

A new type of shell structure in a phosphatic brachiopod from the Cambrian of Estonia

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Abstract. Shell structures of *Ungula ingraca*, *U. inornata*, and *Ungula* sp. 1 (Kallavere and Ülgase formations) from Cambrian sandstones of the Mäekalda section in Tallinn, Estonia, were studied. Specific alterations were recorded in the shell structures of *U. ingraca* and *Ungula* sp. 1. Several generations of precipitation of phosphatic matter inside the shells could be distinguished, marking (1) original biomineralization events, (2) phosphatization of soft tissues, and (3) later diagenetic alteration of mineral matter and/or structures inside the shells. The shells of *U. inornata* and *U. ingraca* were found to represent the baculate structure type typical of the genus. The shell structure of *Ungula* sp. 1 is different, consisting of alternating compact and primarily organic-rich laminae. No *bacula* were found in the latter laminae. Compact laminae are penetrated by *tubuli*, filled with phosphatized organic matter. This structure type is termed here as tubulate shell structure.

Key words: Lingulata, *Ungula*, shell structure, Cambrian, Estonia.

INTRODUCTION

Lingulates are known since the Early Cambrian and represent the oldest survived group of organisms characterized by phosphatic biomineralization. One of the diagnostic features of the class Lingulata is a native chitino-phosphatic shell (Gorjansky & Popov 1986).

The shell structures of lingulates, both fossil and Recent, have been described for more than a century (Gratiolet 1860). However, detailed studies of shell structure as a diagnostic tool have mainly been carried out in the last three decades (Iwata 1981; Pan & Watabe 1988; Holmer 1989; Ushatinskaya 1990; Williams & Holmer 1992; Williams et al. 1994, 1998, 2004; Williams & Cusack 1999; Skovsted & Holmer 2003; Streng & Holmer 2005). These studies have revealed several structure types of Cambrian–Ordovician lingulates: columnar (characteristic of acrotretids), baculate (obolids), and laminar (paterinids). Siphonotretid brachiopods have a specific shell structure, typically with prismatic laths and rods in the secondary layer

(Williams et al. 2004). A unique shell structure of one of the oldest lingulates – *Mickwitzia* – differs from all other types, showing, however, some features, close to that of acrotretids. These structure types can be used as a tool in taxonomic studies.

In the present research the shell structures of *Ungula* sp. 1 of Popov and Khazanovitch (in Popov et al. 1989), *U. inornata* (Mickwitz), and *U. ingrlica* (Eichwald), originating from the Mäekalda section, Estonia, are studied and compared in order to clarify their affinity and preservation history.

GEOLOGICAL SETTING

The Upper Cambrian–Lower Ordovician succession of the northeastern part of the East European Platform is represented by siliciclastic sandy rocks with lens-like or cross-bedded structure and numerous gaps of different duration (Mens et al. 1990). The Upper Cambrian rock units of the Baltic palaeobasin are incomplete, both vertically and laterally (Heinsalu & Viira 1997; Mens & Pirrus 1997). Layers rich in intact shells and shell fragments of lingulate brachiopods, forming phosphorite deposits of commercial interest, occur at certain levels of this succession (Raudsep 1987). In Estonia the main accumulations of such lingulate coquinas are attributed to the Ülgase (*U. inornata* Biozone), Tsitre (*Schmidtites celatus* Biozone), and Kallavere (*U. ingrlica* Biozone) formations. In the Mäekalda section only the Ülgase and Kallavere formations crop out (see also fig. 5 in Mens et al. 1999). Preservation of shells is quite variable, especially in the Kallavere Formation where the basal coquina consists mostly of repeatedly redeposited shell fragments. In the other specified formations the lingulate shells are typically better preserved.

Starting from the first palaeontological description of *Obolus apollinis* (Eichwald 1829), the systematic position of lingulates from the above-mentioned formations has been a topic of discussion for about two centuries. The present knowledge on the palaeontology of lingulates from these beds is summarized in Popov et al. (1989) and Puura (1996).

L. E. Popov and K. K. Khazanovitch (in Popov et al. 1989) described a new specimen from the basal conglomerate of the Ülgase Formation at Ülgase Village near Tallinn. As the shells were poorly preserved, but differed from the lingulate species formerly known in the region, they were referred to as *Ungula* sp. 1. Mens et al. (1999) documented phosphatic shells from the basal conglomerate of the Ülgase Formation in the Mäekalda section and assigned them tentatively to *Ungula* sp. 1 *sensu* Popov and Khazanovitch. However, due to poor preservation of shells, the precise systematic position of this species is not known. The material studied in this paper is tentatively referred to as *Ungula* sp. 1. Although the systematic position of that brachiopod is uncertain, its shell structure is of interest as it differs from those of the other Cambrian lingulate brachiopods identified in the same region. Presumably the pebbles that yielded the specimens originate from the eroded part of the earliest Upper Cambrian (Mens et al. 1999).

