksarina and Pelman 1978; Popov and Tikonov 1990; ?Holmer et al. 2001), Australia (Roberts and Jell 1990; Brock 1999), North Greenland (Popov et al. 1997; herein), North America (Walcott 1905; Rowell 1977; herein).

Family TOMTELUVIDAE nov.

LSID. urn:lsid:zoobank.org:act:9E6287A7-F291-4110-83FC-62808C43E518

Diagnosis. Strongly ventribiconvex shell with high conical ventral valve whose umbo curves anteriorly; interarea cactyl to procline, convex in lateral profile, with pedicle foramen at the beak. Pedicle foramen connects interiorly to a dorsally widening pedicle tube which extends from the beak along inner posterior valve slope to at least 50% of valve height and is supported anteriorly by septa. Ventral interarea long with narrow deltidium or symphytium (or pseudodeltidium). Dorsal interior with paired anteriorly pointing plate-like cardinalia.

Genera included. Tomteluva gen. nov., Nasakia gen. nov., and Anomalocalyx Brock, 1999.

Remarks. The unusual shape of the ventral valve with an internal pedicle tube, unmatched in any other brachiopod taxon, suggests a close relationship between the three constituent genera and justifies the erection of a new family, the Tomteluidae. The pedicle tube is considered to be homologous to the visceral platform and anteris of other naukatids, representing a lateral fusion of these two structural elements.

Occurrence. Uppermost lower Cambrian (Ovatoryctocara granulata Biozone) to lower middle Cambrian of Laurentia (Ehmaniella Biozone) (herein), reaching into the late middle Cambrian in Australia (P. punctuosus Biozone; Brock 1999).

Genus TOMTELUVA nov.

LSID. urn:lsid:zoobank.org:act:A39E1B8F-2C02-4C24-97DF-E5EFE2C0DF09

Derivation of name. From the Swedish word tomteluva meaning Santa’s hat, reflecting the hat-shaped ventral valve; gender feminine.

Type species. Tomteluva perturbata sp. nov., basal thick Stephen Formation, south-eastern slope of Odaray Mountain, British Columbia, Canada; early middle Cambrian (Ehmaniella Biozone; above ROM locality ‘ORU’).

Diagnosis. Tomteluid with multicostellate ornamentation and unisulcate anterior commissure; ventral valve with strongly anteriorly curved umbo. Ventral interarea smooth with narrow, about parallel-sided convex deltidium. Dorsal interarea catacline with ventrally extending, long chilidium.

Remarks. Tomteluva differs from Anomalocalyx Brock, 1999 in lacking concentric ornament and having finer radial elements. The pedicle tube of Anomalocalyx is characterized by two processes (‘teeth’) and a longitudinal groove, features not observed in Tomteluva. Furthermore, the dorsal valve of Tomteluva has a well-developed orthoclinc interarea with elongated chilidium. Such a configuration is incompatible with the current interpretation of the dorsal interarea of Anomalocalyx, for which an open notothyrium was described (Brock 1999). However, the shells of Tomteluva have been replaced by silica and those of Anomalocalyx are preserved as coatings of epidote, processes that do not provide perfect replication of the original shell (see also Remarks on Anomalocalyx below).

Among other naukatids, Tomteluva is best compared with the lower middle Cambrian (Ordian) Bynguanoia from Australia (Roberts and Jell 1990). Both taxa are multicostellate, ventribiconvex, have a unisulcate anterior commissure and an apical foramen (see also Affinity of Tomteluidae above).

Occurrence. Type locality only.

Tomteluva perturbata sp. nov.

Figures 3–6

LSID. urn:lsid:zoobank.org:act:7E761D84-37FB-4538-9AEE-BECA445A3FB1

Derivation of name. From the Latin perturbatus meaning confusing, an allusion to the resemblance of the species to small cnidarians of the same age.
Material. Specimens of Tomteluva perturbata were found in 2 samples within the amalgamated carbonate bed. Sample ROM63413 yielded most of the specimens with 27 articulated shells, 12 ventral valves and 5 dorsal valves, and at least 16 identifiable larger shell fragments. 6 articulated shells, 6 ventral valves and one dorsal valve were recovered from sample ROM63412.

