

Phosphatized organic nanostructures in the Cambrian linguloid brachiopod *Ungula inornata* (Mickwitz)

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Abstract. Scanning electron microscopy of untreated and uncoated fracture sections of a secondary shell of a Cambrian (Furongian) linguloid brachiopod *Ungula inornata* (Mickwitz) in concurrent backscattered electron and secondary electron imaging regimes revealed phosphatized organic fibril-like nanostructures, less than 200 nm in diameter. By analogy with published data on a living lingulate genus *Disciniscia*, the nanofibrils are interpreted as parts of the organic biopolymer matrix, which are composed of axial protein strands of bacula connected by chitin and participate in the formation of baculate sets. The nanofibrils are relevant structural units in the hierarchical structure of lingulate brachiopods with baculate shell structure. It is concluded that these structures are preserved by instant *post-mortem* precipitation of apatite. The shell structure of *U. inornata* is most similar to the other species of the genus *Ungula* Pander and the species of the genus *Obolus* Eichwald.

Key words: Brachiopoda, *Ungula inornata*, shell structure, scanning electron microscopy, Cambrian, Estonia.

INTRODUCTION

Phosphatized fibril-like organic nanostructures in shells of fossil linguloid brachiopods have been documented in rare occasions (Lang & Puura 2009; Lang et al. 2011). By analogy with studies of some modern linguloids (Merkel et al. 2007; Schmahl et al. 2008), these nanofibrils have been interpreted as biopolymer strands preserved by immediate *post-mortem* phosphatization of organic tissues (Lang et al. 2011). The nanofibrils are relevant in the formation of *bacula*, minute apatitic rods (cf. Holmer 1989, p. 31) forming baculate sets. The resulting baculate structure, characterized by alternation of compact and baculate laminae, is found in many modern and fossil lingulate taxa. The phylogenetic context of chemico-structural features of lingulate brachiopods has been discussed by Cusack et al. (1999) and Williams & Cusack (1999, 2007).

The obolids from the Cambrian–Ordovician *Obolus* Sandstone of Estonia, described by Mickwitz (1896) as various species and varieties of the genus *Obolus* Eichwald, 1829, part of which are today assigned to the genera *Ungula* Pander, 1830, *Schmidtites* Schuchert & LeVene, 1929 and *Oepikites* Khazanovitch & Popov, 1984 (in Khazanovitch et al. 1984), have attracted attention as models for the baculate shell structure type. Already Mickwitz (1896) included to his monograph a study of polished cross-sectional thin sections of fossil linguloid brachiopod shells. Holmer (1989) referred to *Ungula ingrlica* (Eichwald, 1829) as to the stratigraphically oldest species

with the baculate structure he studied. Cusack et al. (1999) established *Obolus apollinis* Eichwald, 1829 as a typical representative of the baculate symmetrical shell structure.

The present study describes flexible nanofibrils in a Cambrian linguloid brachiopod *Ungula inornata* (Mickwitz, 1896). These are treated as relevant structural units in the hierarchical structure of the organo-phosphatic shell.

MATERIAL AND METHODS

Material, locality and geological setting

After pilot examination of more than 10 specimens of *Ungula inornata* from different levels in the Mäekalda (Mens et al. 1989), Iru (Puura 2000) and Ülgase (described below) outcrops, a specimen with the best-preserved shell structure was selected for detailed scanning electron microscopy (SEM) study. The studied specimen in the collection of Natural History Museum, University of Tartu (TUG 1323-4; coll. Leonid Popov), originates from the Ülgase Formation (Furongian, Cambrian) of the Ülgase outcrop (Fig. 1). Other illustrated specimens (Fig. 2) from the Iru section (at the eastern margin of Tallinn, 10 km west of the Ülgase section; description in Puura 2000) are from the collection of the Institute of Geology, Tallinn University of Technology (abbr. GIT).

The Ülgase exposures are located 15 km east of the centre of Tallinn, near Ülgase village. These can be found by a landmark: ruins of the abandoned phosphate-

