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CAMBRIAN LINGULOID SHELL STRUCTURES AND TAPHONOMIC CHANGES

MSc thesis

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I propose for this part of paleontology the name of "TAPHONOMY", the science of the laws of embedding […]. It stands on the border of paleontology, uniting it both with geology and biology into one general geo-biological historical method of study. […]. Taphonomical research allows us to glance into the depth of ages from another point of view than that which is in general use in paleontology.

Ivan Efremov, 1940
(Taphonomy: new branch of paleontology. "Pan-American Geologist")

Nothing in palaeontology makes sense except in the light of taphonomy and diagenesis.

Stefan Bengtson and Graham Budd, 2004 ("Science")

ABSTRACT

This MSc thesis is a comparative study of taphonomy of Cambrian linguloid brachiopods from different diagenetic settings. It focuses on three commonest genera – *Ungula*, *Obolus* and *Schmidtites* from the northern East Baltic "*Obolus* Sandstones", "Middle Cambrian" to the "Upper Cambrian" (Furongian) in age. The studied material originates from eight outcrops and two drill cores in Estonia and Ingria (Leningrad Region) in north-western Russia. An environmental scanning electron microscope (ESEM) equipped with detectors for back-scattered electron imaging and energy-dispersive x-ray spectroscopy (EDS) was used to study untreated fracture sections of linguloid valves, to minimize the eventual loss of information on microstructure caused by chemical and mechanical treatment and coating.

The shell structure of *Obolus apollinis* displays a typical preservation of baculate laminae. The structure of *Obolus ruchini* shows the "fibrils" of mineralized organic framework that form a substrate for mineralization of *baculi* and the precipitation of authigenic minerals, such as hematite covering the *baculi* and filling the pore space released after the destruction of organic matter. Similar situation is illustrated by *Ungula convexa* from the Furongian of the NW Russia. Baculate shell structure of *Ungula ingrica* can be observed in rare cases, because it is often masked by the precipitated apatite that has filled all the space left after the degradation of organic matter. Similar structureless appearance, with fragmentary "windows" showing baculate shell structure, is also characteristic of *Ungula inornata* and *Schmidtites celatus* from the Furongian of Estonia. In addition to the precipitated apatite, local occurrences of precipitated pyrite occupying the space left after degradation of organic matter in baculate layers can be observed, e.g., in *Schmidtites celatus* and *Ungula* sp. from the pebbles from the basal Furongian of Estonia.

These observations show how similar initial shell structures (all baculate symmetrical) may turn into rather different observable structures in the fossil state, depending on diagenetic scenarios. This study of linguloid brachiopod taphonomy illustrates the heterogeneity of phosphatic fossils as geochemical archives. It implies that, where applicable, it is advisable to combine the geochemical intepretations with shell structure and taphonomy studies.

CONTENTS

1. INTRODUCTION

Studies on taphonomy of fossils have gained increasing attention in the context of modern geochemical and geological studies. The term taphonomy (from Greek "taphos" (burial) and "nomos" (law)) was introduced by Efremov (1940) to signify a branch of palaeontology dealing with "the laws of embedding" and standing "on the border of paleontology, uniting it both with geology and biology into one geo-biological method of study". At present, the research foci of taphonomy (*sensu lato*) are subdivided into *biostratinomy*, dealing with interpretation of fossils and strata to reveal the scenarios of mechanical accumulation and sorting of fossils (e.g. Behrensmeyer et al., 2000) and taphonomy *sensu stricto* dealing with physico-chemical post-mortem changes during fossilization and diagenesis. In this study, the term *taphonomy* is used in the latter narrow sense, following the mainstream scientific articles since 1990s.

Alongside with some other invertebrates, the shells of brachiopods have attracted interest as geochemical archives. It is usually assumed that more or less "pristine" material would allow using these signals as proxies of past palaeoclimatic and palaeoenvironmental parameters. When high-resolution analytical techniques became available, geochemical heterogeneity of the composition of fossil shells, both calcitic and phosphatic, became common knowledge. Still, as often it is difficult to be selective about the fossil samples, many geochemical and isotope studies tend to use bulk samples of any available skeletal material. In these cases, the knowledge of the taphonomic factors, potentially causing biased results, is relevant. Depending on the diagenetic scenarios, the resulting shell structures look very different and the knowledge of the wide spectrum of taphonomic alteration is helpful for their interpretation.

This thesis focuses on a comparative study of Cambrian linguloid brachiopods from different diagenetic settings. The studied material originates from the Cambrian "Obolus Sandstones" of Estonia and Ingria and north-western Russia and is represented by three most common genera in these strata: *Obolus*, *Ungula* and *Schmidtites*. One of its aims is to demonstrate how initially similar shell structure may turn into rather different structures observable in a fossil state, depending on diagenetic situation and to provide a context that can support further interpretation of fossil linguloid shell structures.

2. LINGULATE SHELL STRUCTURES

2.1. Main shell structure types of lingulates in phylogenetic context

According to modern classification (e.g., Williams et al., 1996; Holmer and Popov, 2000), phylum Brachiopoda is subdivided into three subphyla: Rhynchonelliformea (former "articulate brachiopods"), Craniiformea (former "inarticulate brachiopods" with calcium carbonate shell) and Linguliiformea (former "inarticulate brachiopods" with phosphatic shell). Brachiopods with chitino-phosphatic shells belonging to Class Lingulata in Subphylum Linguliiformea are referred to as "lingulate brachiopods" or "lingulates". Lingulates include superfamilies Acrotretoidea (acrotretoids), Siphonotretoidea (siphonotretoids) and Linguloidea (linguloids). After providing the general context of lingulate shell structures, this study focuses on linguloids.

The organophosphatic shells of lingulate brachiopods are stratiform, with a thin, outer primary layer of relatively constant thickness and an inner secondary layer composed of laminae (Williams et al., 1992). Laminae differ in composition and/or fabric of their biomineral and organic components. The graphical overview after Williams and Cusack (1999) of main structures of secondary shell: baculate, columnar and botryoidal is given in Fig. 1. and their interpretation of the distribution of the lingulate shell structures in the phylogenetic context in Fig. 2.

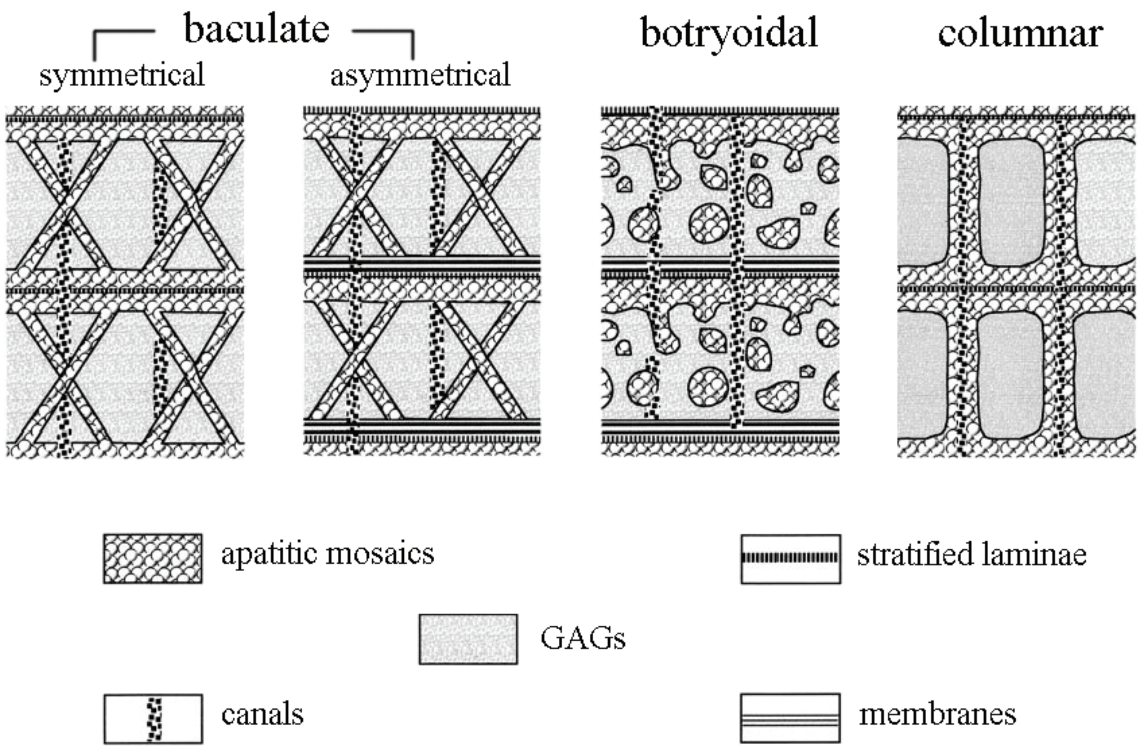

Figure 1. Graphical overview of the main structure types of the secondary layers of lingulate brachiopods: the baculate structure, which is composed of apatitic rods in trellised way, like they are in secondary layers of obolids (baculate-symmetrical) and Recent *Glottidia* (baculate-asymmetrical); botryoidal, which is composed of botryoidal sets composed of spherular apatite, like the structure of the secondary layer of Recent *Lingula*; and columnar, which is composed of apatitic "columns (modified after Williams and Cusack, 1999).

The baculate structure of secondary shell of extinct linguloids is typified by the Cambrian obolids (Cusack et al., 1999). *Obolus apollinis* has a homogeneously apatitic primary layer, which is underlain by a secondary layer composed of baculate sets. The biomineralized succession of baculate sets of *Obolus* is symmetrical about its medial plane with the rhythm of compact-baculate-compact laminae. Cusack et al. (1999) have observed that this rhythm is reduced to compact, virgose (and/or rubbly) laminae in the mid-region of the shell.

In the secondary layers of living, apatitic-shelled lingulid and the discinid brachiopods, baculate sets are dominant in *Glottidia* but are absent in another lingulid *Lingula*. In discinids they are present in both valves of *Discina* and the ventral body platform of *Discinisca* and are developed in *Pelagodiscus* (Williams and Cusack, 1999).

Baculate structure in *Glottidia* and discinids is symmetrical, but that of Cambrian linguloids is asymmetrical (Figs 1 and 2).

The botryoidal structure of secondary shell is characteristic of Recent *Lingula*. The replacement of baculate sets by botryoidal and virgose sets in *Lingula* is considered to be as a major change in this phylogenetic lineage (Cusack et al., 1999). Compact laminae separated by cavernous laminae with recrystallized rods have been traced back to the Carboniferous *Lingula squamiformis* (Cusack and Williams, 1996) and may also be typical of the Caradoc `*Lingulella*` sp. from Ontario. Virgose sets within the secondary layer of the body platform developed as correlatives of marginal baculi in Palaeozoic linguloids. The virgose sets of *Eoobolus* and *Paterula* are interpreted as an ancient fabric precursory to the development of baculation.

The columnar secondary shell is characteristic of the acrotretides. Columnar sets occur in the acrotretides together with the camerate sets, as in *Acrotreta* (Holmer, 1989). Compact laminae, in the form of roofs and floors of chambers, were secreted; but the glycosaminoglycans (GAGs) exuded between these plates contained sufficient quantities of apatite to fill potential chambers with spherular mosaics (Cusack et al., 1999).

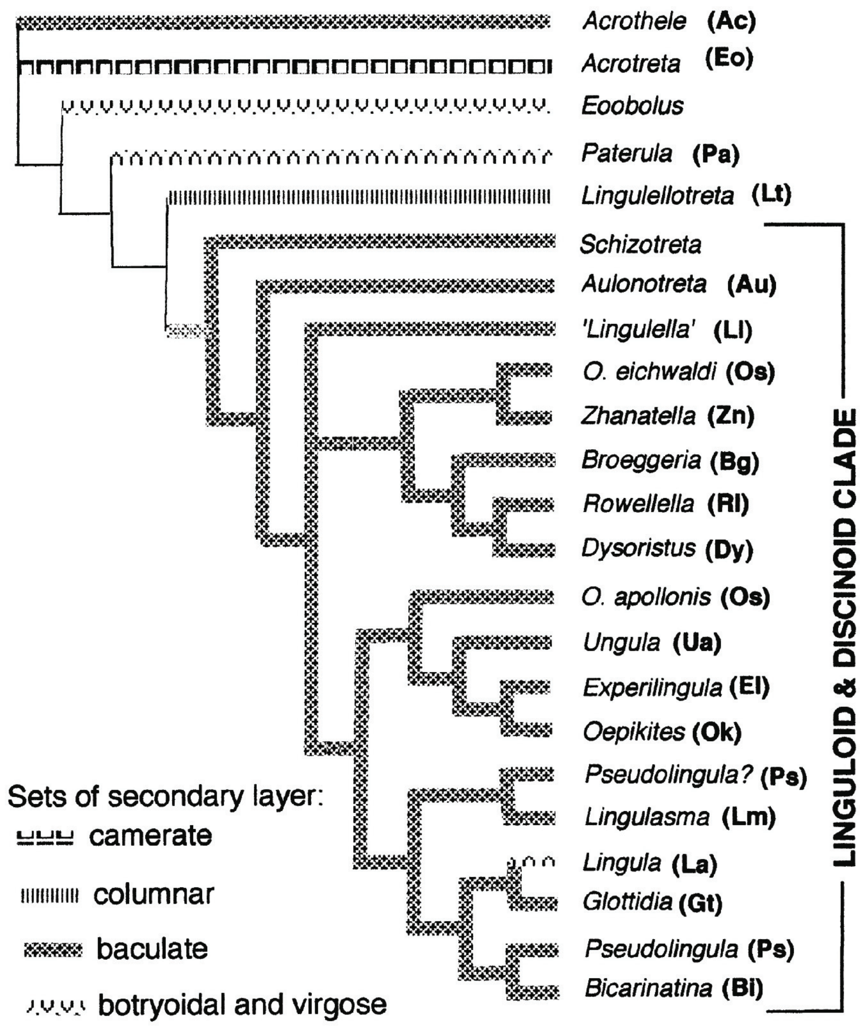

Figure 2. A cladogram showing the phylogeny of linguloid and discinoid brachiopods based mainly on the structure of secondary shell (modified after Cusack et al., 1999).

Some less common structures have been reported in phosphatic non-linguloid brachiopods. **Canaliform** structure has been described in *Paterina* (Williams et al., 1999).

Nemliher (2006) has described a shell structure of HCl- and H_2O_2-treated fragments of a phosphatic brachiopod from the basal Furongian of Estonia assigned conditionally to "*Ungula* sp. 1" by Popov et al. (1989). He reports that the shell structure of *Ungula* sp. 1 consists of an alternation of compact and organic layers, no baculate lamina was detected, while the structure of the compact laminae resembles that of the baculate shell structure. The compact laminae in the fragments are said to be penetrated by "tubular" structures, typically about 4 μm in diameter and filled with phosphatized organic matter; the shell structure is referred to as a new, "tubulate" type. As the systematic position of this phosphatic brachiopod remains unknown, it is possible that it may be a paterinid with a canaliform structure, but the structure can be obscured by taphonomic or treatment-related effects.

Among the organophosphatic brachiopods from the family Curticiidae, *Curticia? pattersonensis* sp. from the upper "Middle Cambrian" of the Great Basin, USA has been reported to have a baculate secondary layer and a columnar tertiary layer. Wedging-out columnar layers are observed in the apical region of the ventral valve building up a thickening, which supports the propareas; in a more marginal position the apatitic rods form a criss-cross pattern of the baculate structure of linguloids (Streng and Holmer, 2005).

2.2 The shell structure of stem-group brachiopods

From the point of view of the origin of the lingulate brachiopod shell structures, the studies of the Cambrian fossils assigned to brachiopods or stem-group linguliform brachiopods are of growing interest. Recent studies have focussed on three stem-group linguliform brachiopods: *Mickwitzia*, *Micrina* and *Askepasma* (Fig. 3).

The shell structure of the stem group of linguliform brachiopod *Askepasma* from the "Lower Cambrian" of South Autralia has been reported to be canaliform. The shell of *Askepasma* sp. is perforated by a single type of phosphatic hollow tubular canals invariably oriented subparallel to the shell lamination. Most of them are rather short, extending only up to 200 μm (Holmer et al., 2006).

In *Mickwitzia* cf. *occidens* Walcott, 1908 from the Ella Island Formation in North-East Greenland, acrotretoid-like columnar laminae, perforated by vertical tubes, have been described (Skovsted and Holmer, 2005).

In *Micrina* Laurie, 1986 laminar sets are arranged like a stack of increasingly larger, eccentric bowls with thick rims, laminae are platy (not granular) and the apatitic aggregates in the chamber are spherulitic (not spherular). Williams and Holmer (2002) have concluded that such differences suggest that the calcifying proteins responsible for the mineralization of the *Micrina* sclerites were not the same as those controlling the development of the lingulate shell. The platy lamination is also typical to the secondary layer of organophosphatic shell of siphonotretide brachiopods, consisting of prismatic laths and rods arranged in monolayers (Williams et al., 2004).

