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# DISCOVERY OF PLYWOOD STRUCTURE IN *SPHENOTHALLUS* FROM GUROVO FORMATION (MISSISSIPPIAN), CENTRAL RUSSIA

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**Abstract**: *Sphenothallus* specimens are reported for the first time from the Mississippian of Central Russia. All *Sphenothallus* specimens have a phosphatic composition and a characteristic laminar structure, which is best observable in the thickened lateral parts of a tube. Most of the lamellae in the tube wall are straight, but some have a wavy morphology and a few are so wrinkled that they form hollow “ribs”. The wrinkled lamellae presumably had an originally higher organic content than the straight lamellae. There are borings on the surfaces of some lamellae that are similar in morphology to the bioerosional traces in various hard, biomineral substrates. Lamellae in the inner parts of the tube wall are composed of fibres. The fibres are parallel to the surface of the tube wall and in successive laminae they differ in orientation by irregularly varying angles. It is possible that the plywood microstructure in *Sphenothallus* was originally organic and was later phosphatized during fossilization. An alternative, but less likely explanation is that the plywood structure was originally mineralized and therefore is comparable to the phosphatic lamello-fibrillar structures of vertebrates.

**Key words**: Scyphozoa, biomineralization, tube microstructure, ultrastructure, mineral composition, Carboniferous.

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## INTRODUCTION

*Sphenothallus* is a genus of phosphatic, tubicolous fossils that has a stratigraphic range from the early Cambrian (Zhu *et al*., 2000; Li *et al*., 2004) to the Carboniferous (Neal and Hannibal, 2000). The genus originally was assigned to the plants (Hall, 1847) because the flattened and often slightly curved tubes are somewhat branch-like. It was later affiliated variously with conulariids, hydroids, annelids and even graptolites, owing to the slightly conical shell (Van Iten *et al*., 1992, 1996, 2013; Vinn and Kirsimäe, 2015). *Sphenothallus* was an encruster of hard substrates and it encrusted various hard substrates, ranging from brachiopod shells (Neal and Hannibal, 2000) to carbonate hardgrounds (Bodenbender *et al*., 1989). Detached *Sphenothallus* tubes often can be found without any holdfast. On the other hand, their holdfasts without tubes are common on brachiopod shells and hardgrounds of Palaeozoic age (Bodenbender *et al*., 1989; Neal and Hannibal, 2000). *Sphenothallus* tubes have an apatitic composition (Vinn and Kirsimäe, 2015) and microlamellar structure (Van Iten *et al*., 1992, 1996, 2013). Some *Sphenothallus* specimens demonstrate a clonal budding that is characteristic for many cnidarians (Van Iten *et al*., 2019). They were most likely phylogenetically related to the conulariids and probably both of them were scyphozoans (Van Iten *et al*., 1992; Ford *et al*., 2016).

The aims of this paper are to: (1) report the first *Sphenothallus* fossils from the Mississippian of Russia; (2) describe the tube microstructure of *Sphenothallus*; (3) discuss the formation of various tube microstructures; and (4) discuss the microbioerosion associated with *Sphenothallus* tubes.

## GEOLOGICAL BACKGROUND AND LOCALITY

The *Sphenothallus* specimens described here are found in a small quarry, 150 km southwest of Moscow (Fig. 1). This locality is named the Borshchevsky Quarry (54°25′25.0″N, 36°48′37.3″E); it is widely known among Russian amateur fossil collectors, but remains undescribed