Type specimens. Holotype: conjoined shell (ROM63413.1; Figs 3E, 5F), sample ROM63413, thick Stephen Formation, ca. 13.4 m above base of formation, southern slope of Odaray Mountain, Cambrian Stage 5, Ehmannella Biocene. Paratypes: five conjoined shells (ROM63413.2, ROM63413.3, ROM63412.3, ROM63413.11 and ROM63413.12), five dorsal valves (ROM63412.2, ROM63413.4, ROM63413.5, ROM63412.4 and ROM63412.5) and six dorsal valves (ROM63412.1, ROM63413.6–9 and ROM63413.10) from the same bed as the holotype.

Diagnosis. As for genus.

Description based on SEM study. Shell strongly ventribiconvex, transversely oval in outline with distinct unisulcate anterior commissure (Fig. 3C), up to 3.8 mm wide with shell width roughly equal to shell height in all measured specimens (n = 14; see Measurements below). Outer shell surface ornamented by fine costae that multiply by intercalation; interareas smooth.

Ventral valve high conical with procline to catacline interarea; interarea convex in lateral view, with curvature most prominent at umbo, that is umbo strongly bent anteriorly (Fig. 3I, L). Anterior valve slope concave at umbo but becomes convex more distally. Lateral slopes variable: slightly concave at umbo and straight, gently convex or concave distally (Fig. 3A, C, E). Interarea distinct, lacks multicoistal ornamentation, poorly defined laterally, but somewhat flattened in relation to remainder of shell surface (Fig. 3D); convex, about parallel-sided deltidium divides interarea medi ally; suture between left and right deltidial plate occasionally visible (Fig. 3M). Ventral margin of interarea with small median notch that accommodates the apex of the dorsal valve when valves are closed (Fig. 4A, D–E). Proximal part ofumbo typically poorly preserved, but better preserved specimens indicate the presence of a small pedicle foramen at beak. No fold developed along anterior slope despite unisulcate commissure. Ventral interior characterized by tube-like structure (pedicle tube) extending dorsally from apex, that is from the pedicle foramen along posterior valve slope to at least around 50% of valve height. Pedicle tube widens dorsally, typically incompletely silicified with anterior facing part of tube missing (Figs 4I–J, 5B). Tube is an autonomous structure which is distinct from posterior shell slope, that is posterior valve slope is not the posteriorly facing wall of the tube. However, posteriorly facing tube wall and posterior valve slope tend to merge proximal to apex but gape distally (Fig. 4I–J). Diameter of pedicle tube increases dorsally, reaching diameters of up to 1 mm. Generally, diameter of tube about half to one-third of respective shell length, leaving an umbonal cavity between tube and anterior and lateral valve slopes. No other internal features, such as muscle scars or mantle canal patterns observed. Interior surface of adult shell smooth (Fig. 4G–H, K).

Dorsal valve convex in lateral profile with strongest convexity near umbo; distinct median sulcus originates close to the beak and becomes broader and deeper anteriorly (Figs 3B–C, G, 4B–C). Interarea catacline, well developed along posterior valve margin consisting of a central, ventrally elongated chilidium which is bordered laterally by a pair of lower, ridge-like propareas (Fig. 5F–G). Transition from smooth interarea to costellate shell surface distinctly marked. Interior of dorsal valve divided into left half and right half by sulcus; two plate-like cardinals emerging from posterior valve slope dorsolaterally to chilidium. Cardin alia extend a short distance anteriorly with their ventral surfaces tilted towards the midline of the valve (Fig. 4A–B, F). Interior shell surface smooth, no signs of mantle canal patterns or muscle scars have been observed.

Measurements. Recovered shells of Tomteluva perturbata range in size from 1.7 to 3.4 mm long (n = 14), 1.9 to 4.0 mm wide (n = 15) and 2.0 to 3.9 mm high (n = 11), with maximum width at around midlength. Height/width ratio ranges from 0.85 to 1.19 (mean = 1.00, n = 11); length/width ratio varies from 0.76 to 0.94 (mean = 0.86, n = 14).

