**New early Cambrian sclerites of *Lapworthella schodakensis* from North-East Greenland:
advancements in the knowledge of lapworthellid taxonomy, sclerite growth and
scleritome organization**

Short title– Early Cambrian lapworthellid from Greenland

Original Article

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Abstract– The Cambrian Stage 4 upper Bastion Formation of Albert Heim Bjerge and CH Ostenfeld Nunatak, North-East Greenland, yielded 34 excellently preserved sclerites of *Lapworthella schodackensis* among other Small Shelly Fossils. Lapworthellids have been interpreted as members of the camenellans, a basal tommotiid group. Little is known about this group although the morphological and ultrastructural features of their sclerites allow a potential reconstruction of a lophophorate body plan. The exquisite material from Greenland provides significant new data for the revision of the species taxonomy but also for the comprehension of the scleritome structure of lapworthellids and the mode of formation of their sclerites. Two morphotypes of *L. schodackensis* sclerites are identified: one with simple apex, occurring in sinistral and dextral forms and one bilaterally symmetrical sclerite with two apices. All bear a similar ornamentation constructed of repeated growth sets consisting of a reticulate inter-rib groove with tubercles, a densely denticulate rib and a striated sub-rib area. The new data on the ornamentation and observations of the laminar shell microstructure of *L. schodackensis* enable us to propose a refined hypothetical reconstruction of the shell formation and to improve the reconstruction of growth in lapworthellids. Finally, the morphological features of the two types of sclerites provide new information for the reconstruction of the bilaterally symmetrical multi-component lapworthellid scleritome with evidence of the fusion of adjacent sclerites during early ontogeny.

Key words: Lapworthellid, tommotiid, sclerite, scleritome, Cambrian, Laurentia, Greenland.

1. Introduction

The first half of the Cambrian period witnessed the emergence and rapid diversification of biomineralizing metazoans (Bengtson, 2004). Many of the earliest skeletal fossils are found as problematic spines, shells or sclerites among the so called Small Shelly Fossils (SSF), which are commonly retrieved from acid resistant residues of marine limestone samples. Although some SSF's remain problematic in terms of their function and biological affinity, it has been discovered that others represent stem group members of different modern lineages, including molluscs (Vinther, 2009), lobopods (Liu *et al.* 2011; Caron *et al.* 2013) and chaetognaths (Szaniawski, 1982, 2002).

Tommotiids are among the most common and conspicuous SSF's (Matthews & Missarzhevsky, 1975; Bengtson *et al.* 1990). Their organophosphatic, cone-shaped sclerites with distinct co-marginal growth are found throughout the first half of the Cambrian Period and on all Cambrian paleocontinents. Recently, tommotiids have been extensively studied and discussed as potential members of the stem group of the phyla Brachiopoda and Phoronida (Williams & Holmer, 2002; Skovsted *et al.* 2011, 2014, 2015; Balthasar *et al.* 2009; Murdock *et al.* 2012, 2014; Kouchinsky *et al.* 2010, 2015; Devaere *et al.* 2014, 2015 and references therein). The phosphatic sclerites and rare partially articulated specimens of tommotiids preserve both morphological and ultrastructural features that allow a potential reconstruction of the lophophorate body plan evolution (Skovsted *et al.* 2011, 2014). In particular, the so called eccentrothecimorph tommotiids show great similarities to paterinid brachiopods and other members of the earliest known brachiopod communities (Balthasar *et al.* 2009 Larsson *et al.* 2014). However, a large remaining problem is our very poor understanding of the function and morphology of the camenellans, a large group of tommotiids hitherto considered as basal members of the phoronid-brachiopod total group (Skovsted *et al.* 2009).

The eccentrothecimorph tommotiids are, based on articulated specimens, known to have a tube-shaped scleritome structure where the tube is constructed by multiple ring shaped units formed by several sclerites (Skovsted *et al.* 2011, 2014; Holmer *et al.* 2008; Larsson *et al.* 2014). The scleritome structure of camenellans is not known from articulated material but has generally been assumed to be radically different from its eccentrothecimorph counterpart and almost all proposed reconstructions are based on a slug-like animal with an imbricated array of dorsal sclerites (Bengtson, 1970, 1977; Evans & Rowell, 1990; McMenamin, 1992; Demidenko, 2004; Skovsted *et al.* 2009, 2015). To a large degree the current uncertainties concerning camenellans and their relationships to other tommotiids is a consequence of our lack of understanding of the lapworthellids – the largest and most diverse group of tommotiids. Lapworthellids are among the first tommotiids to occur in the fossil record and have the longest stratigraphical range (Maloof *et al.* 2010; Kouchinsky *et al.* 2012). Their sclerites are often simple cones with distinct co-marginal ribs and are highly variable in shape, dimensions and ornament. The sclerites may or may not bear internal septa. Unlike most other camenellans where the sclerites occur in two or three recurrent sclerite types, no fixed sclerite types have been identified in lapworthellids. Here we describe sclerites of *Lapworthella shodackensis* (Lochman, 1956) from the Bastion Formation of North-East Greenland. The recovered sclerites are few, but the excellent preservation allows us to revise both the lapworthellid scleritome structure and the mode of formation of *Lapworthella* sclerites.

2. Geological Setting

The lower Cambrian Bastion Formation is part of a late Proterozoic to Ordovician sedimentary sequence cropping out in the Caledonian region of North-East Greenland (Stouge *et al.* 2001). The clastic dominated Bastion Formation contains mainly sand- and siltstones in

the lower part and dark shales with minor limestone layers and nodules in the upper part (Cowie & Adams, 1957). Based on well preserved olenellid trilobites in the upper Bastion Formation, the age of this unit is likely within Cambrian Stage 4 and a similar age is likely for the overlying carbonate dominated Ella Island Formation (Stouge *et al.* 2001; Skovsted, 2006; Stein, 2008). In addition to trilobites, the upper Bastion Formation of Albert Heim Bjerge and CH Ostenfeld Nunatak has yielded a rich shelly fauna including brachiopods (Skovsted & Holmer, 2003, 2005), hyoliths (Malinky & Skovsted, 2004), molluscs (Skovsted, 2004) and diverse Small Shelly Fossils including the lapworthellid specimens described herein (Skovsted, 2006). The stratigraphical succession of the upper Bastion Formation and the geographical location of the Albert Heim Bjerge and CH Ostenfeld Nunatak sections were summarized by Skovsted (2006).

3. Materials and Methods

Available material of *Lapworthella* from the Bastion Formation of North-East Greenland is limited to 34 more or less complete sclerites and numerous shell fragments. The specimens come from acid resistant residues of limestone samples digested in buffered 10% acetic acid at the Geological Museum in Copenhagen and Uppsala University. Selected specimens were coated by gold-palladium alloy and studied using Scanning Electron Microscope at Uppsala University and the Swedish Museum of Natural History in Stockholm. Lapworthellid specimens were recovered from GGU samples 314809, 314837 and 314838 of the Albert Heim Bjerge region and GGU samples 314901, 314902, 314904, 314908, 314910, 314931, and 314933 of CH Ostenfeld Nunatak (Skovsted, 2006). However, the majority of complete

sclerites (N=25) were found in a single sample, GGU sample 314837 from Albert Heim Bjerge.