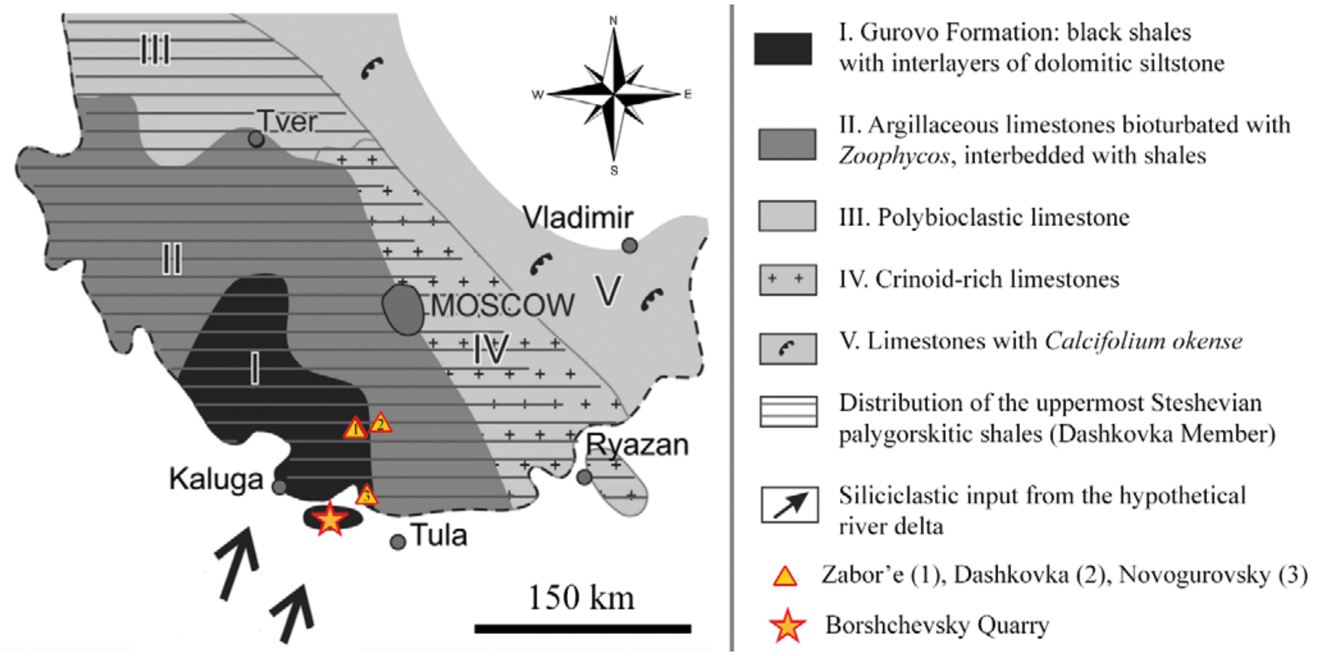

**Fig. 1.** Steshevian (early Serpukhovian) facies and zones in Central Russia. Triangles mark previously described Steshevian localities: 1 – Zabor'e, 2 – Dashkovka (Kalinovskie vyselki), 3 – Novogurovsky. The star marks the Borshchevsky Quarry(54°25′25.0″N, 36°48′37.3″E), from which the *Sphentothallus* specimens were collected. The figure is modified after Kabanov *et al*. (2014).

in the literature. Nevertheless, this section is very similar to the well-known locality Zabor'e of the same age (Kabanov, 2003). *Sphenothallus* specimens were found in a relatively thin (about 30 cm) interlayer of dolomitic siltstones, embedded in thick (more than 2 m) layers of dark grey palygorskite shales. These shales belong to a lower part of the Dashkovka Member (Kabanov *et al*., 2014), which is equivalent to the upper part of Member 7 (Kabanov, 2003), of the Mississippian Subsystem, Serpukhovian Stage, Steshevian regional Substage, Gurovo Formation, conodont *Lochriea ziegleri* Zone (Kabanov *et al*., 2014). *Sphenothallus* specimens previously were found in the same beds at the Zabor'e locality (approximately layer 40, according to Kabanov, 2003), but these findings were never recorded (A. S. Alekseev, MSU, Moscow, oral communications).

The Steshevian Gurovo Formation, consisting of dark clays and shales with thin interlayers of dolomitic siltstone, significantly differs from other Carboniferous formations of Central Russia, which are represented by light-coloured dolomites and limestones. Dark clays and shales most likely were formed under anoxic or hypoxic conditions. They contain a large number of remnants of a pelagic fauna, such as conodonts, graptolites and fish scales and teeth, whereas corals, gastropods and bivalves are absent, and discoveries of mobile benthos, such as sea urchins and trilobites, are extremely rare (Kabanov, 2003). In some shale layers, there is an almost monotypic complex of brachiopods *Eomarginifera lobata*, accompanied by rare *Conularia*, whereas in other layers a benthic fauna is completely absent (Kabanov, 2003).