Microtomography. Two conjoined shells of T. perturbata were analysed using laboratory and synchrotron microtomography. The inside of both specimens is filled with blocky silica crystals as well as empty space (Fig. 6L); the latter was probably occupied by micrite that was dissolved during acid preparation of the sample. The tripartite division of the ventral interior into umbonal pedicle tube, umbonal cavity and supposed mantle cavity (Fig. 6B) matches SEM observations. The pedicle tube itself is incompletely replaced by silica except for its posterior wall, but is recognizable in the tomograms as empty space that is distinct from the silica crystal infilling of the umbonal cavity (Fig. 6B, E, I). The pedicle tube extends from the apex for about two-thirds of the valve height. The tube’s posterior wall is in contact with the shell of the interarea proximal to the apex (Fig. 6D–E; see also Fig. 5B) but becomes detached from it distally (Fig. 6G–I; see also Fig. 4I–J). Within the posterior wall of the tube, a small canal runs from the umbo dorsally, parallel to the suture of the deltidium. Near the umbo, the canal appears to merge with the tube-like structure, whereas the dorsal end of the canal seems to be an opening in the brim of the tube-like structure (compare Fig. 4J). The canal is transversely oval in outline and has a width of about 150 μm throughout its length.

The umbonal cavity contains several vertical septa which most likely supported the pedicle tube, although contacts between septa and the tube are not preserved. The tomograms show a pair of left and a pair of right lateral septa and a medium septum. Whereas the lateral septa are distinct throughout the umbo (Fig. 6D–G), the median septum is only visible where the umbo is narrowest (Fig. 6D–E). The angle between the median septum and the inner lateral septa is about 35° (Fig. 6E). Other features observed in the tomograms match the description of the specimens above, such as the overlap of dorsal and ventral interareas (Fig. 6K), a long chilidium (Fig. 6F), the plate-like cardinals (arrows in Fig. 6L) and a median suture between left and right deltidial plates.
Remarks. Definite septa in the umbonal cavity supporting the tube-like structure have been observed in only one specimen, namely one of the specimens studied by microtomography (Fig. 6). In the majority of the recovered ventral valves, the umbonal cavity is filled by blocky silica crystals and/or other minerals preventing the possible observation of septa (Fig. 4f, l). One specimen (Fig. 4l) shows remnants of probable septa in the form of ridges on the anterior wall of the tube displaying an equivalent configuration as that seen in the tomograms: a pair of lateral septa and a medium septum are preserved. As N. thulensis bears analogous septa (Fig. 7g, i–j), support of the pedicle tube by a series of septa might represent a novel feature of the Tomteluvida, although septa are not identified in A. cawoodi.

Genus NASAKIA nov.

LSID. urn:lsid:zoobank.org:act:D1EAFEB6-148E-49A1-B809-56F039AD21ED

Derivation of name. After the Greenlandic word nasak (or nasaq), meaning hat; gender feminine.

Type species. Nasakia thulensis sp. nov.; late early Cambrian (Ovatoryctocara granulata Biozone), upper member of the Henson Gletscher Formation, North Greenland.

Diagnosis. Tomteluid with smooth exterior shell surface lacking radial ornamentation; only ornamentation consists of fine, regularly spaced concentric fila. Shell transversely oval in outline with unisulcate anterior commissure. Ventral valve with long, slender, anteriorly curved umbo, typically longitudinally compressed. Ventral interarea procline with narrow deltidium.

Remarks. Nasakia differs from Tomteluva in lacking radial ornamentation and by having a more slender, less curved and compressed ventral umbo. The ventral interarea in Tomteluva is flattened and laterally more distinctly defined, in comparison with the transversely convex interarea in Nasakia (Fig. 7j). A fold present in juvenile growth stages of Nasakia is not observed in ventral valves of Tomteluva. Nasakia is delimited from Anomalocalyx by its lack of any type of radial ornamentation and its more regular concentric ornamentation. Tooth-like processes as seen on the tube-like structure of Anomalocalyx are not known from Nasakia.

Occurrence. Late early Cambrian (Ovatoryctocara granulata Biozone), upper member of the Henson Gletscher Formation, southern Freuchen Land and south-west Peary Land, North Greenland.

