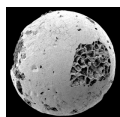


Phosphatized spherical microfossils from the Silurian (Motol Formation, Sheinwoodian, Wenlock) of the Barrandian area, Czech Republic

VERONIKA CHOLEVOVÁ & MICHAL MERGL



Two phosphatized spherical fossils (approximately 2.5 mm in diameters) observed in limestone of Silurian age (Sheinwoodian, Wenlock) in Central Bohemia, Czech Republic, likely represent phosphatized remains of original organic object. Specimen A exhibits a suggested cellular pattern within a smooth external membrane. The phosphatization of the cell walls, polyhedral and hexagonal outline of the cells, phosphatization of the shrunken protoplast inside the cells, and the differentiation of central and peripheral cell layers presumably indicate the algal affinity of the fossil. Specimen B is larger and lacks the distinct cellular pattern. Below the external smooth membrane, columns of botryoid microcrystals are developed around radially arranged fibres. The central part of Specimen B is formed by a plexus of irregularly spaced fibres with aggregated microcrystalline coatings. A poorly defined break lies between the central region and the peripheral layer. This body is interpreted as a simply structured biological object affected by decay processes and simultaneous phosphatization. The taxonomic affinity of Specimen B is uncertain. It could be an animal egg with the phosphatized outer membrane (chorion). Although very rare in the locality, both spherical fossils indicate the similar taphonomic processes and the unique preservation in the Silurian. So far, a similar preservation was so far known only in the Ediacaran and the lower Cambrian of South China, Siberia, and north-western Canada. • Key words: Sheinwoodian, Silurian, phosphatization, Barrandian, algae, problematic microfossils.

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Mechanisms of phosphatization of tissues and weakly sclerotized cuticles in fossil record have been intensively studied in the last decades (Müller 1992, Prévot & Lucas 1992, Jin & Copper 2010, Dornbos 2011, Schiffbauer *et al.* 2014). The phosphatization involves the nucleation and precipitation of authigenic minerals on organic templates, which are encrusted and replicated. Excellent preservation of details has been revealed by the use of modern laboratory and imaging techniques. Especially the application of scanning electron microscopy has remarkably increased our knowledge of phosphatized remains of arthropods (Müller 1979, 1981, 1983; Müller & Wallosek 1985a, b, 1986a, b, 1987, 1988; Walossek & Szaniawski 1991; Wallosek 1993, 2003; Maas *et al.* 2006, 2007; Stein *et al.* 2008; Olempska 2012; Olempska & Wacey 2016; Olempska *et al.* 2019; and others), palaeoscolecoid cuticles (Müller & Hinz-Schallreuter 1993, Maas *et al.* 2007), brachiopods (Jin & Copper 2010), and other diverse organic remains (*e.g.* Yin *et al.* 2007, Zhang *et al.* 2011, Han *et al.* 2013, Xiao *et al.* 2014,

Liu *et al.* 2014a, Donoghue *et al.* 2015, Peel & Willmann 2022).

Recently, two specimens of spherical objects preserved by phosphatization have been observed during the laboratory sorting of other phosphatic or phosphatized fossils from the Silurian limestone at the locality Špičatý vrch near Loděnice in Central Bohemia. The SEM investigation of the first object indicates a multicellular composition of the original organism. The second object possesses regular internal architecture without a distinct cellular arrangement. These structures resemble structures described in some phosphatized late Precambrian and Cambrian biota from China (Xiao *et al.* 1998, 2004) and North Greenland (Peel & Willman 2022). We tentatively refer the first spherical object to the chlorophytes or rhodophytes, while the second object is left unassigned. Definite taxonomic determination is hindered by the rareness of specimens. However, the uniqueness of these weird spherical structures in the Silurian fossil record justifies their publication.

