The enigmatic cnidarian *Martsaphyton moxi* gen. et sp. nov. from the Darriwilian (Middle Ordovician) of Estonia

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Abstract. On the basis of detailed SEM-EDS study and computer tomography scanning, the single specimen of the enigmatic *Martsaphyton moxi* from the Aseri Stage (Darriwiliar; Middle Ordovician) of Estonia was identified as a member of the phylum Cnidaria and subphylum Medusozoa, with unspecified (*incertae sedis*) class placement. Our results confirm a number of similarities in the morphology and chemical composition with previously described *Sphenothallus* Hall 1847 and *Torellella* Holm 1893, also interpreted as cnidarians. All three show tubiculous morphology, lamellar skeleton structure and calcium phosphatic composition. The new species differs from the previously described members in its unique root-like appendages, widened apertural chamber and lack of a laterally thickened skeleton wall.

The element analysis revealed an unexpected chemical composition – high content of silica, iron, aluminium, potassium and sodium – of the rock matrix surrounding the specimen, which suggests possible involvement of material of volcanic origin in the sediment.

Key words: Martsaphyton, Cnidaria, Medusozoa, Ordovician, Darriwilian, Estonia.

INTRODUCTION

Sometimes, even without good scientific reasons, some fossils turn into legends. People remember having seen and talked about them, but when looking back in time, recall no more than vague rumours. Geology students at the University of Tartu in the 1970s and 1980s remember the late charismatic palaeontology professor Arvo Rõõmusoks (1928–2010), long-time head of the department, who used to show students a peculiar fossil, which he called Martsaphyton moxi, declaring it the oldest land plant in the world. The fossil itself, which he kept in his office in an old-looking cardboard box, was deeply hidden in the rock matrix, revealing no more than a narrow strand of an elongate structure which seemed to bear a few short side branches. One extremity of the fossil showed a dark, transversely arranged ovate object, with a sharp tip at one end. That object was called a 'bud' - until one year the professor admitted, it was lost.

Years passed and, after all the (geo)political transformations, scientific and structural reorganizations that the university had gone through, the fossil had found its place in the repository of the Natural History Museum of the University of Tartu. It was catalogued under an ambiguous tag '*incertae sedis*', which is commonly used for enigmatic organisms with uncertain taxonomic placement.

The history of the fossil, however, starts much earlier. It was the year 1925 when a young teaching assistant at the University of Tartu, Artur Luha (1892–1953), took a group of interested school teachers on a geological field trip to Northeast Estonia. Among other localities, they examined a small limestone quarry close to the edge of the North Estonian Klint near the humble Martsa village (Fig. 1), west of the town of Toila. An ardent school teacher Aleksander Moks (1885–1944), head of the Viljandi primary school, noticed a slab with this peculiarlooking fossil and handed it to Luha, who wrote the first label (Fig. 2B), naming the collector and indicating the locality. The elongated fossil reminded him of an axis of early land plants, and he suggested that the transverse object on the tip could be an oddly arranged sporangium.

The fossil itself, however, has never been properly described and published. The only photo of the fossil in its original appearance (Fig. 2A) was published in a local popular science journal (Luha 1967). The manuscript of the text was found among Luha's papers after his death and edited for publication in honour of his 75th birthday

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Fig. 1. Location of the study area (A) and Martsa quarry (B) in Northeast Estonia.

by Einar Klaamann. Although not dated, the text where Luha analysed the evolution of terrestrial ecosystems and speculated that the mysterious fossil could be one of the representatives of early plants, was plausibly the same which he had presented in 1926 at the Estonian Naturalists' Society (Perlitz 1927). There he concluded that the fossil did not belong to any faunal group and, referring to the obscure structure on the tip, stated that no animal possessed such organs that could be seen on that specimen. He compared the fossil to a group of Devonian plants, which, according to the classification of that time (Taylor et al. 2009), were known as psilophytes.

Later, thanks to its 'legendary' status, the enigmatic fossil was mentioned in another local popular science journal in the context of Earth history (Klaamann & Nestor 1976) and in a geological guidebook compiled by Nestor et al. (2007). In 2013, the fossil was retrieved from the repository of the Natural History Museum of the University of Tartu to be examined by undergraduate geology students Raili Hantson and Armin Kuningas in the course of a student project.