Illustrated specimens of *Lapworthella shodackensis* are deposited in the collections of the Geological Museum of Copenhagen (MGUH) and the Swedish Museum of Natural History in Stockholm (SMNH).

4. Systematic palaeontology

Phylum uncertain

Class uncertain

Order TOMMOTIIDA Missarzhevsky, 1970 emend. Matthews, 1973

Family LAPWORTHELLIDAE Missarzhevsky in Rozanov & Missarzhevsky 1966 emend.

Landing 1984

Genus *Lapworthella* Cobbold, 1921

Lapworthella schodackensis (Lochman, 1956)

Figures 1–4

1956 *Stenothecopsis schodakensis* Lochman, p. 1394-1395, pl. 4, figs. 1-2.

?1962 *Stenothecopsis schodakensis* Lochman – Fisher, p. W138, fig. 83.

- ?1966 *Lapworthella* ex. gr. *schodaka* – Rozanov & Missarzhevsky, p. 92, pl. XIII, fig. 3.
- ?1969 *Lapworthella dentata* Missarzhevsky – Rozanov *et al.*, p. 164, pl. VI, figs. 9, 14, 19.
- ?1975 *Lapworthella dentata* Missarzhevsky – Matthews & Missarzhevsky, pl. 3, fig. 12.
- ?1983 *Lapworthella dentata* Missarzhevsky – Bengtson, fig. 6.
- ?1984 *Lapworthella schodakensis* (Lochman) – Landing, p. 1395, figs. 2a–o, 3d, 5a–e
- ?1996 *Lapworthella schodakensis* (Lochman) – Landing & Bartowski, fig. 9.18-19.
- 2006 *Lapworthella schodakensis* (Lochman) – Skovsted, p. 1103, fig. 10.14-10.17.
- 2007 *Lapworthella schodakensis* (Lochman) – Skovsted & Peel, p. 742-743, fig. 6G.
- 2010 *Lapworthella schodakensis* (Lochman) – Rozanov *et al.*, p. 88, pl. 58, figs. 1-7.

Emended diagnosis. The sclerites are completely hollow and exhibit at least two morphotypes. The most numerous morphotype (B) is elongated, asymmetrically pyramidal with a single apex. Its cross section is subquadrangular due to the organization of the sclerite into four surfaces or fields: (1) a narrow, planar field perpendicular (with marked angular ridges) to (2) a planar to slightly concave broad field and to (3) a convex broad field and opposite to (4) a narrow, convex field. The rarest morphotype (A) is elongated, subsymmetrically conical to pyramidal with two apices. The external ornamentation of both morphotypes consists of co-marginal grow-sets constituted of densely denticulate (>25 denticles/mm) commarginal ribs, apertural sub-rib slopes with fine transverse striations parallel to the rib and apical inter-rib grooves covered with a polygonal network variably associated with tubercles.

Remarks. The specimens described in this study are assigned to *Lapworthella schodackensis* because they exhibit densely denticulate (>25 denticles/mm) comarginal ribs, a character that is considered diagnostic of the species by Landing (1984) and Landing *et al.* (2008). However, the diagnosis of the species is emended due to new observations on the ornamentation that are based on the present study and illustrations of specimens assigned to *L. schodackensis* by Rozanov *et al.* (2010). The newly observed polygons sometimes associated with tubercles in the apical inter-rib groove are restricted to and therefore diagnostic of this species of *Lapworthella*. We note that previous descriptions of lapworthellids have not reported morphologically distinct sclerite morphs and most researchers have emphasized continuous variation of a single sclerite type for *Lapworthella*. We define the bilaterally symmetrical sclerites in our collection with twinned apices as a specific sclerite morph. The sclerites described by Landing (1984), Landing & Bartowski (1996) and Landing *et al.* (2008) as *L. schodackensis* exhibit variable cross sections with the smallest specimens having a circular cross-section. Those differences may be related to the size (and therefore growth stage, as suggested by Lochman in 1956) as the sclerites from Greenland are larger than those described by Landing (1984). In any case, the lack of data on the inter-rib groove ornamentation prevents definite synonymization with the specimens presented herein and therefore the inclusion of the variability of sclerite cross section in the emended diagnosis of *L. schodackensis*.

The morphological terms used to describe *L. schodackensis* follow the terminology introduced by Skovsted *et al.* (2015) for *Dailyatia* Bischoff, 1976 when applicable.

Description. The completely hollow sclerites exhibit two morphotypes that will be differentiated hereafter. In both morphotypes, the sclerite walls are variable in thickness depending on the specimen and location, ranging from 20 to 60 μm (Figs. 1a-e, g, i). Composition is phosphatic and the microstructure is finely laminar (Figs. 1b-c, e-g, i) when not completely recrystallized. The outermost and innermost shell laminae are thickest (Figs. 1b-c).

[Fig. 1 should be placed approximately here]

Two specimens amongst the 34 recovered exhibit two smooth, conical apices (Figs. 2a-c, e-l). These are referred to as sclerite morphotype A. They form subsymmetrical pyramidal sclerites, the axis of symmetry passing between the two apices (Figs. 2a, h, j, k), with an elongation parallel to the axis of symmetry (Fig. 2h). The apices are coiled toward the lateral extremities of a slightly planar to concave surface or field (Figs. 2f, h, i, l), the other fields being slightly convex (Figs. 2a, e, f, h-l). Breakage of the apertural margin of the two specimens prevents determination of the accurate dimensions of the sclerites (Figs. 2a, e, h, i-l) but the cross section can be estimated as ovoid with a truncated extremity corresponding to the planar to concave field through the observation of the shape of the distalmost preserved growth set (Fig. 2h).

[Fig. 2 should be placed approximately here]

The second and most common sclerite type, noted B, (32 specimens out of 34) has a single apex and an asymmetrical, elongated pyramidal shape (Figs. 3a-c, e-f, h-j, Figs. 4a-b, d, g, j-l). The height (maximal distance between the apertural margin and the apex) ranges from 660 μm to 2.23 mm (mean height is 1.5 mm); the width (maximal distance between the two broadest fields of the sclerite) ranges from 265 μm to 840 μm (mean width is 500 μm); and the length (maximal distance between the two narrowest fields of the sclerite) ranges from