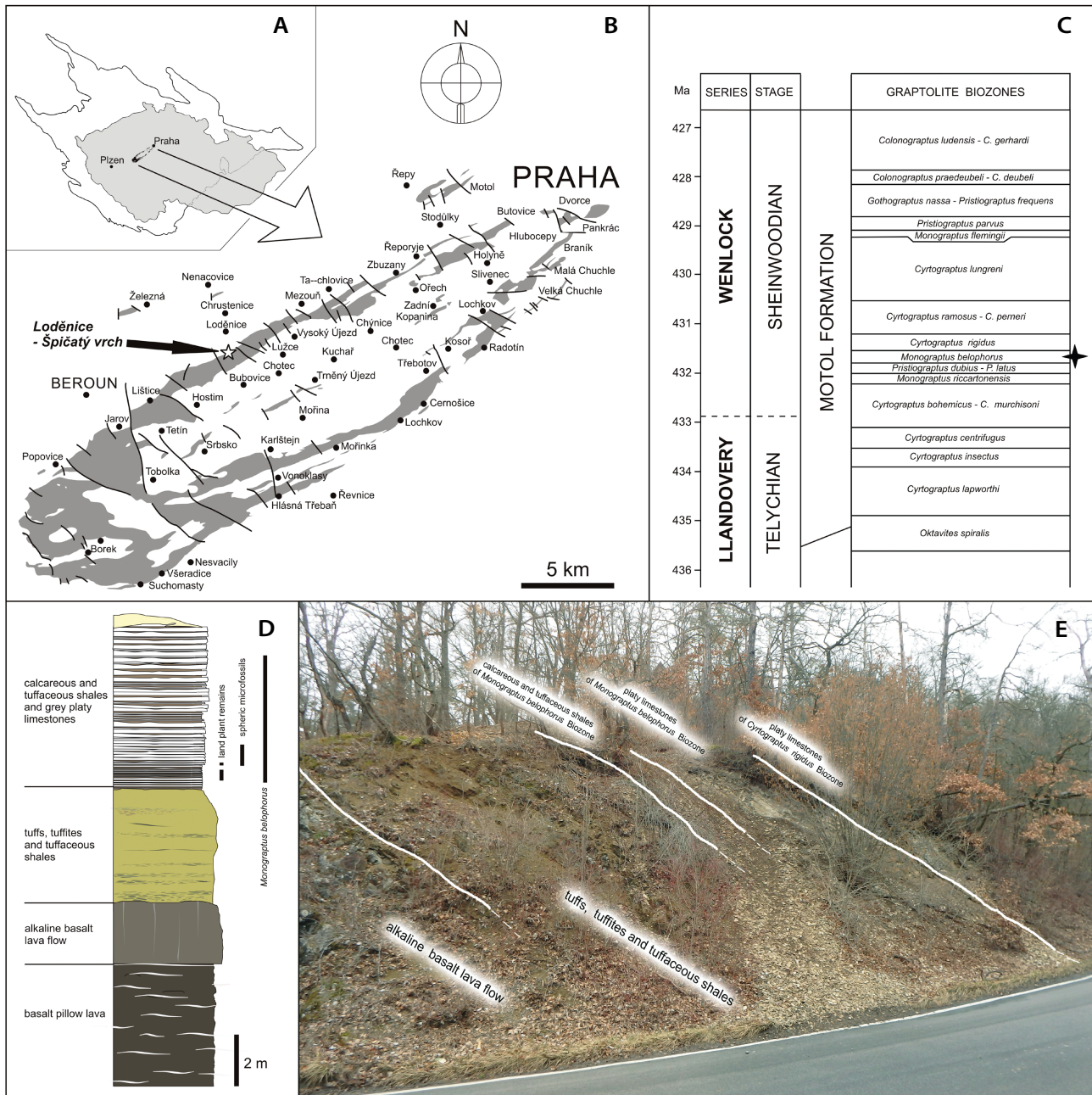


Figure 1. Schematic map of the Bohemian Massif, Czech Republic, and the Silurian of the Barrandian area. • A, B – map of the Silurian outcrop area with position of the Loděnice-Špičatý vrch locality (arrow). • C – stratigraphical position of spherical microfossil-bearing beds within graptolite zones of the Motol Formation (after Štorch 2023, modified). • D – schematic section of the Loděnice-Špičatý vrch locality, with marked position of the occurrence of the examined spherical objects, the earliest records of *Cooksonia*, and the index graptolite *Monograptus belophorus*. • E – road-cut section at Špičatý vrch – Barrandovy Jámy near Loděnice (modified after Mergl 2023).

Geological settings and previous studies

Both phosphatized spherical fossils came from the road cut south of Loděnice on the western slope of the small hill named Špičatý vrch in Central Bohemia (Fig. 1A, B). The road cut has been a rich source of Silurian fossils since the 1940s when the road was built, but nearby localities were

exploited by Joachim Barrande since the middle of the 19th century. The limestone beds outcropping on the east side of a sharp curve of road from Loděnice to Bubovice (Fig. 1E) are currently covered by scree.

The geology and palaeontology of the road section was first described by Bouček (1941a, b; 1951). Details of the locality were provided by Horný (1955, 1962,

1965) and Kříž (1984, 1992). All authors noted richly fossiliferous tuffaceous shales (“*Miraspis* Shale”) and thinly bedded limestones (“*Miraspis* Limestone”) overlying the submarine alkaline basalt lava and bedded tuffs and tuffites (Fig. 1C–E). Abundant fossils belong to the *Miraspis* Assemblage (Chlupáč 1987), or the *Miraspis-Mezounia* Community (Havlíček & Štorch 1990, 1999), respectively. Lists and descriptions of benthic fossils are covered in several publications (Bouček 1941a; Šnajdr 1980; Kříž 1984, 1992; Havlíček & Štorch 1990, 1999; Havlíček 1995; Mergl 2001, 2024). The locality is sig-

nificant for yielding the oldest terrestrial plant remains in the Barrandian area (Libertín *et al.* 2018). Spores, prasinophytes and scolecodonts were described in detail by Bek *et al.* (2022).

Taxonomic composition of trilobites and brachiopods indicate a quiet-water, well oxygenated, subtidal moderately deep environment of benthic community 4–5 (*sensu* Boucot 1975; see Havlíček & Štorch 1990, Bek *et al.* 2022). However, the fragmental nature of skeletal fossils indicates their transport outside their original habitat. The clear lamination, the absence of trace fossils, and the

