Alleged cnidarian *Sphenothallus* in the Late Ordovician of Baltica, its mineral composition and microstructure

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Sphenothallus is a problematic fossil with possible cnidarian affinities. Two species of *Sphenothallus*, *S*. aff. *longissimus* and *S. kukersianus*, occur in the normal marine sediments of the Late Ordovician of Estonia. *S. longissimus* is more common than *S. kukersianus* and has a range from early Sandbian to middle Katian. *Sphenothallus* had a wide paleobiogeographic distribution in the Late Ordovician. The tubes of *Sphenothallus* are composed of lamellae with a homogeneous microstructure. The homogeneous microstructure could represent a diagenetic fabric, based on the similarity to diagenetic structures in *Torellella* (Cnidaria?, Hyolithelminthes). Tubes of *Sphenothallus* have an apatitic composition, but one tube contains lamellae of diagenetic calcite within the apatitic structure. *Sphenothallus* presumably had originally biomineralized apatitic tubes. Different lattice parameters of the apatite indicate that biomineralization systems of phosphatic cnidarians *Sphenothallus* and *Conularia* sp. may have been different.

Key words: Cnidaria?, *Sphenothallus*, apatite, microstructure, Ordovician, Sandbian, Katian, Estonia.

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Introduction

Sphenothallus is a genus of tubicolous fossils known from the early Cambrian (Zhu et al. 2000; Li et al. 2004) to the Carboniferous (Neal and Hannibal 2000). Their tubes encrust various hard substrates from brachiopod shells (Neal and Hannibal 2000) to carbonate hardgrounds (Bodenbender et al. 1989). *Sphenothallus* tubes that are broken from the substrate have often been found without the holdfast. Their holdfasts are common on brachiopod shells and hardgrounds of Palaeozoic age (Bodenbender et al. 1989; Neal and Hannibal 2000). The genus was originally assigned to plants (Hall 1847) because their flattened and often slightly curved tubes resemble somewhat branches of plants. It was later affiliated variously with conulariids (Ruedemann 1896), hydroids, and graptolites (Price 1920) due to their slightly conical shells. In the "Treatise on Invertebrate Paleontology" (Moore and Harrington 1956) it was placed within the Conulata. Later they have also been affiliated with annelid worms (Mason and Yochelson 1985) and cnidarians (van Iten et al. 1992, 1996). The latter opinion has recently been supported by most of the authors (Zhu et al. 2000; Li et al. 2004; Peng et al. 2005; van Iten et al. 2013). The exact ecology of *Sphenothallus* is poorly known, but they probably were sessile predators (Peng et al. 2005).

Sphenothallus had a wide geographic distribution in the Ordovician. Their fossils have previously been known from the Lower Ordovician of China (van Iten et al. 2013) and Korea (Choi 1990). Their fossils also occur in the Upper Ordovician of North America (Bolton 1994; van Iten et al. 1996; Neal and Hannibal 2000) and Brittany (Bouček 1928). In 1927 Öpik described two tubicolous fossils from the Sandbian oil shale of NE Estonia under the names: *Serpulites kukersianus* sp. nov. and *Serpulites longissimus* Murchison, 1939. However, the true taxonomic affinities of these possible worm tubes have remained unresolved.

The aims of this paper are to: (i) determine whether *Serpulites kukersianus* sp. nov. and *Serpulites longissimus* Murchison, 1939 of Öpik (1927) belong to *Sphenothallus* Hall 1847; (ii) analyze mineral composition and tube microstructure of these fossils; (iii) determine whether these fossils were originally biomineralized; and (iv) discuss the palaeobiogeographic distribution of *Sphenothallus* in the Late Ordovician.

Institutional abbreviations.—TUG, Natural History Museum (Museum of Geology), University of Tartu, Estonia; GIT, Tallinn University of Technology, Institute of Geology, Tallinn, Estonia.

Other abbreviations.—ATR, attenuated total reflectance; EDS, Energy-Dispersive X-ray Spectroscopy; FTIR, Fou-

rier Transformed Infrared Spectroscopy; N, number of specimens; sd, standard deviation; XRD, X-ray diffraction.

Geological background

The Ordovician sequence of North Estonia is relatively complete. It is represented mostly by carbonate rocks except for the terrigenous Lower Ordovician part. The area of modern Estonia (Fig. 1) was covered by a shallow epicontinental sea in the Late Ordovician. The most common rocks in the Late Ordovician of northern Estonia are limestones. They are exposed in northern Estonia as a wide belt from the Narva River in the east to Hiiumaa Island in the west (Nestor and Einasto 1997).