Nasakia thulensis sp. nov.

Figures 7, 8

LSID. urn:lsid:zoobank.org:act:EE90035A-7C0C-46F1-8EEC-FBE510CE499D

Derivation of name. After Ultima Thule, a remote northern place beyond the known world.

Material. 21 ventral valves from 4 samples from the upper member of the Henson Gletscher Formation of southern Freuchen Land (GGU samples 298550, 301346, 301347 and 301350). One ventral valve (GGU sample 218583) from the same unit in south-west Peary Land. No dorsal valves known.

Type specimens. Holotype: ventral valve (PMU28783; Figs 7f–h, k, l, 8a, e–f, k, l), GGU sample 301346, Henson Gletscher Formation, collected about 1 m above the base of the upper member, southern Freuchen Land, North Greenland, late early Cambrian, Ovatoryctocara granulata Biozone. Paratypes: five ventral valves (PMU28784–PMU28788) from the same locality as the holotype.

Description. As for genus.
phatized internal mould of pedicle tube shows faint transverse annulations and longitudinal striations (Fig. 8G–H, J) in addition to a pair of distinct longitudinal grooves on postero-lateral surfaces (Figs 7C, 8G, J); annulations deflected across grooves. Diameter of mould increases dorsally measuring 160 µm at its narrowest and 253 µm at its widest preserved part; dorsal end of mould with thin rod-like extension, 100 µm in diameter, also showing faint longitudinal striation (Fig. 8I). Beak with external foramen well preserved in only one specimen displaying circular pedicle opening of about 105 µm in diameter (Fig. 8F).

**Measurements.** No complete valve of *N. thulensis* is preserved preventing the measurement of shell dimensions and calculation of proportions. The largest recovered shells measure up to 1.95 mm from beak to posterior margin (Fig. 7H) and up to 1.83 mm in width (Fig. 7B).

**Remarks.** The median fold only present in the umbonal part of *N. thulensis* might be unrelated to the unisulcate suture. As the umbo appears longitudinally compressed, the fold might simply be a reaction to the presence of the internal pedicle tube.

The presence of a potential valve floor with mantle canal patterns sealing of the umbonal cavity is reminiscent of the configuration of certain acrotretid genera, such as *Dactylotreta* or *Prototreta* (see Tomteluidas and acrotretoid brachiopods, above), in which the apical process fills the apex only being penetrated by the pedicle tube. The existence of an equivalent valve floor in *T. perturbata* is likely. Although such a valve floor is not preserved in any specimen, the virtual reconstruction of specimen ROM63413.11 suggests the original presence of a shell layer between umbonal cavity and dorsal remainder of shell. The blocky silica crystals filling the interior of the shell leave a distinct gap in a position where such a layer should have been present (Fig. 6B).

**Occurrence.** As for genus.

Genus **ANOMALOCALYX** Brock, 1999 emend.

**Type species.** Anomalocalyx cawoodi Brock, 1999 by original designation; late middle Cambrian (*P. punctuosus* Biozone); unit 1 of Murrawong Creek Formation, north-eastern New South Wales, Australia.

**Species included.** Type species only.

**Emended diagnosis.** Coarsely costellate tomkeluid with presumably unisulcate anterior commissure; umbo of ventral valve slightly curved anteriorly. Ventral interarea catacline to steeply procline, variably defined laterally, divided by parallel-sided median ridge (?pseudodeltidium). Tooth-like processes on distal end of pedicle tube.