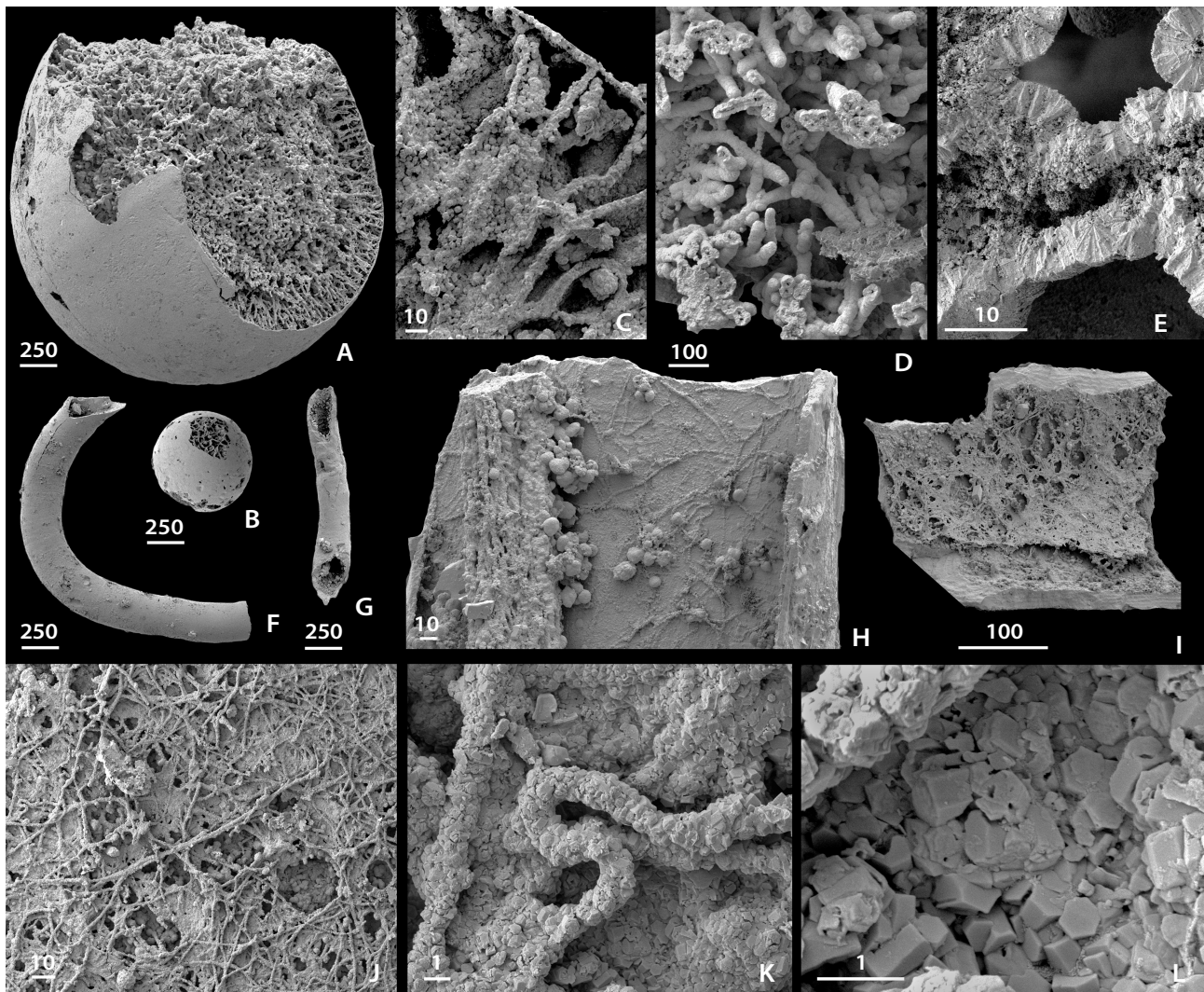


Figure 2. Modes of phosphatization of organic remains from the Špičatý vrch locality, Loděnice, Central Bohemia; Motol Formation, Sheinwoodian, Silurian. • A, D, E – Specimen B (PCZCU 3012), entire partly broken object (A), threads encrusting by botryoidal coatings of apatite in central portion of the object (D), and radially arranged crystals forming a continuous layer surrounding a canal after an organic fibre (E). • B, C – Specimen A (PCZCU 3013), entire partly broken object (B), and section of peripheral part showing crystallic coatings of suggested cell walls (C). • F, G – two tubes of byronids (PCZCU 3014, 3015); the left tube shows a phosphatized internal plexus of treads. • H – fragment of byronid tube (PCZCU 3016) with phosphatized columnar structure, likely a collapsed body of byronid, and thin threads and spheroid bodies (mycelium and sporangia?) of suggested fungi or actinomycetes attached on the internal side of the byronid tube. • I–L – plexus of mycelium covering the internal wall of a byronid tube fragment (I) (PCZCU 3017), detail of phosphatized filaments and globular sporangia (J), detail of filaments covered by apatite crystals (K), and a detail of plexus surface showing hexagonal crystals of mineral coating (L). Bar length in µm.

preservation of graptolite rhabdosomes indicate hypoxic conditions likely just near or immediately below the water/sediment interface of the sediment.

The nearby volcanic island(s) formed an ecospace for the growth of the early terrestrial plants (Bek *et al.* 2022). The sea on shoals of volcanic accumulations supported the development of rich marine communities with diverse groups of invertebrates. Surrounding deeper basinal floor with hypoxic waters hosting only graptolite macrofauna covered the extensive sea floor in the Prague Basin. The Sheinwoodian age (*Monograptus belophorus* Biozone) of the phosphatized spherical objects is proved by the occurrence of the eponymous graptolite (Bek *et al.* 2022, Štorch 2023). Conodonts have not been studied in this section.

Material, methods and terminology

The primary objective of the rock etching from the described locality was study of organophosphatic brachiopods, which was already published (Mergl 2024). Brachiopods, other diverse phosphatic and phosphatized fossils were derived from 20 kg of laminated limestone which was broken into small pieces about 10 g in weight prior to maceration in 15 % solution of acetic acid for four to five days. The residue was sieved, cleaned by water, air-dried, and all fossils from the fraction larger than 0.25 mm were hand-picked under a stereomicroscope. Fossils, in a descending abundance, include phosphatic byronid tubes (*Byronia* sp.), their attachment discs (*Phosphannulus* sp.), fragments of organophosphatic brachiopods (Mergl 2024), fragments of conulariid tests (Mergl 2023), conodonts, small phosphatized coprolites, scolecodonts, and siliceous sponge spicules. In total, several hundred phosphatic, phosphatized or organic-walled fossils were recovered.

Two observed spherical objects (Fig. 2A, B) are exceptional among the phosphatic fossils in the residue, and indicate rarity of this mode of preservation. Other originally organic-walled structures are moderately abundant in the residues, indicating common rapid phosphatization after their burial in an unconsolidated sediment. The phosphatized plexus of thread-like organisms, likely fungi, and similar thread-like structures frequently cover internal walls of some undeformed and 3D preserved byronids having originally phosphatic thecae (Fig. 2F, G, I). Botryoidal aggregations of small, more or less uniformly sized hexagonal microcrystals (Fig. 2L), likely of hydroxyl apatite, form thin coatings on external surfaces of the originally organic-walled filaments, likely fungal hyphae (Fig. 2J, K). The preservation of both spherical objects displays the same features as the assumed filaments of the mycelium (Fig. 2C, D, E).

Experimental studies have demonstrated, that decay of soft structures in seawater occurs within days after death. Phosphatization then occurs rapidly, in days to weeks, when a favourable microenvironment is created (Sagemann *et al.* 1999, Jin & Copper 2010). Nevertheless, the intrinsic mechanism of phosphatization of described both spherical objects is not resolved herein.

The specimens have been visualized with a Scanning Electron Microscope (JSM-7401F JEOL) at the Biology Centre of the Academy of Sciences of the Czech Republic at České Budějovice, South Bohemia.

As much as possible, we use morphologic descriptive terminology to avoid confusion with biological terminology because the biological affinity of both specimens is unclear.

Both specimens are housed in the palaeontological collections of the Centre of Biology, Earth and Environmental Sciences in the Faculty of Education of the University of

West Bohemia in Plzeň, Czech Republic (specimens PCZCU 3012, 3013).

Description of spherical microfossils

Specimen A

Figures 2B, C; 3

Material. – One spherical body (PCZCU 3012), broken into part and the corresponding counterpart of nearly same size, together showing the internal structure as well as the outer partly exfoliated surface.