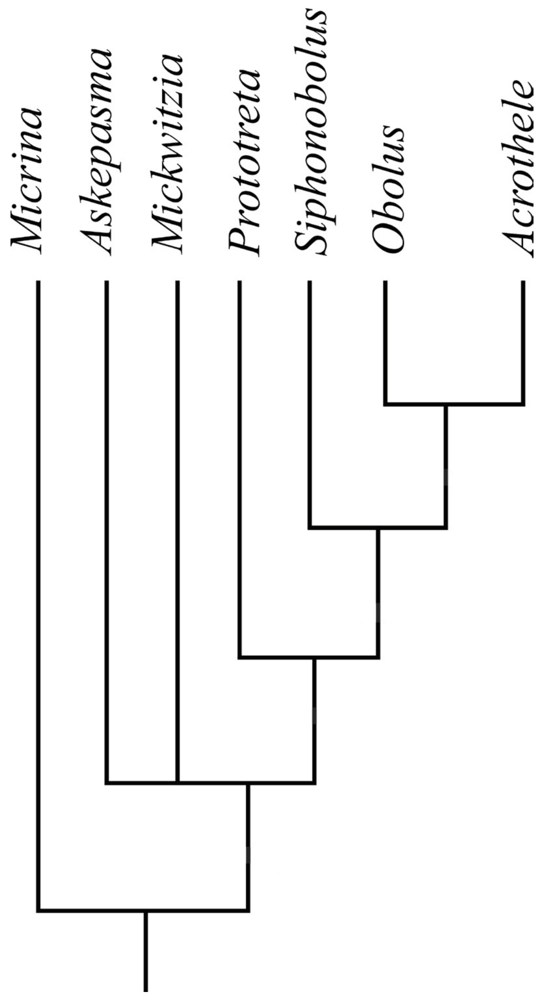

Figure 3. Phylogenetic relationship of *Micrina* and five linguliform genera representing the superfamilies Acrotretoidea, Paterinoidea, Siphonotretoidea, Linguloidea, and Acrotheloidea; modified after Holmer et al, 2002, 2006.

2.3. Detailed laminar structure of baculate linguloid shells

The linguloid brachiopods shells are stratified, with a thin outer primary layer and inner secondary layer composed of laminae. Laminae, either singly or in sets, may be no more than a few micrometres thick. They may cover several square millimetres and may succeed older laminae unconformably with overlap and be involved in lateral facial changes.

In living lingulides, the periostracum is an organic sheet and the underlying primary layer is composed of protein coated apatitic granules dispersed in acidic glycosaminoglycans (GAGs) (Williams et al., 1994). Other superficial features, described as ornamentation, include: radial ribs and capillae; concentric lamellae, fila and rugellae (Popov and Holmer, 1994); and microscopic pits (Cusack et al., 1999).

The basic stratiform secondary layer of linguloids is characterized by a rhythmic succession of laminae composed of organic sheets, apatite and variable quantities of apatite in organic matrix. β-chitinous sheets and wholly apatitic laminae have been the components of the secondary layer since the Early Cambrian. Transformations have repeatedly changed those laminae consisting of various aggregates of spherular apatite (baculi, rods and botryoids) suspended in GAGs and held together by a scaffolding of fibrous proteinaceous struts and chitinous platforms (Cusack et al., 1999).

The lingulid shell is permeated by a canal system erected orthogonally to the secreting plasmalemma (Williams et al., 1994). Canals, less than 1 μm in diameter, can be traced continuously through sequences of all kind of laminae which consequently must have been secreted by same group of epithelial cells. Vertical and horizontal changes in the chemico-structure of the shells are, therefore, more likely to result from phased molecular changes within the same kind of cells than from epithelial differentiation (Cusack et al., 1999)

The characteristic set of the secondary layers of the linguloid and discinoid stem groups is an outwardly convex plate of three biomineralized laminae that are thinnest posteriomedially and thickest around most of the wedge-shaped margin. The laminae were secreted as a compact-baculate-compact sequence. These sets were traversed by regularly disposed trellises of baculi subtended between compact apatitic laminae seldom more than

1 μm thick. The baculi had been recrystallized into aggregates of prismatic apatite about 500 nm thick (Williams and Cusack, 1999).

Williams and Cusack (1999) suggest that despite the degrading and recrystallizing effects of fossilization, the biomineral constituent and locations of the original organic components of the living shell are identifiable. Each set was contained within chitinoproteinaceous membranes with groups of sets segregated by relatively thick membranous laminae. The compact laminae were originally composed of apatitic mosaics, as were baculi, although some of these were also made up of stacked pinacoidal plates. Both types of baculi accreted around fibrous polymers and were sporadically supported by membranes coated with spherules. The trellised framework of baculi accreted within GAGs (with dispersed apatitic spherules) which were the principal components of the swollen margin of the set.

The first phase of biomineralization was the exocytosis of protein-coated granules of apatite and their aggregation into chitin-bound spherules that nucleated on membranes or existed freely in GAGs. This laminar exoskeleton was then strengthened by chitinous pillars, the so-called canal system. In the second phase of biomineralization, the spherules in association with fibrous proteins, accreted as coats of canals and/or chitinous walls secreted intercellularly (the columnar and camerate states, respectively, of Holmer, 1989) or as baculi (as composed of stacked pinacoidal plates) and botryoids (Williams et al., 1994, 1998). The biomineralized secondary layer of the linguliform shell has always been mainly or exclusively composed of one of the five fabrics: stratified alterations of organic and phosphatized laminae and columnar, camerate, baculate or mosaic sets (Cusack et al., 1999).

4. MATERIAL AND METHODS

In this thesis, the traditional stratigraphic subdivision into "Lower Cambrian", "Middle Cambrian" and the Furongian as an equivalent of "Upper Cambrian" is used, for the purpose of better communication, because the revision of global Cambrian stratigraphy is still in progress and regional stratigraphic schemes for Estonia and NW Russia have not yet adopted new international subdivisions.

The study area (Fig. 4), including Estonia and Ingria (Leningrad district of Russia), is situated in the north-western part of the East European Platform.

The "Middle Cambrian" to lowermost Ordovician succession (Fig. 5) of the north-eastern part of the East European Platform is represented by siliciclastic sandy rocks with lense like or cross-bedded structure and numerous gaps of different duration (Mens et al., 1990). The Furongian rock units of the Baltic palaeobasin are incomplete, both vertically and laterally (Heinsalu and Viira, 1997; Mens and Pirrus, 1997). Many of the studied species occur in abundance in coquinas. Layers rich in intact shells and shell fragments of lingulate brachiopods occur at certain levels of succession. In Estonia the main accumulations of such lingulate coquinas are known from the Ülgase, Tsitre and Kallavere Formations, in NW Russia to the Sablinka, Ladoga and Tosna Formations.

This thesis is based on lingulate brachiopod samples originating from 10 localities. The brief locality information and stratigraphical columns (Figs. 7-15) are given after Puura (1996); for the legend, see Fig. 6. Samples from the Saka, Ülgase and Iru sections were collected by the author during two field works in summer year 2004 and 2005. Additional material was collected during the previous field trips by Ivar Puura.

Figure 4. Locality map.Outcrops are indicated by squares and drill core sites by open circles.

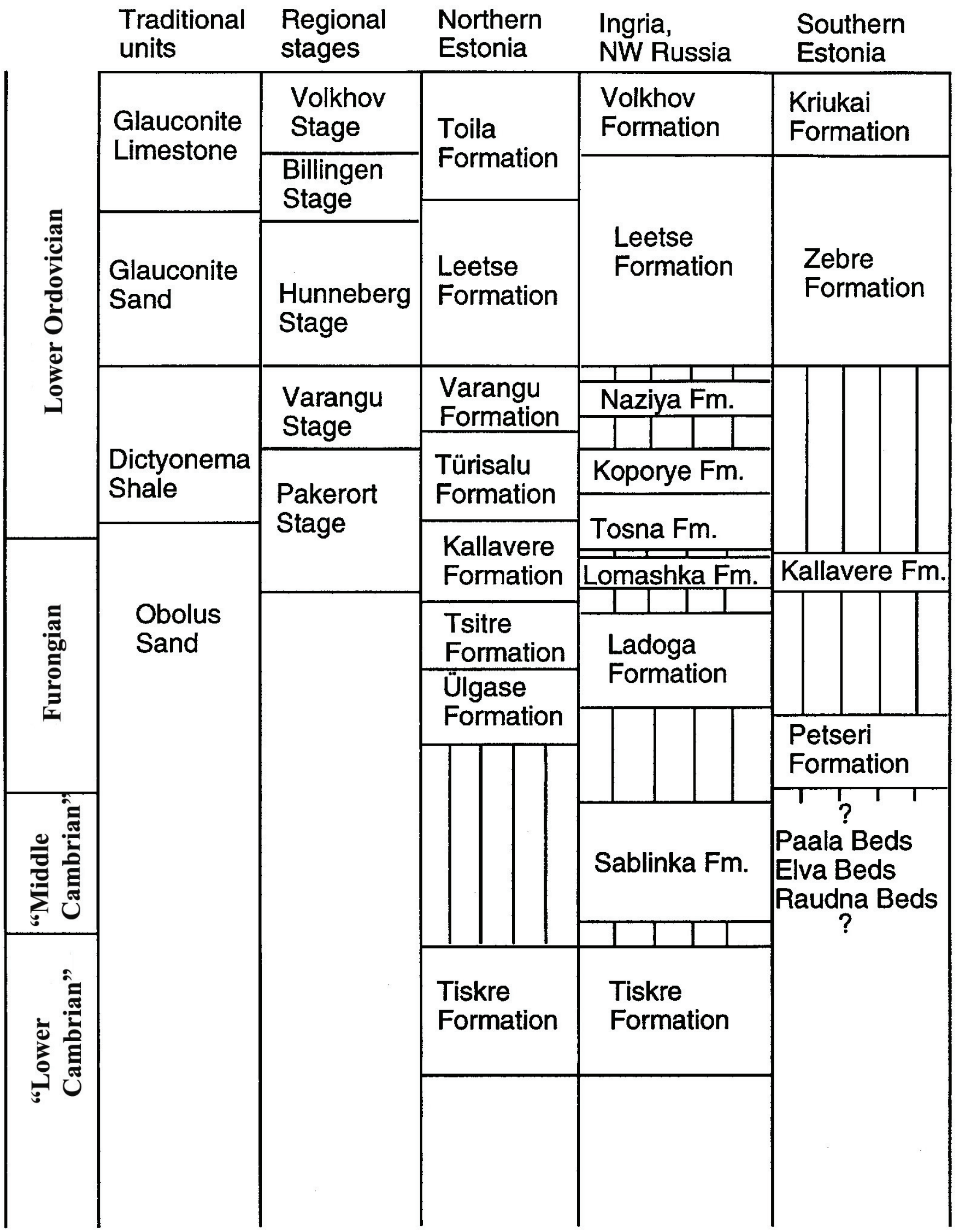

Figure 5. Major chrono- and lithostratigraphic units of "Middle Cambrian" - Hunneberg strata in Estonia and Ingria and their correlation with traditional units (modified after Puura, 1996).

4.1. Localities

Ingria, north-western Russia

Lava River. On the right bank of the Lava River (Fig. 4), the rocks from the Furongian Ladoga Formation to the Lower Ordovician Kunda Stage are exposed (Fig. 7). Raymond (1916) gave a generalized description of this section; the Cambrian-Ordovician boundary beds have been described by Popov et al. (1989). *Obolus apollinis* occurs abundantly in the middle and upper part of the Tosna Formation of the section. The sample of *Obolus apollinis* originates from the middle part of the section.

Sarya River. The sections of Cambrian-Ordovician boundary beds (Fig. 8) on the banks of Sarya River, near Vojbokalo village (Fig. 4) have been described by Rukhin (1939) and Popov et al. (1989). The lower part of the Gertovo Member of the Sablinka Formation is exposed in an outcrop 700 m downstream of Vojbokalo village (outcrop L-6 of Popov et al., 1989).

Another section of the outcrop, where the Ladoga and Tosna Formations are exposed, is located on the right bank of the Sarya River, 550 m upstream from the previous locality, near the bridge in Vojbokalo village. The studied sample *Obolus ruchini* originates from the basal part of the Gertovo Member, Sablinka Formation.

Suma River. An outcrop of the Cambrian-Ordovician boundary beds (Fig. 9) is located on the right bank of the Suma River, 500 m downstream of the bridge on the road connecting the Kaibolovo village with the R-35 road (Fig. 4). This outcrop has been described by Rukhin (1939) and Popov et al. (1989, outcrop L-31). The studied valves of *Obolus apollinis* originate from the Tosna Formation of the section.

Putilovo quarry. The limestone quarry near the Putilovo village, east of St. Petersburg. The Cambrian siliciclastic sequence has been opened in a trench (Artyushkov et al., 2000). The studied sample of *Obolus apollinis* originates from the Tosna Formation.

Volkhov River. Outcrops along the Volkhov River have been described by Rukhin (1939) and Popov et al. (1989; outcrops L-40 and L-41). An exposure of the Cambrian-Ordovician boundary beds (Fig. 10) is situated on the right bank of the Volkhov River, upstream of the southern margin of the Gorchakovskaya village (Fig. 4). The studied sample *Obolus ruchini* originates from the Gertovo Member, Sablinka Formation.

Estonia

Core R-1555** (R-1555 in Fig. 4)**. The site of this core drilled in 1979, is about 15 km east of Rakvere (Fig. 4). The core penetrated the Ordovician and Furongian rocks and reached the uppermost part of the "Lower Cambrian" Tiskre Formation (Fig. 11). The studied sample *Obolus apollinis* originates from the Kallavere Formation, depth interval 95-103.1 m of the core.

Core Värska-6. The drilling site is located in the environs of Värska, south-eastern Estonia (Fig. 4). In this core the "Middle Cambrian" Paala beds are overlain by dark-grey sandstone of Kallavere Formation (Fig. 12). At the base of the Kallavere Formation, depth interval 455.0-455.2 m, occurs lingulate brachiopod coquina, composed of abundant valves of *Schmidtites celatus* and rare *Ungula ingrica*.

Iru. The Iru section (Fig. 13) is located at the eastern margin of Tallinn, near acient Iru stronghold (Fig. 4). The section has been described by Öpik (1928, 1929) and briefly discussed by Popov et al. (1989, p. 61). The studied sample *Ungula ingrica* originates from the exposure of Kallavere Formation, Maardu Member of this section.

Saka. The Saka section (Fig.14), 2 km west of the Saka village (Fig. 4), has been exposed since 1984, as a result of construction of a waste water pipe. Previous descriptions of this section include Kaljo et al. (1986), Heinsalu et al. (1991a, b) and Puura and Holmer (1993). The Tsitre Formation of the section has yielded the studied sample *Ungula* *convexa*, *Schmidtites celatus* occurs in the brachiopod coquina at the base of the Rannu Member, Kallavere Formation.

Ülgase. Cambrian-Ordovician boundary beds are exposed in two sections (Fig. 15) along the clint near the ruins of the phosphate-processing factory of the "Eesti Vosvoriit" company, near Ülgase village (Fig. 4). The Furongian Ülgase Formation is exposed in a wall of abandoned mineworks. This exposure was selected as the stratotype of the Ülgase Formation by Müürisepp (1958) and has been previously described and discussed by Loog and Kivimägi (1968), Rõõmusoks et al. (1975) and Puura and Holmer (1993). In this section, the sandstones of the "Lower Cambrian" Tiskre Formation are overlain by the Ülgase Formation. Another section, 200 m westwards is described as neostratotype of the Maardu Member by Heinsalu et al. (1987).

The studied sample *Ungula inornata* originates from the Ülgase Formation and the sample of *Ungula* sp. from the basal 0.1 m of it, the valves of *Schmidtites celatus* and *Ungula ingrica* originate from the Maardu Member, Kallavere Formation.

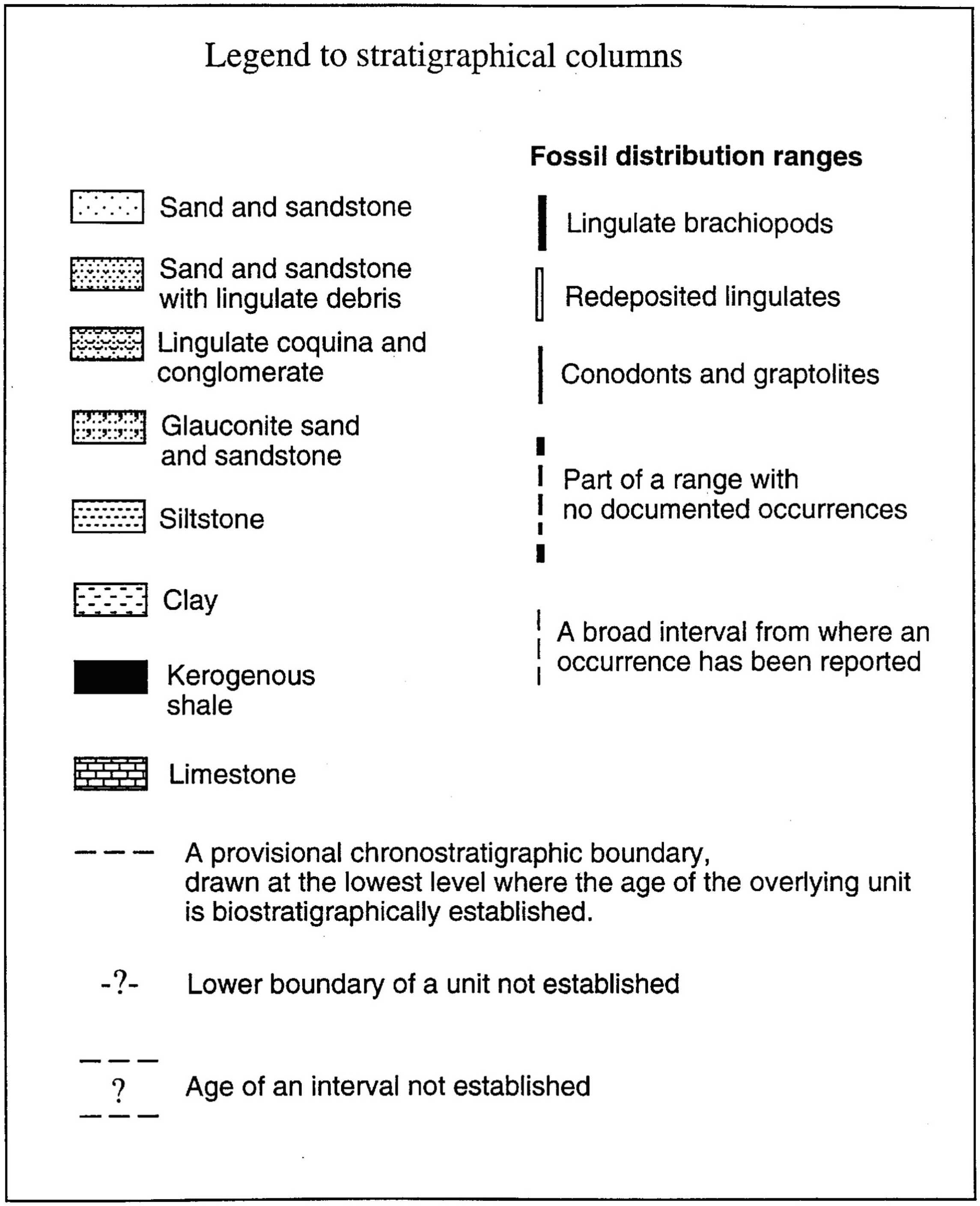

Figure 6. Legend to stratigraphical columns.