In the Ordovician, Baltica drifted from the southern high latitudes to the tropical realm (Torsvik et al. 2012), which caused a drastic climatic change on the palaeocontinent. The sedimentation rate of carbonates increased due to climate warming. As a result of these climatic processes, deposits that are characteristic of an arid and tropical climate appeared in the Estonian Late Ordovician sequence (Nestor and Einasto 1997). These types of tropical deposits were completely lacking in the Early and Middle Ordovician when the Baltic Basin was situated in a temperate climate zone (Jaanusson 1973). The appearance of tabulate corals, stromatoporoids and reefs were the first signs of a warming climate in the early Katian. These fossil groups and reefs became prevalent at the very end of the Ordovician in the Hirnantian (Nestor and Einasto 1997). The oil shale and limestone containing *Sphenothallus* fossils are formed in normal marine conditions on a shallow carbonate shelf. *Sphenothallus* fossils are accompanied by normal marine fauna containing bryozoans, brachiopods, bivalves, gastropods, nautiloids, ostracods, trilobites, echinodermates, graptolites, chitinozoans, and algae.

Sphenothallus kukersianus occurs only in the Viivikonna Formation of the Kukruse Stage (lower Sandbian). This species, though rare, could be characteristic for the early Sandbian rocks of NE Estonia. The larger and more common specimens of *S.* aff. *longissimus* also appear in the Viivikonna Formation, but have a stratigraphic range to the Tudulinna Formation of Vormsi Stage (middle Katian).

Palaeobiogeography

Sphenothallus kukersianus is not known from the outside of the Sandbian oil shale deposits of NE Estonia. *S. kukersianus* could be endemic for Sandbian of Baltica, if it is not a junior synonym of *S.* aff. *longissimus*. The latter species occurs in the Ludlow of England (Avalonia) (Murchison 1854), but it is not known from the Late Ordovician outside of Baltica. The genus *Sphenothallus* has a wide distribution in the Late Ordovician. In addition to Baltica it occurs in the Late Ordovician of Laurentia (North America) (Bolton 1994; van Iten et al. 1996; Neal and Hannibal 2000) and Ar-
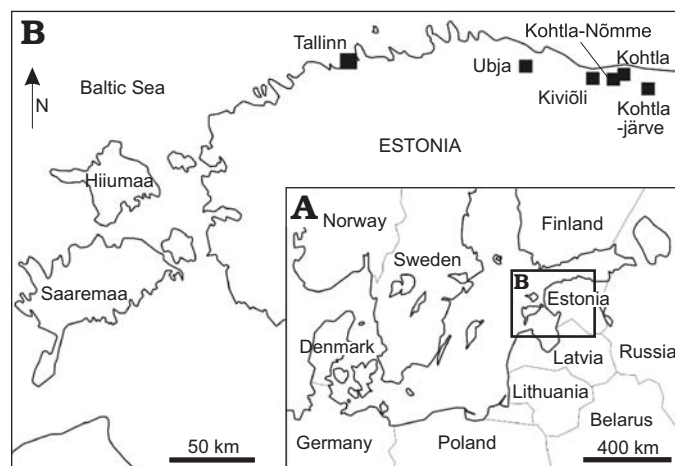

Fig. 1. Location of study area (**A**) and studied sections (**B**).

morica (Brittany) (Bouček 1928). The occurrence of *Sphenothallus* both in tropical Laurentia and more temperate Armorica close to Gondwana shows the climatic tolerance of the genus.

Material and methods

Eleven tubes of *Sphenothallus longissimus* from the Viivikonna Formation and one tube from the Tudulinna Formation were studied, along with a single tube of *S. kukersianus* from the Viivikonna Formation. One specimen of *Conularia* sp. (Cnidaria) from Viivikonna Formation was studied for comparison.

Scanning electron microscopy (SEM) imaging and analysis of samples was performed on a variable pressure Zeiss EVO MA15 SEM equipped with Oxford X-MAX energy dispersive detector system and Aztec Energy software for element analysis. Samples were studied as: (i) freshly broken surfaces perpendicular to bedding in uncoated and coated state with the coated samples prepared by depositing 5 nm thick Pt conductive layer using Leica EM SCD 500 high-resolution sputter; and (ii) polished slabs embedded in epoxy resin. The polished resin blocks were studied uncoated in a variable pressure mode.