Description. – Specimen A has a spherical form approximately 670 µm diameter and displays different structures in the peripheral layer and at its centre (Fig. 3A). The peripheral zone consists of polyhedral and irregularly shaped chambers, likely the remains after cells of varying size, with the larger cells 36.1–81.9 µm long (mean = 54.4 µm, SD = 10.3 µm, N = 15) and 19.5–44.5 µm wide (mean = 33.6 µm, SD = 11.1 µm, N = 15). The suggested cell walls are preserved by coatings of botryoidal microcrystals, in some places arranged in two discrete layers. A thin gap present between these layers suggests the original presence of intercellular space or this space remained after a disintegration of cell walls (Fig. 3C: ic). Irregular clusters of microcrystals form discrete bodies inside almost each chamber, regularly adjoining to one of cell walls (Fig. 3C, D: pt) that may represent the phosphatized remain of shrunken protoplast because their regular presence in each chamber.

The surface of Specimen A is formed by a continuous, similarly bilayered, smooth microcrystalline coating (Fig. 3B, C, D) with a narrow slit separating the two layers. The

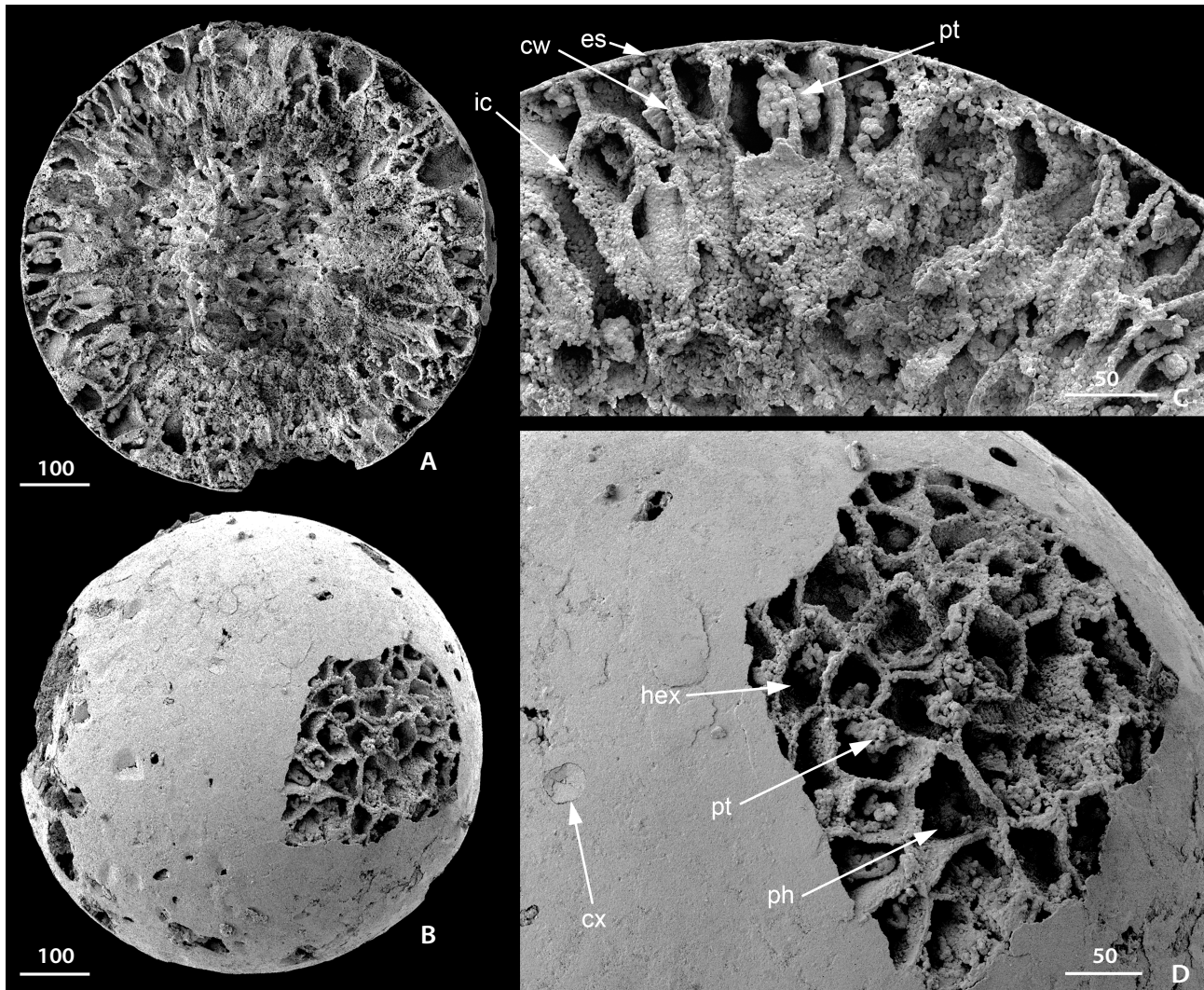


Figure 3. Specimen A. Locality Špičatý vrch, Loděnice, Central Bohemia; Motol Formation, Sheinwoodian, Silurian. • A–D – Specimen A (PCZCU 3013), natural cross-section showing its internal structures (A); the second part of Specimen A showing the external surface and cellular structure close to its surface (B); cellular architecture beneath the surface of object showing the shrunken protoplast (pt), the intercellular space (ic), the slit in external surface layer (es), and the bilayered mineral coating of the cell wall (cw) (C); peeled surface of object external membrane showing hexagonal (hex) to polyhedral (ph) shape of cells, ghost cracks (cx), and phosphatized shrunken protoplasts (pt) (D). Bar length in µm.

slit was observed in several places at the broken spheroid surface (Fig. 3C: es). The slit is likely a hollow after the original organic membrane surrounding the whole body of the object.

The elongation of cells in the surface layer indicates their clearly centripetal arrangement from the outer membrane (Fig. 3A). Although cell outlines just beneath the external layer of object are clearly polyhedral (Fig. 3D), the hexagonal outlines are also visible (Fig. 3D: hex). The polyhedral structure below the outer membrane is copied by a ghost cracks pattern on the surface of external layer (Fig. 3B, D: cx).