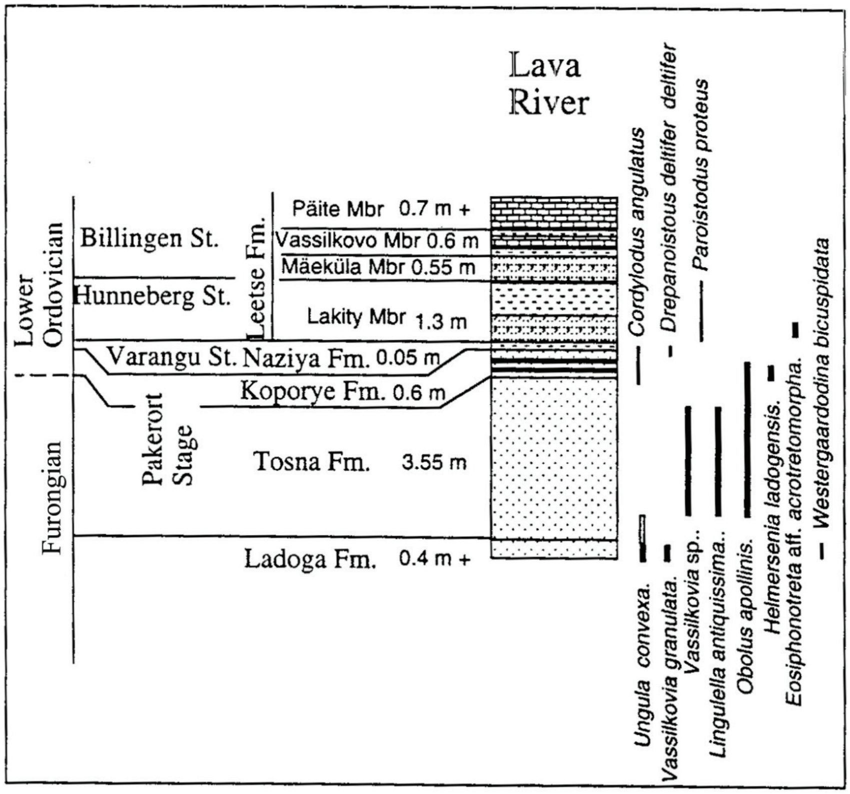

Figure 7. Stratigraphical description and distribution of lingulate brachiopods and selected conodonts in a section on the Lava River (modified after Popov et al., 1989, Dronov et al., 1995, Puura, 1996).

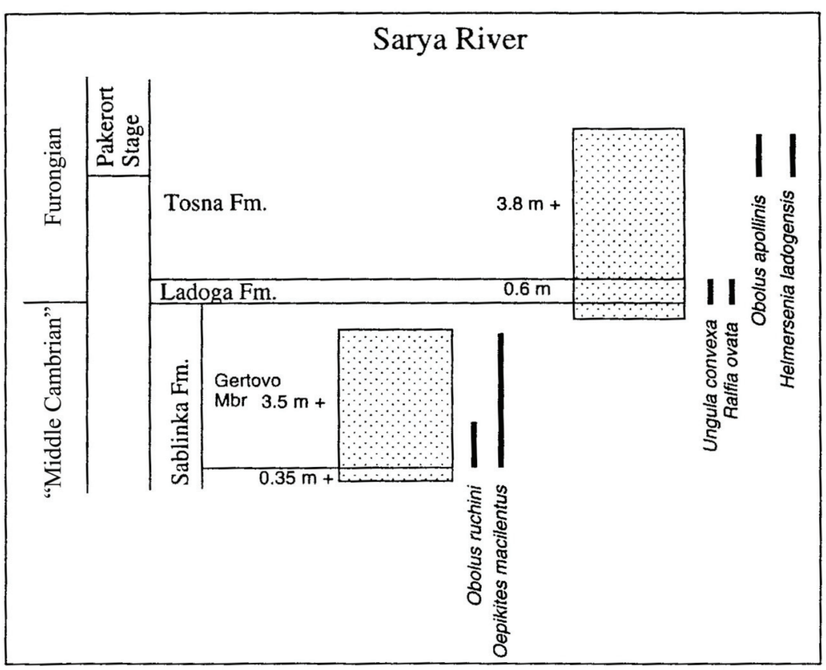

Figure 8. Stratigraphical description and distribution of lingulate brachiopods and selected conodonts in a section along the Sarya River (modified after Popov et al., 1989, Dronov et al., 1995; Puura, 1996).

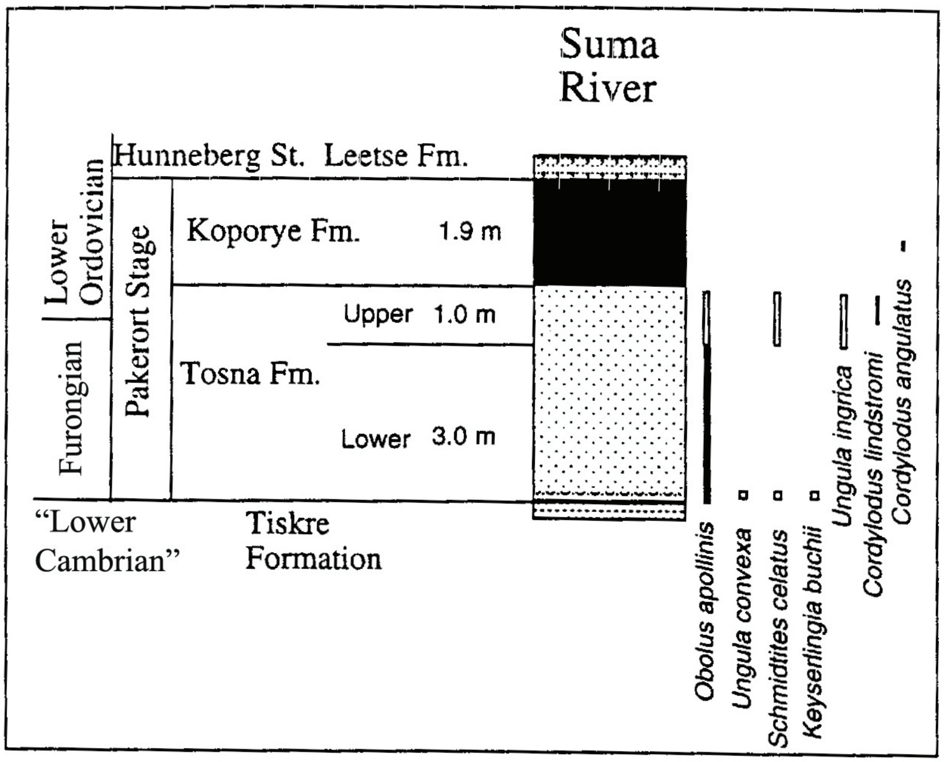

Figure 9. Stratigraphical description and distribution of lingulate brachiopods and selected conodonts in a section on the Suma River (modified after Popov et al., 1989; Puura, 1996).

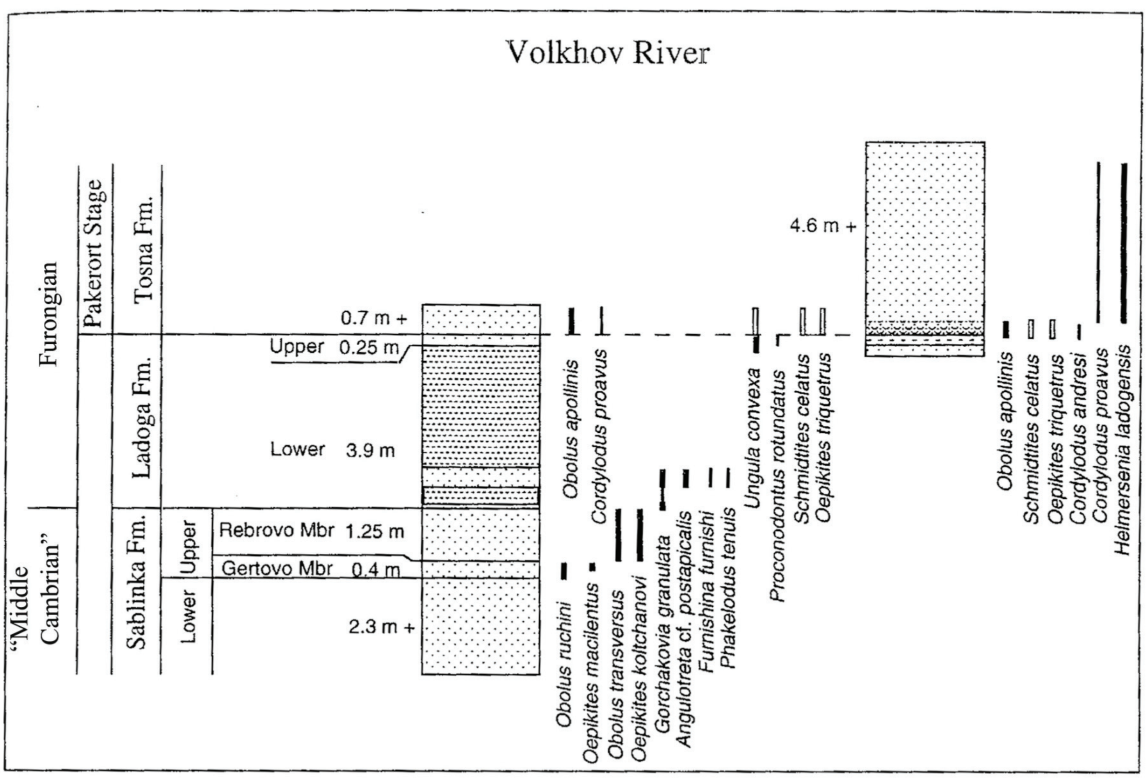

Figure 10. Stratigraphical description and distribution of lingulate brachiopods and selected conodonts in a section along the Volkhov River (modified after Popov et al., 1989; Puura, 1996).

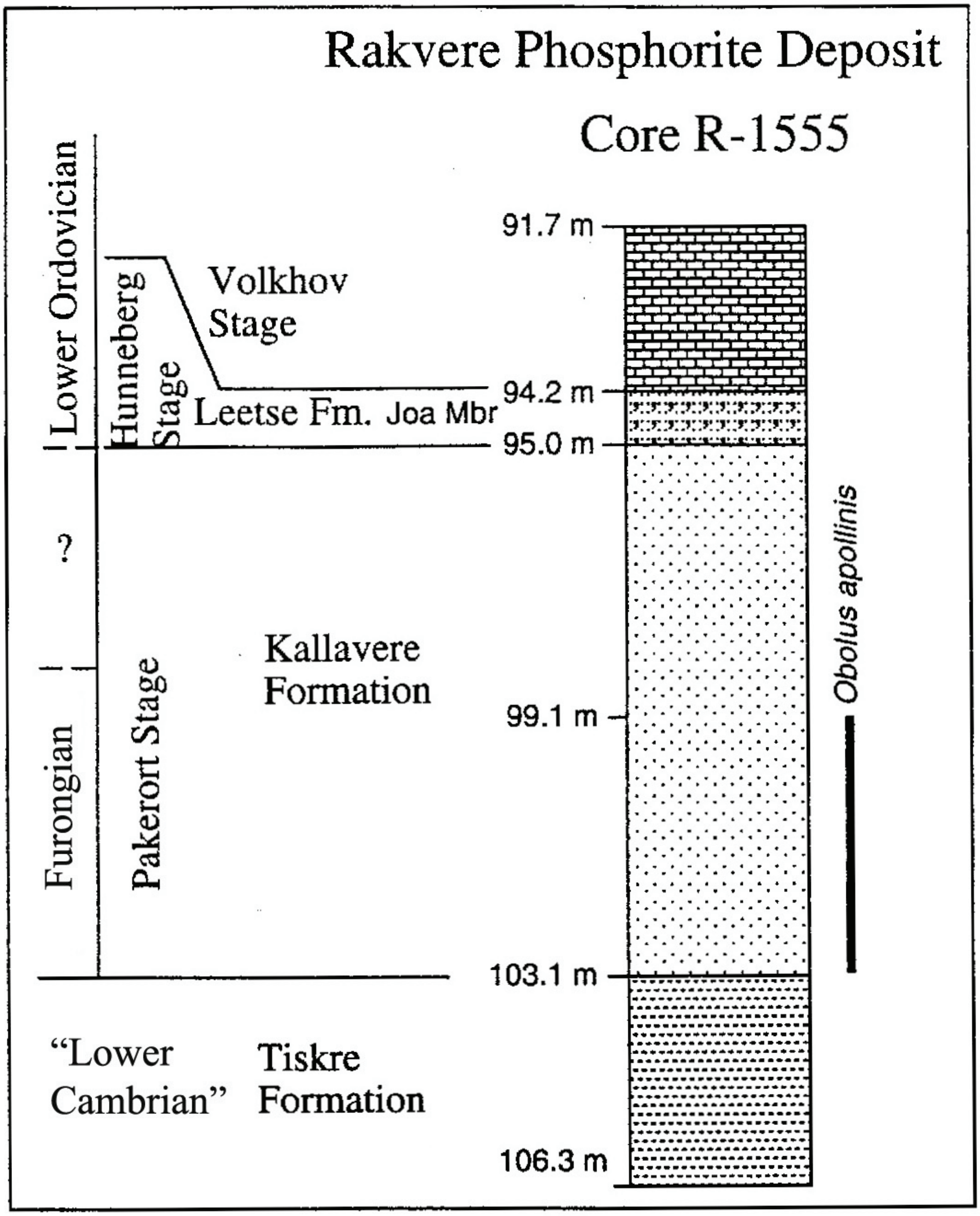

Figure 11. Lingulate occurrence and stratigraphical description in core R-1555, east of Rakvere (modified after Puura, 1996).

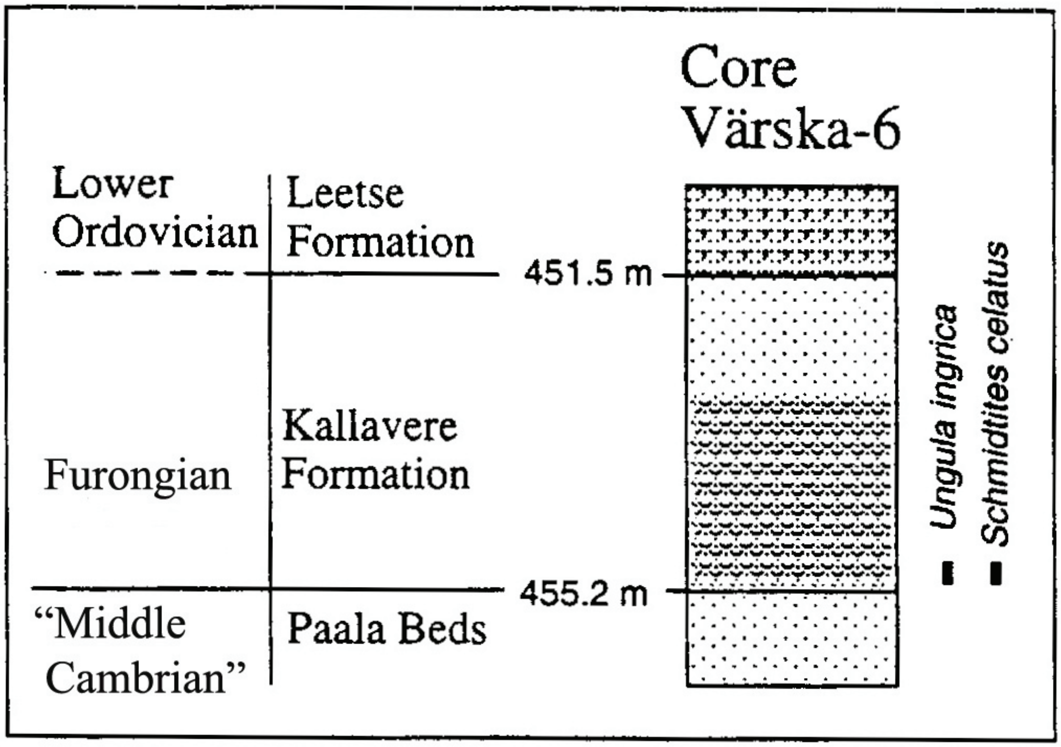

Figure 12. Lingulate occurrence and stratigraphical description in core Värska-6, SE Estonia (modified after Puura, 1996).