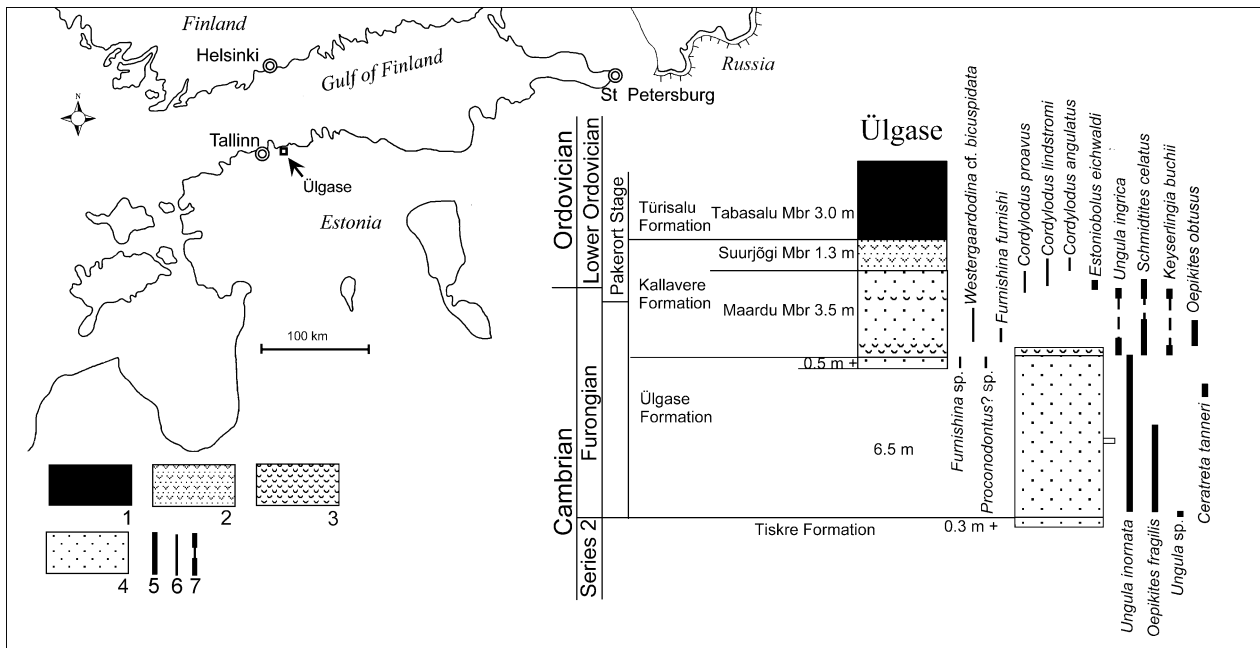


Fig. 1. Generalized map of Estonia and adjacent areas, showing the location and the sections of the Ülgase outcrop (after Puura 2004). The described specimen of *Ungula inornata* is collected from the sandstones from an interval 3.0–3.2 m above the base of the Ülgase Formation (marked with an open rectangle on the right side of the lithological column). 1, kerogenous shale; 2, sand and sandstone yielding lingulate debris; 3, lingulate coquina and conglomerate; 4, sand and sandstone; 5, lingulate brachiopods; 6, conodonts and graptolites; 7, part of a range with no occurrences documented. Mbr, Member.

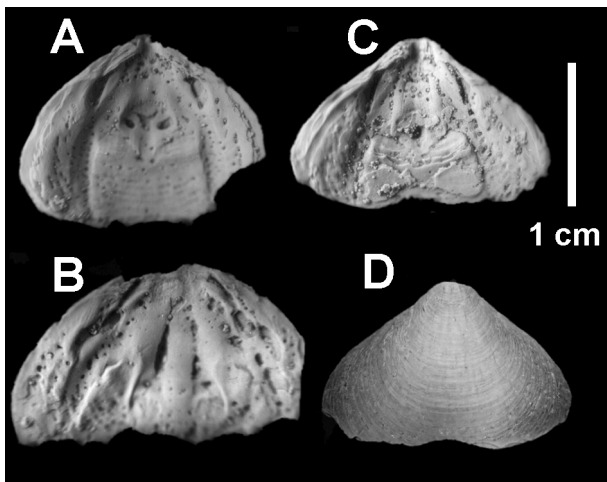


Fig. 2. Valves of *Ungula inornata* (Mickwitz) from the Iru section at the eastern margin of Tallinn, northern Estonia. The valves are redeposited from the Ülgase Formation to the lowermost Maardu Member of the Kallavere Formation (Cambrian, Furongian). **A**, ventral valve interior (GIT 275-40) with a well-preserved heart-shaped depression; **B**, dorsal valve interior (GIT 275-43); **C**, ventral valve interior (GIT 275-42); **D**, ventral valve exterior of specimen C (GIT 275-42).

processing factory of the ‘Eesti Vosvoriit’ company that was destroyed in a fire in 1938. The Upper Cambrian Ülgase Formation, Cambrian, Furongian (previously Upper Cambrian), is exposed in a wall of abandoned mineworks (59°29’21”N, 25°05’08”E) in a phosphorite mine that was exploited during 1921–1938. The Ülgase Formation, 6.5 m in thickness, overlies white sandstones of the Tiskre Formation (Cambrian, Series 2, previously Lower Cambrian) and is represented mainly by light grey silty sandstones, intercalated with two greenish-grey clay beds: a 10 cm thick clay bed 0.73 m above the base and a 4 cm thick clay bed 1.09 m above the base (Loog & Kivimägi 1968). The sample with *U. inornata* (TUG 1323-4) originates from the interval 3.0–3.2 m above the lower boundary of the Ülgase Formation.