X-ray diffraction (XRD) patterns were collected with a Bruker D8 Advance diffractometer with Cu$K\alpha$ radiation in the 2θ range 3–72°, with step size 0.02° 2θ and counting time 0.1 s per step using a LynxEye linear detector. The X-ray tube was operated at 40 kV and 40 mA. Minute pieces of a tube were powdered by hand using agate mortar under ethanol and XRD preparations were made dropping dense suspension on a low background silicon mono-crystal sample holder for mineral analysis. Mineral composition and structure refinement of apatite was modeled using Rietveld algorithm based code Siroquant 3.0 (Taylor 1991). The CO_3^{2-} ion substitution in carbonate-fluorapatite was determined using an empirical equation (Schuffert et al. 1990) that relates position of 004 and 410 reflections of carbonate-fluorapatite structure
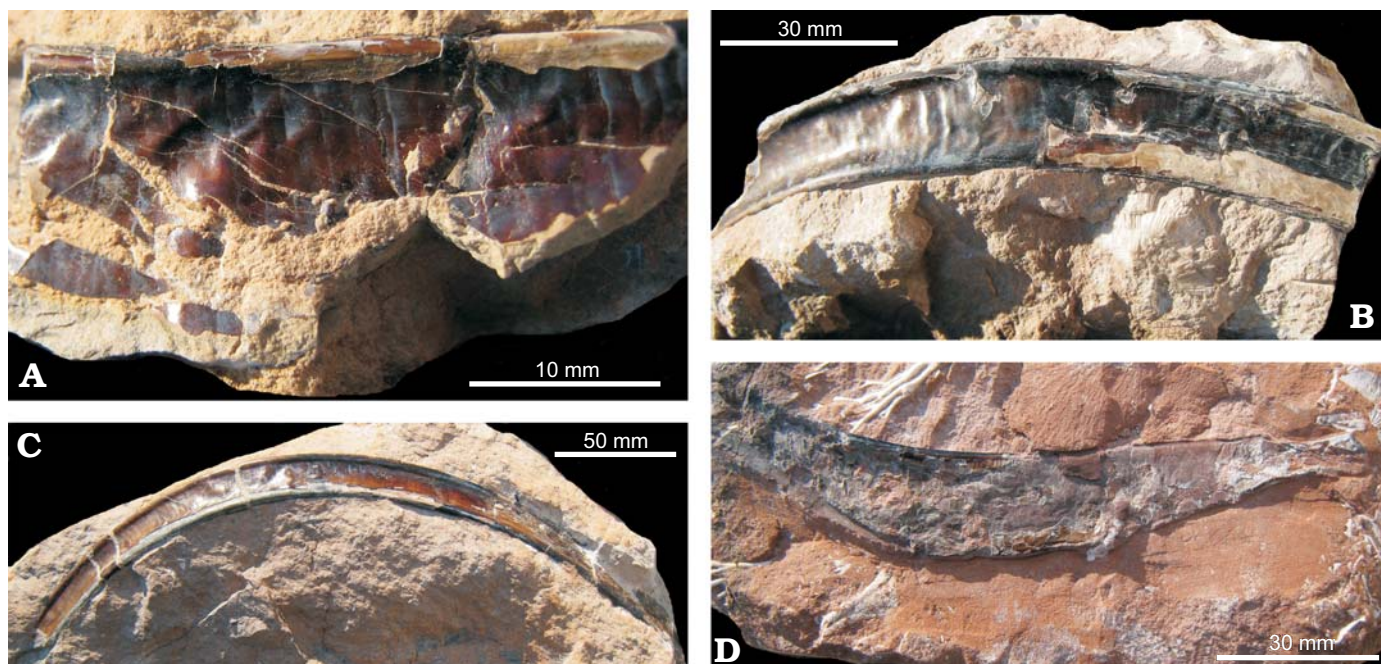
Fig. 2. Tubes of *Sphenothallus* aff. *longissimus* (**A–C**) and *Sphenothallus kukersianus* (Öpik, 1927) (**D**) Viivikonna Formation, lowermost Sandbian, NE Estonia. **A**. TUG 73-37 from Kohtla-Järve. **B**. TUG 1087-14 from Kohtla. **C**. TUG 2-551 from North East Estonia, oil shale basin. **D**. TUG 1087-12 from Kohtla-Järve.

on X-ray diffraction pattern and concentration of CO_3^{2-} in carbonate-substituted fluorapatite.

Infra-red spectrum of *Sphenothallus longissimus* tube was registred on Nicolet 6700 Fourier Transformed Infrared (FTIR) spectrometer with diamond micro-ATR (attenuated total reflectance) accessory in the 4000–550 cm^{-1} range.

We follow the classification by van Iten et al. (2013) for *Sphenothallus*.

Systematic palaeontology

Phylum Cnidaria Hatschek, 1888

Subphylum Medusozoa Peterson, 1979

Class uncertain

Genus *Sphenothallus* Hall, 1847

Type species: *Sphenothallus angustifolius* Hall, 1847, New York, Middle Ordovician.

Sphenothallus kukersianus (Öpik, 1927)

Fig. 2D.

1927 *Serpulites kukersianus*; Öpik 1927: 27, pl. 2: 14.

Material.—One complete specimen TUG 1087-12 from Kohtla-Järve, NE Estonia; Viivikonna Formation, lowermost Sandbian.

Description.—Large flattened slightly curved tube with very thin wall. Distal part of the tube is slightly tapering. Tube grew relatively fast in diameter 1.6 mm per 10 mm of length. Tube wall has two lateral thickenings 180° apart that are 0.4 mm

thick. The tube wall between lateral thickenings is 0.15 mm thick. Tube external surface is smooth and glossy, with very fine somewhat irregular perpendicular wrinkles. There are six to seven wrinkles per 5 mm. Tube wall has a lamellar structure.