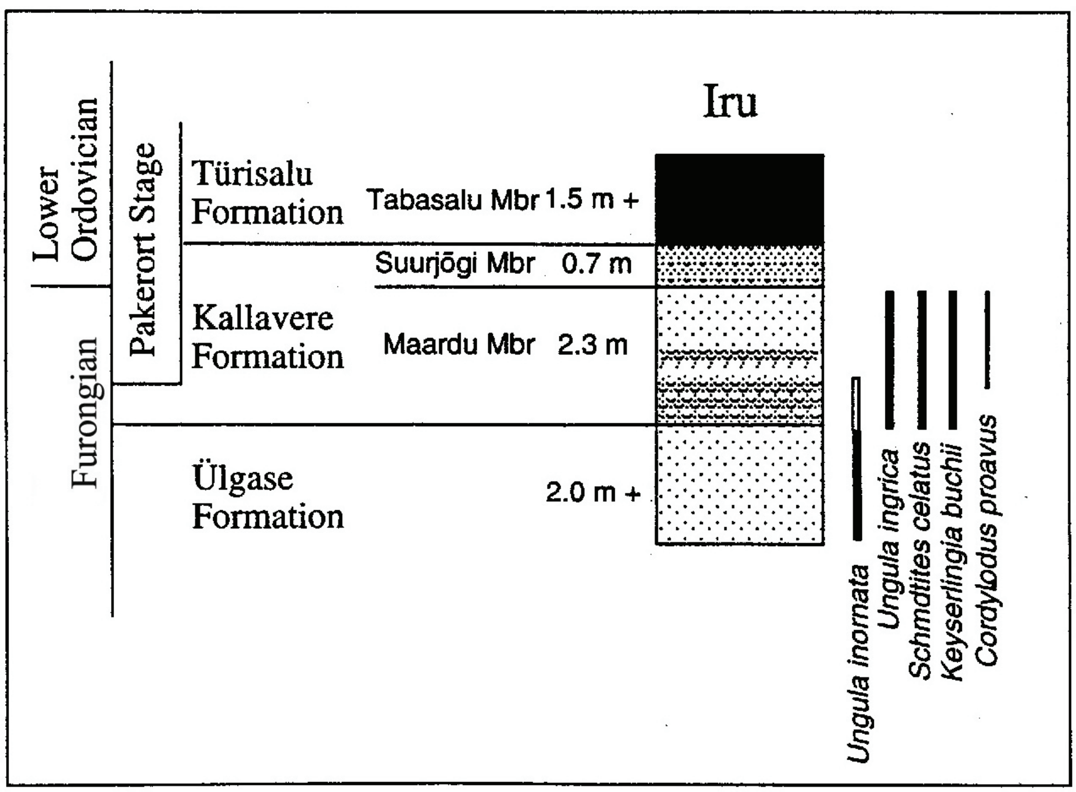

Figure 13. Section at Iru, Tallinn, showing distribution of lingulate brachiopods and selected conodont occurrences and stratigraphical distribution (modified after Puura, 1996).

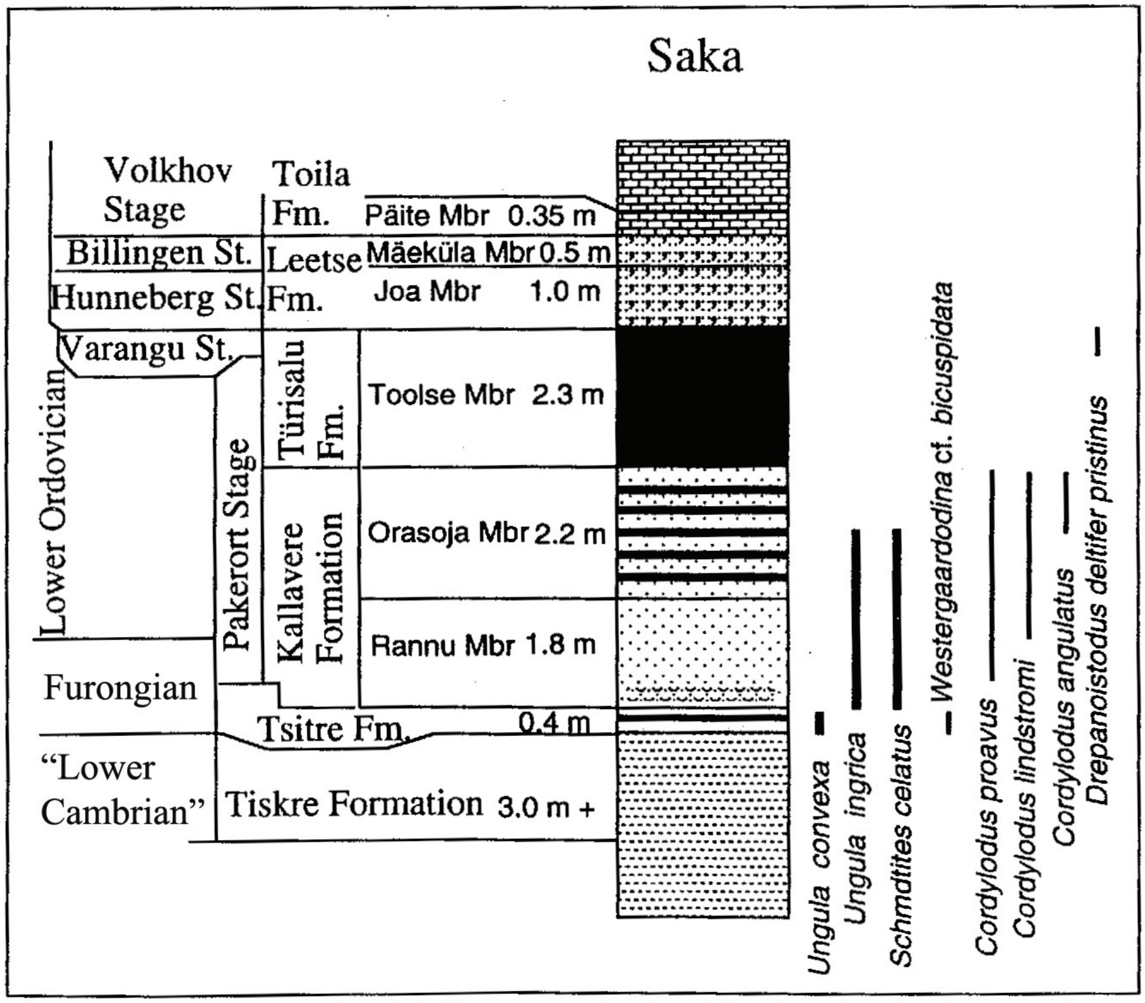

Figure 14. Stratigraphical description and distribution of lingulate brachiopods and selected conodonts in the Saka section (modified after Puura, 1996).

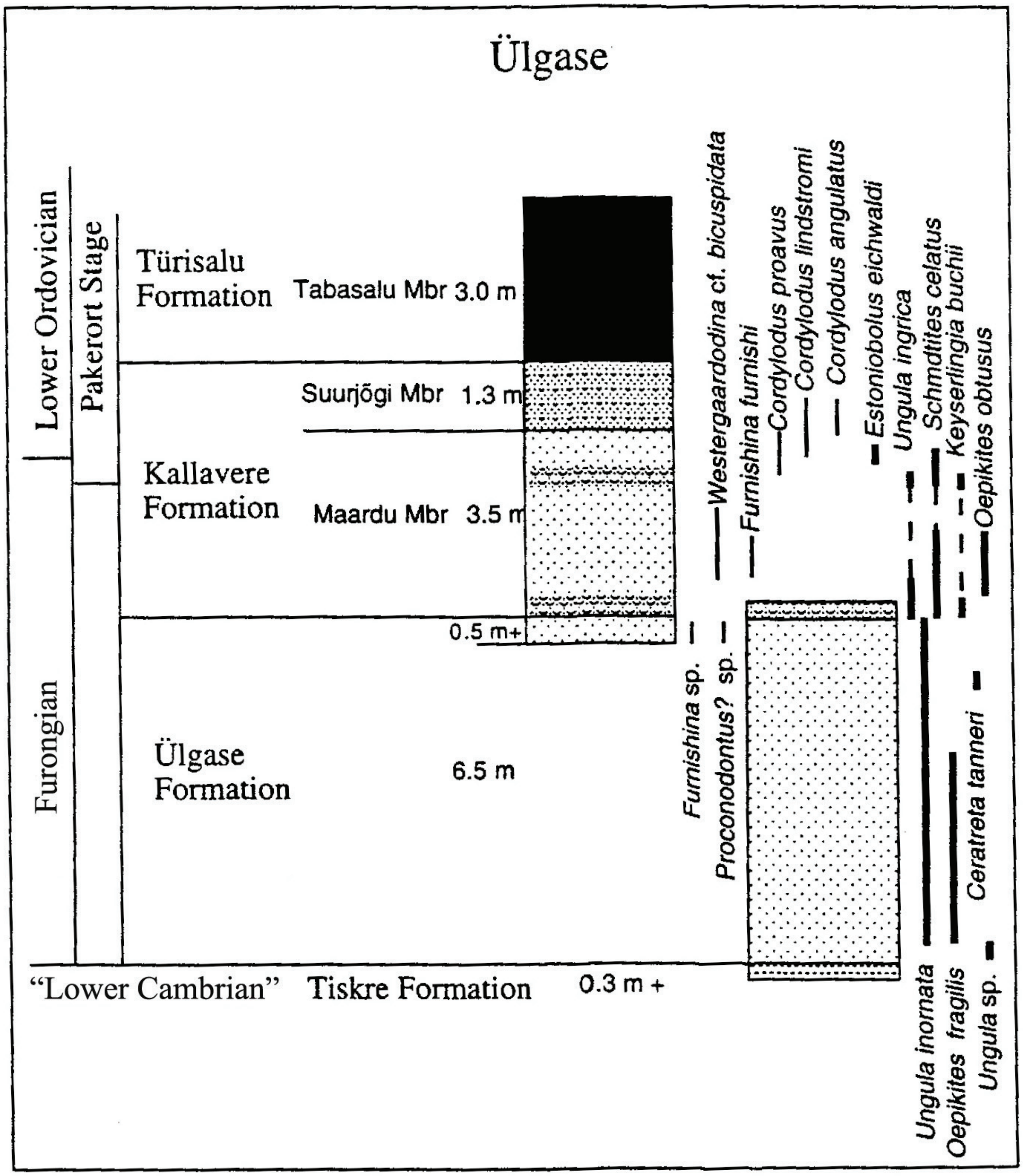

Figure 15. Stratigraphical description and distribution of lingulate brachiopods and selected conodonts in the secions at Ülgase (modified after Puura, 1996).

4.2. Methods

The shells of lingulate brachiopods were investigated by means of analytical environmental scanning electron microscope (ESEM) equipped with a back-scattered electron imaging (BS) detector and energy dispersive X-ray analyzer (EDS).

Sample preparation

Fossils were cleaned from sedimentary surroundings and cracked to expose the fracture section of shells internal surface and mounted on sample holders. No coating was performed.

ESEM-EDS studies

For viewing back scattered electron scans and achieving energy dispersive X-ray microanalysis LEO 1450VP "environmental" scanning electron microscope (ESEM) was used at the microscopy laboratory of the Norwegian Geological Survey (NGU) in Trondheim. Instead of the specimen chamber being maintained at high vacuum, at ESEM it can be operated at a relatively high pressure (e.g. 10^{-1} torr), which allows to study fractured sections of uncoated specimens. The study of uncoated and untreated surfaces of shells proved to be relevant for avoiding the treatment-related information loss; the study of fracture sections allowed to view the shell structures three-dimensionally. The studies at the ESEM laboratory were carried out by the author in 2005 and 2006.

5. RESULTS AND DISCUSSION

5.1. Case studies of shell structures

***Obolus apollinis* Eichwald**

The studied sample of *Obolus apollinis* from the Tosna Formation from the locality on the right bank of the Lava River in the Leningrad district shows a rather unique preservation of baculate structure that is not common in the valves filled with authigenic apatite, e.g. *Ungula*. Well-expressed baculate structure is observable, characterized by several layers of trellised baculate sets separated by dense compact laminae. The baculi consist of spherical apatite aggregates that can be interpreted as resulting from early diagenetic change. The space left by the degradation of organic matter is mostly empty, i.e. not filled with authigenic apatite or other minerals. Exceptionally, some spots containing Fe-hydroxide, hematite, can be observed. The Fe-hydroxide was identified by EDS spot analysis and has been previously identified as hematite by XRD studies. As heavier elements are lighter in back-scattered electron images, hematite spots are lighter than background apatite (Plate 1). Spherical apatite aggregates can be also observed in the baculi of *Obolus apollinis* from the Tosna Formation in the Suma River (Plate 1, Photo 3).

Obolus apollinis from the Kallavere Formation, from the R-1555 core section, depth 103.7-104.0, shows a wide compact-baculate laminae sequence. The structure is best preserved in the middle part of the shell, where there is less secondary infilling (Plate 2).

Obolus apollinis from the Tosna Formation from the Putilovo quarry in NW Russia shows good overview of rather thin baculate laminae (less than 10 μm) alternating with compact laminae (Plate 3; Plate 4, Photo 1). Within another sample from same locality it can be observed hematite precipitation into baculate laminae mimicking, that hematite crystallization is following the baculate laminae of the shell (Plate 4, Photo 2).

Obolus ruchini Khazanovitch and Popov

Obolus ruchini from the outcrop on a bank of the Volkhov River close to the Gertovo village in Russia shows an excellent preservation. The structure of the baculate laminae is clearly visible (Plate 5). In many parts of the shell apatitic baculi are coated with hematite. In this sample, hematite spherules and hematite coatings on the quartz crystals can be observed in the host rock (Plate 5, Photo 1). The baculate laminae of *Obolus ruchini* appear to be wider than those of *Obolus apollinis*.

Exclusive preservation of this specimen of *Obolus ruchini* allows to observe fragile flexible stuctures interpreted here as mineralized organic fibrils that could be part of the polymer framework for accretion of baculi (Plate 5, Photo 3). Usually two parallel sub-micron size flexible fibrils run parallel, almost vertically, about 1 μm from each other and are connected with horizontal ties forming bridges between the fibrils. In some cases, the fibrils appear to be organized to column-like sets reminding a framework of a bacula (Plate 5, Photo 2). These structures show exclusive preservation that is a result of many coinciding favourable conditions of fossilization.

The studied sample *Obolus ruchini* from the Sarya River outcrop shows differential preservation of the shell structure (Plate 6). The baculate laminae can be best observed in the middle part of the shell. Within the other parts of the shells the infill rate of the precipitated authigenic apatite is greater. In some places, hematite precipitation can be observed. On the Plate 6, Photo 3 can be followed that the hematite is crystallized preferably within the baculate layer of the shell.

Ungula convexa Pander

The *Ungula convexa* from the outcrop on a bank of Lava River section (Tosna Formation) shows a spherical apatite mineralization within the baculate laminae (Plate 7, Plate 8, Photo 1). Apatitic baculi of the shell are coated with hematite.

Another sample of *Ungula convexa* from the same locality shows a quite extensive hematite precipitation (Plate 8, Photo 2). Hematite coating baculi is forming characteristic spherical aggregates.

The shell structure of *Ungula convexa* from the Tsitre Formation, Saka locality is masked by authigenic apatite precipitated to the space between the baculi.

***Ungula ingrica* Eichwald**

Ungula ingrica from the basal conglomerate of the Kallavere Formation in the Ülgase outcrop shows locally, in the middle of the shell, alteration of baculate and compact laminae (Plate 9, Photo 1).

A sample of *Ungula ingrica* from the Iru locality shows locally the structures were can be observed the alteration of baculate and compact laminae (Plate 9, Photo 2). Other parts of the shell have massive, homogenous appearance, due to the precipitation of authigenic apatite. In another sample, the baculate shell structure is almost completely masked, but with the background knowledge, we can distinguish hardly visible compact and baculate laminae. On the shell surface there is a Fe-rich and apatite- containing crust, containing some crystals of baryte. Baryte is also visible within the shell fracture section.

***Ungula inornata* Mickwitz**

The valve *Ungula inornata* from the Ülgase Formation in the Ülgase outcrop shows baculate layers in various preservation conditions and contains precipitated authigenic apatite in different extent. Some samples are locally more porous and with some crystals of precipitated pyrite (Plate 9, Photo 3).

***Ungula* sp.**

Ungula sp. from pebbles of the basal conglomerate of the Ülgase Formation shows a quite well observable baculate lamina with locally precipitated pyrite (Plate 9, Photo 4).