The significant differences of the Gurovo Formation from the associated limestones have led to a lengthy discussion about the conditions of its formation. In the first description of the Steshevian shales, Shvetsov (1932) considered these facies to have been formed under deep-water conditions. However, this author later changed his opinion and reinterpreted them as shallow-water, lagoonal deposits, owing to their limited geographic extent (Shvetsov, 1938, 1948). The hypothesis of the formation of dark shales in a shallow "Steshevian lagoon" had become widely accepted by researchers in the 20th century (Osipova and Belskaya, 1965; Belskaya *et al*., 1975; Makhlina *et al*., 1993). However, Kabanov (2003) put forward a new hypothesis, according to which Steshevian dark shales were formed at relatively great depths under the pycnocline and below the wave base. Later, another hypothesis was proposed, according to which the "Steshevian basin" could have been formed by a persistent influx of terrigenous particles, coming from a low-energy delta attached to the Voronezh Land (Kabanov *et al*., 2012). The terrigenous suspension could have caused eutrophication, suppressed carbonate production and formed a shallow (a few metres deep) basin with a generally hypoxic bottom layer (Kabanov *et al*., 2012). According to recent publications, it is still unclear whether the bottom hypoxia and black shale formation were caused by increased sea depths *versus* eutrophication in front of a large, southerly located delta (Kabanov *et al*., 2014). However, the existence of the early Serpukhovian transgression is supported by various lines of evidence, such as a dramatic increase in conodont numbers and the abundance and diversity of echinoderms and cephalopods (Kabanov *et al*., 2014).

The Steshevian clays of the Gurovo Formation have been studied in several sections and drill holes in Central Russia (Kabanov *et al*., 2014). The Borshchevsky Quarry is the southernmost of known points of distribution of the Gurovo Formation (Fig. 1); it is located closer to the hypothetical delta (see Kabanov *et al*., 2012, fig. 6) than all other sections. Nevertheless, in the Borshchevsky Quarry the Steshevian clays contain a large number of pyritized cephalopod shells. Although Kabanov (2003) mentioned discoveries of small cephalopod shells in the Steshevian shales in the quarries that he studied, such shells were extremely rare in all these outcrops, whereas at Borshchevsky they are very numerous. The significantly larger number of cephalopod shells in the Borshchevsky Quarry, by comparison with other Steshevian sections, contradicts the hypothesis that explains the formation of clays by the influence of a delta, since cephalopods are generally stenohaline animals and cannot tolerate desalination. A clear increase in their numbers at Borshchevsky by comparison with other sections indicates a more offshore location of the basin in this territory. It is worth noting that the cephalopods, which are common at Borshchevsky (representatives of the nautiloid orders Orthocerida, Pseudorthocerida and Nautilida), led a pelagic mode of life in the water column. All of them, including the medium-sized nautilids *Lyroceras* and *Catastroboceras*, have small, embryonic shells and it cannot be ruled out that they could have had floating clusters of eggs, so their reproduction would not have depended on the conditions at the bottom (Mapes and Nutzel, 2009).

Therefore, it is most likely that the appearance of the *Sphenothallus* in Central Russia in the Carboniferous is related to the maximum height of rising sea levels during Steshevian time (Kabanov *et al*., 2012). This coincided with the spread of anoxic conditions in the bottom water layers. *Sphenothallus* tubes are preserved in dolomitic siltstones together with very numerous fish remains, flattened conulariids, dissolved nautiloid shells (*Lyroceras, Catastroboceras* sp.), graptolites *Dictyonema* sp. and rare brachiopods *Orbiculoidea* sp.

## MATERIAL AND METHODS

SEM images were taken of the small fragments of ten *Sphenothallus* tubes. They are from both the thin-walled central parts and thickened lateral parts of the tubes. The specimens were coated with gold and palladium and examined under the scanning electronic microscopes SEM TESCAN VEGA II and III at the Palaeontological Institute of the Russian Academy of Science, in Moscow. All images were made using two detectors (SE and BSE). Data on the elemental composition of the specimens studied were obtained using Energy dispersive X-ray Analysis (EDX) on the SEM-coupled INCA Energy Dispersive X-ray Spectroscopy Detector. The specimens studied are housed at the Palaeontological Institute of Russian Academy of Science (PIN RAS), Moscow, Russia, collection number 5804.