MATERIAL AND METHODS

The Mäekalda section, which is no longer accessible, was exposed along a road cut in the city of Tallinn (see Mens et al. 1989, 1999 for location and stratigraphical details). The section was sampled during fieldwork in 1987 as follows: pebbles from the basal conglomerate of the Ülgase Formation (N-62), lingulate brachiopod shells from the Ülgase Formation (N-63 and N-63A), and basal lingulate shell coquina of the Kallavere Formation (N-60). All samples are deposited in the Department of Collections of the Institute of Geology at Tallinn University of Technology.

Valves of *Ungula* sp. 1 (*sensu* Popov and Khazanovitch) were extracted mechanically from pebbles of the basal conglomerate of the Ülgase Formation. Besides, a number of pebbles were cut with a diamond saw in order to reveal the cross-sections of shells. Valves of *U. inornata* (Mickwitz) from the Ülgase Formation and *U. ingrlica* (Eichwald) from the Kallavere Formation were picked out of weakly cemented sandstone.

Fractured and polished cross-sections of shells, untreated and treated with 10% HCl (30 s) or 20% H₂O₂ (about 3 min), were studied. After treatment shells were washed with distilled water, dried, mounted, covered with gold, and examined under SEM, Tesla BS 300 equipment, operating at 20 KeV. Altogether, 51 cross-sections were examined.