The structure of the central region of Specimen A, which occupies about a half of body diameter, has a less

distinct architecture (Fig. 3A). The alternation of chambers and sheets suggests a cellular structure, but without a distinct radial pattern. Thick thread-like structures are visible (Fig. 3A).

Remarks. – The natural cross section in the broken part of the peripheral layer of Specimen A indicates: (i) the nearly same thickness of the double layered partitions, (ii) weakly convex to weakly concave, but mostly planar contacts between suggested cells, (iii) hexagonal cell outline similar to cell outlines in the tissues of extant organisms, and (iv) radial but otherwise fairly irregular spacing of elongate cells that differs from the regular cell arrangement of the embryonal morula of metazoans. An

animal affinity of Specimen A also seems less probable due to the absence of any larger hollow space inside the object that is characteristic for blastula or gastrula stages.

The less regular structure of the central area of the object may be a result of partial decay of the tissues or alteration by diagenetic processes. The observed thick thread-like structures are similar to structures observed in the second studied spherical object, where a decay process is suggested. However, it cannot be determined conclusively if the original object had a nearly homogenous cellular structure or displayed functional and morphological differentiation of the central and peripheral zones.

Specimen B

Figures 2A, 4

Material. – One subspherical object (PCZCU 3013), broken into one smaller and much larger opposite pieces, showing the internal structure as well as outer surface of the object.

Description. – Specimen B has a weakly elongate subspherical shape of approximately 2.5 mm diameter (Fig. 2A). The outer surface of Specimen B is smooth, without any noticeable surface pattern (Fig. 4A, C). A thin but distinct gap between the outer and the inner microcrystalline layers is developed, suggesting the original presence of an organic membrane (Fig. 4I). The interior of the specimen is filled with phosphatized fibrous structures that extend inwards from the surface membrane (Fig. 4B, D). The original organic fibres are preserved as thin canals enveloped by a layer of botryoidal microcrystals with radial crystal structure (Fig. 2E, 4G).

Specimen B shows a differentiation into a peripheral layer composed of radially arranged, thicker fibres with a diameter of 15.90 μm (SD = 2.51 μm ; N = 50). These fibres are laterally branched into thinner fibres having a half diameter (8.07 μm ; SD = 2.00 μm ; N = 30) (Fig. 4D, H, I). The thinner secondary fibres regularly adjoin to inner side of the surface membrane or interconnect the radial fibres in the outer peripheral region (Fig. 4H) of the object. Despite their uneven sizes some fibres size has a blind end (Fig. 4G). Thinner fibres extend nearly or just perpendicularly from the thicker fibres (Fig. 4H, I).

The central part of the object shows a more random network-like, intertwined character of similarly-sized fibres (Fig. 4C, E, F) and its total volume significantly exceeds the volume of the peripheral layer. The fabric of the central part is more compact and less clearly differentiated into the main (thicker) and the secondary (thinner) fibres. A boundary between the interior with irregular fabric and the peripheral layer with radially

arranged fibres is abrupt (Fig. 4B, C). The radial fibres of peripheral layer are quite often disconnected with thinner and much randomly arranged fibres of the internal layer. Fractures of mineral coatings of radial fibres are distinct (Fig. 4D, G). Unlike this, the distal ends of fibres of the internal fabric are naturally terminated by interrupted mineral botryoidal coatings (Fig. 4F). Therefore, it is suggested that any unpreserved barrier between the internal area and the peripheral layer occurred at 170–200 m below the surface of Specimen B.

Remarks. – Is not clear whether the described internal fibrous structure represents the original fabric of the organism or represents structures related with a decay process of originally differently structured organism. The growth of microcrystals forming the radial structure clearly began on the surface of threads or fibres that densely filled the interior of the apparently undifferentiated envelope of the object. These fibres have a distinct arrangement in the outer, radially arranged peripheral layer, where radially arranged microcrystals form regularly spaced columns. The central part of the specimen displays a less regular, three-dimensional plexus of threads clearly indicated by their microcrystal coatings. The fibres of the peripheral layer were firmly attached to inner side of the external membrane, generally with several further branched and likely originally thinner fibres. Cellular tissue of the type observed in Specimen A is not seen. There are also distinct differences in size and shape between Specimen A and Specimen B. Specimen A is smaller, forming a perfect sphere, while Specimen B is much larger and slightly elongate.

Discussion

Specimen A

External membrane. – The nature of the surface-covering membrane is considered to be an important criterion for taxonomic identification (Zhang & Zhang 2022). In metazoan embryos, the outer covering membrane constitutes an independent, smooth external layer that does not contact internal multicellular structures (see Steiner *et al.* 2014, fig. 4; Willman *et al.* 2020).

A layering of the surface membranes in these developmental stages, with one of the multiple layers exhibiting the external ornamentation, has been observed in fossils by Xiao & Knoll (2000), Xiao *et al.* (2014), Yin *et al.* (2004), and Cunningham *et al.* (2017). A smooth external membrane has also been documented in microfossil algae, where, apart from *Wengania* specimens (Zhang *et al.* 1998), it generally forms an independent external envelope of morphologically distinct cell