***Schmidtites celatus* Volborth**

The valve of *Schmidtites celatus* from the Ülgase outcrop shows a relatively homogenous carbonate fluorapatite composition with some more Fe-rich, pyrite-containing layers (Plate 9, Photo 5).

The shell of *Schmidtites celatus* from the Saka section shows a good overview of laminated structure with relatively homogenous apatitic composition

The oblique view of fracture section of the shell of *Schmidtites celatus* Volborth from the Kallavere Formation in the Värska-6 core section, depth 455.0-455.2 m, reveals the alternation of compact and baculate laminae. Apatite is locally mineralized in the form of needle-like crystals; pyrite is covering the fossil shell and quartz minerals in the host rock (Plate 9, Photo 6).

5.2. Discussion and conclusions

The composition and structure of a fossil brachiopod shell is the result of *in vivo* development of soft and hard tissues and their *post-mortem* degradation, fossilization and diagenesis. Thus, for interpretation of the fossil shell structures, the knowledge of the structure of Recent shells is a good starting point.

The shells of Recent lingulate brachiopods are stratiform, consisting of periostracum and biomineralized primary and secondary layers under it (Cusack et al., 1999; Williams and Cusack, 1999). Usually, periostracum is not preserved in fossil brachiopods (Williams, 2000).

The secondary layer is composed of laminae that differ in their composition and in thickness. In linguloid shells, there are two distinctive types of laminae – compact laminae and baculate laminae. The closest modern analogue to the fossil linguloids, having baculate shell structure, is Recent genus *Glottidia*.

This study of the shell structures of linguloid brachiopods showed that the shell structure of the studied valves consist of trellised apatitic rods (baculi) of baculate laminae which are associated with lamina of compacted mosaics and spherules of apatite (compact laminae). The shell structure can be classified as baculate symmetrical with the secretory rhythm of compact lamina – baculate lamina – compact lamina. The structure elements are best preserved in the specimens from the genus *Obolus* Eichwald, 1829 and *Schmidtites* Schuchert and Levene, 1929. In the samples of *Ungula* Pander, 1830, the shell structure of fossil valves is mostly masked by precipitated authigenic apatite, giving the shell a massive, homogenous appearance.

In the higher magnifications, the compact laminae were mostly preserved in the compact form and it is logical to conclude that although they are most likely passed through chemical and mineralogical diagenetic changes, they have preserved their position in the shell. The scenarios of changes of baculate layers are more diverse.

The ESEM observations of shell structure presented above allow to interpret taphonomic changes of shell structures, as compared to most common situations. First, the shell structure of *Obolus apollinis* Eichwald from the Furongian (previously "Upper Cambrian") of Estonia and NW Russia, chosen as a typical baculate structure for extinct linguloid by Cusack et al. (1999) was studied in greater detail and magnification, focusing on the preservation of baculi. Second, *Obolus ruchini* Khazanovitch and Popov from the "Middle Cambrian" of NW Russia showing the unique preservation is studied. It is shown how fibrils of mineralized organic polymers and associatied tiny apatite crystals form a framework for accretion of baculi. It is likely that the *post-mortem* fossilization was rapid, allowing the conservation of the early stages of accretion of baculi around the fibrous polymers.

The same shell allows to observe results of various diagenetic processes that have shaped the baculi in a fossil shell, e.g. formation of apatite spherules and precipitation of hematite covering the baculi. Similar situation is illustrated by *Ungula convexa* Pander from the Furongian of the NW Russia; however, in some cases the hematite is precipitated in the form of larger spherules between the baculi. In case of *Ungula ingrica* from the Furongian of Estonia, baculate structure is observed in rare cases; it is masked by the precipitation of apatite into the space left after the degradation of organic matter.

This massive and structureless apparance is also characteristic of *Ungula inornata* Mickwitz and *Schmidtites celatus* Volborth from the Furongian of Estonia. In some cases, local occurrences of precipitated pyrite can be observed in *Schmidtites*. Pyritization is also observed in case *Ungula* sp. from the pebbles from the basal Furongian of Estonia.

From these observations, it can be concluded that the stage for the taphonomic events which change the appearance of shells is set by the degradation of organic matter in the baculate laminae, leaving free space for fluids and precipitation of authigenic minerals that can be compared to pore space in the host rocks. We have observed that in some cases (genera *Ungula* and *Schmidtites*) this pore space is almost entirely filled with authigenic apatite (and sometimes, pyrite); while in other cases (within valves of *Obolus*) baculate sets are well exposed.

A pore space like microenvironment may develop in a lingulate valve, where the organic matter or the space left after its degradation is enveloped by the mineral part, after its burial under sediments. Back-scattered electron imaging shows that the space occupied *in vivo* by organic tissue is filled with pyrite in many valves. The sedimentary pyrite precipitation is considered to be initiated by sulphate reducing bacteria (Berner, 1984) and to occur below oxic-suboxic interface in the water or sedimentary column or in pore space with similar geochemical regime (Allison, 1988). In contrast, the precipitation of Fe-hydroxides, such as hematite, is considered as indicator of oxic environment.

Experimental work has demonstrated that bacteria are able to mediate apatite formation trough the action of their enzymes (Lucas and Prévôt, 1991). Possible pathways of bacterially mediated mineralization of organic tissue depending on burial conditions and early diagenetic environment can be viewed in the context of the sequence of oxic, suboxic, anoxic zones in the bottom water and sediment column. The XRD studies by Nemliher and Puura (1996) and Puura and Nemliher (2001) have revealed that in many linguloid shells from the "*Obolus* Sandstone", two apatite varieties with different lattice parameters can be distinguished. They have suggested that the organic material was first degraded by bacteria and the free space was subsequently filled with diagenetic apatite. This assumption is strongly supported by SEM observations in this study.

This spectrum of possible scenarios leads to the following conclusions which have implications to our understanding of linguloid shells as geochemical archives:

(1) In some cases, of exclusive preservation, early stages of the accretion of baculi around fibrous polymers can be observed.
(2) A pore-space like microenvironment developing within baculate laminae of linguloid valves, where the organic matter or the space left after its degradation is enveloped by the mineral part, after the burial in the sediment, plays a significant role as the main stage of physico-chemical processes during the diagenesis.
(3) The chemical conditions of the diagenetic environment influence the spectrum of minerals precipitated in the pore space.
(4) The presence of iron minerals, either pyrite or hematite, indicates that in many cases, the valves are open systems and the outside fluids can reach the pore space in the valves.

Altogether, these observations showed that when rather similar initial shell structures (all baculate symmetrical) are influenced by different diagenetic scenarios, the final appearance of their microstructure and mineral composition can be very different. It shows also that shell structure and taphonomy studies are relevant for geochemical interpretations, because the extent of precipitation of different apatite phases may result in a mixture of different geochemical signatures.

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7. SUMMARY IN ESTONIAN

Kambriumi linguloidide koja struktuur ja tafonoomilised muutused

Käesolevas magistritöös uuriti kaltsiumfosfaadist kojaga fossiilsete käsijalgsete ülemsugukonna *Linguloidea* kojastruktuure ning neis toimunud tafonoomilisi ja diageneetilisi muutusi kolme "oobolusliivakivis" enimlevinud perekonna *Ungula*, *Obolus* ja *Schmidtites* näitel. Uuritud kivistisi sisaldavad proovid pärinevad viiest paljandist Loode-Venemaal ning kolmest paljandist ja kahest puursüdamikust Eestist (joonis 4), kihtidest, mille vanus ulatub "Kesk-Kambriumist" – Furongini (varasem Hilis-Kambrium).

Erinevatest sedimentatsioonitingimustest pärinevate apatiitsete lingulaatide koja struktuuride ja mineraalse koostise uurimiseks kasutati analüütilist skaneerivat elektronmikroskoopi (ESEM – "environmental" SEM) koos tagasipeegeldunud elektronide detektori ja EDS-analüsaatoriga, mis võimaldas madala vaakumi reziimil analüüsida töötlemata ja katmata murdepinna preparaate. See võimaldas mikrostruktuure vaadelda 3-mõõtmelisena ning vältida info kadumist töötlemisel.

Kokkuvõtvalt võib skeletistruktuuride tafonoomiliste muutust kohta läbi viidud ESEM uuringute põhjal järeldada alljärgmist: 1. Eesti ja Loode–Venemaa Furongi kihtidest pärit *Obolus apollinis'*e ristlõikes on hästi jägitav bakulaarsete ja kompaktsete kihtide järgnevus, viidates bakulaarsele sümmeetrilisele koja struktuuri tüübile Williams and Cusacki (1999) järgi. 2. Loode-Venemaal „Kesk-Kambriumist" pärit *Obolus ruchini* kojapoolmed on markantseks näiteks unikaalsest struktuuri säilimsest; ESEM abil on võimalik jälgida baakulate mineraliseerumise varajasi staadiume ümber elastsete polümeerikiudude. Autigeensete mineraalide (nt. hematiidi) ladestumine järgib bakulaarse kihi piire, kus poorsus on võrreldes kompaktsete kihtidega suurem. Eelnevaga sarnane tafonoomiline pilt on jälgitav ka *Ungula convexa* kojapoolmetel Furongist Loode-Venemaalt, kus hematiit on ladestunud sfääriliselt.

Bakulaarne koja struktuur on aimatav ka Iru paljandist (Furong) *Ungula ingrica* koja ristlõike põhjal. Erinevalt perekonnast *Obolus* on *Ungula*'te kojas rohkesti autigeenset apatiiti, mis baakulate vahelist pooriruumi täites on maskeerinud bakulaarse struktuuri. Selline väheste struktuurielementide säilivusega olukord tuli ilmsiks ka Ülgase paljandist pärinevate *Ungula inornata* Mickwitz and *Schmidtites celatus* Volborth kojapoolmete murdepindadel. Lisaks autigeensele apatiidile on orgaanika lagunemise järel vabanenud ruumi laiguti täitnud ka püriit, mida on võimalik jälgida *Schmidtites celatus*e ja Ülgase kihistu basaal konglomeraadist pärineva *Ungula s*p. näitel. Vaatamata sellele, et kõigi uuritud liikide puhul on tegu bakulaarse sümmeetrilise struktuuritüübiga, võib öelda, et fossiilsetes kodades jälgitavad kojastruktuurid võivad tafonoomiliste ja diageneetiliste protsesside tagajärjel olla väga eri-ilmelised.

Tafonoomiliste muutuste kaardistamine võimaldab täpsustada kojastruktuuride interpreteerimist fülogeneetilises kontekstis, samuti ka sekundaarsete muutuste rolli geokeemilistes uuringutes.

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PLATES

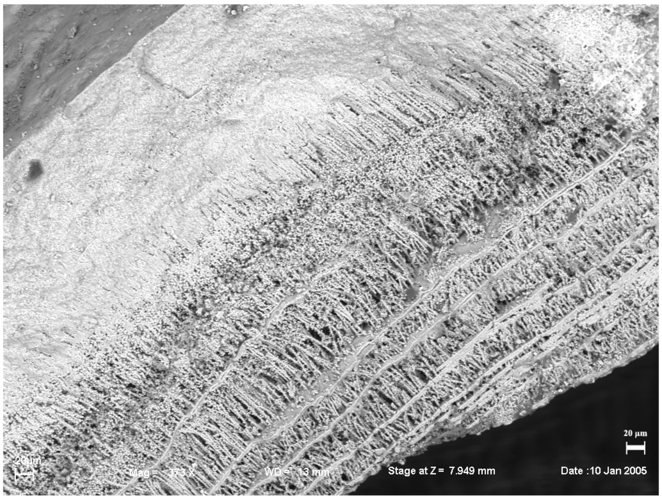
Plate 1

Back-scattered electron images of fracture sections of *Obolus apollinis* Eichwald from the Cambrian (Furongian) of Ingria.

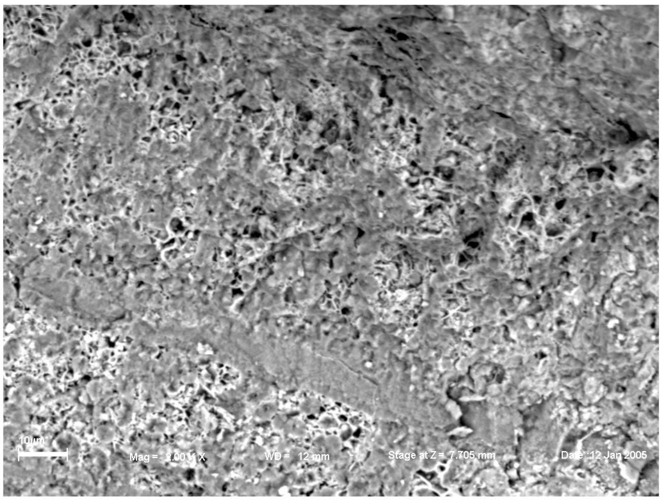
Photos 1 and 2: A specimen from the Tosna Formation, Lava River outcrop in Ingria, NW Russia showing alternation of compact and baculate laminae. Note the diagenetically changed baculi with spherical aggregates, maintaining their position in the trellised baculate sets. There are lighter patch indicating hematite precipitation on the right upper corner of Photo 1. Scale bars 20 μm and 10 μm, respectively.

Photo 3: *Obolus apollinis* from the Tosna Formation, Suma River section in Ingria, NW Russia; with the baculate sets, slightly masked by precipitated apatite. Scale bar 10 μm.

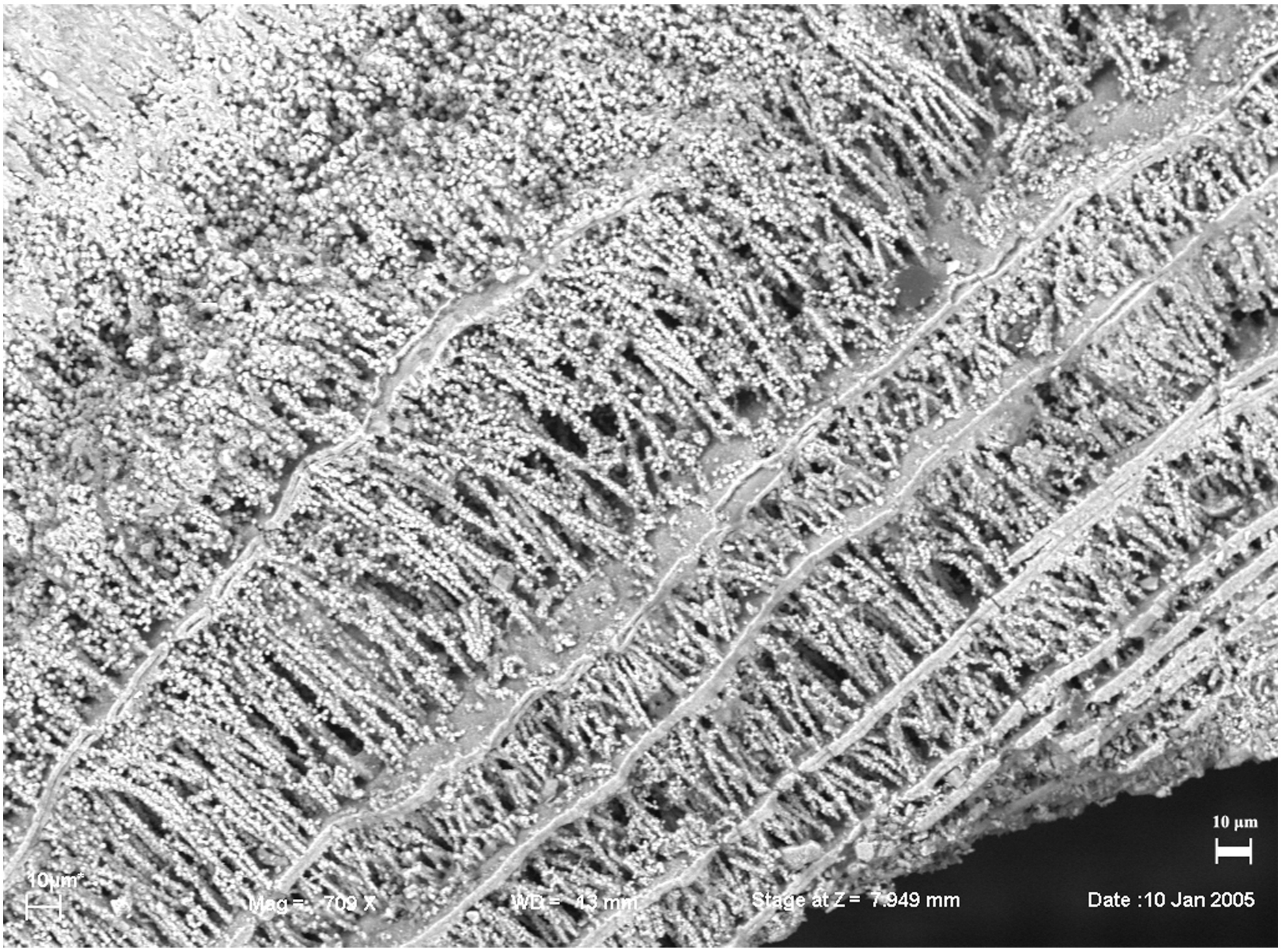
PLATE 1


20 µm
20µm
Mag = 373 X
WD = 13 mm
Stage at Z = 7.949 mm
Date :10 Jan 2005

1


10µm
Mag = 2.00 K X
WD = 12 mm
Stage at Z = 7.705 mm
Date :12 Jan 2005

3


10 µm
10µm
Mag = 709 X
WD = 13 mm
Stage at Z = 7.949 mm
Date :10 Jan 2005

2

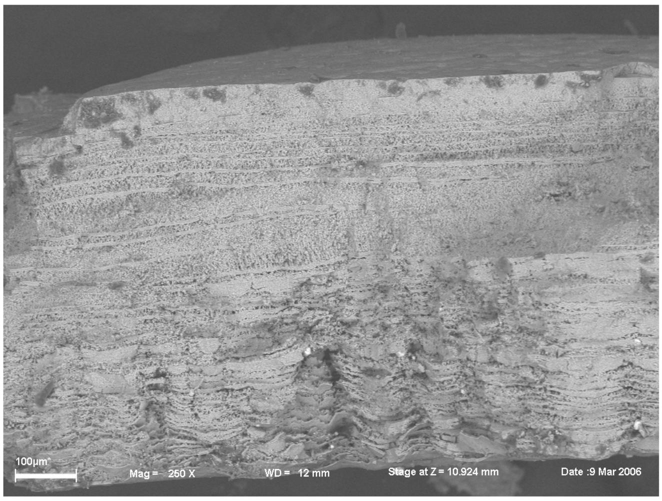
Plate 2

Back-scattered electron images of a fracture section of *Obolus apollinis* Eichwald from the Kallavere Formation, core R-1555 near Rakvere, depth 99.1-103.1 m.