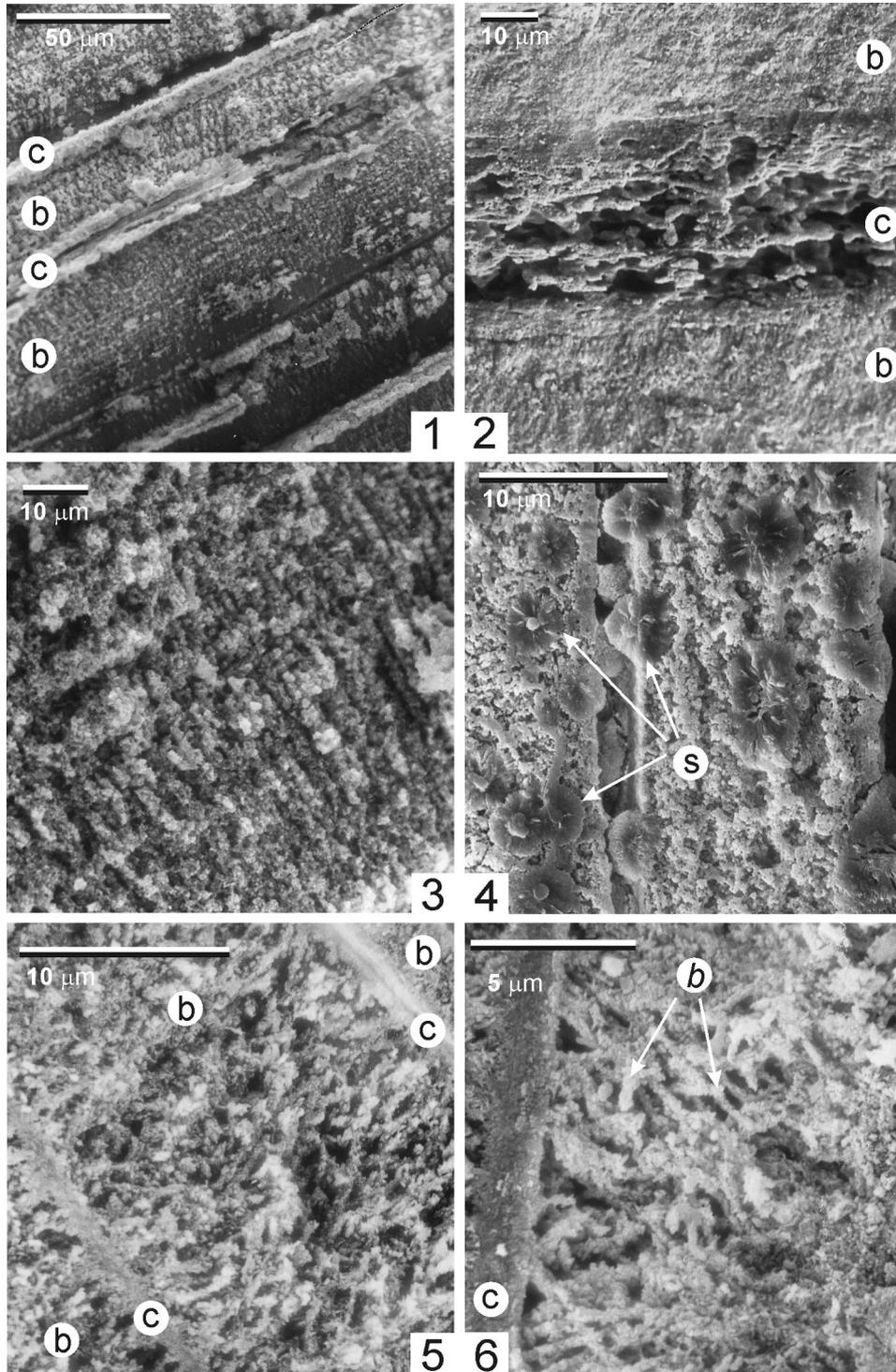
RESULTS AND DISCUSSION

Representatives of the genus *Ungula* have a baculate shell structure. Holmer (1989) established this structure type on specimens of *U. ingrlica* from the basal beds of the Kallavere Formation in the Jägala-Joa section, Estonia.

Shell architecture of the studied samples of *U. ingrlica* and *U. inornata* was identified as belonging to the baculate type. This structure is typically an alternation of compact (primarily, layers with a higher mineral content) and baculate laminae. The latter are primarily organic-rich layers in the shell, containing a large number of originally mineralized particles forming the *bacula*. This shell architecture should be considered as the primary shell structure type of the genus *Ungula*.

***Ungula ingrlica*.** The typical shell structure of this species shows an alternation of thin compact (c) (commonly ranging from a few micrometres to 10 µm) and much thicker baculate (b) (20–30 µm) laminae (Pl. I, fig. 1). However, the structure of the specimens from the Mäekalda section is variously preserved, presumably due to the influence of taphonomic processes on the accumulation of shells and diagenetic alteration of different extent and intensity. So, valves showing an almost homogeneous appearance of the shell in cross-section are abundant. Etching, however, brings forth alternation of compact (c) and baculate (b) laminae (Pl. I, fig. 2), while compact laminae have a multi-lamellae (*sensu* Holmer 1989) structure. It is assumed that homogenization of baculate laminae has taken place due to a large amount of secondarily added apatitic material, formed via phosphati-

PLATE I



zation of the organic compound in baculate laminae. This second generation of apatitic matter inside shells has a characteristic structure and has been termed as collophanous calcium phosphate (CCP) by Holmer (1989).

Phosphatization of organic matter requires an alkaline and reducing (micro-) environment (Briggs & Kear 1993). Such conditions in the earliest stages of *post mortem* development of lingulate valves are confirmed by the typical dark colour and high pyrite content (detected by the X-ray diffraction method) of *U. ingrlica* shells from the Mäekalda section (Nemliher & Puura 1996a). Nemliher et al. (2004) have identified the presence of both, primarily secreted and secondarily added apatite varieties in shells of lingulate brachiopods from the *Obolus*-sandstone of the Northeastern European Platform. This serves as another evidence of the conditions conducing to organic matter phosphatization in shells at the very early diagenetic stages.

A common structure observed in shells of *U. ingrlica* is chains of spherical phosphatic particles inside baculate laminae, arranged perpendicular to the compact lamina (Pl. I, fig. 3). This structure, similar to the structural unit “walled lamina” in terms of Williams et al. (1994), is also interpreted here as being formed *post mortem* as a result of phosphatization of the original structure of the organic matter in the shell.

The above-described variations in shell architecture of *U. ingrlica* have been complicated by later diagenetic alteration. Among them the third generation of apatite can be clearly distinguished (Pl. I, fig. 4), building well-distinguishable

Explanation of Plate I

Fig. 1. Fractured cross-section of a dorsal valve of *Ungula ingrlica*, etched with 10% HCl, sample N-60-27, basal coquina of the Kallavere Formation. Alternation of compact (c) and baculate (b) laminae.