610 μm to 2.10 mm (mean length is 1.27 mm). The apical angle, measured on the broadest field, varies between ca. 30° (Fig. 4g) and 75° (Fig. 4l). The apex is a simple smooth cone with circular to oval cross-section (Figs. 1f, i, 3c, e, f, i, 4g, j, L). The apertural cross-section is subquadrangular (Figs. 3a, e, j, 4a, d, o-p). The subquadrangular shape of the cross-section results from the presence of roughly four surfaces or fields of the sclerites organized into a pair of opposite, rather broad fields and a pair of opposite, rather narrow fields. Paired opposite fields are dissimilar and angles between the fields variable, which contribute to the asymmetry of the sclerites. One of the narrow fields is almost planar, corresponding to a rectilinear portion of the apertural margin (np on Figs. 3e and 4p) while the other is convex, corresponding to a curved portion of the apertural margin (nc on Figs. 3e and 4p). The transition between the narrow, planar field and neighboring broad fields is abrupt, almost orthogonal, with a marked angular ridge (Fig. 4j) while the transition between the other, narrow, convex field with the broad fields is more transitional, without any angle (Fig. 4k), which gives a curved shape to the corresponding portion of the apertural cross-section (Figs. 3e, 4o-p). One of the broad fields is convex (bc on Figs. 3e and 4p) while the other is planar to slightly concave (bp on Figs. 3e and 4p). The apertural margin is undulating in lateral view due to differences in growth rates (Figs. 3b, c, h-i, 4b, g, l). The apertural margins of the two broad fields are arched apically and the two narrow fields are consequently longer in comparison with the medial part of the broad fields (Figs. 3b, i, h, 4b, g, l). The sclerites are asymmetrically curved, from few degrees (Fig. 4l) for the smallest sclerites up to 70° (Figs. 3i) and invariably coiled toward the planar narrow field of the sclerite which is either located on one side of the sclerite (Figs. 3a, j, 4d) or the other (Figs. 3e, 4a). Variations in the position of the narrow, planar field either on one side of the sclerite or the opposite (relative to the broad planar and concave field) and the direction of the coiling toward the narrow, planar field allow differentiation of sinistral and dextral sclerites. Of the 32 sclerites of this

morphotype, it was possible to identify the orientation in 16 sclerites of which 9 are sinistral and 7 dextral. Some specimens exhibit roughly polygonal imprints organized into a reticulate pattern on the internal surface of the sclerite (Figs. 1h, 3g). The internal cavity is otherwise not subdivided by any structure (Figs. 3e, 4o, p).

[Figs. 3 and 4 should be placed approximately here]

Although slightly variable, depending on preservation and/or intraspecific variability, both sclerite morphotypes are ornamented externally according to the same general pattern. The ornamentation consists of 8 to 29 coarse annulations parallel to the apertural margin that have been referred to as co-marginal growth sets (cf. Skovsted *et al.* 2015). Each co-marginal growth set is constituted of three zones characterized by different ornamentations (defined in Fig. 5a and reported in Fig. 4c, partly using the terminology introduced for *Dailyatia* by Skovsted *et al.* 2015 when applicable): (1) the rib, located in the medial part of the co-marginal growth set and noted s; (2) the apertural sub-rib zone, located on the apertural slope of the rib and noted a and; (3) the apical inter-rib groove, located apically of the rib crest and noted g. The ribs, varying in density between 5.6 and 28.8/mm, are transverse, undulating parallel to the apertural margin and they bear apically directed denticles with a density ranging from 25 denticles/mm to 77 denticles/mm. The denticles vary in size and shape, from rounded (Figs. 2d, 3d, l) to pointed (Figs. 4c, e, m-n). Fine transverse striations parallel to the rib are present at the apertural sub-rib slope (Figs. 2d, 3d, l, 4c, e, h, m, n) which is inclined at 5 to 47° to growth axis. The surface of the apical inter-rib groove is generally covered with a polygonal network (Figs. 2d, 3d, l, 4c, e, h, i, m-n), the polygons constituted of small walls surrounding depressions with an average diameter of 11.3 µm (Fig. 4i). The inter-rib groove is separated from the apertural sub-rib zone of the preceding growth set by a narrow, depressed, smooth furrow (Figs. 3l, 4c, e-f, h, m-n). On the distal surface of the apical inter-rib groove, tubercles can be seen on some specimens (Figs. 3d, h, l, 4c, e-f, h-i, m-n). They

can be large, globular and fused with the denticles, obscuring the polygonal network (Figs. 3k) or high and grouped or dispersed along a line parallel to the rib (Figs. 2d, 3d, l, 4c, e-f, h-i, m-n).

Comparisons. Several lapworthellid species can be directly differentiated from *Lapworthella schodackensis* (Lochman, 1956) on the presence/absence of fused sclerites in the scleritome. In the genus *Lapworthella*, fused sclerites have only been reported in *Lapworthella schodackensis* by Landing (1984) and *Lapworthella fasciculata* Conway-Morris & Bengtson in Bengtson *et al.*, 1990 which ornamentation otherwise completely differs from the specimens described herein by the presence of multiple fine longitudinal ribs on the entire surface. However, identification of fused sclerites in the scleritome of *Lapworthella* species is probably greatly dependent on taphonomic conditions and is insufficient to confidently identify and differentiate species at the moment. Therefore, other characters need to be considered. The presence/absence of denticles/tubercles/nodes on the comarginal rib is a useful character for discriminating lapworthellid species. The specimens described herein exhibit denticles on the comarginal rib that differentiate it from species that lack any denticles (also referred to as tubercles or nodes) on the rib such as *Lapworthella rete* Yue, 1987, *L. bornholmiensis* (Poulsen, 1942), *L. ludvigseni* Landing, 1984, *L. puttapensis* Bengtson & Conway Morris in Bengtson *et al.*, 1990 and *L. bella* Missarzhevsky in Rozanov & Missarzhevsky, 1966 although the latter is too poorly illustrated and most probably preserved to conclude the validity of the species. Among the species that have, as described herein, a denticulate rib, the differentiation is based on the ornamentation of the apical inter-rib groove and apertural sub-rib zones when available. The fine transverse growth lines parallel to the rib seen on the apertural sub-rib surface of the specimens described herein, corresponding to growth laminae of the wall, are observed in several other *Lapworthella* species (i.e., *L. cornu*

(Wiman, 1903), *L. filigrana* Conway Morris & Fritz, 1984; *L. tortuosa* Missarzhevsky in Rozanov & Missarzhevsky, 1966). On the other hand, the polygons associated with the tubercles in the apical inter-rib groove seem to be restricted to the specimens described herein. A roughly similar ornamentation of the apical inter-rib groove is observed in the specimens assigned to *Lapworthella schodackensis* (Lochman, 1956) figured by Rozanov *et al.* (2010; pl. 58, figs. 1-7): here, polygons are weakly expressed and the presence of associated tubercles is difficult to assess as this character is not well-figured. Similarities in the organization and ornamentation of the apertural sub-rib and apical inter-rib grooves of *Lapworthella* specimens with a denticulate transverse rib are often encountered. In this case, Bengtson (1980), Landing (1984) and Bengtson *et al.* (1990) proposed to consider the number of denticles per mm for differentiation, although the taxonomic significance of this character has been legitimately questioned by Hinz (1987). On this basis, Landing (1984) and Landing *et al.* (2008) proposed *L. schodackensis* as senior synonym of *L. dentata* Missarzhevsky in Rozanov *et al.* 1969 due to their similar dense denticulation. The specimens assigned to *L. schodackensis* by Rozanov *et al.* (2010) exhibit between 28 and 43 denticles/mm on the transverse rib, which is within the range of variation observed in the present specimens but it is slightly less than the variation described for the species in the emended diagnosis of Landing (1984). Based on this new, well-preserved material, an emendation of the diagnosis of *L. schodackensis*, to which the specimens studied herein have been (Skovsted 2006) and are being assigned, is proposed in order to take into account the new data. Apart from the denticulate *L. schodackensis* and *L. dentata*, the similarly ornamented denticulate *L. cornu* (Wiman, 1903), *L. nigra* Cobbold, 1921 and the four morphotypes of *Lapworthella* described by Hinz (1987) have been proposed by Hinz (1987) and Landing *et al.* (2008) as synonyms due to their overlapping scattered number of denticles per mm (12-25/mm). Although the number of denticles per mm seems to be relatively significant for the taxonomy of denticulate

lapworthellids, we recommend the use of apical inter-rib groove surface ornamentation for identification and therefore to sample and observe a large number of well-preserved specimens. We also note that in the camenellan genus *Dailyatia*, closely related species can be differentiated based on small differences in both morphology and sclerite ornament, including the presence/absence and distribution of denticles (pustules *sensu* Skovsted *et al.* 2015), that are only expressed in some of the characteristic sclerite morphotypes (Skovsted *et al.* 2015). Consequently, species identification in camenellans should ideally be based on different lines of evidence from large numbers of sclerites or multiple sclerite morphs, rather than a single characteristic.