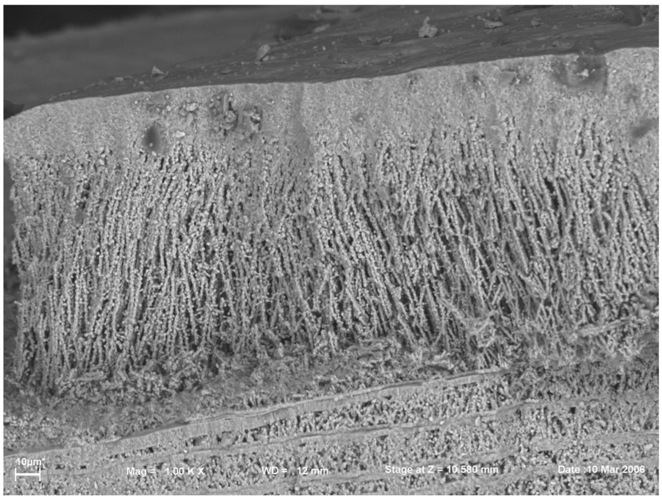
Photo 1: General view, showing the alteration of compact and baculate laminae, scale bar 100 μm.

Photos 2, 3: Details of the shell structure, scale bars 10 μm. Longer baculate sets near the outer margin of the shell (Photo 2) and alternation of compact and baculate laminae in the middle part of the shell (Photo 3). Note different preservation of the baculi: in some baculate layers the baculi are fused together.

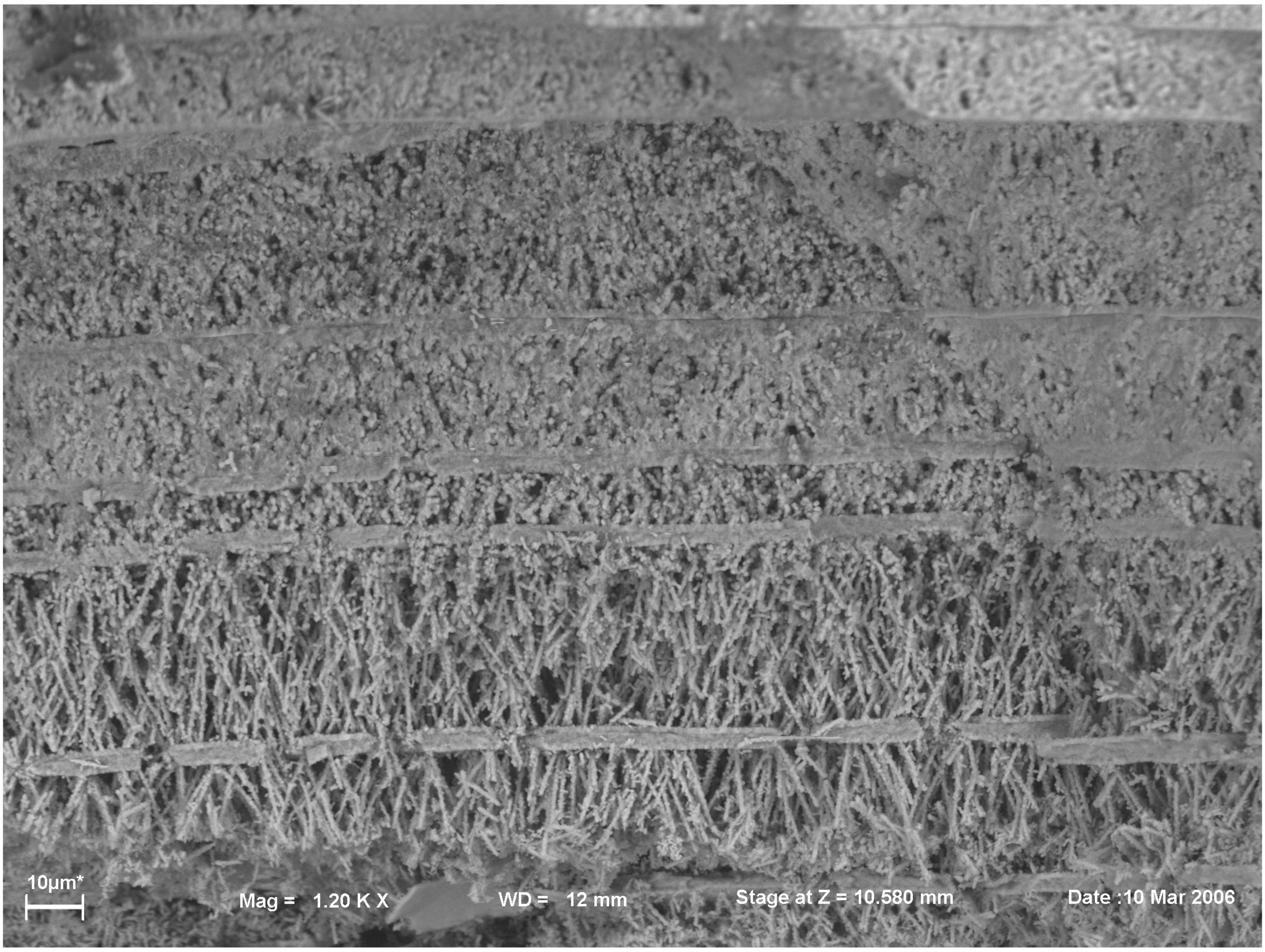
PLATE 2


100µm*
Mag = 250 X
WD = 12 mm
Stage at Z = 10.924 mm
Date :9 Mar 2006

1


10µm*
Mag = 1.00 K X
WD = 12 mm
Stage at Z = 10.580 mm
Date :10 Mar 2006

2


10µm*
Mag = 1.20 K X
WD = 12 mm
Stage at Z = 10.580 mm
Date :10 Mar 2006

3

Plate 3

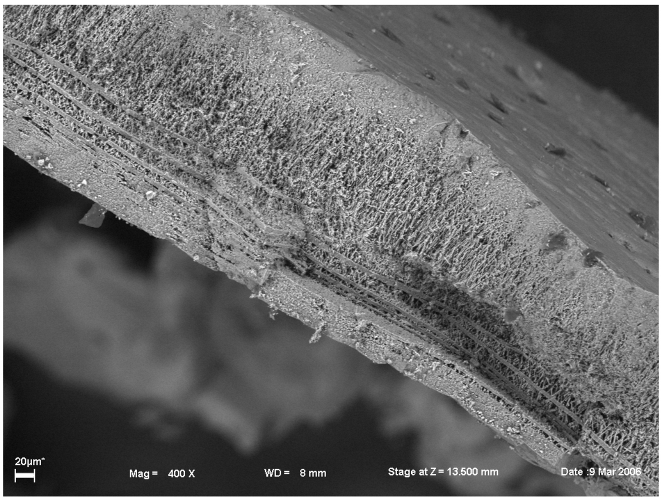
Back-scattered electron images of a fracture section of *Obolus apollinis* Eichwald from the Tosna Formation, Putilovo quarry, East of St. Petersburg, NW Russia.

Photo 1: General view of alternating baculate and compact laminae. Scale bar 20 μm.

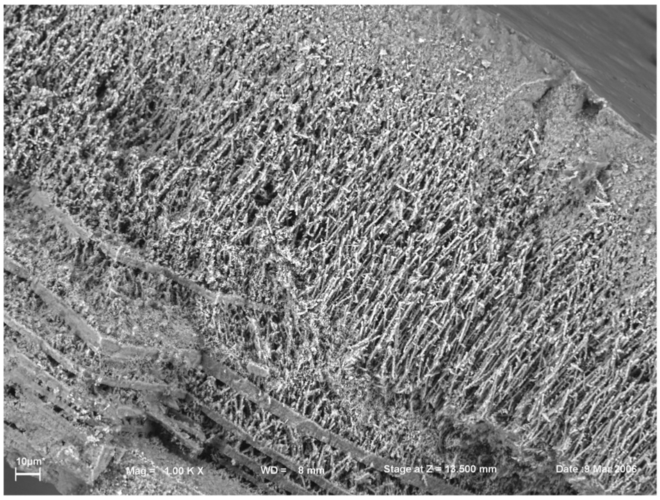
Photo 2: Detail of photo 1 showing an oblique three-dimensional view of well-preserved baculate sets. Scale bar 10 μm.

Photo 3. Detail of compact and baculate laminae in lower part of the shell. Note the baculi composed of spherical aggregates of apatite. Scale bar 2 μm.

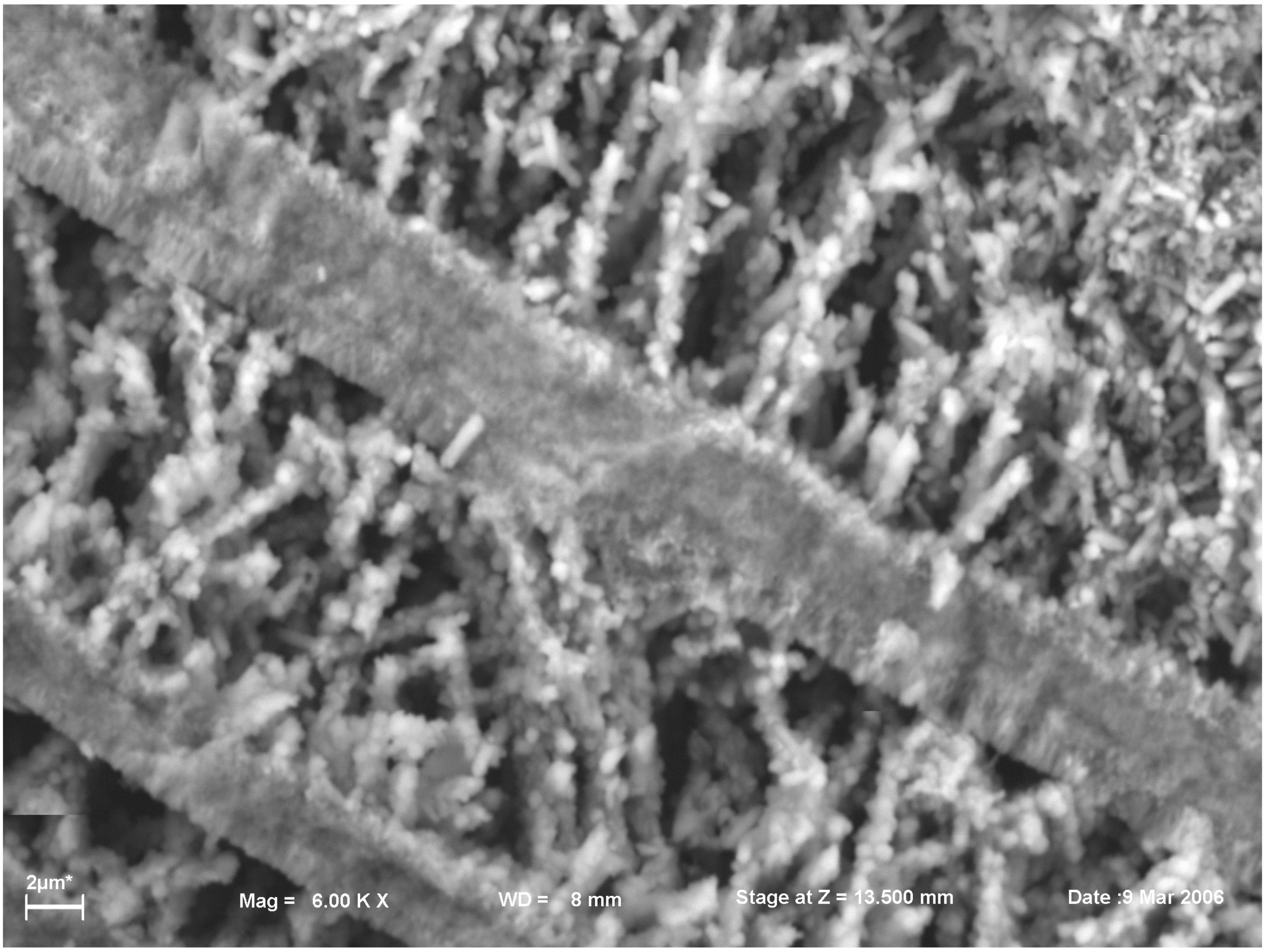
PLATE 3


20µm*
Mag = 400 X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

1


10µm*
Mag = 1.00 K X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

2


2µm*
Mag = 6.00 K X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

3

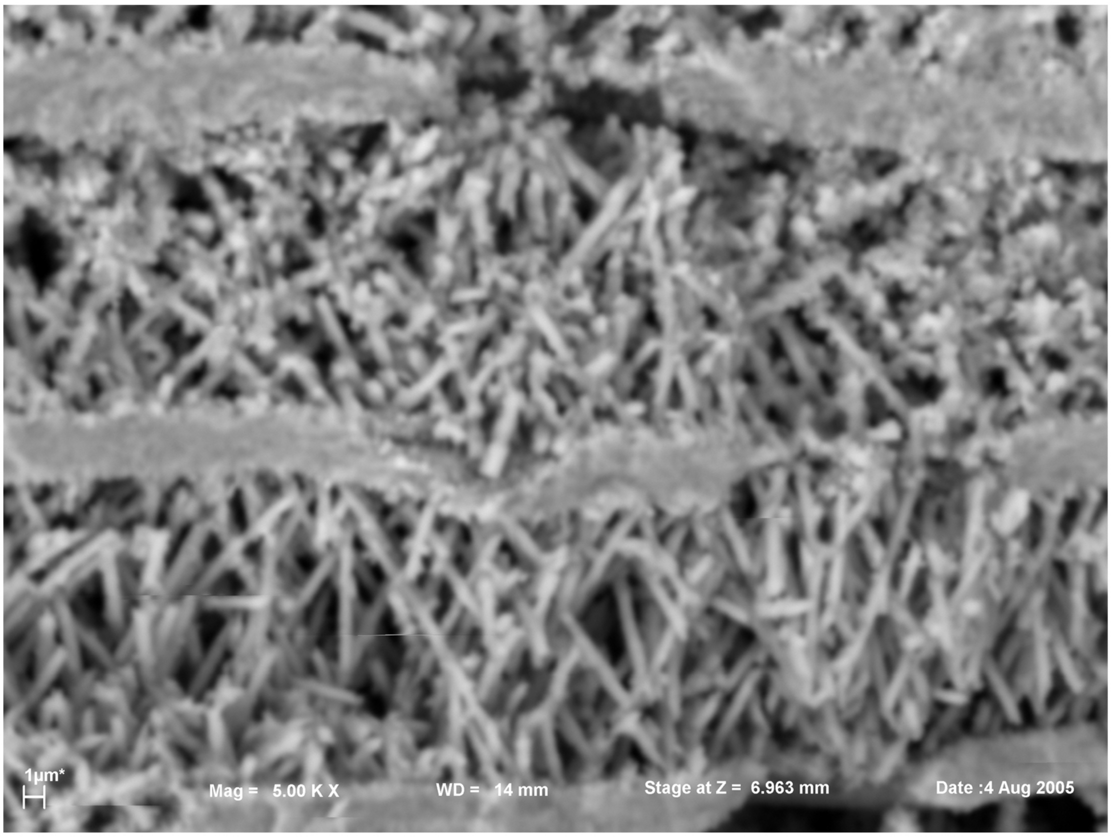
Plate 4

Back-scattered electron images of a fracture section of *Obolus apollinis* Eichwald from the Tosna Formation, Putilovo quarry, East of St. Petersburg, NW Russia.