## RESULTS

The specimens studied (Fig. 2A, B) (diameters 2.0 mm to 8.7 mm, mean 6.0 mm, $\sigma = 1.77$ mm, $n = 8$; tube fragments are up to 53.0 mm long) somewhat resemble in size and general morphology *Sphenothallus* cf. *S. angustifolius* from the Mississippian Bear Gulch Limestone of central Montana (Hill, 1978). There is another somewhat similar species *Sphenothallus stubblefieldi* (diameters 1.0 mm to 1.5 mm) known from the Carboniferous, but the tubes of the present authors are larger (Schmidt and Teichmüller, 1956). All specimens have a laminar structure (Figs 2C–F, 3A–D), which is best expressed in the thickened lateral parts of tube. The laminar tubes can easily fall apart into separate layers. The thickness of the lamellae is variable. They can be 3.0 µm to 50 µm thick. The thickest lamellae occur in the external part of the tube wall at the lateral thickenings. Thin lamellae are more common in the inner parts of the tube wall. Some laminae have a wavy structure (Fig. 3B) and some are so wrinkled that they form hollow “ribs”, mostly in lateral parts of the tube, where the wall is thicker (Fig. 3A). The external surface of these specimens is smooth, devoid of any micro-ornamentation and pores. Surfaces of most of lamellae are also smooth and their microstructure is homogeneous. However, lamellae in the inner parts of the tube wall are composed of fibres, best observed in lateral parts of the tube wall (Figs 2C, D, F, 3C, D). The fibrous part of the tube wall can be up to 70 µm thick (Fig. 3D). The fibres are long, at least tens of micrometres long and 1.5–2.0 µm thick. The fibres are parallel to the surface of tube wall and in successive laminae they differ in orientation by irregularly varying angles. In some lamellae, the fibres are accompanied by somewhat spherical phosphatic granules of variable shape which are similar in size to the fibre diameters (Fig. 3C, D). In one specimen PIN 5804/3–2, multiple borings of relatively constant diameter (2.0–2.5 µm) are visible on the surface of an inner lamella (Fig. 2E). Borings are preserved mostly in the form of shallow slightly curved to straight grooves on the surfaces of the lamella, but some burrows reach to the interior of the lamella in the form of cylindrical shafts. The lamella with borings has a smooth surface and is not composed of fibres. The whole surface of the lamella is crowded with borings. On the surface of one fibrous lamella, there are small circular to semicircular pits (Fig. 2F), but it is unknown whether they penetrate the whole lamella. There is no pattern in the location of the pits. Some pits form groups or are fused, whereas others are solitary. The dimensions of the pits are variable (3–8 µm). In the cracks between the lamellae, crystals of pyrite are visible (Fig. 4). EDX analysis detected that there is no chemical difference between smooth, fibrillar and globular layers of the *Sphenothallus* test; they all are phosphatic. The small crystals between the lamellae are pyrite, but they are slightly dissolved. The surrounding rock consists of dolomite crystals cemented by clay.

## DISCUSSION

### Laminar microstructure

The laminar structure described is very typical of *Sphenothallus* (Van Iten, 1992, 1996, 2013). However, the hollow ribs discovered have not been previously described in *Sphenothallus*. It is possible that these “ribs” are not original shell structures but were formed during fossilization. The mode of formation of the hollow ribs can tell us something about the original composition of lamellae. Most likely the organic content varied in different lamellae.

Lamellae with a higher organic content became wrinkled, owing to contraction after the decay of the organic material. Most organic-rich lamellae formed hollow ribs; the less organic-rich lamellae became wavy, whereas the mainly mineral lamellae preserved their original volume and stayed even in thickness. Conulariid tests were composed of alternating organic-rich and mineral lamellae (Ford *et al*., 2016). The large variation in organic content of the *Sphenothallus* lamellae is like the situation in the conulariids. This similarity corroborates the idea about a close phylogenetic relationship between *Sphenothallus* and the conulariids.