It should be noted that accurate comparisons with *Lapworthella marginita* Meshkova, 1969, *L. cancellata* Jiang in Luo *et al.*, 1982, *L. hubeiensis* Qian & Zhang, 1983, *L. sinensis* Duan, 1984 (synonym with *L. ablorta* Duan, 1984 and *L. subrectangulata* Duan, 1984 according to Qian & Bengtson, 1989), *L. annulata* Qian & Yin, 1984 and *L. gezhongwuensis* Qian & Yin, 1984 are difficult due to poor illustrations and preservation. Bengtson *et al.* (1990) provided an exhaustive list of other specimens that have, previously to their study, been referred to *Lapworthella* but that they reassessed as non-*Lapworthella* species.

5. Ornament and the process of shell formation

The surface of the sclerites of all camenellans, including lapworthellids, is characterized by repeated growth sets, consisting of distinct annulations that are parallel to the apertural margin and constituted of co-marginal ribs and inter-rib grooves (Skovsted *et al.* 2009, 2015), herein complemented by the differentiation of a distinct sub-rib zone on the apertural side of the rib

crest. Growth sets are typically separated by narrow furrows and details of the surface ornament of consecutive growth sets is typically identical on each sclerite. Each co-marginal rib is interpreted to correspond to the apertural inflation of selected shell laminae of an internal conical/pyramidal growth element. All growth elements and shell laminae are interpreted by Bengtson (1983), Landing (1984) and later authors to be produced by basal internal accretion.

Following the interpretations of the growth and ornamentation of lapworthellids, a reconstruction of the organization of soft tissues secreting the sclerites was first proposed for *Lapworthella rete* by Conway Morris & Chen (1990) and then extended to Kennardiidae (*Dailyatia*) by Wrona (2004). According to this model, new growth increments (growth sets) were covered by epithelium during formation, reflected in the fossils by the external reticulate network representing molds of epithelial cells.

[Fig. 5 should be placed approximately here]

The new data from the Greenland specimens of *Lapworthella schodackensis* and comparison to the recently described shell structure of *Dailyatia* (Skovsted *et al.* 2015) enable us to complement the hypothetical reconstruction of the association of soft tissues with the sclerites and their growth for *L. schodackensis* (Fig. 5). Skovsted *et al.* (2015) showed that in *Dailyatia ajax*, where the entire surface of the sclerites is covered by a reticulate network, the surface of each growth set is formed by a single shell lamina while subsequent shell laminae reinforce the shell by adding thickness without incremental shell growth. Our interpretation of the shell growth of the Greenland specimens of *L. schodackensis* is similar in that a single shell lamina appears to form the surface of the apical inter-rib area and the rib crest itself (Figs. 1b-c, 5a).

A similar organization of the shell laminae is also observed in the section of a sclerite

assigned to *L. dentata* (possibly synonym with *L. schodackensis*) by Bengtson (1983, figs. 6D, E) although the type of associated ornamentation is difficult to assess. In the present specimens of *L. schodackensis*, these areas are covered by the reticulate network. The apertural sub-rib area with its fine concentric striations represents conventional co-marginal accretion of shell material, and here no traces of epithelial imprints can be found. Consequently, reticulate external surface patterns in *Lapworthella*, as well as in kennardiids, appear to represent elongation of single surface forming laminae. As discussed by Skovsted *et al.* (2015), this could be an adaptation to facilitate rapid shell growth. The elongated laminae would have been formed under an epithelium, while the growing edge of the sclerite was embedded in soft integument (Fig. 5B). During growth the sclerites are interpreted to have periodically erupted from the shell forming tissue, presumably in concert with the formation of new growth sets. The formation of subsequent shell laminae supporting the surface forming lamina and forming the apertural inter-rib zone could have been formed either while the sclerite margin was embedded in soft tissue or after the eruption. The polygons observed on the apical inter-rib zone would correspond to imprints of large epithelial cells (Conway Morris & Chen, 1990; Wrona, 2004) and interpreted, in *L. schodackensis* with the help of the tubercles, as ‘anchorage’ devices for the sclerites in the soft tissues. The reticulate network present on the sclerite interior of *L. schodackensis* from Greenland is composed of smaller polygonal cells compared to the external reticulate ornament and is interpreted to be only involved in secreting the shell material.

6. Scleritome construction and sclerite fusion in lapworthellids

Bilaterally symmetrical sclerites (A sclerites) constitute a large percentage of all sclerites in the camenellans *Kennardia* Laurie, 1986 and *Dailyatia* (Bischoff, 1976; Laurie, 1986; Evans & Rowell, 1990) and at least in *Dailyatia*, the symmetrical A sclerites always exhibit twin apices (Skovsted *et al.* 2015). The A sclerites in *Dailyatia* constitute about 12-25% of all sclerites in assemblages from South Australia (Skovsted *et al.* 2015) and were interpreted by Evans & Rowell (1990) and Skovsted *et al.* (2015) as straddling the mid-line of the dorsal scleritome of a slug-like animal. The asymmetrical B and C sclerites of *Dailyatia* occur in sinistral and dextral symmetry variants and were interpreted to be arranged symmetrically along the midline of the same scleritome (i.e. equal numbers of opposing sinistral and dextral sclerites on the left and right hand sides of the scleritome). If other camenellan tommotiids (mainly *Camenella* Missarzhevsky, 1970, *Kelanella* Rozanov & Missarzhevsky, 1966 and *Lapworthella*) were also slug-like animals with a dorsal scleritome, the most likely arrangement of their asymmetrical sclerites would be forming symmetrical sclerite pairs along the midline of the scleritome.

The two specimens of sclerite morph A in *L. schodackensis* are characterized by two equal apices and appear to be bilaterally symmetrical. The twin apices in each specimen are of the same morphology but appear to have been formed independently and were fused to form a united sclerite during early ontogeny. Similar lapworthellid specimens showing ontogenetic sclerite fusion have been documented before (Landing, 1984) but have usually been interpreted as fortuitous examples of sclerite malformation. However, such examples have been used as evidence for a bilaterally symmetrical multi-component scleritome in tommotiids (Landing, 1984; Qian & Bengtson, 1989; Demidenko, 2004; Li & Xiao, 2004). The bilaterally symmetrical sclerite composites (morph A) in *Lapworthella schodackensis* documented here could be interpreted to represent early ontogenetic fusion of two adjacent sclerites of sinistral and dextral morph B on either side of the mid line of the scleritome (Fig.