The Ülgase Formation is overlain by sandstones of the Maardu Member of the Kallavere Formation, which is exposed in full thickness in another outcrop, 200 m westwards. Here, the Kallavere Formation is up to 4.8 m thick and is overlain by black shales of the Türişalu Formation, exposed in a thickness of 3.0 m (Fig. 1). According to the correlation with the GSSP in the Green Point Section in Newfoundland, the Cambrian–Ordovician boundary is defined in this section within

the Maardu Member of the Kallavere Formation by the first appearance of the conodont *Cordylodus lindstromi*, 2.9 m above the base of both units (Fig. 1; for the criteria for tracing the Cambrian–Ordovician boundary in Baltoscandia, see Puura & Viira 1999, 2004).

The lower boundary of the Kallavere Formation is marked by the lingulate coquina containing numerous valves of linguloid brachiopods *Ungula ingrlica*, *Schmidtites celatus*, rare *Keyserlingia buchii* and *Oepikites obtusus*. Early conodonts *Westergaardodina* cf. *bicuspidata* and *Furnishina furnishii*, found in a sample 0.7 m above the base of the Kallavere Formation, allow correlation of this interval tentatively to the *Peltura scarabeoides* trilobite Biozone (Heinsalu et al. 1987).

The Ülgase Formation has yielded lingulate brachiopods *Ungula inornata* from all levels above the basal coquina, *Ceratreta tanneri* from the upper 3 m and *Ungula* sp. from only the basal coquina, 0.1 m thick. The conodonts *Furnishina* sp. and *Proconodontus* sp. and the acritarch assemblage found from two levels in the Mäekalda section near the centre of Tallinn (15 km west of the Ülgase section) allow tentative correlation of the Ülgase Formation in Tallinn and its environs with the *Olenus* trilobite Biozone (Mens et al. 1989). The studied sample of *U. inornata* originates from the interval 3.0–3.2 m below the upper boundary of the Ülgase Formation (Fig. 1).

During the Furongian and the Cambrian–Ordovician transition, the Baltica palaeocontinent was located on the southern hemisphere, presumably at the southern latitudes 20–40° (Cocks & Torsvik 2005). According to Artyushkov et al. (2000), the Cambrian quartzose sands found in northern Estonia were deposited in the peritidal zone in a shallow epicontinental sea.

Scanning electron microscopy (SEM)

Ten shells out of those examined by means of light microscope were selected for pilot SEM study. The best-preserved specimen was selected for detailed shell structure study. For SEM observations, the valve was cleaned and broken along the medial axis and mounted on the sample holder using conductive aluminium tape. The fracture surfaces were left untreated and uncoated while studied with the Zeiss EVO MA15 SEM at the Department of Geology, University of Tartu (Estonia). The variable pressure mode was used in two concurrent regimes: backscattered electron imaging (BSE) and secondary electron imaging (SE). Backscattered electrons are elastically scattered electrons excited from the specimen by a beam of primary electrons. The scattering induced by the incident electron beam is controlled by the average atomic number of the specimen. Secondary electrons are

inelastically ejected from the specimen surface (within a few nanometres) and describe the topography of the specimen. The SEM images of BSE and SE regimes are displayed pairwise (Fig. 3A–H and A'–H', respectively), to take into account the information from both regimes and to allow comparison with earlier publications using either of the two regimes.

The terminology used in describing baculate shell structures in lingulate brachiopods stems from Holmer (1989) and Cusack et al. (1999) and is updated in Williams & Cusack (2007).

SYSTEMATIC PALAEOLOGY

- Phylum BRACHIOPODA Duméril, 1806
- Subphylum LINGULIFORMEA Williams et al., 1996
- Class LINGULATA Goryanskij & Popov, 1985
- Order LINGULIDA Waagen, 1885
- Superfamily LINGULOIDEA Menke, 1828
- Family OBOLIDAE King, 1846
- Genus *Ungula* Pander, 1830

Type species. *Ungula convexa* Pander, 1830; Cambrian, Furongian, Ladoga Formation, NW Russia.

Other species. *Obolus ingrlicus* Eichwald, 1829, Cambrian, Furongian, Estonia; *Obolus triangularis* Mickwitz, 1896, Cambrian, Furongian, Estonia.

Distribution. Furongian of Estonia, NW Russia and Sweden.

Remarks. The genera *Obolus* Eichwald, 1829 and *Ungula* Pander, 1830 have been recognized by Popov and Khazanovitch in Popov et al. (1989), who assigned the above three species to the genus *Ungula*. This nomenclature has been followed by most researchers and in the *Treatise of Invertebrate Palaeontology*. Prior to that publication, many authors assigned all the species of the above two genera to the genus *Obolus* (e.g., Mickwitz 1896). The majority of the authors agree that the two genera are related and they resemble each other in shape and shell structure to the extent that has led to some taxonomic debate (e.g., Emig 2002; Popov & Holmer 2003). However, we consider that challenging or revision of the current well-established taxonomy of linguloids and in particular, obolids, would need more evidence and a better understanding of the characters of taxonomic value, including the shell structure and eventual taphonomic overprint. Therefore, and for the consistence and clarity in comparing the shell structure information with previous works, the classification of Popov et al. (1989) and the *Treatise* is followed here.