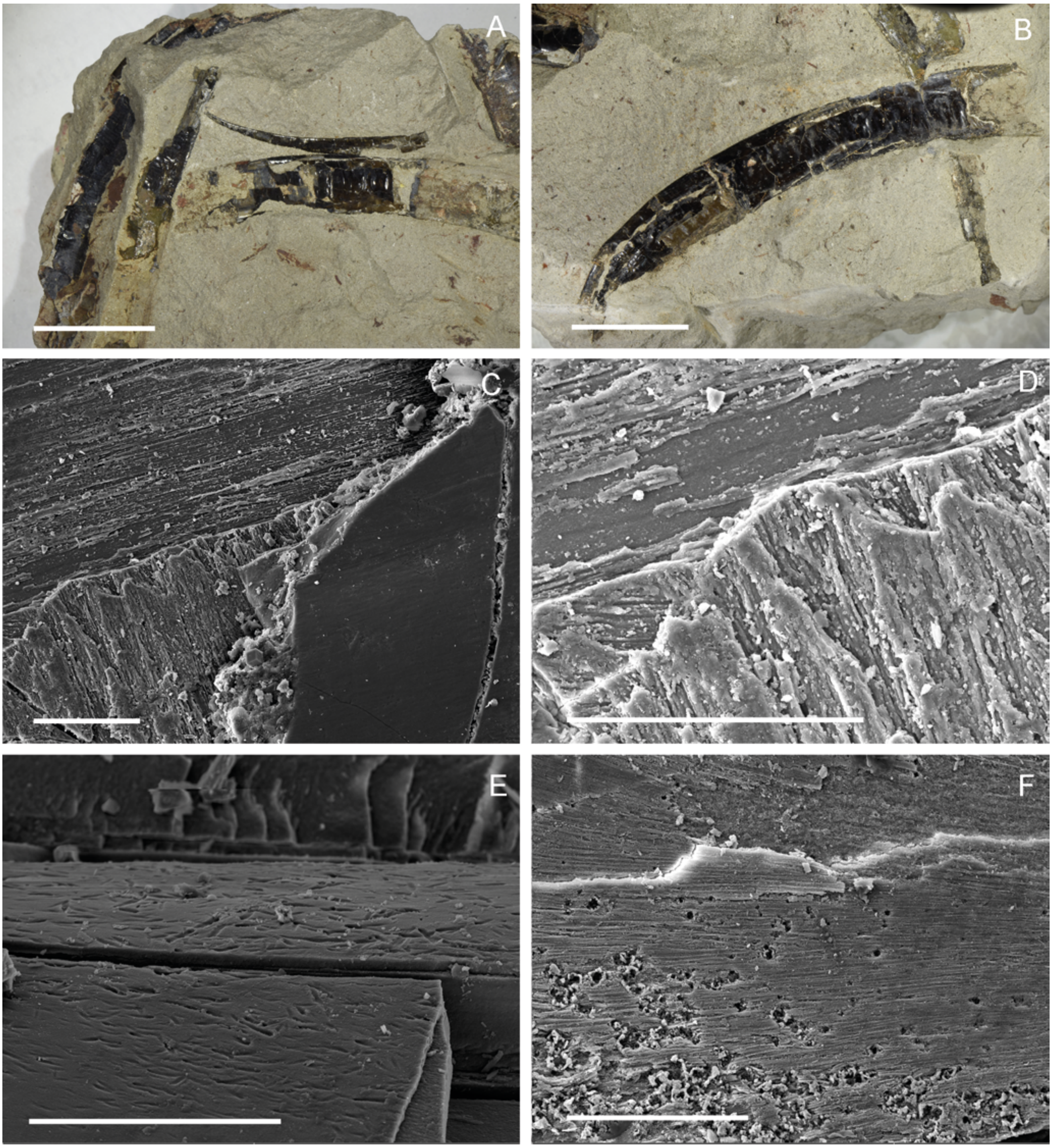

**Fig. 2.** *Sphenothallus* cf. *S. angustifolius* from the Borshchevsky Quarry, Central Russia, Gurovo Formation (Mississippian, Serpukhovian Stage). **A, B.** General views of specimens PIN 5804/1 and PIN 5804/2, respectively. **C, D.** Horizontal view of natural fracture surface showing plywood structure, lateral region of the tube, specimen PIN 5804/3–1. **E.** Borings on the surface of smooth lamella, lateral region of the tube, specimen PIN 5804/3–2. **F.** Pits on the surface of a fibrous lamella, lateral region of the tube, specimen PIN 5804/3–3. Scale bar for A, B equals 1 cm, for C–F it equals 100 µm.