6). The more numerous B sclerites were likely oriented in symmetrical pairs along the mid line of the scleritome (Fig. 6b). Both sclerites of morph A and B are oriented with their apices directed posteriorly following assumptions for *Dailyatia* in Skovsted *et al.* (2015). Growth sets on the concave sub-apical field of the A sclerite (bp) curve strongly in the apical direction, corresponding to a deep arch in the apertural margin. We interpret this arch as an accommodation to the curved surface of the animal body in transverse section. Similar arched apertural margins are present on the broad fields of the B sclerites described herein. Based on these observations we suggest that broad B sclerites were arranged in pairs on either side of the mid line of the scleritome with the convex broad fields (bc) oriented forwards and the convex narrow sides (nc) meeting at the midline (Fig. 6b). In this configuration the arched apertural margins of the broad fields in B sclerites would accommodate the curved body of the animal and the apices would be directed backwards and laterally, in a presumably defensive stance (Fig. 6).

[Fig. 6 should be placed approximately here]

Although the exact structure of the scleritome remains elusive, we consider symmetrical sclerite composites (morph A) to be a normal part of the scleritome of *Lapworthella schodackensis*. The relative position of A and B sclerites respectively is not possible to determine. By comparison to the proposed scleritome of *Dailyatia* (Skovsted *et al.* 2015), the A and B sclerites of *L. schodackensis* would, in terms of position in the scleritome, correspond to A and B sclerites of *Dailyatia*. It is possible that other types of asymmetrical sclerites, such as described by Landing (1984) could occupy other positions in the scleritome, but this is presently difficult to assess. Ontogenetically fused sclerites assigned to *L. schodackensis* by Landing (1984) have been described from the Taconic allochthon, eastern New York. The assignment of those specimens to *L. schodackensis* needs to be assessed through additional data on the surface sculpture of the sclerites. The synonymy with the

present specimens is therefore uncertain. One specimen is bilaterally symmetrical and comparable to the fused specimens described herein whereas the other is asymmetric and could possibly correspond to fusion of sclerites in a different part of the scleritome of *L. schodackensis* or to sclerite fusion in a different species.

The ubiquitous presence and large number of symmetrical sclerites with twinned apices in *Dailyatia* suggest that sclerite fusion in this tomotiid occurred as a programmed event early in sclerite ontogeny and by comparison may suggest that sclerite fusion in *Lapworthella schodackensis* was also a normal phenomenon in sclerite ontogeny in a particular part of the scleritome. Similar bilaterally symmetrical sclerite composites (albeit with more than 2 apices) were documented by Demidenko (2004) for *Lapworthella fasciculata* from Horse Gully in the Stansbury Basin of South Australia. Fused sclerite composite specimens of *L. fasciculata* with two apices only have been discovered in the Donkey Bore Syncline of the Arrowie Basin in South Australia (Topper 2006; T.P. Topper, pers. comm. 2015).

Consequently, it is not unlikely that given sufficient sample size, bilaterally symmetrical sclerite morphs could perhaps be discovered in other lapworthellids in the future. However, it may be worth considering that fused sclerite composites of the Greenland *L. schodackensis*, as well as the Australian *L. fasciculata* from both the Stansbury Basin (Demidenko, 2004) and the Arrowie Basin (T.P. Topper pers. comm. 2015) are derived from single samples and the observed pattern could possibly represent differences between populations or even individuals.

7. Conclusions

Excellent preserved specimens of *Lapworthella schodackensis* from the Cambrian Stage 4 upper Bastion Formation at Albert Heim Bjerge and CH Ostenfeld Nunatak, North-East Greenland provide significant novel data on the species taxonomy and for comprehension of the scleritome structure of lapworthellids and the mode of formation of their sclerites. In the Greenland assemblage, two sclerite morphotypes of *L. schodackensis* were identified: one with simple apex, occurring in sinistral and dextral forms and one bilaterally symmetrical with two apices. The excellent preservation provide exquisite new details on the sclerite ornamentation which is constructed of repeated growth sets constituted of a reticulate inter-rib groove with tubercles, a densely denticulate rib and a striated sub-rib area. The new data on the ornamentation and shell microstructure of *L. schodackensis* in combination with the results of Skovsted *et al.* (2015) on *Dailyatia* also enabled us to propose that the surface of the apical inter-rib area and the rib crest itself is formed by a single shell lamina while subsequent shell laminae reinforce the shell by adding thickness and laminar structures in the sub-rib area. Finally, new information for the reconstruction of bilaterally symmetrical multi-component lapworthellid scleritome were deduced from the recovered *L. schodackensis* sclerites with twin apices that have been formed independently and were fused to form a united sclerite during early ontogeny. The orientation of the ontogenetical fusion suggests that at least, a certain number of *L. schodackensis* sclerites formed symmetrical pairs along the midline of the scleritome.

Acknowledgements

The authors thank Prof. John S. Peel (Uppsala) for access to collections and geological information from North-East Greenland. Dr. Timothy P. Topper is thanked for valuable

discussions on sclerite morphology and ultrastructure. This work was supported by the European Community – Research Infrastructure Action under the FP7 ‘Capacities’ Specific Programme (LD, SYNTHESYS grant SE-TAF-4164 performed at the Swedish Museum of Natural History). LD is also indebted to Drs Daniela Kalthoff and Thomas Mörs for their hospitality and the Swedish Museum of Natural History staff for the support. We are grateful to the editor and the external reviewers whose reviews greatly improved the quality of the final manuscript.

References

- BALTHASAR, U., SKOVSTED, C. B., HOLMER, L. E. & BROCK, G. A. 2009. Homologous skeletal secretion in tommotiids and brachiopods. *Geology* **37**, 1143–1146.
- BENGTSON, S. 1970. The Lower Cambrian fossil *Tommotia*. *Lethaia* **3**, 363–392.
- BENGTSON, S. 1977. Aspects of problematic fossils in the early Palaeozoic. *Acta Universitatis Upsaliensis, Abstracts of Uppsala Dissertations from the Faculty of Science* **415**, 1–71.
- BENGTSON, S. 1980. Redescription of the Lower Cambrian *Lapworthella cornu*. *Geologiska Föreningen i Stockholm Förhandlingar* **102**, 53–55.
- BENGTSON, S. 1983. The early history of the Conodonta. *Fossils and Strata* **15**, 5–19.
- BENGTSON, S. 2004. Early skeletal fossils. In *Neoproterozoic–Cambrian Biological Revolutions* (eds J.H. Lipps & B.M. Waggoner), p. 67–77. The Paleontological Society Papers no. 10.

BENGTSON, S., CONWAY MORRIS, S., COOPER, B. J., JELL, P. A. & RUNNEGAR, B. 1990. Early Cambrian fossils from South Australia. *Memoirs of the Association of Australasian Palaeontologists* **9**, 1–364.

BISCHOFF, G. C. O., 1976. *Dailyatia*, a new genus of the Tommotiidae from Cambrian strata of SE Australia (Crustacea, Cirripedia). *Senckenbergiana Lethaea* **57**, 1–33.

CARON, J-B., SMITH, M. R. & HARVEY, T. H. P. 2013. Beyond the Burgess Shale: Cambrian microfossils track the rise and fall of hallucigeniid lobopodians. *Proceedings of the Royal Society B* **280**, 20131613.