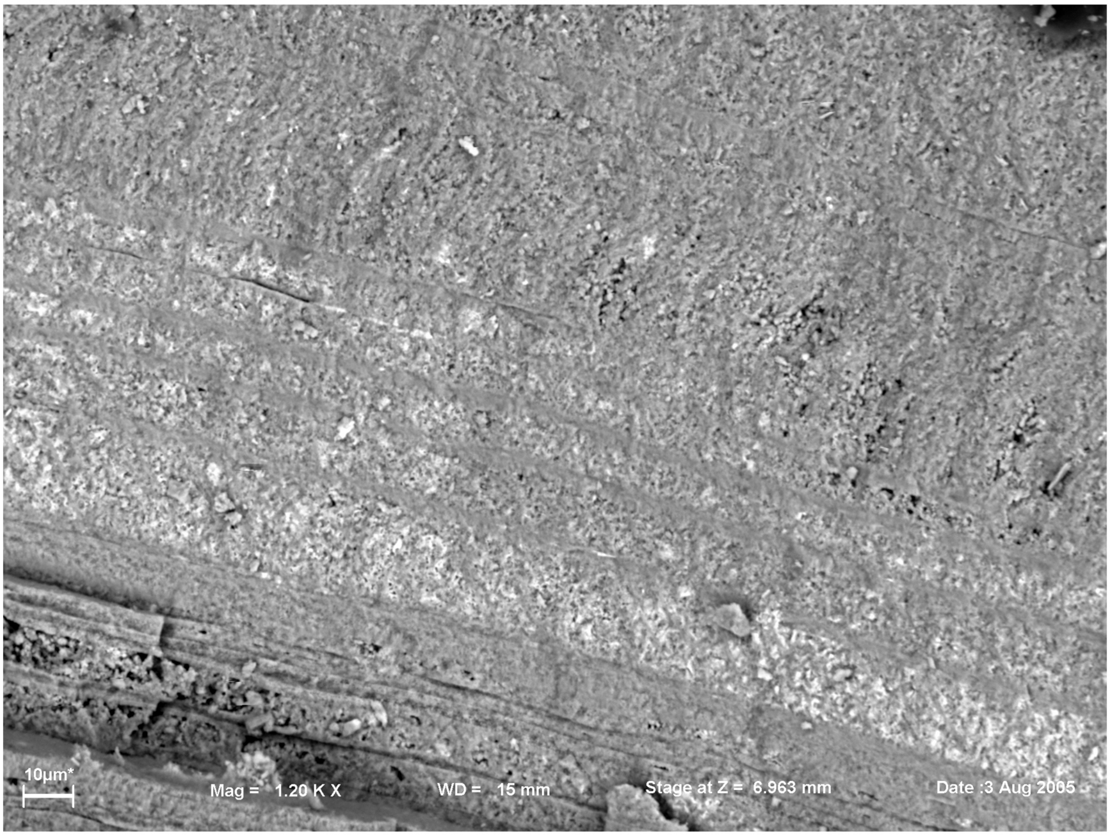
Photo 1: Detail of compact and baculate laminae. Scale bar 1 μm.

Photo 2: General view of alternating baculate and compact laminae. Note the hematite precipitation preferably within the baculate layer of the shell. Scale bar 10 μm.

PLATE 4


1µm*
Mag = 5.00 K X
WD = 14 mm
Stage at Z = 6.963 mm
Date :4 Aug 2005

1


10µm*
Mag = 1.20 K X
WD = 15 mm
Stage at Z = 6.963 mm
Date :3 Aug 2005

2

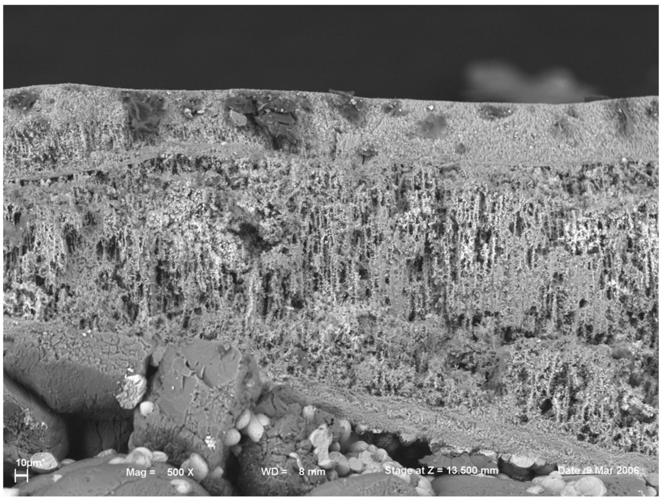
Plate 5

Back-scattered electron images of a fracture section of *Obolus ruchini* Khazanovitch and Popov from the "Middle Cambrian" Sablinka Formation, on the bank of Volkhov River near the Gertovo village, NW Russia.

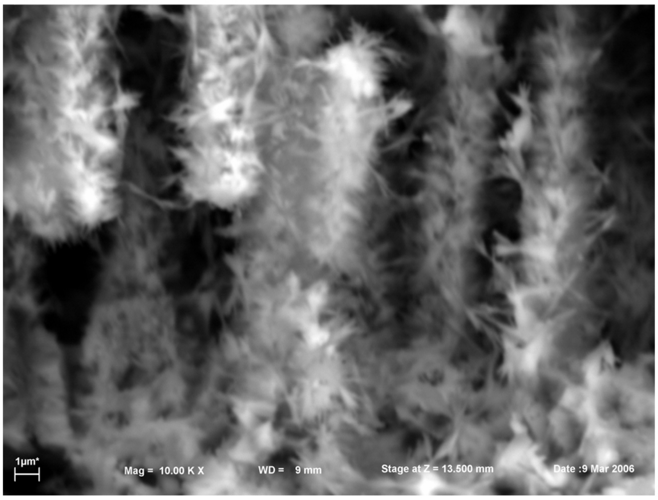
Photo 1: A general view of the valve, with baculate sets. Note the lighter color zones of hematite precipitation and light spherical hematite aggregates on the dark quartz grains below the valve. Scale bar 10 µm.

Photos 2 and 3: Close-up images of mineralized polymer matrix acting as a supporting "backbone" for mineralization of baculi. Photo 2 shows the development of mineralization and formation of the baculi as three-dimensional rod-like structures. Photo 3 shows flexible parallel fibrils interpreted as part of mineralized polymer network, tied together pairwise, accompanied by needle-like apatite crystals. Scale bars 1 µm.

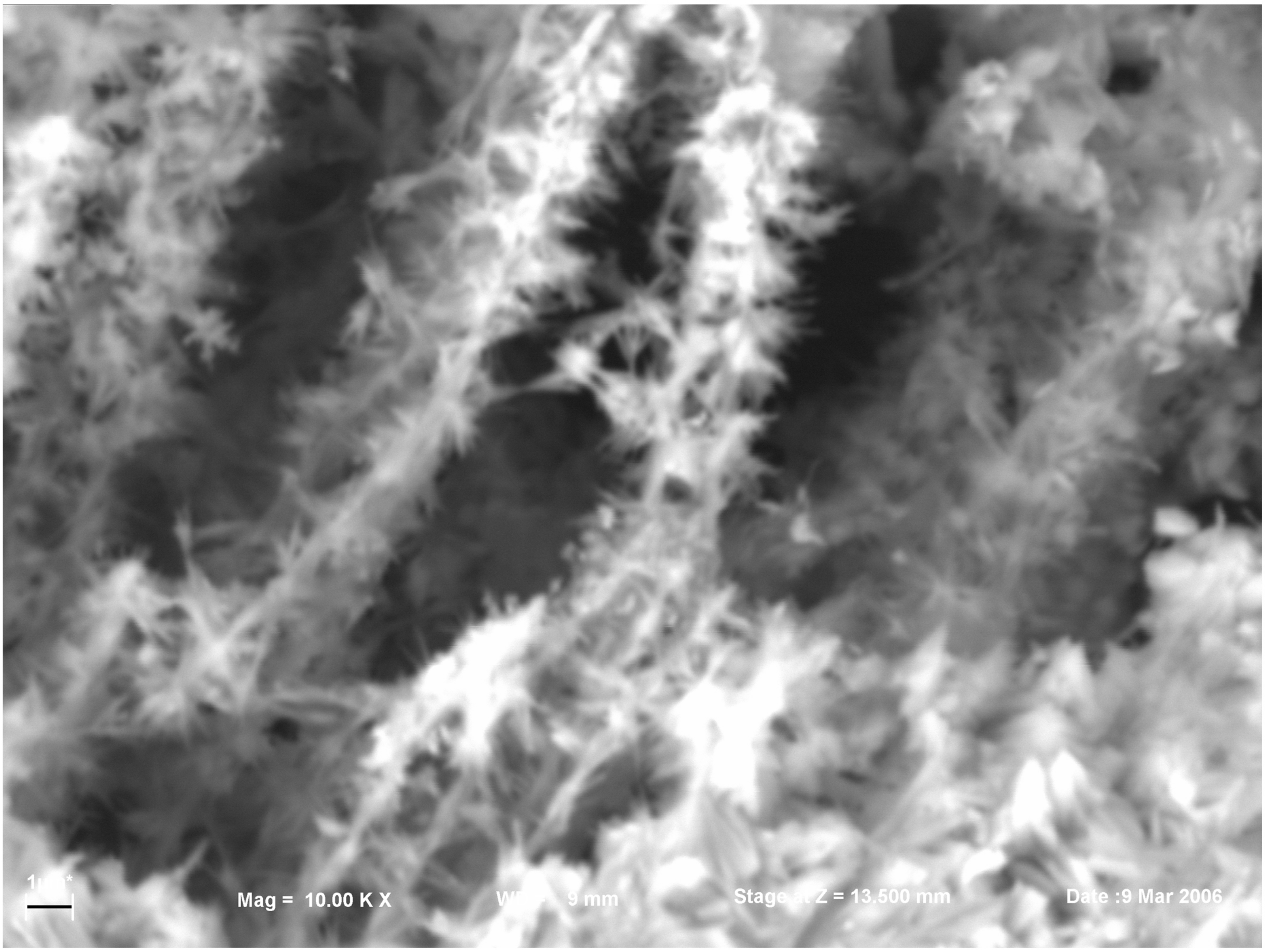
PLATE 5


10µm*
Mag = 500 X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

1


1µm*
Mag = 10.00 K X
WD = 9 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

2


Mag = 10.00 K X
9 mm
Z = 13.500 mm
Date :9 Mar 2006

3

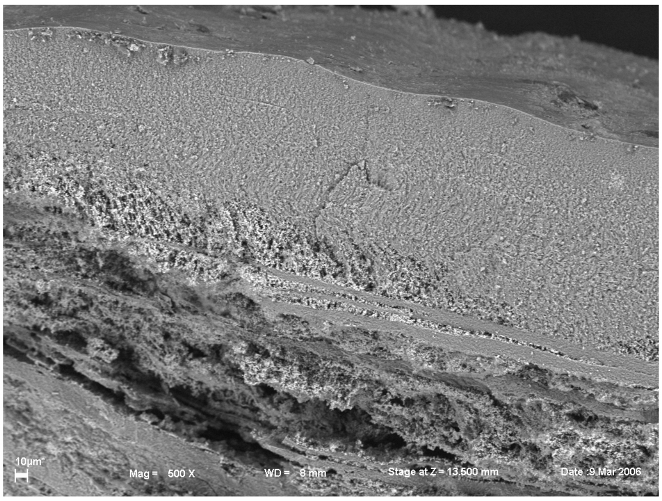
Plate 6

Back-scattered electron images of a fracture section of *Obolus ruchini* Khazanovitch and Popov from the “Middle Cambrian” Sablinka Formation Sarya River near the Gertovo village, NW Russia.

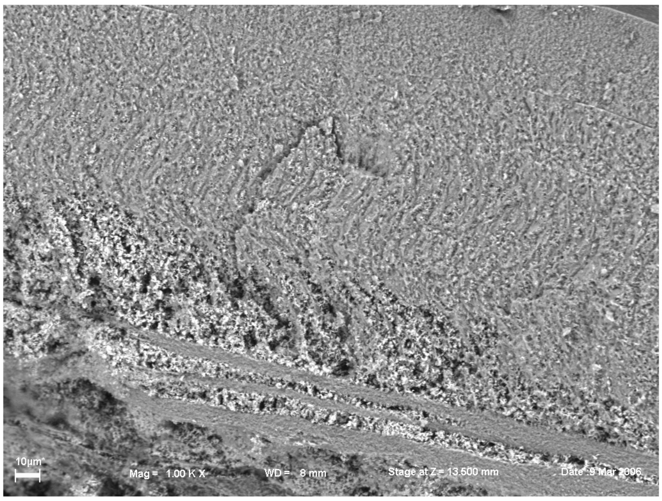
Photos 1 and 2: General views, showing alternation of compact and baculate laminae. Scale bars 10 μm.

Photo 3: A close-up image showing alternation of compact and baculate laminae. Note the hematite precipitation (with lighter color on back-scattered electron image) into the baculate laminae mimicking, so that the hematite precipitation is following the baculate laminae. Scale bar 1 μm.

PLATE 6


10µm*
Mag = 500 X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

1


10µm*
Mag = 1.00 K X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

2


1µm*
Mag = 5.00 K X
WD = 8 mm
Stage at Z = 13.500 mm
Date :9 Mar 2006

3

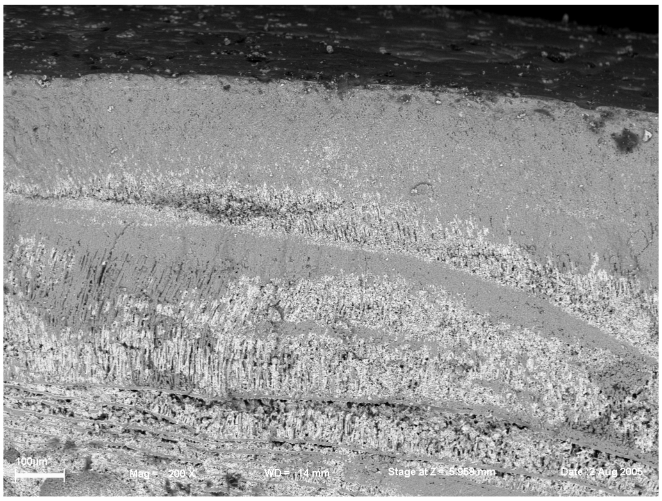
Plate 7

Back-scattered images of a fracture section of *Ungula convexa* Pander from the Tosna Formation, Lava River section in Ingria, NW Russia.

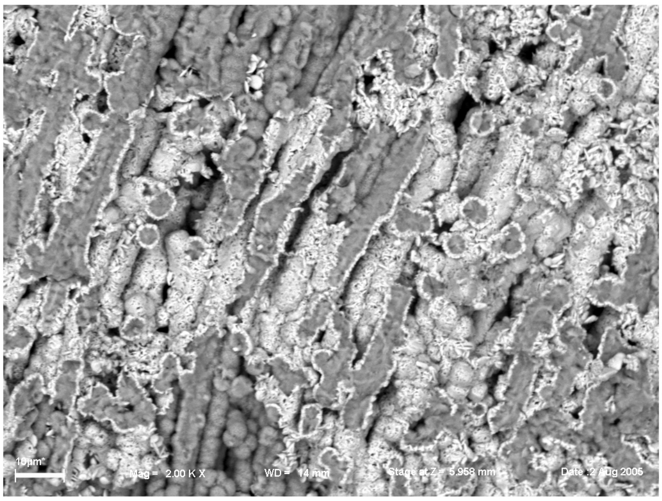
Photo 1: A general view, showing alternating compact and baculate laminae. Lighter zones mark hematite precipitation. Scale bar 100 μm.

Photos 2 and 3: Close-up views showing spherical apatite aggregates forming the baculi; and hematite light-coloured coatings and aggregates of precipitated hematite. Scale bars 10 μm and 2 μm, respectively.