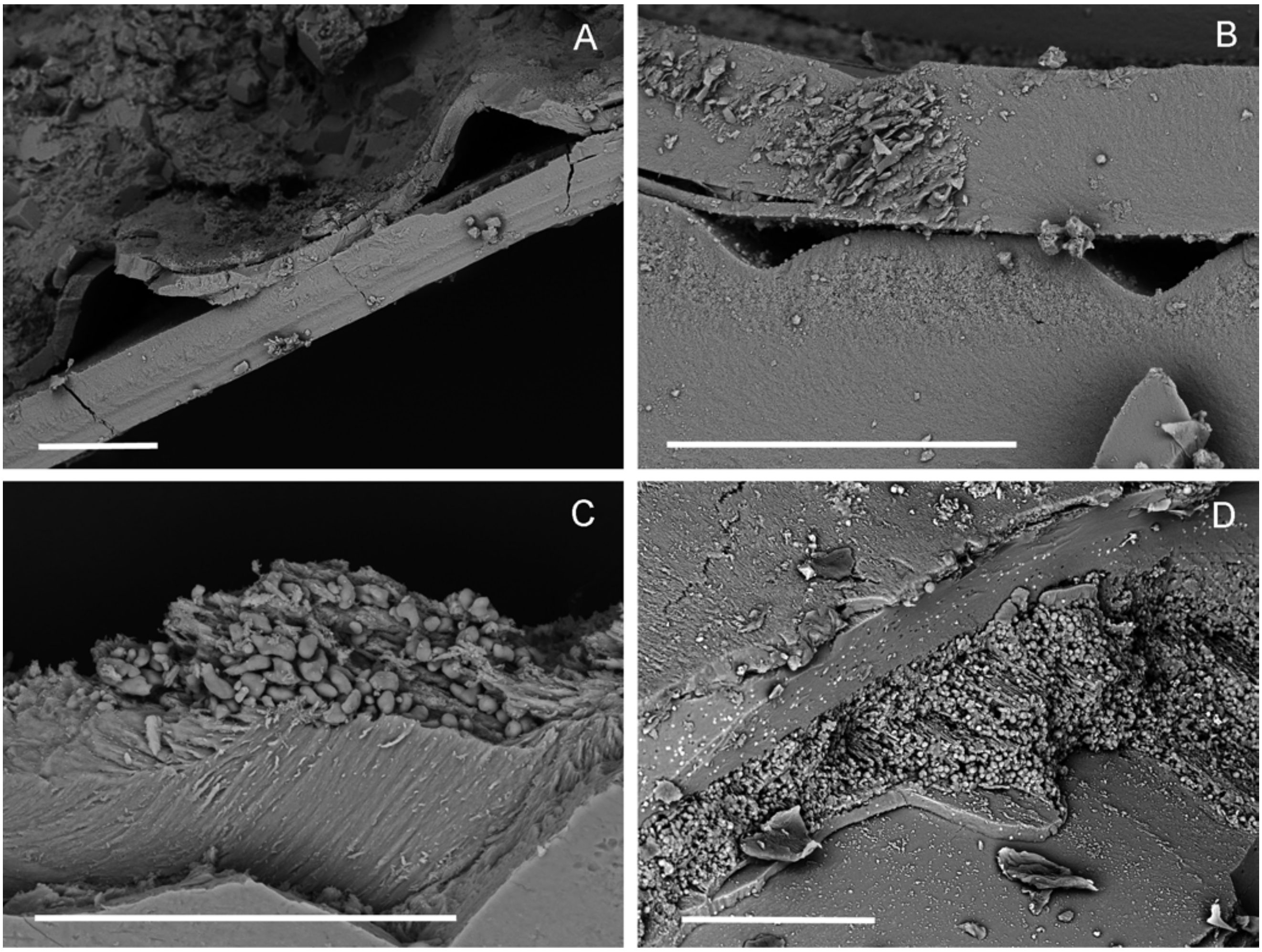

**Fig. 3.** *Sphenothallus* cf. *S. angustifolius* from the Borshchevsky Quarry, Central Russia, Gurovo Formation (Mississippian, Serpukhovian Stage). **A.** “Hollow ribs”, specimen PIN 5804/4–1. **B.** Wavy lamella, specimen PIN 5804/4–2. **C.** Plywood structure with phosphatic granules, lateral region of the tube, specimen PIN 5804/3–4. **D.** Fibrous layer with phosphatic granules, lateral region of the tube, specimen PIN 5804/3–5. Scale bar equals 100 µm.