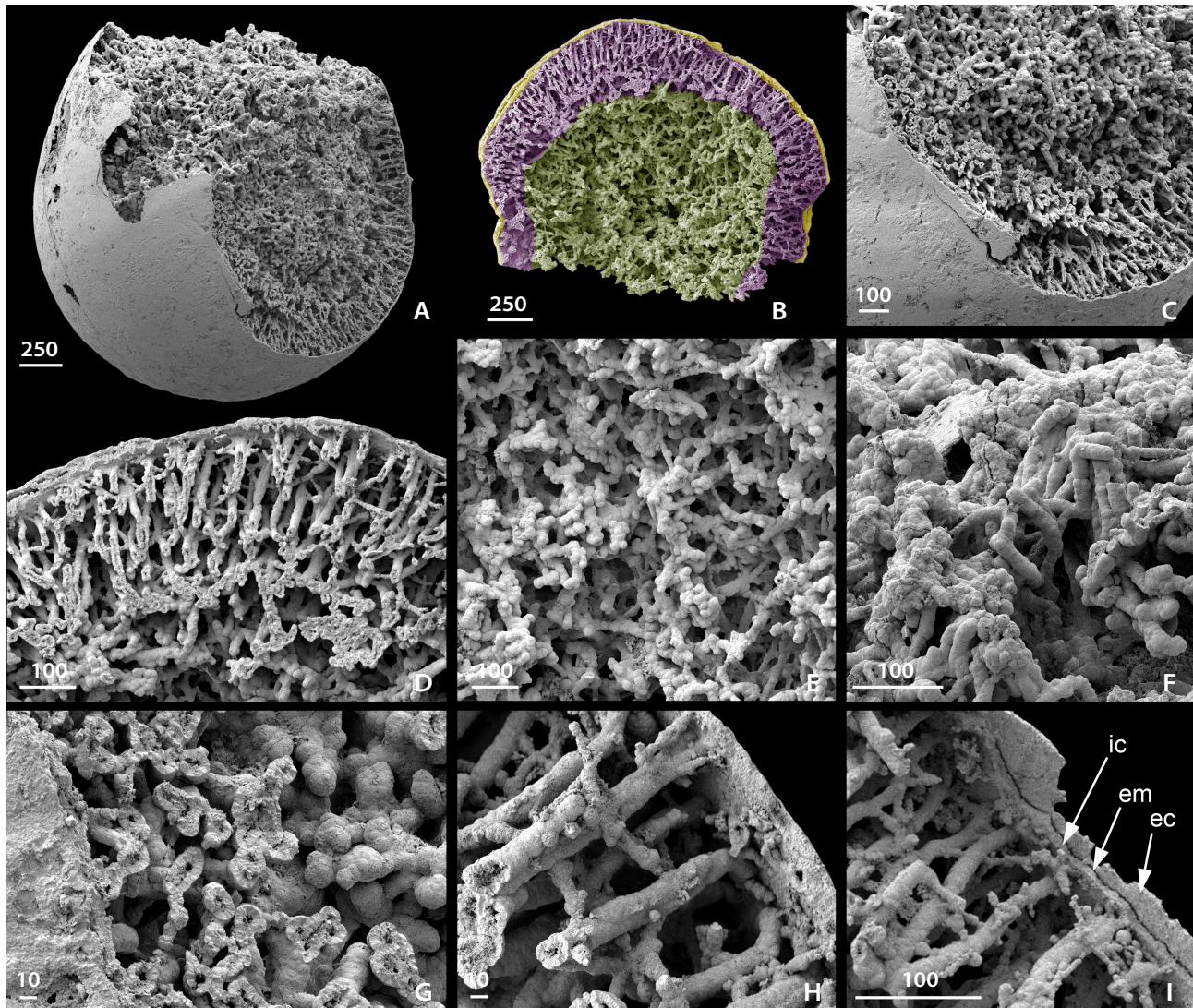


Figure 4. Specimen B. Locality Špičatý vrch, Loděnice, Central Bohemia; Motol Formation, Sheinwoodian, Silurian. • A–I – Specimen B (PCZCU 3012), natural cross-section showing its internal structures (A); the peeled smaller second part of Specimen B showing the external membrane (yellow), peripheral radially arranged layer (violet) and a distinct surface between the peripheral layer and the central part (green) (B); a part of Specimen B from which a fragment was peeled off (C); columnar peripheral layer (D), detail of central part (E), chaotic arrangement of phosphatized fibres in the central part (F), the interface between peripheral layer and central part with cross-sections of phosphatized fibres (G), columnar architecture of the peripheral layer just below the external membrane of the object with thinner fibres branched from thicker radial fibres (H), bilayered coatings (ic = internal coating; ec = external coating) of the external membrane (em) in the broken part of the objects; note branched columns attached to the internal surface of the external membrane. Bar length in μm .

aggregates (Zheng *et al.* 2021, Tang *et al.* 2022). The smooth outer surface of the multicellular alga *Thallophyca* Zhang, 1989, is formed by distinctly differentiated cortical layers composed of smaller cells, or of cells differently oriented compared to those in the deeper layers of the thallus (Zhang *et al.* 1998, Xiao *et al.* 2004). Indeed, the layering of the external membrane is not restricted to metazoan embryos, as it has also been documented in the thalli of certain *Wengania* specimens (Zhang *et al.* 1998).

Specimen A exhibits a single external cell membrane connected to the peripheral cell layer (Fig. 3C). It is not an

independent external membrane. This feature is evident in peeled parts of the external membrane, where the interior with polygonal cells of the peripheral layer is exposed (Fig. 3D). Although it represents the outer surface of peripheral cells, no individual cell outlines or regular ornamentation are distinguishable on the outer surface of the spherical object. Regular structures are commonly observed in extant green algae and red algae as well as in the peripheral cells of pseudo-parenchymatous fossils (Zheng *et al.* 2021, Tang *et al.* 2022). There, the question arises how the growth of such structures proceeds without

leaving the outlines of individual surface cells. For a possible explanation, we apply a hypothetical model derived from modern algae and plants possessing rigid cell walls, where cell expansion is driven by internal turgor pressure acting on the cell wall (Cosgrove 2005). This mechanism involving enzymatic loosening of the wall and simultaneous synthesis of new wall material through the cooperation of enzymes (e.g. endoglucanases in vascular plants), and proteins such as expansins (Cosgrove 2016). This mechanism cannot be directly confirmed in fossils, but serves as the useful analogy for the phosphatized specimen.

Although the composition of algal and vascular plant cell walls differs, the mechanism is considered broadly applicable (Ortega 2023), even though Boyer (2016) suggests that cell wall growth in *Chara corallina* Willdenow, 1805 (Charophyta, Charophyceae) can proceed in the absence of enzymatic activity. While the outlines of surface thallus cells are visible in extant multicellular red algae and green algae, the fossil preservation of Specimen A without discernible outlines of individual cells could hypothetically be explained by enzymatic remodelling of the cell walls (Cosgrove 2005) or by continuous expansion of a coherent external wall associated with the exocytosis of wall components. The possibility that the smooth external membrane is merely a phosphatization product cannot be ruled out. Yet phosphatized fossils show that external cell outlines are often preserved (e.g. Chai *et al.* 2022), indicating that phosphatization does not necessarily erase the surface morphology. It thus seems more plausible that a smooth surface of Specimen A reflects areal biological property of the peripheral cells rather than a purely taphonomic artefact.