Fig. 2. Fractured cross-section of a dorsal valve of *Ungula ingrlica*, etched with 10% HCl, sample N-60-3, basal coquina of the Kallavere Formation. Structure of a poorly preserved but obviously multilayered primarily compact (c) lamina between possibly primary baculate laminae (b).

Fig. 3. Fractured cross-section of the dorsal valve of *Ungula ingrlica*, etched with 10% HCl, sample N-60-27, basal coquina of the Kallavere Formation. Altered structure of a baculate lamina, displaying the arrangement of apatitic particles, formed during phosphatization of organic matter inside the shell, perpendicular to the compact lamina.

Fig. 4. Polished and etched (10% HCl) cross-section of a dorsal valve of *Ungula ingrlica*, sample N-60-60, basal coquina of the Kallavere Formation. Spherulitic apatite bodies (s) of the third generation of apatite, displaying typical radial structure.

Fig. 5. Fractured cross-section of a dorsal valve of *Ungula inornata*, treated with 20% H₂O₂, sample N-63A-17, Ülgase Formation. Typical baculate structure, showing alternation of baculate (b) and compact laminae (c).

Fig. 6. Fractured cross-section of a dorsal valve of *Ungula inornata*, treated with 20% H₂O₂, sample N-64A-15, Ülgase Formation. Structure of a baculate lamina, displaying the characteristic shape of the *bacula* (b). Note the small amount of secondary apatite filling the space between the *bacula*.

spherical bodies (s) inside the shell. Typically, the dimensions of these spherulites are about 2–3 μm . They have a radial structure and have been reported to be common in secondarily altered biological phosphates (Nemliher 2001) as well as in phosphates of diagenetic origin (Nemliher & Puura 1996b).

***Ungula inornata*.** Compared to *U. ingrlica*, the shell structure of *U. inornata* from the studied section of the Ülgase Formation is much less variable. Only the baculate shell structure type has been identified (Pl. I, fig. 5), resembling that of *U. ingrlica* structure in compact laminae as well as in the nature and orientation of *bacula* (b in Pl. I, fig. 6). Possibly, due to preservation of only primarily mineralized shell components (the first apatite generation), the shell structure is the same as in *Tilasia rugosa* (Holmer 1991) or *Obolus apollinis* (Williams & Cusack 1999). This interpretation is supported by the light colour of *U. inornata* shells from the Ülgase Formation of the Mäekalda section as well as by the absence of pyrite in the shells, indicating lack of strong reducing environmental conditions.

***Ungula* sp. 1.** As in all lingulates, shells of this species are built up of a rhythmic alternation of laminae marking different mineralized tissue secretion events (Pl. II, fig. 1). They are called here “organic layers” (o in Pl. II, fig. 1) due to the lack of *bacula* in primarily organic-rich layers. However, the fine microstructure of these organic layers is very similar to that of the baculate layer in *U. ingrlica* (cf. Pl. I, fig. 1 and Pl. II, fig. 1), which refers to the CCP nature of the former. Thus, it is assumed here that those layers were initially organic-rich (= baculate layer of *U. ingrlica*), filled with the apatite formed due to phosphatization of organic matter inside the valve.

Explanation of Plate II

Fig. 1. Polished cross-section of a phosphatized pebble containing a valve of *Ungula* sp. 1 (?), etched with 10% HCl, sample N-62-54, basal conglomerate of the Ülgase Formation. Alternation of compact (c) and primarily organic-rich laminae (o). Q, quartz grain, p, phosphatic cement of the pebble. Note the similarity between the structures of organic layers and phosphatic cement.