**Remarks.** Unit 1 of the Murrawong Creek Formation, the type level of *Anomalocalyx*, is a ca. 85-m-thick polymictic paraconglomerate in the lower part of the formation (Cawood 1980; Leitch and Cawood 1987; Brock 1999). Among the components of the conglomerate are fossiliferous limestone boulders yielding a rich fauna of trilobites, brachiopods and molluscs among others (Sloan 1991; Engelbretsen 1993, 1996; Brock 1998a, b; Sloan and Laurie 2004), as well as *Anomalocalyx*. Initial trilobite studies indicated that the conglomerate contains blocks of different age ranging from the *Acidius atavus* to *Lejopyge laevigata* biozones (Sloan 1991 *fide* Brock 1998a), an interpretation that was later revised and rendered more precisely to an interval spanning the *Psychagnostus punctuosus* to *Lejopyge laevigata* biozones (Sloan and Laurie 2004). Brock (1998a, b) stated that the boulders he studied for molluscs and brachiopods were void of faunal elements indicating the *L. laevigata* Biozone and suggested an age range of *A. atavus* to *P. punctuosus* for the studied fauna following initial age determinations by Sloan (1991). As *Anomalocalyx* is from the same boulders as these mollusc and brachiopod faunas (Brock 1999), and considering the age revision by Sloan and Laurie (2004), *Anomalocalyx* probably is of late middle Cambrian age (Drumian, *P. punctuosus* Biozone), representing the youngest tomkeluid currently known.

*Anomalocalyx* is distinguished from *Tomteluva* and *Nasakia* by its coarse, typically ramicostellate ornamentation and its less coiled umbo. Furthermore, Brock (1999) described the presence of paired teeth in almost all ventral valves of *Anomalocalyx* and an open notothyrium in the dorsal valves. No teeth have been observed in any ventral valve of *Tomteluva* or *Nasakia*. The only illustrated specimen of *Anomalocalyx* with such teeth clearly visible is the holotype of *Anomalocalyx cawoodi* (Brock 1999, fig. 4A, E), an incompletely preserved ventral valve with a large part of the distal shell missing (comparable in preservation with *N. thulensis* and some specimens of *T. perturbata*, e.g. Fig. 3H). The same appears to be true for the figured paratypes. Hence, the observed teeth might not have been associated with the shell margin and used for articulation but are situated in the valve interior where they are either constitute a part of the pedicle tube or represent platforms for muscle attachment.

Brock (1999) described the delthyrium of *Anomalocalyx* as narrow and covered for its entire length by a convex pseudodeltidium, a configuration generally equivalent to *Tomteluva*. However, within the dorsal valve, he described a wide open notothyrium unlike the configuration in *Tomteluva* where an elongated chilidium extends ventrally
from the apex. Dorsal valves of *Anomalocalyx* are poorly preserved, and it is likely that the described open notothyrium is a preservational artefact.

From the same sample yielding *A. cawoodi*, Brock (1998a, p. 616, fig. 8.1–8.3) briefly described a single dorsal valve under open nomenclature. This dorsal valve is more completely preserved than those assigned to *A. cawoodi* and shows matching features with dorsal valves of *Anomalocalyx* and *Tomteluva*, that is a sulcate valve ornamented by coarse costae that multiply by intercalation, and more importantly, internally with an anteriorly directed plate originating from the posterior valve slope (‘socket plate’ of Brock 1998a). No notothyrium appears to be present in this valve, but an irregularly silicified medially situated shell thickening occurs on the posterior shell margin (‘cardinal process’ of Brock 1998a). We interpret the single ‘socket plate’ preserved in this specimen to be homologous to the left process of the paired cardinalia (the right one is not preserved) and the ‘cardinal process’ as a potential chilidium, thus resembling the configuration of the dorsal valve of *T. perturbata*. It would be tempting to synonymize the single valve with *A. cawoodi*, but external ornamentation is coarser and sulcation stronger in *A. cawoodi* (G. A. Brock, pers. comm. 2015). It is likely that the single valve represents a nauktid taxon close to the tomteluidvs (see also Brock 1998a).

**Occurrence.** Type locality only.

*Anomalocalyx cawoodi* Brock, 1999

*1999 Anomalocalyx cawoodi* Brock, p. 184, fig. 4A–P. 2007 *Anomalocalyx cawoodi* Brock, 1999; Popov and Williams, fig. 1720.

**Diagnosis.** As for genus.

**Remarks.** For the description of *A. cawoodi*, see Brock (1999) qualified by Remarks on *Anomalocalyx* above. New material of *A. cawoodi* is needed to resolve the nature of the paired ‘teeth’ in the ventral valve.

**Occurrence.** As for genus.

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**DATA ARCHIVING STATEMENT**

Additional data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.rd247

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