Ungula inornata (Mickwitz, 1896)

Figures 2, 3

- 1896 *Obolus triangularis* n. sp.; Mickwitz, p. 145, pl. II, figs 7–9.
- 1896 *Obolus panderi* n. sp.; Mickwitz, p. 149, pl. II, fig. 13.
- 1906 *Obolus triangularis* Mickwitz; Moberg & Segerberg, p. 65.
- 1912 *Obolus triangularis* Mickwitz; Walcott, p. 419.
- 1969 *Obolus (Obolus) triangularis* Mickwitz; Goryanskij, p. 24, pl. I, figs 21, 22.
- 1989 *Ungula inornata* (Mickwitz); Popov & Khazanovitch, p. 121, pl. 6, figs 1–4, 14; pl. 7, figs 19, 22–24.
- 1993 *Ungula inornata* (Mickwitz); Puura & Holmer, p. 219, fig. 2G–J.
- 1999 *Ungula inornata* (Mickwitz); Cusack, Williams & Buckman, p. 803, pl. 6, fig. 9; pl. 9, figs 5, 6 (shell structure).
- 2003 *Ungula inornata* (Mickwitz); Popov & Holmer, p. 7, fig. 3B.
- 2006 *Ungula inornata* (Mickwitz); Nemliher, p. 264, pl. 1, figs 5, 6 (shell structure).

Diagnosis. See Puura & Holmer (1993).

Remarks. *Ungula inornata* is the replacement name for *Obolus triangularis* Mickwitz, 1896. It was proposed by Popov & Khazanovitch (1989), who recognized the synonymy of *O. triangularis* Mickwitz, 1896 and *O. triangularis* var. *inornatus* Mickwitz, 1896. If the species *O. triangularis* were assigned to the genus *Ungula*, *U. triangularis* would have become a junior secondary homonym of *U. triangularis* Pander, 1830. Therefore, the assignment of the replacement name was necessary. *Ungula inornata* (Fig. 2) differs from the other species of the genus, *U. ingrlica* and *U. convexa* Pander,

1830 (see Popov et al. 1989) by the presence of well-developed concentric rugae on both valves and by the subtriangular outline of the ventral valve. The posterior part of the shell is thinner than that of *U. ingrlica* and the heart-shaped depression in the ventral valve is shallower. The distinct sulcus on the dorsal valve does not occur in other species of the genus.

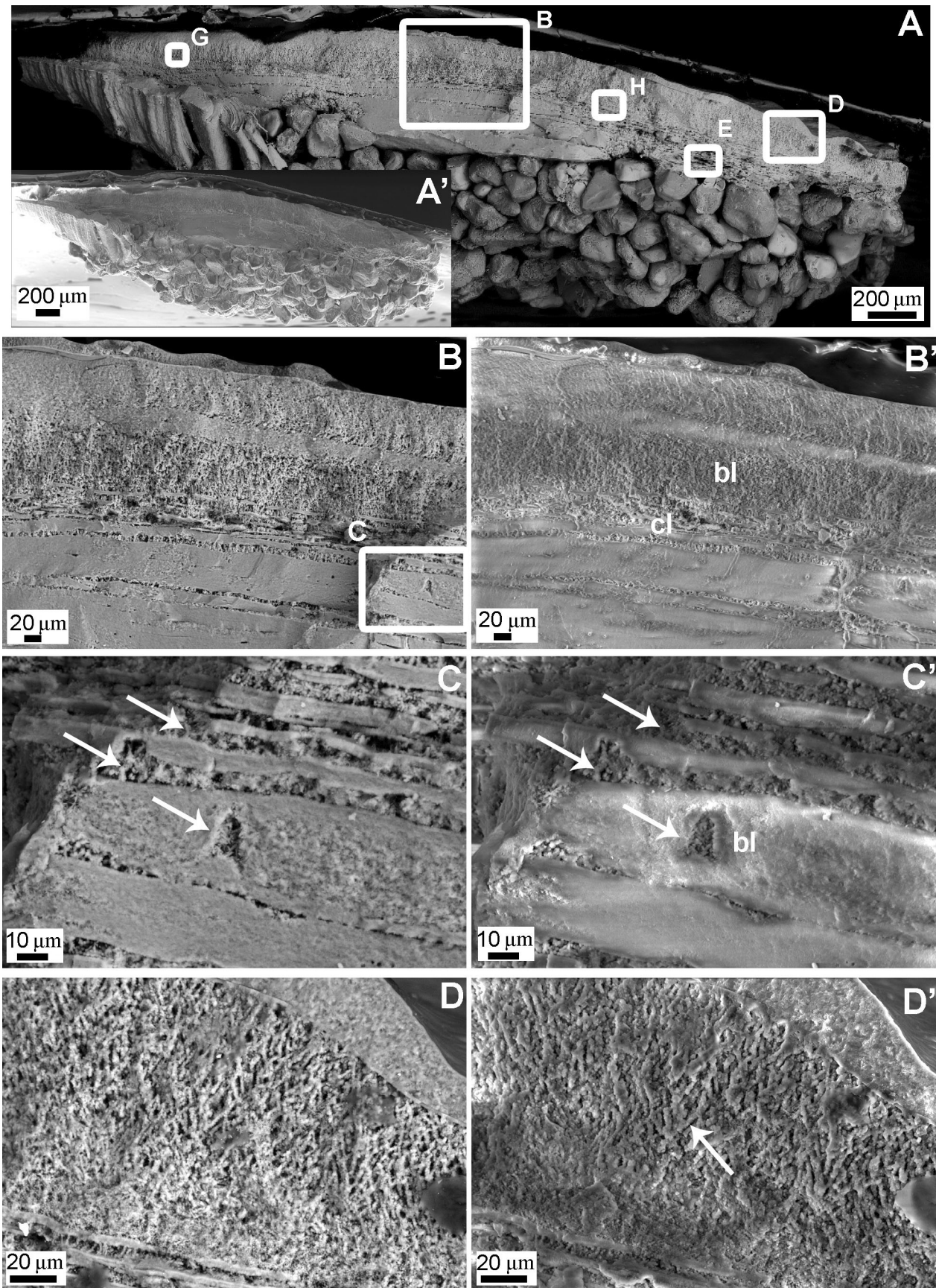
RESULTS AND DISCUSSION**Shell structure of *Ungula inornata***