It is also possible, by analogy with animal embryos (e.g. Xiao & Knoll 2000, Yin *et al.* 2004, Xiao *et al.* 2012, Cunningham *et al.* 2017) and algal thalli (Zhang *et al.* 1998), that more than one external membrane was originally present in Specimen A. In such a case, the object may display only the internal membrane. Despite described findings of structurally comparable algal thalli, particularly from the Wengan Biota, observations based on two-dimensional thin sections (Zhang 1989, Zhang *et al.* 1998, Xiao *et al.* 2004, Liu *et al.* 2014b) do not permit adequate comparison of surface structures.

Cells and cell division. – The mode of cell division is an important criterion for distinguishing metazoan embryos from algae. Palintomic cell division in which daughter cells do not grow to their original size, has often been associated with metazoan embryos (Xiao *et al.* 1998, Cunningham *et al.* 2017), though this has occasionally been questioned (Huldtgren *et al.* 2011). However, the densely packed polygonal cells in our specimen differ

significantly from the palintomic cell arrangement found in metazoan embryos, where cells are of uniform size and shape, and more closely resemble the cellular arrangement seen in algal thalli (Zhang 1989, Zhang *et al.* 1998, Xiao *et al.* 2004, Zheng *et al.* 2021, Tang *et al.* 2022).

While *Wengania*-fossils exhibit a similar cell morphology in a spheroidal thallus, none of the described *Wengania* species show comparable cell arrangement and/or cell sizes in relation to the overall thallus size (Zhang 1989, Zhang *et al.* 1998, Xiao 2004). It is tempting to suggest that our specimen represents an early developmental stage of a *Wengania*-like species. However, the dimensions of the thallus and cells in known *Wengania* species do not correlate with those of our Specimen A. Thalli of *W. globosa* Zhang, 1989, and *W. exquisita* Zhang *et al.*, 1998, show significantly smaller, regularly arranged cells that diverge or are arranged in parallel rows (only in the periphery in *W. exquisita*), with similar thallus sizes. Additionally, *W. exquisita* exhibits the irregular cell arrangement in thallus interiors (Zhang *et al.* 1998, Liu *et al.* 2014b). The thallus of *W. minuta* reaches only one-third of the size of our specimen at its maximum, with an inner cell size ranging between 3 to 8 μm (Xiao 2004).

It has been suggested that *Wengania* species could represent early developmental stages of florideophyte pseudo-parenchymatous thalli (Shang & Liu 2022). However, the different internal arrangement and/or cell size are evident in the thalli of pseudo-parenchymatous species of *Thallophyca* Zhang, 1989, *Thallophycoides* Zhang & Yuan, 1992, *Paramecia* Zhang & Yuan, 1992, and other genera (Zhang & Yuan 1992, Zhang *et al.* 1998, Xiao *et al.* 2004, Shang & Liu 2022). For these reasons, we do not consider that our specimen is developmental stage of these genera.

An alternative suggestion is that Specimen A represents an early developmental stage of an aggregate algal microfossil. Zheng *et al.* (2021) considered that aggregate algal microfossils consist of variously sized, more or less spheroidal clusters of cells. During early development, such an alga could form a multicellular internally differentiated spherical thallus. However, a comparison of the sizes of aggregate fossils (Zheng *et al.* 2021) with our specimen shows that our specimen is much larger than the partial, sphere-like components of the aggregate thallus observed so far. The internal differentiation of the aggregate microfossils observed by Zheng *et al.* (2021) shows a pyramidal shape and a distinct arrangement of peripheral cells, which constitute up to half the volume of the aggregate. Moreover, in the proposed life cycle of such aggregated algae, the initial stage involves the formation of uniformly-sized outer cells corresponding to a constant proliferation rate. In contrast, our algal spheroid does not show identical cell shape and size in its periphery. The

irregularly shaped *Calathophycus irregulatus* Tang, 2022, documented by Tang *et al.* (2022), closely resembles our specimen in terms of cell shape and compactness. However, several differences are evident, including the overall thallus habitat, which displays a distinct central concavity, the arrangement of cells into clumps separated by clear gaps, and smaller only 20–35 µm long cells.

Reproductive structures. – The spherical structures could also represent reproductive bodies of certain algae, which may form either (i) in specialized parts of the thalli or (ii) through separation from the original mother thalli. Similar nearly spherical structures observed in the thalli of the Doushantuo biota have been interpreted as putative carposporangia (Xiao *et al.* 1998, Zhang *et al.* 1998, Xiao *et al.* 2004). However, carposporangia are always part of the thallus and do not form separate reproductive structures. Other differences are present in the arrangement and/or size of the cells and the overall carposporangium.

Structures resembling the thallus of Specimen A were observed at the periphery of the thallus of *Thallophyca* cf. *corrugata* Zhang & Yuan, 1992 (Liu *et al.* 2014b). However, the internal arrangement of small cells (approximately 3 × 3 µm) in rows more closely resembles the internal structure of *Wengania* than the structure of Specimen A. If Specimen A was a reproductive body broken off from the mother thallus, we would expect to observe a cleavage site or scar on the surface of the spheroid but these are not evident.

The significance of Specimen A lies in the unique combination of characters – a large spheroidal thallus, irregularly sized peripheral cells, and the potential for multiple external membranes – none of which has previously been documented together in either metazoan embryos or described algal species. This combination broadens the morphological spectrum currently recognized in sphaeromorphic microfossils. Although the alternative interpretations cannot be entirely excluded, the observed combination of characters is most consistent with the interpretation of this specimen as a separate organism rather than a developmental stage or taphonomic variant of a previously described taxon.