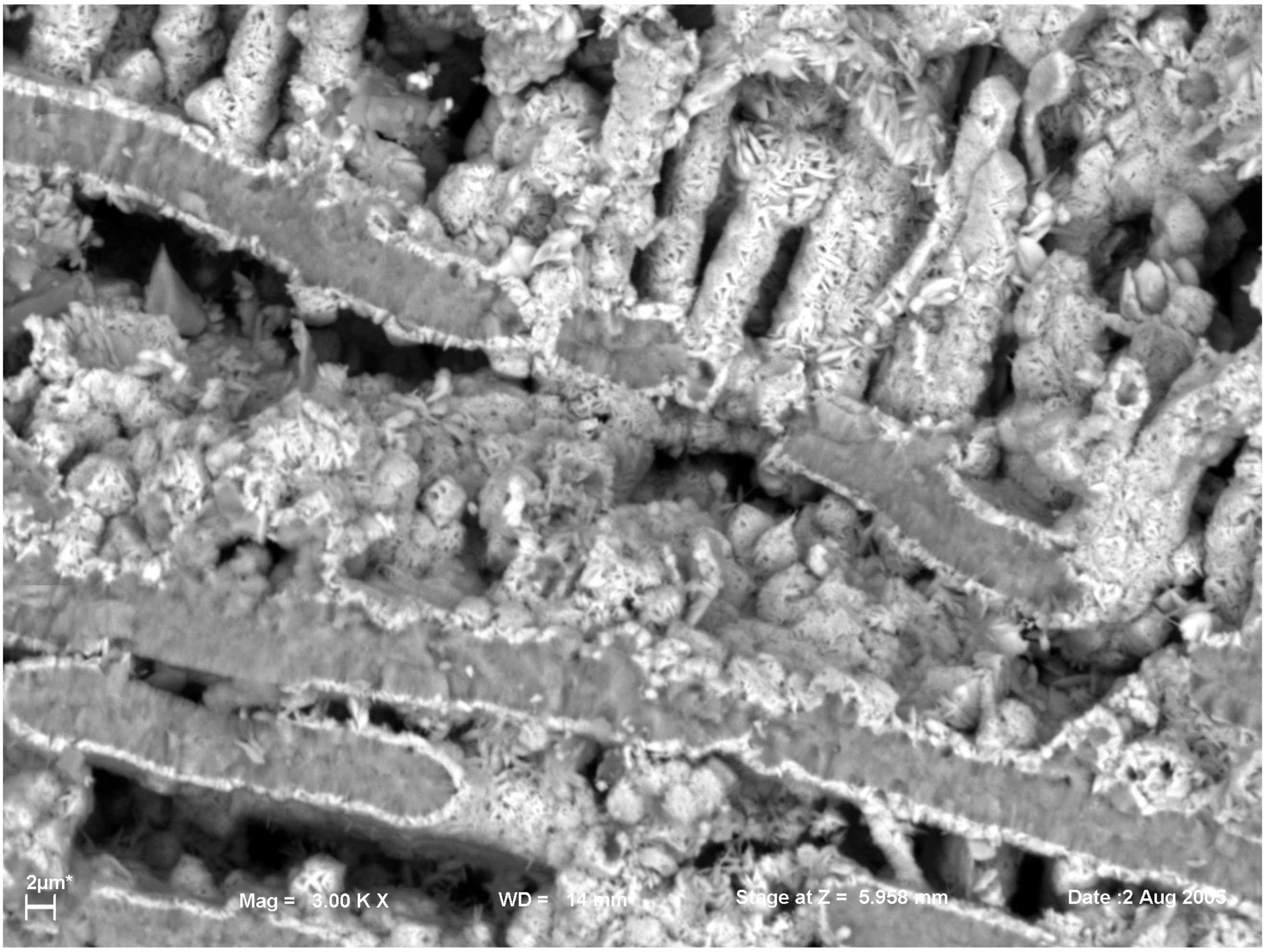
PLATE 7


100µm*
Mag = 200 X
WD = 14 mm
Stage at Z = 5.958 mm
Date :2 Aug 2005

1


10µm*
Mag = 2.00 K X
WD = 14 mm
Stage at Z = 5.958 mm
Date :2 Aug 2005

2


2µm*
Mag = 3.00 K X
WD = 14 mm
Stage at Z = 5.958 mm
Date :2 Aug 2005

3

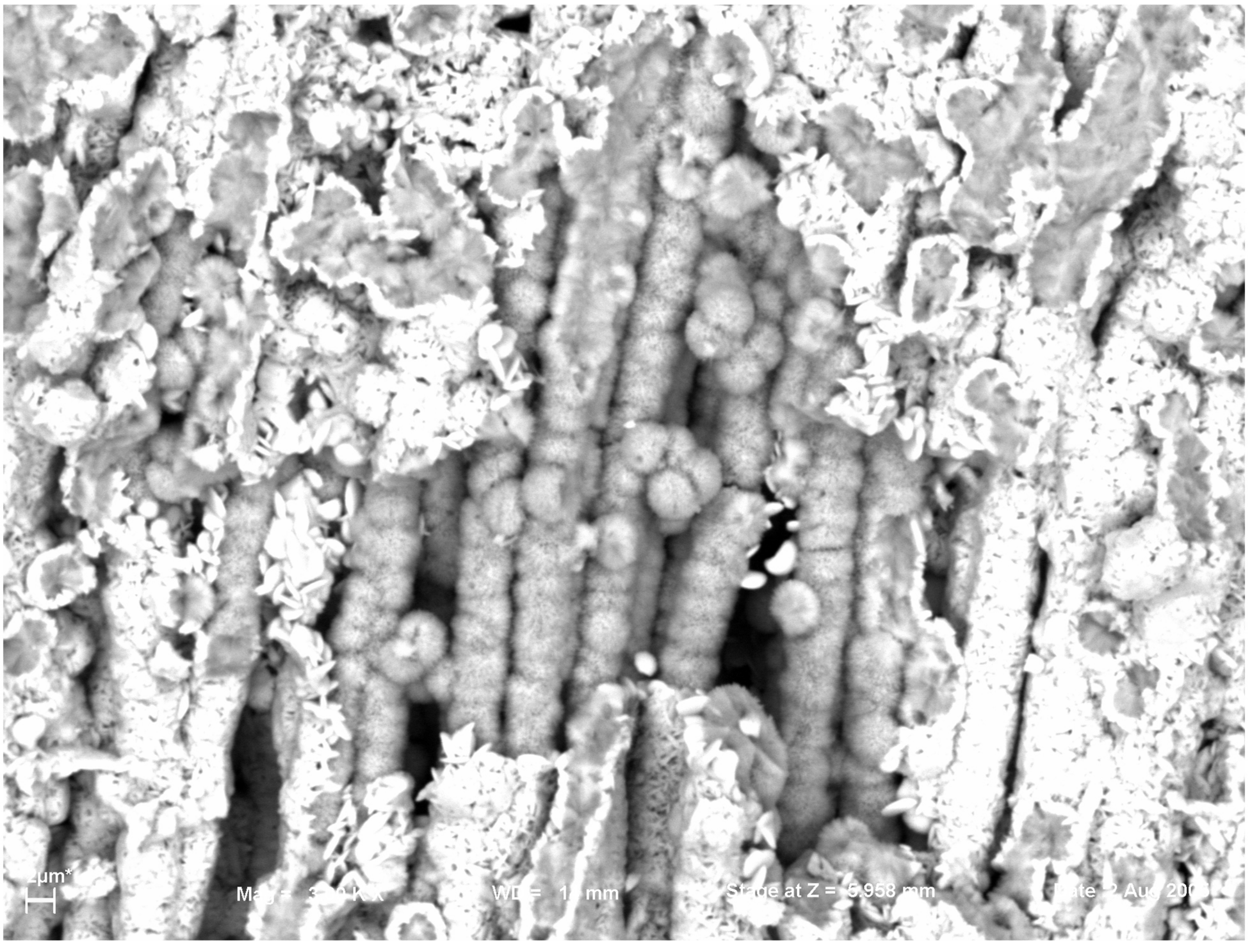
Plate 8

Back-scattered electron images of fracture sections of *Ungula convexa* Pander from the Tosna Formation, Lava River section in Ingria, NW Russia.

Photo 1: Apatite aggregates forming the baculi and hematite light-coloured coatings and aggregates of precipitated hematite. Scale bar 2 μm.

Photo 2: A close-up image of another specimen showing baculate sets and hematite precipitation in the form of spherical aggregates and amorphous infill. Scale bar 10 μm.

PLATE 8



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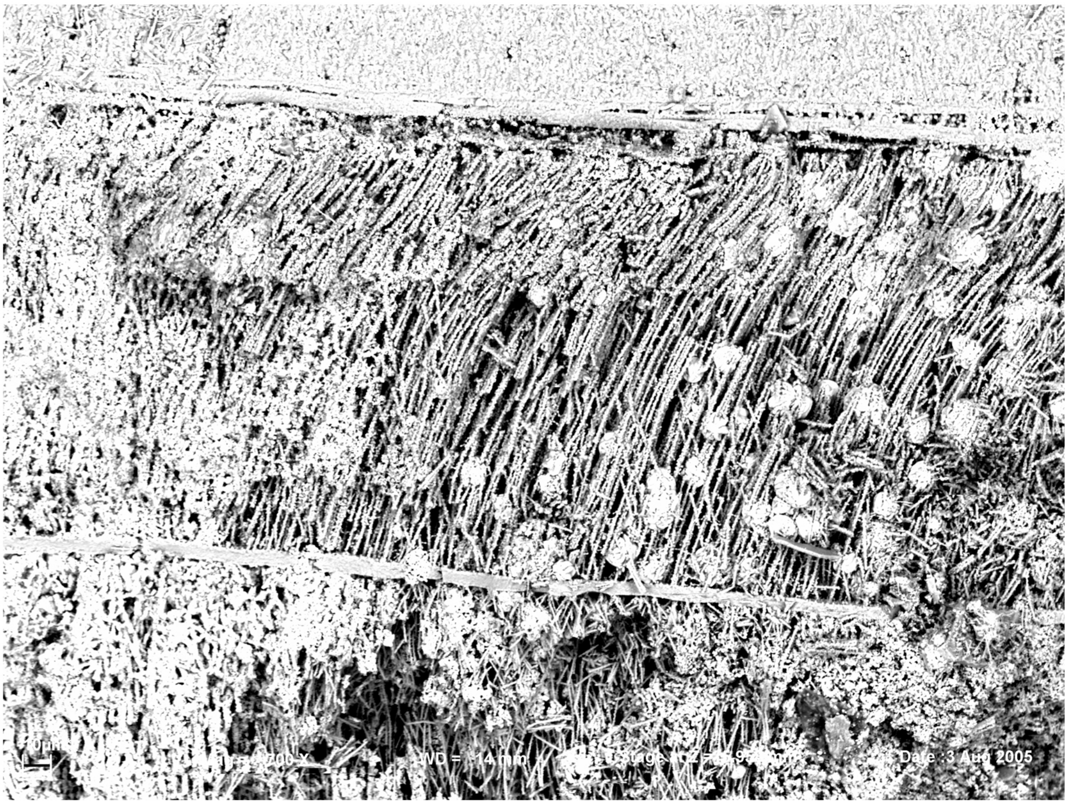


2

Plate 9

Back-scattered electron images of fracture sections of obolids from the Cambrian (Furongian) Ülgase and Kallavere Formations of Estonia.

Photo 1: *Ungula ingrica* Eichwald from the basal conglomerate of the Kallavere Formation, from the Ülgase section. A close-up image of fracture section of the valve showing alternation of compact and baculate laminae. Note rather well-expressed baculate structure. Scale bar 10 μm.

Photo 2: *Ungula ingrica* from the Kallavere Formation in the Iru section. Alteration of baculate and compact laminae is homogenized because of authigenic apatite precipitation and fusion of baculi. Baculate sets can be vaguely observed in the lower part of the valve. Scale bar 10 μm.

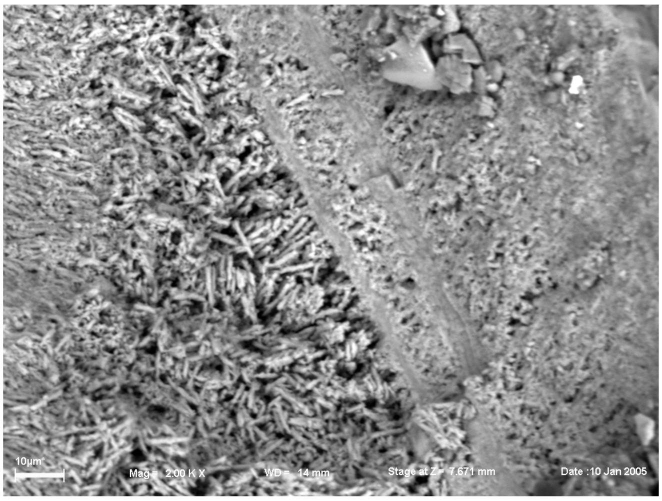
Photo 3: *Ungula inornata* from the Ülgase Formation, from the Ülgase outcrop in Estonia. The baculate structure is almost entirely masked by the precipitation of authigenic apatite. Local lighter spots of precipitated pyrite can be observed. Scale bar 10 μm.

Photo 4: *Ungula* sp. from pebbles of the basal conglomerate of the Ülgase Formation, Ülgase outcrop in Estonia. Alternation of compact and baculate laminae can be observed. Lighter zones show pyrite precipitation. Scale bar 10 μm.

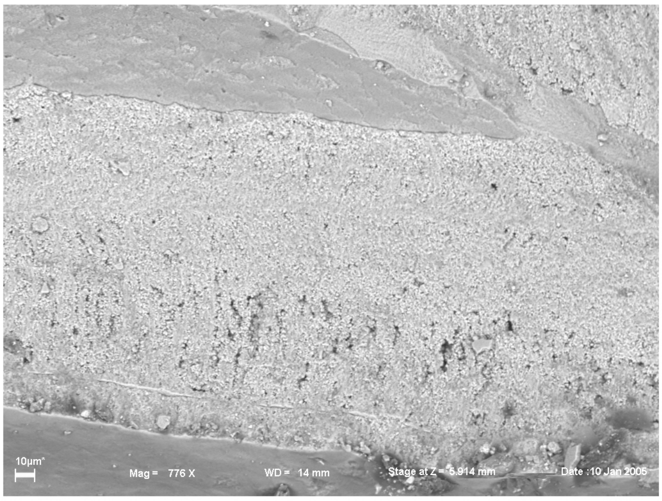
Photo 5: *Schmidtites celatus* from the Kallavere Formation, Ülgase outcrop. Alternation of compact and baculate laminae is vaguely observable. Lighter zones show pyrite precipitation. Scale bar 10 μm.

Photo 6: *Schmidtites celatus* from the Kallavere Formation, core Värska 6 in south-eastern Estonia, depth 455.0-455.2 m. An alternation of compact and baculate laminae can be observed. Lighter zones show pyrite precipitation. Scale bar 10 μm.

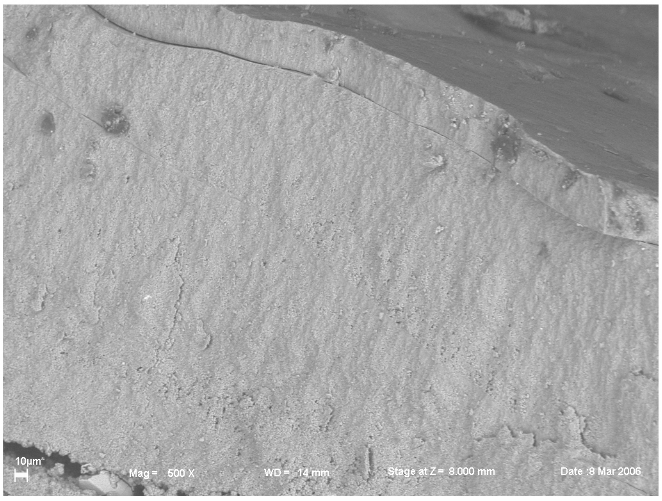
PLATE 9



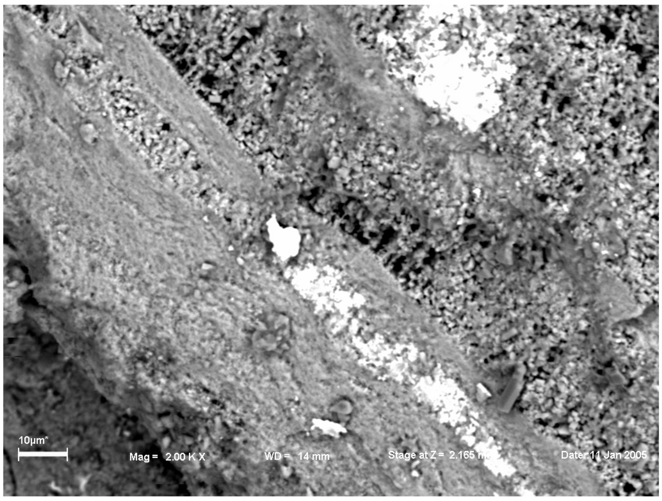
1



2



3



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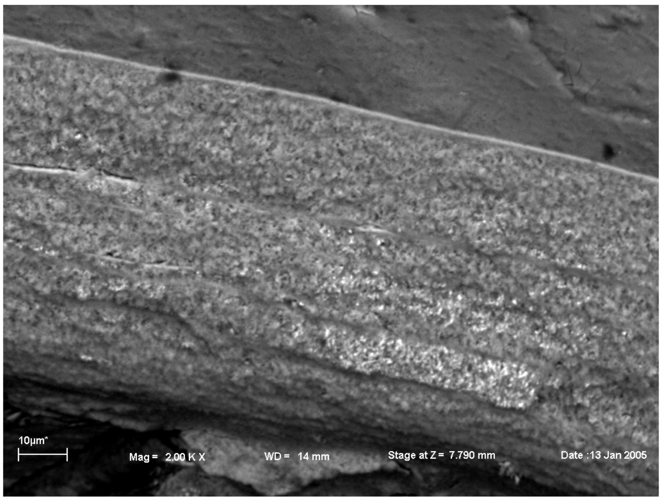
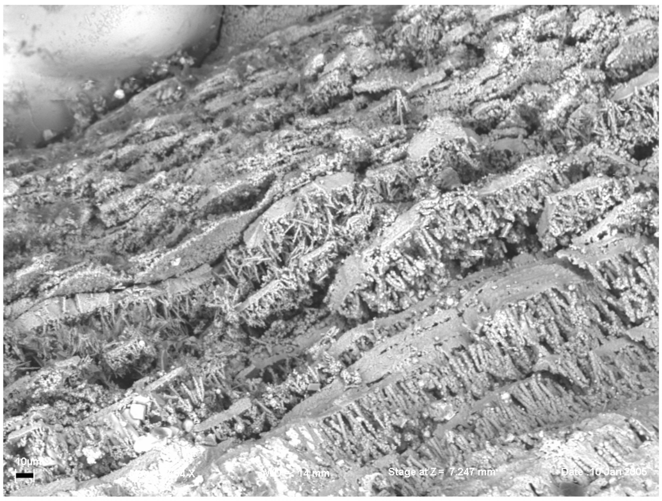


5



6