Previous pilot studies have documented the presence of the baculate symmetrical structure in *U. inornata*. Backscattered electron images of the shell structure published by Cusack et al. (1999, pl. 6, fig. 9; pl. 9, figs 5, 6) show the baculate structure, rather poorly expressed due to precipitation of secondary apatite. Secondary electron images of a fragment of a dorsal valve treated with 20% H₂O₂ have revealed baculate lamination, with 20 µm distance between observed compact layers (Nemliher 2006, pl. 1, figs 5, 6). In both cases, the material originates from the Ülgase Formation of the Mäekalda section in Tallinn, Estonia, which was temporarily exposed in the course of the road construction near the centre of the town (Mens et al. 1989).

The secondary shell of the *U. inornata* ventral valve has baculate lamination, characteristic of the baculate symmetrical type (see Cusack et al. 1999). The total observable thickness of the studied valve is 460 µm. Densely mineralized compact laminae alternate with baculate laminae (Fig. 3A–E). The thickness of fully developed compact laminae, usually occurring symmetrically in both sides of a membranous lamina, is 1–2 µm.

The baculate laminae reach their maximum thickness in the medium part of the valve and it decreases to 80–100 µm in the posterior and anterior parts (Fig. 3A).

Fig. 3. Pairs of SEM photos of *Ungula inornata* (TUG 1323-4) from the Ülgase Formation (Cambrian, Furongian) of the Ülgase outcrop in backscattered electron (BSE; A–H) and secondary electron (SE; A'–H') imaging regimes. **A/A'**, general view of the studied valve with rectangles indicating the locations of subsequent images (B, D, E, G, H). **B/B'**, close-up of a part of A showing the alternation of compact (cl) and baculate (bl) laminae; the rectangle indicates the location of images C. **C/C'**, close-up of a part of B, showing varying preservation of baculate laminae (pointed by arrows) alternating with compact laminae. Note that the baculate structure observable in the BSE regime (C) is in part obscured in the SE image (C') by likely remains of organic matter (see arrows). **D/D'**, close-up of a part of A showing a wide baculate lamina in the upper part of the shell. The white arrow is pointing to a baculum. **E/E'**, compact and baculate laminae at the lower part of the shell showing thin fibrils, well observable both in BSE (E) and SE (E') regimes; the rectangle indicates the location of image F. **F/F'**, close-up of nanofibrils observable in E. Note the effect of BSE (F) and SE (F') regimes on the observable width of the fibrils. **G/G'**, bacula from the upper middle part of the shell covered with aggregates of apatite (spherulites), creating an impression of rather thick bacula in cross section. Note the better observable bacula in BSE images (G) and better expressed crust-like surface features observable in SE images (G'). **H/H'**, alternation of baculate (bl) and compact (cl) laminae in the middle part of the shell; both laminae are composed of aggregates of apatite needles. Compact laminae occur usually in pairs, separated by a membranous lamina (ml). Note the sharper contrast in the BSE image (H) helping to locate membranous laminae within compact laminae and richer information on the sculpture of the broken surface of compact laminae in the SE image (H').