Specimen B

Original nature of the fibrous structures. – In our opinion, the internal fibrous arrangement cannot be of purely inorganic origin. We come to this opinion for the following reasons: (i) if it were a purely inorganic phosphate structure, the surface phosphate coatings would be of uneven size. However, in Specimen B, the thickness of the phosphate coatings is relatively consistent, with

the phosphate layer on the radial fibres of the peripheral layer averaging 5.64 µm (SD = 0.47 µm; N = 35), and the phosphate layer surrounding the internal reticular fibres averaging 4.93 µm (SD = 0.56 µm; N = 20); (ii) the arrangement of the fibres and the differentiation of the internal structure are regular and non-random, indicating a structured internal fabric characteristic of a living organism. Moreover, experimental phosphatization of eggs at various stages of decay demonstrates a close correspondence to the process of phosphatization that occurred hundreds of millions of years ago resulting in faithful preservation of the original internal structures (Hippler *et al.* 2012). For these reasons, we suggest that the central space with the fibrous structure (Fig. 4B, C) was originally traversed by organic fibres, which were radially encrusted by botryoidal layers of apatite microcrystals during phosphatization process. The inorganic origin of these structures is also contradicted by Steiner *et al.* (2014) and Han *et al.* (2018) who interpret a similar asymmetrical intertwining of fibres in the cavities of eggs and embryos as a phosphatized relict of soft tissues.

The hypothesis of a bacterial origin for the fibrous structures (Xiao & Knoll 1999) within the cavities of eggs and embryos was refuted by Steiner *et al.* (2014). The explanation that decaying internal organic material led to the formation of a regular network pattern seems quite unlikely in Specimen B. Decay can hardly have produced such a symmetrical internal arrangement, at least in the peripheral part of the object. This also applies to the hypothetical phosphatized filaments of cyanobacteria, which are known in described cryptoendoliths (Stockfors & Peel 2005). These cryptoendolith filaments which were observed in the Cambrian brachiopods are less regularly arranged and are not regularly branched as can be observed in filaments in the outer layer of Specimen B.

Nevertheless, following the suggestion of Steiner *et al.* (2014), some degradation of the original organic content may occur. The decay process might have assisted the formation of the random fabric in the central region of the object. The same decay processes in more superficial parts of the objects left shrunken regularly spaced protein threads adhered by more smaller threads to inner surface of the external membrane. The distal inward parts of protein threads ended on an unpreserved envelope of the central region. This hypothetical decay structure of the object was used as the template for the earliest generation of phosphate microcrystals. Growth of microcrystals was terminated simultaneously in all internal space of the object.

The complex structure closely resembles structures found inside the vesicle of fish eggs. Hypothetically, the central part of the object might represent a yolk, while the peripheral layer could represent a perivitelline space

with encrusted threads of glycoproteins. In such a case, the external membrane would represent the chorion. The indistinct break between central part and peripheral layer could correspond to the unpreserved vitelline membrane. Similar spherical fossils of comparable size, which were interpreted as a chorion and animal embryos, were described by Broce *et al.* (2014). We refer to the extensive discussion of these authors on a phosphatization of the external membrane (= ?chorion), and the nature of these objects coming from lower Cambrian of South China.

Comparison with similar fossils. – Microfossils with a smooth surface membrane and an internal reticulate structure have been repeatedly documented and interpreted as metazoan eggs and embryos (Xiao & Knoll 1999, Yin *et al.* 2004, Pyle *et al.* 2006, Broce *et al.* 2014, Steiner *et al.* 2014, Donoghue *et al.* 2015, Peel & Willman 2022). In addition to the evident differences in size between eggs and embryos with a similar internal structure (see Steiner *et al.* 2014: fig. 8), morphological differences are apparent in the structure of the surface membrane. In fossilized eggs and embryos (Steiner *et al.* 2014, Willman *et al.* 2020), the surface membrane does not exhibit a double phosphate coating surrounding the original organic membrane, as observed in Specimen B. A diagenetic origin of two-layers on the same surface of the organic membrane seems a less probable, although composite multi-layered coatings of a single structure are described (Stackfors & Peel 2005). Furthermore, the internal fibrous structure of eggs and embryos is random, consisting not only of fibrous but also spherulitic structures, without clear differentiation between the central and peripheral regions.

Some phosphatized fibrous structures found in the cavities of various organisms have also been attributed to fungi (e.g. Xiao & Knoll 2000, Fang *et al.* 2022, Peel & Willman 2022) or actinomycete-like fossils. The green algae are also considered by some authors (Stackfors & Peel 2005). Traces resulting from colonization by endolithic organisms or ambient inclusion trails are commonly preserved on the external surfaces of fossils (e.g. Stackfors & Peel 2005, Yang *et al.* 2017, Peel 2025). Although phosphatization commonly preserves fine-scale surface details, it is hypothetically possible that traces of penetration by symbiotic or saprophytic organisms were obscured during phosphatization. Even if this were the case, the internal organization of the filaments in Specimen B is so regular that it cannot be reconciled with an interpretation as relics of endolithic organisms or ambient inclusion trails. Structurally distinct phosphatized filaments, likely of fungal or bacterial origin, were observed on the surface of byronid fragments within the same sample (Fig. 2F–L). Their arrangement, however, does not exhibit the highly regular fabric observed in the described spherical object.

Conclusions

Two minute spheres recovered from limestone of Silurian age in the Czech Republic likely represent the phosphatized remains of organic bodies.

Specimen A exhibits a suggested cellular structure inside a smooth external membrane. The phosphatization of cell walls, polyhedral and hexagonal outline of cells, phosphatization of shrunken protoplast inside cells, and the differentiation of central and peripheral cell layers suggest an algal affinity.

Specimen B lacks the distinct cellular pattern observed in Specimen A. Below the external smooth membrane, a peripheral layer of columns composed from botryoidal microcrystals encrusting radially arranged fibres is developed. The central part is formed by plexus of irregularly spaced fibres having aggregated microcrystal coatings. A poorly defined break lies between the central part and the peripheral layer. This object is interpreted as a simply structured biological object affected by decay processes and phosphatized nearly simultaneously with the decay processes. The taxonomic affinity of Specimen B is uncertain. Hypothetically, the object could be a phosphatized egg.

The phosphatization of spherical microfossils in the limestone of the Motol Formation (Sheinwoodian, Wenlock) was enhanced by volcanic material admixture into the sediment, a possible source of the phosphate. This important role could play the development of presumed hypoxia or anoxia at or just near to the water/sediment interface, which is evident from the absence of infaunal and benthic scavengers, and the lamination of limestone.

This is the first occurrence of phosphatized spherical microfossils of algal and/or metazoan affinity in the Silurian of the Barrandian area and European peri-Gondwanan units. Together with the problematic mazuelloids (Kremer 2005), the finds improve our knowledge of this type of fossilization in the Silurian Period.

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