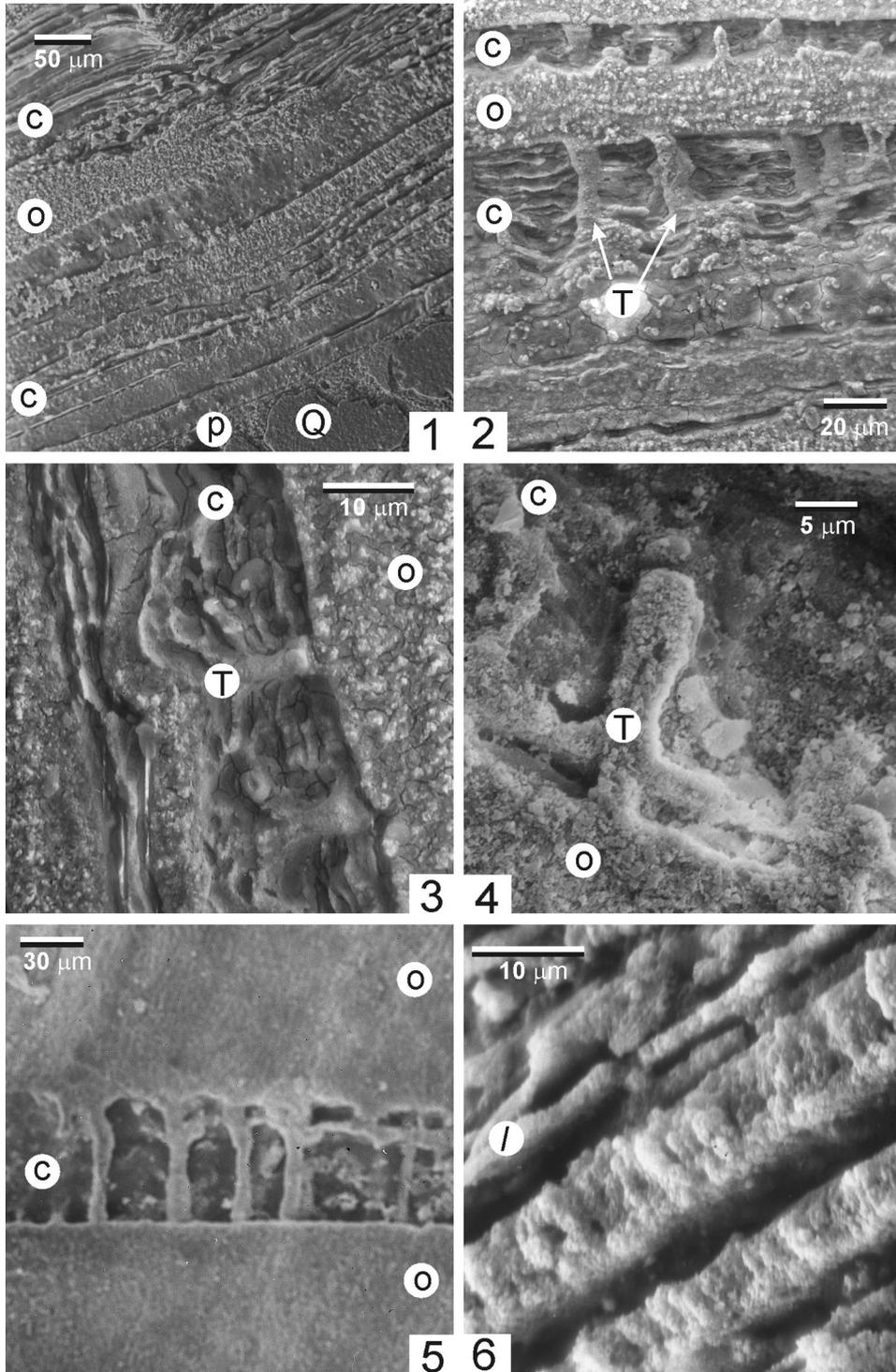
Fig. 2. Polished cross-section of a dorsal valve of *Ungula* sp. 1, etched with 10% HCl, sample N-62-52, basal conglomerate of the Ülgase Formation. Alternation of compact (c) and primarily organic-rich laminae (o). Compact laminae, displaying a multi-lamellae structure, are penetrated by *tubuli* (T).

Fig. 3. Polished cross-section of a dorsal valve of *Ungula* sp. 1, etched with 10% HCl, sample N-62-52, basal conglomerate of the Ülgase Formation. Compact lamina (c), displaying a multi-lamellae structure, is penetrated by a *tubulus* (T).

Fig. 4. Polished cross-section of a dorsal valve of *Ungula* sp. 1, etched with 10% HCl, sample N-62-52, basal conglomerate of the Ülgase Formation. *Tubulus* (T) in the compact (c) lamina. Note the similarity between the structures of apatite filling the organic layer (o) and *tubulus*.

Fig. 5. Polished cross-section of a dorsal valve of *Ungula* sp. 1, treated with 20% H_2O_2 sample N-62-4, basal conglomerate of the Ülgase Formation. The organic layers (o) display a homogeneous structure, while the compact (c) lamina reveals multi-lamellae architecture.

Fig. 6. Polished cross-section of a dorsal valve of *Ungula* sp. 1, etched with 10% HCl, sample N-62-11, basal conglomerate of the Ülgase Formation. The compact lamina is formed of lamellae (l).