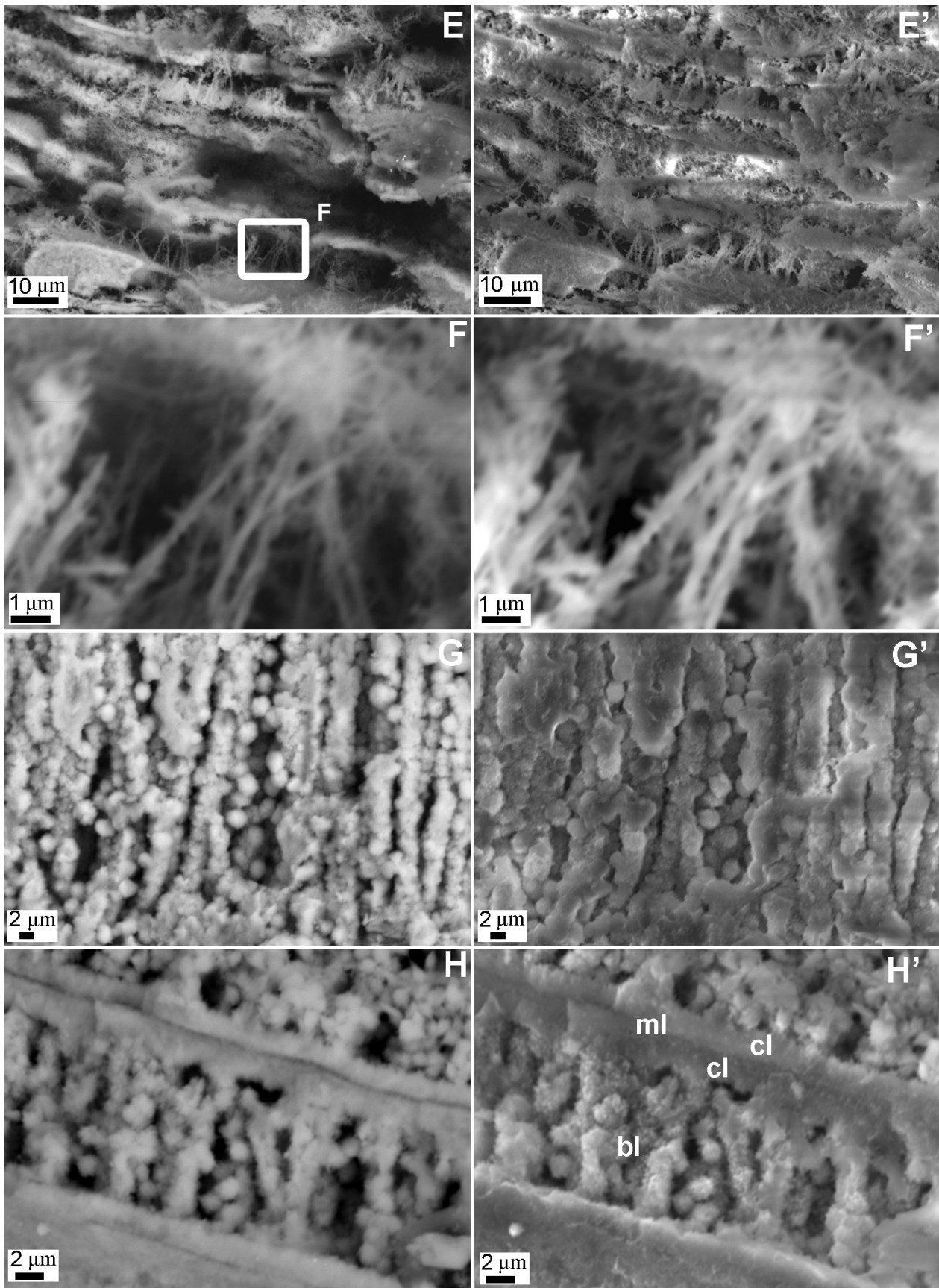


Fig. 3. Continued.

In the cross section of the valve, thicker baculate laminae occur closer to the exterior of the valve (Fig. 3B, D). The thickness of the outermost baculate lamina reaches 140 μm . The next laminae are 80–90 μm and those in about mid-valve about 20 μm thick. Near the internal part of the valve, the thickness of baculate laminae decreases to 2–12 μm and is close to that of compact laminae.

The best-preserved organic nanostructures, flexible nanofibrils connected with nets of thinner fibrils, which presumably preserved by instant *post-mortem* precipitation of apatite, are observable near the internal part of the valve both in BSE and SE regimes (Figs 3E, F and 3E', F', respectively). The phosphatized nanostructures are reminiscent of the baculate sets of a living brachiopod *Discinisca tenuis*, where bacula are embedded in the matrix consisting of biopolymers, such as glycosaminoglycans (GAGs) and chitin (cf. Williams et al. 1998, p. 2012, fig. 7; Williams & Cusack 2007, p. 2444, fig. 1595). From the experiments with modern linguloids, using the digestion of the GAGs matrix of baculate laminae with enzymes, proteinase-K or subtilisin, Williams & Cusack (2007, p. 2442) have concluded that the bacula have axial proteinaceous strands bounded by protease-resistant chitinous strands and meshes.

Some sections near the interior of the valve appear to be homogeneous when observed with lower magnifications (Fig. 3B). However, in higher magnifications, BSE images show the baculate structure (Fig. 3C), especially well recognizable in cavities on the fractured surface. The structure is partly masked in SE images (Fig. 3C').