COBBOLD, E. S. 1921. The Cambrian horizons of Comley (Shropshire) and their *Brachiopoda*, *Pteropoda*, *Gasteropoda*, etc. *Quarterly Journal of the Geological Society* **76**, 325–386.

CONWAY-MORRIS, S. & FRITZ, W. H. 1984. *Lapworthella filigrana* n. sp. (incertae sedis) from the Lower Cambrian of the Cassiar Mountains, northern British Columbia, Canada, with comments on possible levels of competition in the early Cambrian. *Paläontologische Zeitschrift* **58(3/4)**, 197–209.

CONWAY MORRIS, S. & CHEN, M. 1990. Tommotiids from the Lower Cambrian of south China. *Journal of Paleontology* **64(2)**, 169–184.

DEMIDENKO, Y. E. 2004. New data on the sclerite morphology of the tommotiid species *Lapworthella fasciculata*. *Paleontological Journal* **38**, 134–140.

DEVAERE, L., HOLMER, L. E., CLAUSEN, S. & VACHARD, D. 2015. Oldest mickwitziid brachiopod from the Terreneuvian of Southern France. *Acta Palaeontologica Polonica* **60(3)**, 755–768.

- DEVAERE, L., CLAUSEN, S., MONCERET, E., VIZCAÍNO, D., VACHARD, D. & GENGE, M-C., 2014. The tommotiid *Kelanella* and associated fauna from the early Cambrian of southern Montagne Noire (France): implication for camenellan phylogeny. *Palaeontology* **57**, 979–1002.
- DUAN, C. 1984. Small Shelly Fossils from the Lower Cambrian Xihaoping Formation the Shennongjia district, Hubei province - hyoliths and fossil skeletons of unknown affinities. *Bulletin of the Tianjin Institute of Geology and Mineral Resources* **7**, 141–188.
- EVANS, K. R & ROWELL, A. J. 1990. Small Shelly Fossils from Antarctica: An Early Cambrian Faunal Connection with Australia. *Journal of Paleontology* **64**, 692–700.
- FISHER, D. W. 1962. Small conoidal shells of uncertain affinities. In *Treatise on Invertebrate Paleontology – Miscellanea* (ed. R. C. Moore), p. W98–W143. Geological Society of America and University of Kansas Press, Lawrence.
- HINZ, I. 1987. The Lower Cambrian microfauna of Comley and Rushton, Shropshire/England. *Palaeontographica Abteilung A* **198(1/3)**, 41–100.
- HOLMER, L. E., SKOVSTED, C. B., BROCK, G. A., VALENTINE, J. L. & PATERSON, J. R. 2008. The Early Cambrian tommotiid *Micrina*, a sessile bivalved stem group brachiopod. *Biology Letters* **4**, 724–728.
- KOUCHINSKY, A., BENGTSON, S. & MURDOCK, D. J. 2010. A new tannuolinid problematic from the lower Cambrian of the Sukharikha River in northern Siberia. *Acta Palaeontologica Polonica* **55**, 321–331.
- KOUCHINSKY, A., HOLMER, L. E., STEINER, M. & USHATINSKAYA, G. T. 2015. The new stem-group brachiopod *Oymurania* from the lower Cambrian of Siberia. *Acta Palaeontologica Polonica* **60(4)**, 963–980.

KOUCHINSKY, A. V., BENGTSON, S., RUNNEGAR, B., SKOVSTED, C., STEINER, M. & VENDRASCO, M. 2012. Chronology of early Cambrian biomineralisation. *Geological Magazine* **149**(2), 221–251.

LANDING, E. 1984. Skeleton of lapworthellids and the suprageneric classification of tommotiids (Early and Middle Cambrian phosphatic problematica). *Journal of Paleontology* **58**(6), 1380–1398.

LANDING, E. & BARTOWSKI, K. E. 1996. Oldest shelly fossils from the Taconic allochthon and late early Cambrian sea-levels in eastern Laurentia. *Journal of Paleontology* **70**(5), 741–761.

LANDING, E., JOHNSON, S. C. & GEYER, G. 2008. Faunas and Cambrian volcanism on the Avalonian marginal platform, southern New Brunswick. *Journal of Paleontology* **82**, 884–905.

LARSSON, C. M., SKOVSTED, C. B., BROCK, G. A., BALTHASAR, U., TOPPER, T. P. & HOLMER, L. E. 2014. *Paterimitra pyramidalis* from South Australia: scleritome, shell structure and evolution of a lower Cambrian stem group brachiopod. *Palaeontology* **57**, 417–446.

LAURIE, J. R. 1986. Phosphatic fauna of the Early Cambrian Todd River Dolomite, Amadeus Basin, central Australia. *Alcheringa* **10**, 431–454.

LI, G. & XIAO, S. 2004. *Tannuolina* and *Micrina* (Tannuolinidae) from the Lower Cambrian of eastern Yunnan, South China, and their scleritome reconstruction. *Journal of Paleontology* **78**, 900–913.

- LIU, J., STEINER, M., DUNLOP, J. A., KEUPP, H., SHU, D., OU, Q., HAN, J., ZHANG, Z. & ZHANG, X. 2011. An armoured Cambrian lobopodian from China with arthropod-like appendages. *Nature* **470**(7335), 526–530.
- LOCHMAN, C. 1956. Stratigraphy, paleontology, and paleogeography of the *Elliptocephala asaphoides* strata in Cambridge and Hoosick Quadrangles, New York. *Bulletin of the Geological Society of America* **67**, 1331–1396.
- LUO, H., JIANG, Z., WU, X., SONG, X. & OUYANG, L. 1982. *The Sinian-Cambrian boundary in eastern Yunnan, China*. Yunnan Institute of Geological Sciences, 265 pp.
- MALINKY, J. M. & SKOVSTED, C. B. 2004. Hyoliths and small shelly fossils from the Lower Cambrian of North-East Greenland. *Acta Palaeontologia Polonica* **49**, 551–578.
- MALOOF, A. C., PORTER, S. M., MOORE, J. L., DUDÁS, F. Ö., BOWRING, S. A., HIGGINS, J. A., FIKE, D. A. & EDDY, M. P. 2010. The earliest Cambrian record of animals and ocean geochemical change. *Geological Society of America Bulletin* **122**, 1731–1774.
- MATTHEWS, S. C. 1973. Lapworthellids from the Lower Cambrian *Strenuella* Limestone at Comley, Shropshire. *Palaeontology* **16**(1), 139–148.
- MATTHEWS, S. C. & MISSARZHEVSKY, V. V. 1975. Small Shelly Fossils of late Precambrian and early Cambrian age: a review of recent work. *Journal of the geological Society of London* **131**, 989–304.
- MCMENAMIN, M. A. S. 1992. Two new species of the Cambrian genus *Mickwitzia*. *Journal of Paleontology* **66**, 173–182.