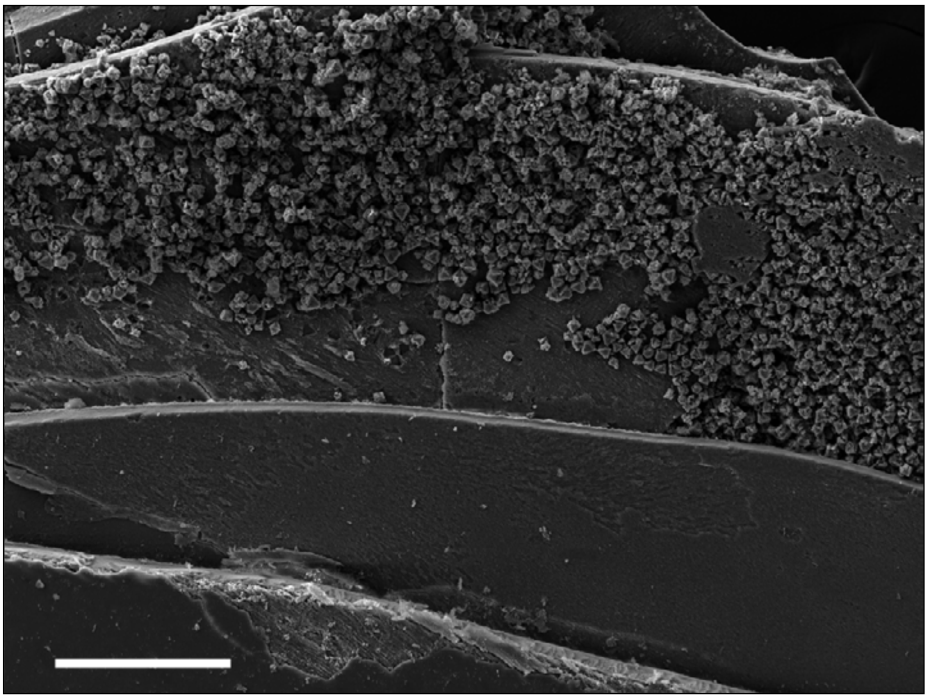

**Fig. 4.** *Sphenothallus* cf. *S. angustifolius* from the Borshchevsky Quarry, Central Russia, Gurovo Formation (Mississippian, Serpukhovian Stage) showing pyrite crystals on the surface of a growth lamella. Scale bar equals 100 µm.

## Borings and pits

The orientation of borings (sub-parallel to the surface of lamella) and their morphology (cutting the surface of a lamella, rather than being surrounded by the tissue) indicates that they probably were not part of the original anatomy of *Sphenothallus*. In this respect, the borings are different from the pores found in conulariids (Van Iten *et al*., 2005). Moreover, the pores in conulariids are oriented perpendicular to the surface of lamellae, whereas borings in *Sphenothallus* are rather subparallel to the surface of lamellae. Borings on the surfaces of lamellae are morphologically similar to the bioerosional traces in various hard biomineral substrates. The size of the borings corresponds to microbioerosion. Presumably, a lamella was bored by some chemical means by microorganisms feeding on the organic compounds of the lamella. These microorganisms probably did not collect their food from seawater, as their borings were not connected to the outer environment. Thus, most likely the borings constitute a feeding trace. The post-mortem nature of the borings is also likely, but the authors cannot rule out the possibility that the tube of *Sphenothallus* housed boring microbes already during the life of the animal. It should be noted that the borings are located only in one lamella and do not pass into others. This fact confirms the hypothesis that the different lamellae varied in organic content and had differences in nutritional value for the boring microorganisms.

Circular to semicircular pits in some fibrous, inner lamellae are superficially similar to the pores of conulariids (Van Iten *et al*., 2005). Conulariid pores range in size from approximately 2 μm to approximately 12 μm (Van Iten *et al*., 2005), which is very similar to the range in size of the pits in some fibrous lamellae (3–8 μm). However, there is an alternative interpretation of *Sphenothallus* pits, as opposed to their homology with conulariid pores. In some of the cracks between the lamellae, crystals of pyrite of similar size to the pits are visible (8 μm). One possibility is that these pits are holes dissolved in the shell owing to diagenesis and form the places of further growth of pyrite crystals. Alternatively, they may be related to bioerosion, but they have edges that are too uneven for ordinary borings.