In the outermost part of the valve, the baculate laminae are the thickest, and the length of bacula may reach over 100 μm (Fig. 3B, D). In some cases, local lense-like compact laminae may occur in this kind of baculate lamina. Bacula occurring in upper wide baculate laminae are well mineralized and rod-like, up to 3 μm in diameter (Fig. 3G, G'). Similar rod-like bacula, but shorter and thinner (around 1 μm in diameter), occur in the parts of the valve where the baculate laminae get narrower, about 4–5 times the thickness of the compact laminae (Fig. 3H, H'). The bacula form symmetrical trellised sets that are partly better observable in BSE images (Fig. 3B, D), while the SE images of the surface structure (Fig. 3B', D') complement the BSE observations.

Shell structure of related genera

Baculate symmetrical shell structure (cf. Williams & Cusack 1999) is characteristic of most genera in the order Lingulida, including the family Obolidae. According to cladistic analysis of the chemico-structural characters of the shell, *Ungula* is phylogenetically closely related to the genera *Obolus* Eichwald, 1829, *Oepikites*

Khazanovitch & Popov, 1984 (in Khazanovitch et al. 1984) from the Cambrian of Baltoscandia, and also *Experilingula* Koneva & Popov, 1983 from the Cambrian of Kazakhstan. This clade is related to another clade including Ordovician *Pseudolingula* Mickwitz 1909, Devonian *Lingulasma* Ulrich, 1889, Devonian–Carboniferous *Bicarinatina* Batrukova, 1969 and modern genera *Glottidia* Dall, 1870 and *Lingula* Bruguière, 1797 (Cusack et al. 1999).

Among the species of the genus *Ungula*, the shell structure of *Ungula ingraca* is best known. While introducing the new terminology for describing baculate structures, Holmer (1989) used *U. ingraca* as a model, relating the new terms to those used by Mickwitz. Drawings of light microscope images of thin sections appeared already in Mickwitz (1896). The structure of *U. ingraca* has been found to be rather homogeneous in early SEM studies, and different methods of etching have been used. Holmer (1989, p. 32, fig. 32) published SE images of baculate structures in a polished cross section of a fragment of a dorsal valve of *U. ingraca* etched with 4% HCl. The SE images of Nemliher (2006) represent a fragment of a dorsal valve etched with 20% H₂O₂, showing compact laminae and baculate laminae with poorly observable bacula.

The BSE image of a fragment of *Ungula convexa* Pander, 1830, the type species of the genus *Ungula*, by Popov & Holmer (2003, fig. 6A–C) shows alternation of compact and baculate laminae resembling that of *U. inornata*. The thickness of the illustrated baculate laminae is 20–100 μm .

Thus, in general terms, the baculate shell structure of *U. inornata* is similar to the other species assigned to this genus. However, there is no published information on the preservation of mineralized organic nanostructures in *U. ingraca* or *U. convexa*.

The type species of the Cambrian genus *Obolus* Eichwald, 1829, *O. apollinis* Eichwald, 1829, occurring in the uppermost Cambrian of NW Russia and sub-surface of Estonia, has been chosen by Cusack et al. (1999, text-fig. 6) as a model of typical shell structure for Palaeozoic obolids and linguloids. The BSE images of a valve in Cusack et al. (1999, pl. 6, figs 3, 4, 6–8) and Williams & Cusack (1999, p. 236, fig. 6; 2007, pp. 2441–2442, figs 1592–1593) show baculate sets, numbering 27, as stated by the authors. The maximum observable thickness of the outermost baculate lamina is 150 μm . The SE image of a fragment of the valve treated with 5% H₂O₂ found in Nemliher et al. (2004) shows baculate sets with 2–35 μm thick baculate laminae. The close-up of a BSE image of baculate sets by Lang et al. (2011, p. 361, fig. 2A) exhibits bacula covered by spherulitic apatite aggregates. No published images of nanostructures of *O. apollinis* are available.

The BSE images of nanostructures in *Obolus ruchini* Khazanovitch & Popov, 1984 (in Khazanovitch et al. 1984) presented by Lang et al. (2011, fig. 3) reveal sets of phosphatized flexible organic nanofibrils. These are interpreted as biopolymer strands resembling those in *U. inornata* (cf. Fig. 3F and Lang et al. 2011, fig. 3F).

The only known BSE image of the shell structure of *Experilingula divulgata* Koneva & Popov, 1983 from the Cambrian (Furongian) of Kazakhstan, published by Cusack et al. (1999), depicts a fragment of a valve with broken bacula recrystallized into prisms. No further information on the shell structure of the genus *Experilingula* is available.

The genus *Bicarinatina* Batrukova, 1969 is illustrated by BSE images of an oblique view of baculate sets in *B. wilsoni* Graham, 1970 from the Carboniferous (Mississippian) of Scotland (Cusack et al. 1999, text-fig. 3G, H) and cross section with baculate sets of *B. bicarinata* Kutorga, 1837 from the Devonian (Eifelian) Narva Stage, Kernavè Formation of Estonia (Lang & Puura 2009, fig. 3). In the innermost baculate laminae, flexible phosphatized organic nanofibres resembling those of *U. inornata* and *O. ruchini* have been observed (Lang et al. 2011, fig. 3F).