- MESHKOVA, N. P. 1969. On the paleontological characterization of the Lower Cambrian deposits of the Siberian platform. *Biostratigraphy and Paleontology of the Lower Cambrian of Siberia and the Russian Far East* (ed. I.T. Zhuravleva), p. 158–174. Nauka, Moscow.
- MISSARZHEVSKY, V. V. 1970. Novoye rodovoye nazvaniye *Tommotia* Missarzhevsky, nom. nov. *Paleontologicheskii Zhurnal* **2**, 100.
- MURDOCK, D. J. E., DONOGHUE, P. C. J., BENGTON, S. & MARONE, F. 2012. Ontogeny and microstructure of the enigmatic Cambrian tommotiid *Sunnaginia* Missarzhevsky 1969. *Palaeontology* **55**, 661–676.
- MURDOCK, D. J., BENGTON, S., MARONE, F., GREENWOOD, J. M. & DONOGHUE, P. C. 2014. Evaluating scenarios for the evolutionary assembly of the brachiopod body plan. *Evolution & Development* **16**, 13–24.
- POULSEN, C. 1942. Nogle hidtil ukendte Fossiler fra Bornholms Eksulanskalk. *Meddelelser fra Dansk Geologisk Forening* **10**, 212–235.
- QIAN, Y. & ZHANG, S. 1983. Small Shelly Fossils from the Xihaoping Member of the Congying Formation in the Fangxian county of Hubei province and their stratigraphical significance. *Acta Palaeontologica Sinica* **2(1)**, 83–94.
- QIAN, Y. & YIN, G. 1984. Small Shelly Fossils from the lowest Cambrian in Guizhou. *Professional Papers of Stratigraphy and Palaeontology* **13**, 91–124.
- QIAN, Y. & BENGTON, S. 1989. Palaeontology and biostratigraphy of the early Cambrian Meishucunian Stage in Yunnan province, south China. *Fossils and Strata* **24**, 1–156.

ROZANOV, A. Y. & MISSARZHEVSKY, V. V. 1966. Biostratigraphy and fauna of the lower Horizons of the Cambrian. *Proceedings of the Geological Institute of the Academy of Sciences of the USSR, Nauka, Moscow* **148**, 1–118.

ROZANOV, A. Y., MISSARZHEVSKY, V. V., VOLKOVA, N. A., VORONOVA, L. G., KRYLOV, I. N., KELLER, B. M., KOROLYUK, I. K., LENDZION, K., MIKHNYAR, R., PYKHOVA, N. G. & SIDOROV A. D. 1969. Tommotskiu jarus i problema nizhney granisty Kembriya. [The Tommotian Stage and the lower boundary problem]. *Trudy Geoligske Institut Leningrad* **206**, 1–379.

ROZANOV, A. Y., PARKHAEV, P. Y., DEMIDENKO, Y. E., KARLOVA, G. A., KOROVNIKOV, I. V., SHABANOV, Y. Y., IVANCOV, A. Y., LUCHININA, V. A., MALAKHOVSKAYA, A. E., MELNIKOVA, L. M., NAIMARK, E. B., PONOMARENKO, A. G., SKORLOTOVA, N. A., SUNDUKOV, V. M., TOKAREV, D. A., USHATINSKAYA, G. T. & KIPRIYANOVA, L. D. 2010. *Fossils from the lower Cambrian Stage stratotype*. PIN RAN, Moscow, 225 pp.

SKOVSTED, C. B. 2004. Mollusc fauna of the Early Cambrian Bastion Formation of North-East Greenland. *Bulletin of the Geological Society of Denmark* **51**, 11–37.

SKOVSTED, C. B. 2006. Small shelly fauna from the upper Lower Cambrian Bastion and Ella Island Formations of North – East Greenland. *Journal of Paleontology* **80**, 1087–1112.

SKOVSTED, C. B. & HOLMER, L. E. 2003. The Early Cambrian stem group brachiopod *Mickwitzia* from Northeast Greenland. *Acta Palaeontologica Polonica* **48**, 11–30.

SKOVSTED, C. B. & HOLMER, L. E. 2005. Early Cambrian brachiopods from North-East Greenland. *Palaeontology* **48**, 325–345.

- SKOVSTED, C. B. & PEEL, J. S. 2007. Small shelly fossils from the argillaceous facies of the Lower Cambrian Forteau Formation of western Newfoundland. *Acta Palaeontologica Polonica* **52**, 729–748.
- SKOVSTED, C. B., BALTHASAR, U., BROCK, G. A. & PATERSON, J. R. 2009. The tommotiid *Camenella reticulosa* from the early Cambrian of South Australia: morphology, scleritome reconstruction and phylogeny. *Acta Palaeontologica Polonica* **54**, 525–540.
- SKOVSTED, C. B., CLAUSEN, S., ÁLVARO, J. J. & PONLEVÉ, D. 2014. Tommotiids from the early Cambrian (Series 2, Stage 3) of Morocco and the evolution of the tannuolinid scleritome and setigerous shell structures in stem group brachiopods. *Palaeontology* **57**, 171–192.
- SKOVSTED, C. B., BETTS, M. J., TOPPER, T. P. & BROCK, G. A. 2015. The early Cambrian tommotiid genus *Dailyatia* from South Australia. *Memoirs of the Association of Australasian Palaeontologists* **48**, 1–117.
- SKOVSTED, C. B., BROCK, G. A., TOPPER, T. P., PATERSON, J. R. & HOLMER, L. E. 2011. Scleritome construction, biofacies, biostratigraphy and systematics of the tommotiid *Eccentrotheca helenia* sp. nov. from the early Cambrian of South Australia. *Palaeontology* **54**, 253–286.
- STEIN, M. 2008. Evolution and taxonomy of Cambrian arthropods from Greenland and Sweden. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* **558**, 1–35.
- STOUGE, S., BOYCE, D. W., CHRISTIANSEN, J., HARPER, D. A. T. & KNIGHT, I. 2001. Vendian–Lower Ordovician stratigraphy of Ella Ø, North-East Greenland: New investigations. *Geology of Greenland Survey Bulletin* **189**, 107–114.

SZANIAWSKI, H. 1982. Chaetognath grasping spines recognized among Cambrian protoconodonts. *Journal of Paleontology* **56**, 806–810.

SZANIAWSKI, H. 2002. New evidence for the protoconodont origin of chaetognaths. *Acta Palaeontologia Polonica* **47**, 405–419.

TOPPER, T. P. 2006. *Lower Cambrian Palaeontology, biostratigraphy and geology of the Donkey Bore Syncline, South Australia*. Unpublished Honours Thesis, Macquarie University, Sydney, 209 p.

TOPPER, T. P., BROCK, G. A., SKOVSTED, C. B. & PATERSON, J. R. 2009. Shelly fossils from the lower Cambrian *Pararaia bunyeroensis* Zone, Flinders ranges, South Australia. *Memoirs of the Association of Australasian Palaeontologists* **37**, 199–246.

VINTHER, J. 2009. The canal system in sclerites of Lower Cambrian *Sinosachites* (Halkieriidae: Sachitida): significance for the molluscan affinities of the sachitids.

Palaeontology **52**, 689–712. WILLIAMS, A. & HOLMER, L. E. 2002. Shell structure and inferred growth, functions and affinities of the sclerites of the problematic *Micrina*. *Palaeontology* **45**, 845–873.

WIMAN, C. 1903. Studien uiber das Nordbaltische Silurgebiet. I. Olenellussandstein, Obolussandstein und Ceratopygeschiefer. *Bulletin of the Geological Institute of the University of Uppsala* **6**, 12–76.