## Plywood structure

Plywood microstructures found in animals can either be organic in composition or biomineral. The organic plywood structures are commonly found in the tubes of various invertebrates, such as cnidarians, polychaete annelids and phoronids. Phosphatic plywood structures so far have been found only in vertebrates (Carter *et al*., 1990). Nevertheless, there are examples of phosphatized plywood structures in invertebrates that originally were aragonitic in composition, such as in the case of middle Cambrian hyoliths (Moore and Porter, 2018). Numerous studies have indicated that the original composition of *Sphenothallus* tubes was organo-phosphatic (Van Iten, 1992, 1996, 2013; Muscente and Xiao, 2015; Ford *et al*., 2016). The *Sphenothallus* test originally contained a substantial amount of organics, at least in the form of organic matrices. It is possible that the test may have been composed of alternating organic-rich mineral to pure organic and mostly mineral lamellae, as in the tests of conulariid (Ford *et al*., 2016). In the latter case, the plywood structures may have been originally organic. If the plywood structure was originally organic in composition, one can compare it with the organic plywood structures of the modern, tubicolous invertebrates. Organic plywood structures in many invertebrates, such as polychaete annelids (Merz, 2015; Vinn *et al*., 2018), amphipods (Neretin *et al*., 2017) and phoronids (Temereva *et al*., 2020) have architecture similar to that of *Sphenothallus*, but the diameters of their fibres are much smaller, usually about a magnitude smaller. Unfortunately, there is no detailed information available on the ultrastructure of organic scyphozoan tests. However, there are some data available on tube-dwelling anemones (Stampar *et al*., 2015). The tubes of the latter invertebrates also are composed of fine fibres in some species, about 10 μm thick and arranged in overlapping layers, creating an arrangement similar to that of manufactured fabric (Stampar *et al*., 2015). Thus, the measurements of fibres arranged in the plywood structure in *Sphenothallus* are in the size range of the fibres in the various organic tube structures of modern invertebrates. Therefore, it is possible to interpret the plywood structure of *Sphenothallus* as a fossilized (phosphatized) organic film. This organic film was either part of the composite structure for increasing the flexibility of the mineral tube or served as an organic template for the growth of apatite crystals. The phosphatic granules, associated with some fibrous laminae, probably are not part of the original tube microstructure, but the result of fossilization of the original fibrous fabric. It is also possible that the phosphatic granules belong to microorganisms that inhabited the fibrous tube layers during the life of *Sphenothallus* or after its death. On the other hand, one would expect to find higher carbon and sulphur content in fossilized organic films than in originally apatitic lamellae, but the EDX analysis detected no differences in composition between smooth and fibrous lamellae. Alternatively, the lamellae of *Sphenothallus* with a plywood structure can be interpreted as the preserved remains of an original phosphatic tube structure. In the latter case, the structure of the *Sphenothallus* test is almost identical to that of the phosphatic lamello-fibrillar structure of vertebrates (Carter *et al*., 1990). In invertebrates, only aragonitic or calcitic lamello-fibrillar structures are known. Lamello-fibrillar structures occur in arthropods, molluscs and annelids (Carter *et al*., 1990; Vinn *et al*., 2008). However, in cnidarians no mineral plywood structures have been described to date (Carter *et al*., 1990), making the interpretation of the *Sphenothallus* structure as a biomineral one less likely than as a fossilized fibrous organic film.

Fibrous lamellae, somewhat similar to those of *Sphenothallus* were described in *Torellella* (Vinn, 2006). However, it is not known whether the fibrous lamellae of *Torellella* also formed a plywood structure. The fibrous structure of *Torellella* was interpreted as an original biomineral microstructure of the tube. The *Sphenothallus* and *Torellella* probably were closely linked phylogenetically; most likely both of them were scyphozoans (Vinn, 2006). In the light of the discovery of a plywood structure in *Sphenothallus* and its possible organic origin, it is possible that the fibrous lamellae in *Torellella* may have similar origin as an organic film. Further studies of the microstructure of the conulariid test should show whether fibrous lamellae or even plywood structures also are present in conulariids.

## CONCLUSIONS

Phosphatic tubes found in the Gurovo Formation (Serpukhovian Stage), Central Russia, belong to *Sphenothallus* cf. *S. angustifolius*. Hollow ribs and wavy lamellae have not been previously described in *Sphenothallus* and most likely indicate variations in the organic content of *Sphenothallus* lamellae, as in the lamellae of conulariids. The wrinkled lamellae originally contained more organic material than the flat lamellae. Microborings occur in one lamella, but their orientation and morphology indicate that they were not part of the original anatomy of *Sphenothallus* and most likely are not homologous to the pores found in conulariids. Circular to semicircular pits found in some fibrous inner lamellae are superficially similar in morphology to the pores of conulariids, but the authors interpret these pits as dissolved holes in the shell due to diagenesis and the sites of later growth of pyrite crystals. *Sphenothallus* tubes contain lamellae and thin layers with a fibrous microstructure. The fibres are arranged like those in organic and mineral plywood structures. It is possible to interpret the plywood structure of *Sphenothallus* both as fossilized (phosphatized), organic film(s) or as the preserved remains of an original phosphatic tube microstructure. No mineral plywood structures have been described previously in cnidarians.

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