The above discussion shows that the overall hierarchical shell structure of *U. inornata* is closely similar to that of the species of the genus *Obolus*. Moreover, the observations in Palaeozoic linguloids are consistent with the scanning and transmission electron microscopy studies of the shell structure of a modern linguloid *Discradisca stella* exhibiting similar flexible nanofibrils in the secondary layer (Merkel et al. 2007; Schmahl et al. 2008). In the nanostructure level, these studies reveal structures relevant in the build-up of baculate sets, laminae and individual bacula of the living species (e.g. from the genera *Glottidia*, *Discina*, *Discinisca*, *Pelagodiscus* and *Discradisca*), which are well comparable to those in the Cambrian species *U. inornata* and *O. ruchini* (see Lang et al. 2011) and offer valuable information for the interpretation of phosphatized organic structures in fossil shells.

CONCLUSIONS

In the light of the new results and earlier data, as expected from the cladistic analysis of the phylogenetic relationships of linguloids (Cusack et al. 1999; Williams & Cusack 1999, 2007), the shell structure of the representatives of the genera *Obolus* and *Ungula* is rather similar. The genus- and species-level differences need further study in a wider context, comparison of the taxon-specific differences in shell structure and consideration of the effects caused by taphonomic changes.

The secondary layer of the studied valve of *Ungula inornata* has baculate symmetrical shell structure (cf. Williams & Cusack 1999), with well-expressed alternation of baculate and 1–2 µm thick compact laminae. In cross section, the maximum thickness of the baculate laminae reaches 140 µm in the outermost part of the valve, 20 µm in the middle part and 2–12 µm in the innermost part, where fine nanofibrils are preserved.

Nanofibrils described in *U. inornata* are similar to those known in *Obolus ruchini* and *Bicarinatina bicarinata* (Lang & Puura 2009; Lang et al. 2011). By analogy with modern genera *Discinisca* and *Glottidia* (Williams et al. 1998; Williams & Cusack 2007), the details of the nanostructures of *U. inornata* and related fossil linguloids allow us to interpret the nanofibrils as biopolymers supporting the formation of bacula. Tentatively, assuming chemico-structural similarities with modern *Discinisca*, these phosphatized biopolymers can be interpreted as proteinaceous axial strands of bacula and sheets and meshes of chitin. The nanofibrils are relevant structural units in the hierarchical structure of lingulate brachiopods with baculate shell structure. Our present and earlier studies have shown that phosphatized organic nanostructures in lingulate brachiopods may not be as rarely preserved as previously thought, and they can be found in a large variety of taphonomic conditions.

Assuming, as a work hypothesis, similar or at least analogous roles of biopolymers in forming nanostructures of fossil lingulates from the Cambrian to the Holocene, the nanostructures and the hierarchical shell structure in general could be interpreted as resulting from the initial chemico-structural properties of the organophosphatic shell and conditions and pathways of *post-mortem* processes affecting the preservation of the shell structure in all hierarchical levels. In the phylogenetic context already known, this opens an opportunity to study the role of taphonomic overprint to the observable structure of fossil lingulate shells.

Our studies have shown that, in many cases, especially in higher magnifications, BSE images bearing compositional information are more informative than SE images for observing nanostructures and shell structure in general. However, both types of images complement each other and without documenting the structures in both regimes, some relevant details may be missed.

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Fosfatiseerunud orgaanilised nanostruktuurid Kambriumi brahhiopoodil *Ungula inornata* (Mickwitz)

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Skaneeriva elektronmikroskoobi (SEM) abil uuriti linguloidide hulka kuuluva fosfaatse kojaga Kambriumi käsijalgse *Ungula inornata* (Mickwitz) koja ristlõike töötlemata ja katmata murdepindu, rakendades režiimi, mis võimaldas samaaegselt kuvada ning salvestada tagasihajunud elektronide (BSE) ja sekundaarsete elektronide (SE) abil saadud kujutisi. Kojas avastati fosfatiseerunud orgaanilised kiulised struktuurid läbimõelduga alla 200 nm, mis on omavahel ühendatud peenemate kiudude võrgustikuga. Võrdlus tänapäevaste käsijalgsete perekonnaga *Discinisca* varem avaldatud tööde põhjal lubab järeldada, et kiire fosfatiseerumine on talletanud 500 miljoni aasta vanuse käsijalgse orgaanilise struktuuri peenimadki detailid, sealhulgas koja ehituses oluliste apatiidist varraste teljeks olevad valgukiud ja nendega ühendatud kitiinist võrgustiku. *Ungula inornata* koja struktuur on kõige sarnasem sama perekonna ja perekonna *Obolus* liikide kodade struktuuridega. Vaadeldud nanostruktuurid on võrreldavad paljude seni uuritud fossiilsete ja praegu elavate lingulaatide, fosfaatse kojaga käsijalgsete struktuuridega.