Generally the shell structure of *Ungula* sp. 1 consists of an alternation of compact and organic layers. A distinctive feature of this taxon is that compact laminae may be penetrated by tube-like structures, typically about 4 µm in diameter (termed here as *tubuli*; T in Pl. II, figs 2, 3), beginning from organic layers and often not reaching the next compact lamina (Pl. II, fig. 4). No *bacula* were detected in the “baculate” lamina (organic layer or chitine layer *sensu* Iwata 1981). On the contrary, the structure of the compact lamina resembles that of the baculate structure type (Pl. II, figs 2, 3, 6). Proceeding from that it might be concluded that *tubuli*, filled with organic matter and emanating from organic layers, penetrate the primarily mineralized (= compact) laminae (Pl. II, fig. 4). Such organization of shell architecture of fossil obolids is called here a tubulate shell structure.

It is important to note that the described feature of the shell structure of *Ungula* sp. 1 is different from the columnar structure of acrotretoid brachiopod shells (Williams & Holmer 1992), as well as from that of *Mickwitzia* shells (Skovsted & Holmer 2003), where columns penetrate initially organic-rich layers.

The shell structure of *Ungula* sp. 1, like that of *U. ingrlica*, occurring in the basal beds of the Kallavere Formation, is variably preserved. However, more or less homogeneous shells without baculate architecture can be found (Pl. II, fig. 5). Similarly to *U. ingrlica*, the multi-lamellae (*l*) structure of the compact lamina has been revealed after etching (Pl. II, fig. 6).

It may be concluded that the tubulate shell architecture of *Ungula* sp. 1 should be regarded as primary and biologically formed one. So, in spite of the similarity in the shell morphology of *Ungula* sp. 1, *U. ingrlica*, and *U. inornata*, the taxonomic position of *Ungula* sp. 1 in the genus *Ungula* is tentative.

CONCLUSIONS

Several generations of phosphatic matter precipitation were recorded in the shells of fossil lingulates from the Cambrian part of the Mäekalda section, marking (1) original biomineralization events, (2) phosphatization of organic matter, and (3) later diagenetic alteration of mineral matter/structures inside fossil shells. The following conclusions can be drawn:

1. Shells of *U. ingrlica* from the Kallavere Formation have a typical baculate structure. Large-scale variation in the preservation of shell structure and the extent of secondary changes indicate different *post mortem*, transportation, and postsedimentary conditions during the Kallavere Age.
2. Shells of *U. inornata* from the Ülgase Formation have also a baculate structure. Variations and the extent of secondary changes in the shell structure of this species are less substantial, indicating constant *post mortem*, transportation, and postsedimentary conditions during the Ülgase Age.
3. Shells of *Ungula* sp. 1 from the basal conglomerate pebbles of the Ülgase Formation have a tubulate structure. For this reason this species cannot probably be assigned to the genus *Ungula*. Large-scale variations in the preservation of

the shell structure with numerous secondary alterations indicate heterogeneity of *post mortem*, transportation, and postsedimentary conditions during the pre-Ülgase Age.

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Eesti Kambriumist pärinevate fosfaatse kojaga käsijalgsete poolmete uus struktuuritüüp

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On uuritud Tallinnas asunud Mäekalda paljandi Kambriumi liivakividest pärinevate *Ungula ingrlica*, *Ungula inornata* ja *Ungula* sp. 1 (Kallavere ja Ülgase kihistud) karbistruktuure. Liikide *Ungula ingrlica* ja *Ungula* sp. 1 poolmetes on tuvastatud spetsiifiliste muutuste olemasolu – võimalik on eristada mitmeid apatiitse ainese generatsioone, mis märgivad: (1) biomineralisatsioonil tekkinud originaalset poolmete struktuuri; (2) poolmetes sisaldunud orgaanilise aine fosfatiseerumist; (3) hilisemat, diageneesi etapil aset leidnud mineraalse ainese poolmesisest ümberjaotumist. On leitud, et *Ungula ingrlica* ja *Ungula inornata* poolmed on tüüpiliselt bakulaatse struktuuriga, mis on sellele perekonnale omane. *Ungula* sp. 1 poolmete struktuur seevastu on üles ehitatud mineraliseerunud ja algselt orgaanikarikaste kihtide vaheldumisena; viimastes pole baakulaid leitud. Mineraalsed kihid on läbistatud torujate struktuuride poolt (*tubuli*), mis on täidetud fosfatiseerunud orgaanilise ainega. Selline struktuuritüüp on nimetatud tubulaatseks poolmete struktuuriks.