WRONA, R. 2004. Cambrian microfossils from glacial erratics of King George Island, Antarctica. *Acta Palaeontologica Polonica* **49(1)**, 13–56.

YUE, Z. 1987. The discovery of *Tannuolina* and *Lapworthella* [sic] from Lower Cambrian in Meishucun (Yunnan) and Maidiping (Sichuan) sections. *Professional Papers on Stratigraphy and Palaeontology* **16**, 73–180.

Figure captions

Figure 1. *Lapworthella schodackensis* (Lochman, 1956) from the upper Bastion Formation of Albert Heim Bjerge and CH Ostenfeld Nunatak. (a-c) Specimen SMNH X6119. a. Internal view of a sclerite fragment, upper boxed area magnified in (b) and lower boxed area magnified in (c). (b-c) Details of the finely laminar shell microstructure. (d-e) Specimen SMNH X6120. (d) Internal view of a sclerite fragment, boxed area magnified in (e). (e) Detail of the finely laminar shell microstructure. (f-i) Specimen SMNH X6121. (f) Broken sclerite of morphotype B, lower left boxed area magnified in (g), lower right boxed area magnified in (h) and upper boxed area magnified in (i). (g) Detail of the finely laminar shell microstructure. (h) Detail of the polygonal imprints organized into a reticulate pattern on the internal surface of the sclerite. (i) Detail of the apical oval cross-section with finely laminar shell microstructure visible. Scale bars: (b, c, e, g, i), 20 μm ; (h), 50 μm ; (a, d, f), 200 μm .

Figure 2. Morphotype A of *Lapworthella schodackensis* (Lochman, 1956) from the upper Bastion Formation of Albert Heim Bjerge and CH Ostenfeld Nunatak. (a-g) Specimen SMNH X6122. (a) General view, boxed area magnified in (b). (b-c, g). Close up at the two apices of the sclerite. (d) Detail of co-marginal growth sets typical ornamentations. (e) Apertural view. (f) Lateral view, boxed area magnified in (d). (h-l) Specimen MGUH 26760. (h) Apical view.

(i, l) Lateral views. (j) Anterior view. (k) Posterior view. Scale bars: (b-d), 50 μm ; (h, k), 100 μm ; (a, e-g, i-j, l), 200 μm .

Figure 3. Morphotype B of *Lapworthella schodackensis* (Lochman, 1956) from the upper Bastion Formation of Albert Heim Bjerge and CH Ostenfeld Nunatak. (a-b, d) Sinistral sclerite, specimen SMNH X6123. (a) Apical view, boxed area magnified in (d). (b) View of the broad convex field of the sclerite. (d) Detail of co-marginal growth sets typical ornamentations: apical inter-rib groove covered with a polygonal network and tubercles, rib with denticles and fine transverse striations parallel to the rib on the apertural sub-rib surface. (c, e, g-h, k) Dextral sclerite, specimen MGUH 27605. (c) Lateral view showing the undulating apertural margin, boxed area magnified in (g). (e) Apertural view showing the subquadrangular cross section; (np) portion of the apertural margin corresponding to the narrow, planar field of the sclerite; (nc) portion of the apertural margin corresponding to the narrow, convex field; (bp) portion of the apertural margin corresponding to the broad, planar to concave field and (bc) portion of the apertural margin corresponding to the broad, convex field. (g) Detail of the polygonal imprints organized into a reticulate pattern on the internal surface of the sclerite. (h) View of the broad, concave field of the sclerite, boxed area magnified in (k). (k) Detail of the ornamentation with rounded fused denticles and tubercles. (f, l) Sinistral sclerite, specimen SMNH X6124. (f) View of the broad, convex field of the sclerite, boxed area magnified in (l). (l) Detail of co-marginal growth sets typical ornamentations in three zones. (i-j) Sinistral sclerite, specimen SMNH X6125. (i) View of the broad, convex field of the sclerite. (j) Apical view showing the subquadrangular apertural cross-section. Scale bars: (d, g, k), 50 μm ; (l), 100 μm ; (a, c, e-f, h, j), 200 μm ; (b, i), 500 μm .

Figure 4. Morphotype B of *Lapworthella schodackensis* (Lochman, 1956) from the upper Bastion Formation of Albert Heim Bjerge and CH Ostenfeld Nunatak. (a-c) Dextral sclerite, specimen SMNH X6126. (a) Apical view showing the subquadrangular apertural cross-section. (b) View of the broad, convex field of the sclerite, boxed area magnified in (c). (c) Detail of co-marginal growth sets typical ornamentations: apical inter-rib groove (g) covered with a polygonal network and tubercles, rib (s) with denticles and fine transverse striations parallel to the rib on the apertural sub-rib surface (a). (d-k) Sinistral sclerite, Specimen MGUH 27604. (d) Apical view showing the subquadrangular apertural cross-section, boxed area magnified in (h). (e) Detail of co-marginal growth sets typical ornamentations. (f) Close up at the ornamentation showing the tubercles associated with the polygonal network. (g) View of the broad, convex field of the sclerite. (h) Apical view of the typical ornamentation of the co-marginal ribs. (i) Close up at the polygonal network and tubercles. (j) Lateral view centered on the angular ridge between the narrow, planar field and the broad convex one, boxed area magnified in (e). (k) View of the narrow, convex field. (l-o) Dextral sclerite, specimen SMNH X6127. (l) View of the broad, convex field of the sclerite, right boxed area magnified in (m) and left boxed area magnified in (n). (m-n) Detail of co-marginal growth sets typical ornamentations. (o) Apertural view. (p) Apertural view of sinistral sclerite, specimen SMNH X6128 (see legend of Fig. 3e for annotations). Scale bars: (i), 10 μm ; (f, m), 20 μm ; (e, h, n), 50 μm ; (c), 100 μm ; (a-b, d, g, j-l, o-p), 200 μm .

Figure 5. (a) Proposed nomenclature to describe the ornamentations in lapworthellids with references to the terminology proposed for *Dailyatia* Bischoff, 1976 in Skovsted *et al.* (2015). (b). Hypothetical reconstruction (modified from Wrona 2004) of the relationship between *Lapworthella schodackensis* (Lochman, 1956) sclerite and secretory tissues during growth,

based on the present observation of surface sculpture of the co-marginal ribs and cross-section of the shell and cross-section of *L. dentata* (Bengtson, 1983).

Figure 6. Hypothetical reconstructions of the orientation of (a) morph A (based on specimen MGUH 26760) and (b) morph B sclerites (based on specimens SMNH X6126 and MGUH 27604) of *Lapworthella schodackensis* (Lochman 1956) relative to the mid-line and anterior and posterior parts of a slug-like animal (see legend of Fig. 3e for annotations). Note that the relative position of A and B sclerites respectively and the distance between morph B sclerites and the scleritome mid line is not possible to determine from the present material and is completely artificial.

a

Apical inter-rib groove (g)

Rib (s)

Apertural sub-
rib zone (a)**b** Thick external surface lamina Thin internal laminae Thick internal surface lamina

} Growth-set

Soft tissues

a

Morph A

b

dextral

Scleritome
mid-line

Post

nc

Morph B

bc

sinistral

np