Dimensions.—Maximal length 8.8 mm, maximal width 13.0 mm

Remarks.—*S. kukersianus* differs from *S.* aff. *longissimus* by its relatively fast growing diameter and tapering distal part of the tube. The tapering distal part of the tube could be caused by lateral compression and is presumably an artifact of preservation. It is possible that the fast growing diameter could also be characteristic of the proximal part of the tube of *S.* aff. *longissimus*. However, the studied material did not contain proximal parts of *S.* aff. *longissimus* tubes. Thus, *S. kukersianus* may be a junior synonym of *S.* aff. *longissimus*.

Geographic and stratigraphic range.—North East Estonia, oil shale basin, Sandbian.

Sphenothallus aff. *longissimus* (Murchison, 1839)

Fig. 2A–C.

1927 *Serpulites longissimus* Murchison, 1839; Öpik 1927: 26, pl. 2: 13.

Material.—Twelve partially preserved tubes TUG 1087-11, TUG 1008-25, TUG 1008-26, TUG 1008-27, TUG 1648-2, TUG 1648-3, TUG 1648-4, TUG 2-548, TUG 2-549, TUG 2-550, TUG 2-551, and GIT 494-14; from Kohtla, Kohtla-Nõmme, Kohtla-Järve, Kiviõli, Ubja from NE Estonia, and Kükita 24 borehole; Viivikonna Formation, lowermost Sandbian to Tudulinna Formation, middle Katian.

Description.—Very large slightly curved and flattened tubes with thin walls. Tubes grew very slowly in diameter 0.3
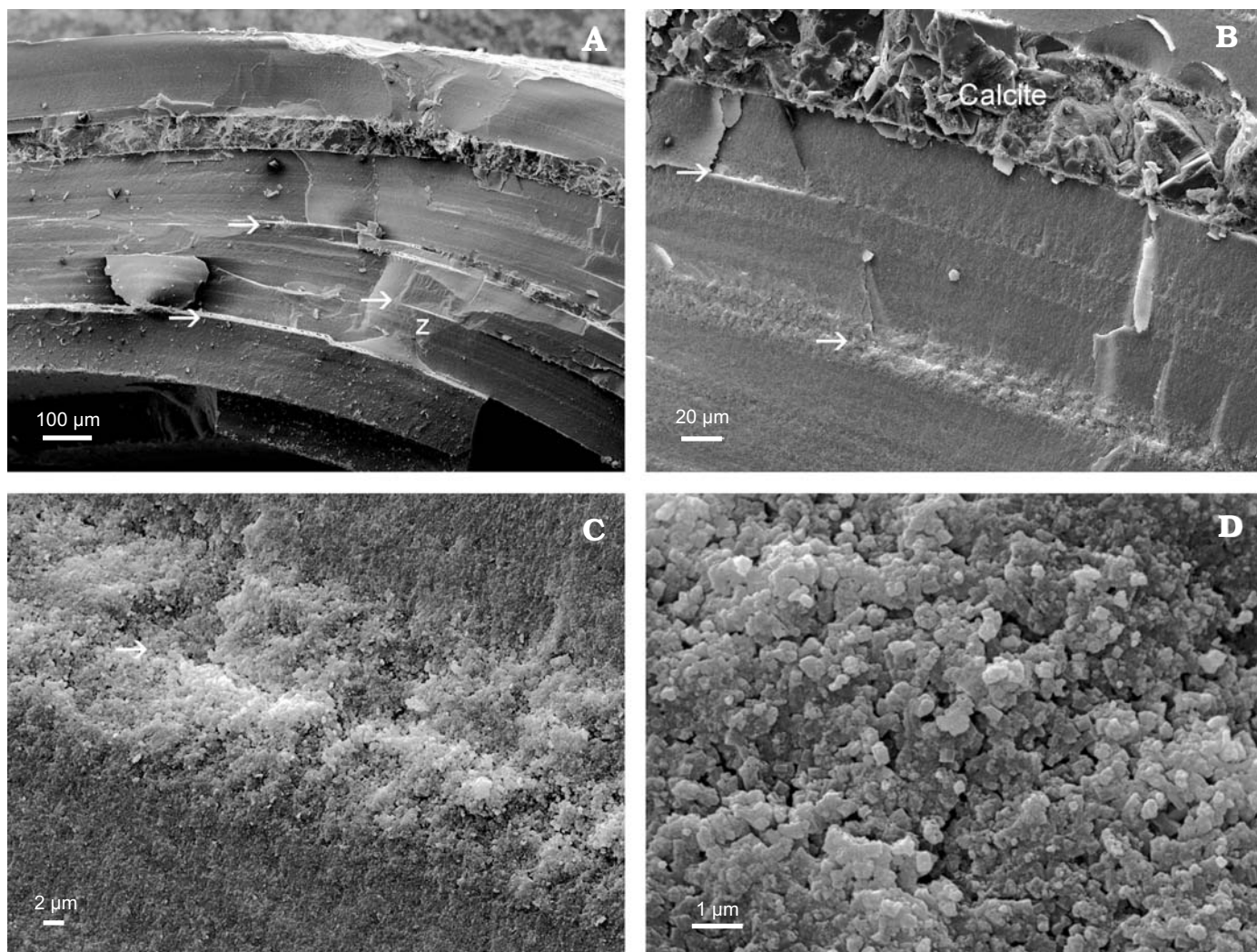
Fig. 3. Tube microstructure of *Sphenothallus* aff. *longissimus* (TUG 1648-2), Viivikonna Formation, lowermost Sandbian, Kohtla-Nõmme. **A**. Laminar microstructure, arrows point to the boundaries of laminae; z, possible thin primary lamination. **B**. Secondary calcitic layer in the tube wall, arrows point to the boundaries between laminae. **C**. Detail view of the boundary between laminae. **D**. Homogeneous microstructure.

to 0.7 mm per 10 mm of length. Tube wall has two lateral thickenings 180° apart that are 0.4 to 0.9 mm thick (N = 7, mean = 0.56 mm, sd = 0.18). The tube wall between lateral thickenings is 0.15 mm thick (N = 6, mean = 0.17 mm, sd = 0.04). Tube external surface is smooth and glossy, but some tubes have fine somewhat irregular perpendicular wrinkles. There are about three wrinkles per 5 mm in wrinkled tubes. In addition, irregular wrinkles in various directions and of various magnitudes occur in many tubes. Tube wall has a lamellar structure, both at thickenings and between them.

Dimensions.—Maximal length >355 mm, maximal width 25 mm (N = 12, mean = 19.3 mm, sd = 4.89)

Remarks.—The studied specimens are affiliated with *Serpulites longissimus* Murchison, 1839 (Murchison 1854: 233, pl. 16: 1) from Ludlow of Great Britain due to their very large and slightly curved tubes. *Sphenothallus* specimens described by Bolton (1994: 2) have somewhat similar shape to *S*. aff. *longissimus*, they also show various wrinkles (Neal and Hannibal 2000: 374–376), but their tubes are much smaller. Another Ordovician species, *S. ruedemanni* (Kobayashi 1934: 527, pl. 1: 9–12; Choi et al. 1990: 3, figs. 3, 4), has also somewhat similar wrinkles to some specimens of *S*. aff. *longissimus*, but it differs by the much smaller size of the tube. It also has much greater angle of expansion of the tube than *S*. aff. *longissimus*.

Results

Preservation.—*Sphenothallus* tubes are compressed, but not completely flattened (Fig. 2). The compaction of tubes is variable: maximal diameter/minimal diameter of the tube is 3.3 to 18 (N = 6, mean = 6.17, sd = 5.80). Tubes contain sediment infilling and show variously developed wrinkles and deformation. Some tubes have fractures filled with sparry calcite or micritic mudstone sediment.

Microstructure.—Tubes are composed of thin apatitic lamellae. The development and thickness of the lamellae is vari-

able. They are 10 to 170 μm thick (Fig. 3A–C). The boundaries of the lamellae have variable sharpness. Some boundaries are real gaps in the mineral structure, while others are caused by differences in crystal size and appear as parallel zones in the tube wall. The development (sharpness) of boundaries of the same lamella can change laterally. In one tube there is a thin lamella of well-crystallized calcite between the apatitic lamella, 50 to 70 μm thick. The microstructure of apatitic lamellae is homogeneous and typically composed of apatite <500 nm size crystallites (Fig. 3D). The crystal size of apatite forming the homogeneous microstructure is variable and can be larger at the boundaries of lamellae.

Mineral composition.—Three analysed tubes of *S.* aff. *longissimus* from oil shale of Viivikonna Formation are composed of carbonate substituted fluorapatite-francolite. Representative X-ray diffraction pattern of *S.* aff. *longissimus* is shown in Fig. 4. The carbonate ion concentrations in studied samples are similar to each other and vary between 9.0–10.7 wt% (Table 1). The lattice parameters of the studied apatite are: Kohtla Nõmme a = 9.319(6) Å, c = 6.903(0) Å; Kohtla a = 9.320(5) Å, c = 6.904(1) Å; Kiviõli a = 9.321(7) Å, c = 6.904(1) Å (Fig. 5). One tube contained calcite in addition to apatite (Fig. 6). *Conularia* sp. shell from oil shale of Viivikonna Formation is also composed of francolite with carbonate ion concentration 8.1 wt%. The lattice parameters of *Conularia* sp. apatite are a = 9.315(7) Å, c = 6.888(3) Å (Table 1).

Table 1. Carbonate content of *Sphenothallus* and *Conularia* apatite according to equation $y = 10.643x^2 - 52.512x + 56.986$, where $Y = CO_2$ wt% and $x = \Delta(004)-(410)$ (Schuffert et al. 1990).

Species	position of XRD peaks, °θ, CuKα			
	410	004	Δ	CO2%
Sphenothallus (Kohtla-Nõmme)	51.870	53.019	1.149	10.7
Sphenothallus (Kohtla)	51.821	53.032	1.211	9.0
Sphenothallus (Kiviõli)	51.857	53.009	1.152	10.6
Conularia (Kohtla-Järve)	51.815	53.060	1.245	8.1

Infrared spectrum of *S.* aff. *longissimus* (Fig. 7) show strongest absorption bands at 1024 cm⁻¹ and 550–600 cm⁻¹, which are due to stretching vibration and bending of phosphate PO_4^{3-} anions, respectively (Elliot 2002). Bands at about 1600, 1400, and 865 cm⁻¹ are assigned to carbonate anions replacing the phosphate in apatite structure. There is no indication of C-H bands typical to organic material in the region 2500–3000 cm⁻¹. Broad maxima between 3000–3400 cm⁻¹ is due to adsorbed molecular water.

Discussion

Tube microstructure.—We interpret the lamellae of *Sphenothallus* as an original tube structure. In addition to well-developed lamella there are zones located parallel to the tube wall. One specimen revealed a zonation with the interval
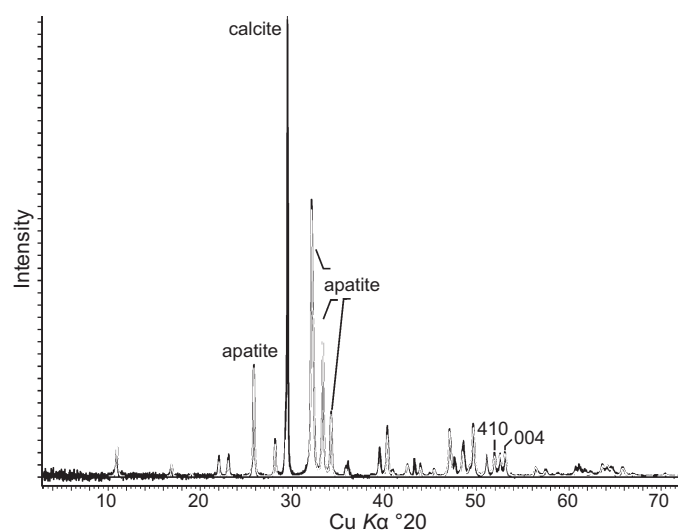

Fig. 4. Representative X-ray diffraction pattern of *Sphenothallus* aff. *longissimus*, Viivikonna Formation, lowermost Sandbian, Kohtla, NE Estonia. Dark gray line indicates modelled apatite pattern fitted to measured pattern. Position of reflections 410 and 004 were used to estimate carbonate ion content in carbonate-fluor apatite structure.
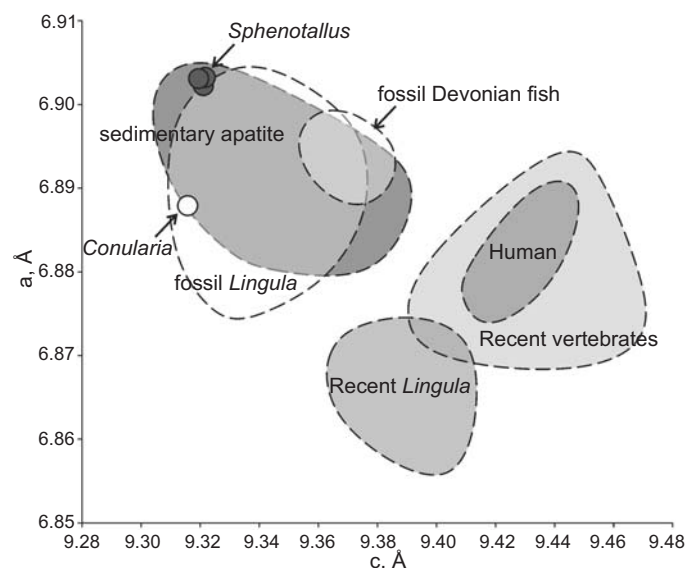

Fig. 5. Lattice parameters of *Sphenothallus* aff. *longissimus* apatite compared with *Conularia* sp. and other biological and sedimentary apatites (data from Nemliher 1999).

of 10 μm that possibly represents the original thickness of the lamellae in the tube wall (Fig. 3A). We did not find any chemical zonation corresponding to this microstructural feature. We interpret the variable thicknesses of the lamellae and their variable development as a result of recrystallization during the diagenesis. Specifically, the laterally changing sharpness of boundaries of lamellae indicates diagenetic alternation of the microstructure.

Homogeneous microstructure is common in various invertebrates (Carter et al. 1990). However, it is possible that the original microstructure of *Sphenothallus* lamellae may have been different. The homogeneous microstructure could be a result of recrystallization during diagenesis. The di-
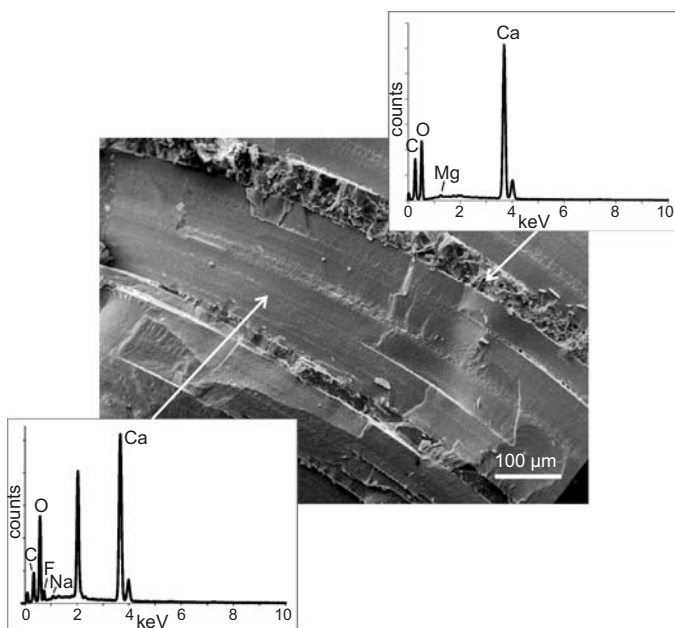
Fig. 6. EDS spectra of the phosphatic *Sphenothallus* tube with diagenetic calcite interlayer. Scale bar 100 μm.

agenetically altered microstructure of the phylogenetically closely related *Torellella* is very similar to that of homogeneous microstructure in *Sphenothallus* (Fig. 3D). In contrast, the unaltered laminae of *Torellella* are composed of fibres oriented parallel to the longitudinal axis of the tubes (Vinn 2006). It is possible that biomineralization systems of phylogenetically closely related animals were similar. Thus, *Torellella* and *Sphenothallus* may have also had a similar tube microstructure if they had a similar biomineralization. Conulariids are the other phosphatic cnidarians presumably related to the *Sphenothallus*. Similarly to the *Sphenothallus* shell of conulariids is composed of thin lamellae (van Iten 1991, 1992a, b). However, it is not clear whether this similarity represents a homology or a convergent development.

Biomineralization and mineral composition.—There are two alternative views to the original composition of *Sphenothallus* tubes. Previous mineralogical analyses have in general showed apatitic composition (Schmidt and Teichmüller 1956; Mason and Yochelson 1985). Feldmann et al. (1986) found possible collophane in the tube wall of *Sphenothallus*. According to an alternative view, *Sphenothallus* may have had originally organic tubes (Bodenbender et al. 1989) and their remains phosphatized later during the fossilization. We found some taphonomic evidence supporting the originally biomineralized tubes. If thin-walled *Sphenothallus* had organic tubes they would likely have been completely flattened due to sediment compaction. However, the tubes studied here show only partial compaction. In addition we did not find any signs of diagenetic phosphatization in other fossils found around the *Sphenothallus* tubes. The limestone and oil shale rocks containing *Sphenothallus* tubes have no elevated phosphorus content and they don't contain any sedimentary phosphorites (Raukas and Teedumäe 1997). Moreover, we did not find any signatures of

organic material in ATR-FTIR spectra of *Sphenothallus* tube (Fig. 7). The selective phosphatization of *Sphenothallus* tubes seems unlikely as the other fossil remains would have offered similarly good surfaces for apatite nucleation.

The lattice parameters as well as the carbonate content in francolite of three studied tubes are very similar, which may indicate little variability of the *Sphenothallus* apatite from the Sandbian oil shale of NE Estonia (Fig. 5). The apatite of the studied tubes has likely been partially or completely recrystallized during diagenesis. Due to the diagenetic changes, lattice parameters of the studied *Sphenothallus* apatite are similar to the other old sedimentary apatites and diagenetically altered bioapatites (Fig. 5). The calcite lamellae in the tube structure of one specimen were presumably deposited into preformed fractures during diagenesis.

It is possible that Palaeozoic tubicolous fossils commonly attributed to *Sphenothallus* belong to different animals with convergent morphology and tubes, which are composed of organics and phosphate. In addition to earlier reports of organic walled *Sphenothallus* finds (e.g., Bodenbender et al. 1989), Wei-Haas et al. (2011) recently described unbranched, straight or slightly bent tubular fossils morphologically similar to *Sphenothallus* in the Martinsburg Formation, Upper Ordovician of Appalachians, USA. However, these tubes are composed of carbonaceous material, rather than Ca-phosphate and show some distinct morphological differences, such as limited evidence for distal widening of the tubes, and lack of holdfasts compared with the phosphatic tubes of *Sphenothallus*. Therefore, Wei-Haas et al. (2011) refer to these as "*Sphenothallus*-like".

On the other hand, a mixed organic-phosphatic composition of *Sphenothallus* tubes has been reported (Fauchland et al. 1986; Yi et al. 2003; Li et al. 2004). Fauchland et al. (1986) and Yi et al. (2003) base their interpretation of organic matter in tubes on C peak appearance on energy dispersive (EDS) microanalysis spectrums. However, our XRD analysis of *Sphenothallus* tubes shows that the tube walls are composed of carbonate-substituted fluorapatite (francolite),
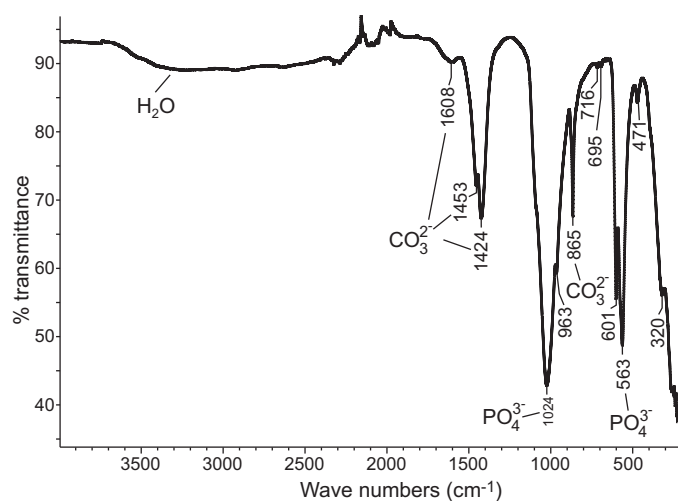

Fig. 7. Representitave ATR-FTIR spectrum of *Sphenothallus* aff. *longissimus* from Viivikonna Formation, Kivõli, NE Estonia.

whereas ATR-FTIR spectra of studied *Sphenothallus* tubes do not reveal adsorption maxima characteristic to organic compounds (Figs. 4, 7). Therefore, the qualitative identification of carbon in a microanalysis spectrum alone does not prove the presence of the organic carbon/matter (sensu stricto) in tubes. Nevertheless, Li et al. (2004) show, in addition to EDS spectra, presence of organic matter-like structures on transmission electron micrographs of HCl and HF treated tube sections, suggesting that tube walls of *Sphenothallus* originally consisted of alternating phosphatic and organic laminae, but organic laminae have been in most cases replaced by diagenetic apatite. Similar microstructure of alternating phosphatic and organic laminae is observed in the Recent lingulate brachiopod *Lingula anatina*, though the organic matter is completely replaced by secondary carbonate-fluorapatite in fossil lingulates (e.g., Lang and Puura 2013). This does not mean that *Sphenothallus* shared biological affinities with lingulates, but it may have had similarities in the biomineralization. Conulariids and *Sphenothallus* possibly share the cnidarian affinities (van Iten 1991, 1992a, b; van Iten et al. 2013) and they also have skeletons with similar apatitic composition. However, the lattice parameters of the *Conularia* sp. and *Sphenothallus* are different (Table 1, Fig. 5). Both *Conularia* sp. and *Sphenothallus* were collected from oil shale of Viivikonna Formation of north eastern Estonia. They were preserved in similar geological conditions. Thus, the different lattice parameters may reflect the original differences in the biomineralization of these phosphatic cnidarians.

Conclusions

- The genus *Sphenothallus* has a wide distribution in the Late Ordovician. The occurrence of *Sphenothallus* both in tropical Laurentia and more temperate Armorica close to Gondwana shows the climatic tolerance of the genus.
- We found taphonomic evidence supporting the originally biomineralized tubes. If thin-walled *Sphenothallus* had organic tubes they would likely have been completely flattened due to sediment compaction. However, the tubes studied here show only partial compaction. In addition we did not find any signs of diagenetic phosphatization in other fossils found around the *Sphenothallus* tubes.
- We interpret the lamellae of *Sphenothallus* as an original tube structure. In addition to well-developed lamella there are zones located parallel to the tube wall with the interval of 10 μm that possibly represents the original thickness of the lamellae in the tube wall. The tube walls of *Sphenothallus* originally consisted of alternating phosphatic and organic laminae, but organic laminae have been in most cases replaced by diagenetic apatite.
- Different lattice parameters of the apatite indicate that biomineralization systems of phylogenetically closely related phosphatic cnidarians *Sphenothallus* and *Conularia* sp. may have been different.

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