MATERIAL AND METHODS

The fossil is catalogued at the Natural History Museum of the University of Tartu as TUG 1303. It consists of three pieces: the main part (TUG 1303-1; Fig. 3A–E), a fragment from the wider upper end of the fossil (TUG

B

Fig. 2. A, original photo of *Martsaphyton moxi* gen. et sp. nov., published in 1967; **B**, the label accompanied by the specimen. The text on the label says: *Martsaphyton moxi*. Problematic from the Martsa quarry, found in 1925 by teach. A. Moks in the teachers' excursion station. Presented by A. Luha as the oldest land plant at the Estonian Naturalists' Society in 1926.



Fig. 3. *Martsaphyton moxi* gen. et sp. nov. **A–E**, holotype TUG 1303-1: A, complete specimen; B, C, details from the side view; **D**, view from above; E, view from below. **F**, fragment of the specimen, broken from the uppermost part of the holotype (TUG 1303-2), side view.

1303-2; Fig. 3F) and the third piece of rock matrix (TUG 1303-3) showing a narrow strip of the outer mould.

The specimen was photographed with the stereomicroscope system Leica S9i and studied with the Zeiss EVO MA15 scanning electron microscope (SEM) backscattered electrons detector (BSE) uncoated in low vacuum regime. The elemental analysis was performed with an Oxford X-MAX 80 energy dispersive detector system (EDS) and Aztec Energy software at the Department of Geology, University of Tartu.

The X-ray computer tomography (CT) scanning was performed at the Laboratory of Industrial Computer Tomography, Institute of Technology, Estonian University of Life Sciences. The CT scanner YXLON FF35 CT was used, the scan was performed with tube voltage 100.0 kV and tube current 750.0 μ A; 3000 projections were made, with the integration time of 0.03 s.

GEOLOGICAL SETTING

The original label which came with the fossil says that the specimen was found at the Martsa quarry in North Estonia, at the edge of the Baltic Klint, near the town of Toila. Orviku (1940) lists two small quarries near the Martsa village, both of which open the same beds of the Aseri Regional Stage of middle Darriwilian age, with the thickness of 2–3 m. However, the preserved documents do not reveal which of these two quarries was the exact site of discovery of the specimen.

During the Ordovician, the modern territory of Estonia was part of the Baltica palaeocontinent in the temperate climate zone in the Southern Hemisphere (Torsvik & Cocks 2013). Apart from the largely terrigenous Lower Ordovician, most of the Ordovician sequence of Estonia is characterized by carbonate rocks, predominantly limestones, which were laid down in a shallow epicontinental sea.

In North Estonia, the Aseri Stage consists of bioclastic limestones (Jaansoon-Orviku 1927; Orviku 1940; Hints 1997), with unevenly distributed light-coloured phosphatic (francolitic) ooids and brown goethitic ooids. Sturesson & Bauert (1994) have suggested that the source material for these ooids came from a land area northwest of Tallinn and that the ooids were formed during a transgression/deepening event.

The Aseri Stage is rich in shallow-water marine fauna, especially invertebrates like trilobites, bryozoans, brachiopods, echinoderms, cephalopods, various ostracods, chitinozoans, etc. (Rõõmusoks 1970; Estonian geocollections database at https://geocollections.info). However, it has also been emphasized (Suyarkova & Koren 2009) that due to the shallow shelf conditions, the whole Darriwilian of the area is rather poor in graptolites. In terms of biozones, the Aseri Stage corresponds to the lower part of the *Pterograptus elegans* graptolite Zone and approximately to the *Eoplacognathus suecicus* conodont Zone (Männik & Viira 1990; Männil 1990; Hints 1997; Meidla et al. 2014).

COMPOSITIONAL ANALYSES

The EDS chemical mapping and element analysis (Figs 4, 5) showed that *Martsaphyton moxi* gen. et sp. nov. largely consisted of calcium phosphatic lamellae, which were, in places, encrusted with thin carbonaceous material (Fig. 5). The elemental analysis of the surrounding rock matrix revealed elevated levels of Si, K, Al, Fe, Mg and Na (in decreasing order of relative abundance) (Fig. 6).



Fig. 4. Elemental composition of *Martsaphyton moxi* gen. et sp. nov. A, EDS view of the lower part of *Martsaphyton moxi* gen. et sp. nov.; B, composite image of the EDS element distribution maps; C–L, EDS element distribution maps.



Fig. 5. Microstructure (A, B) and EDS spectra (C, D) of the *Martsaphyton moxi* gen. et sp. nov. phosphatic tube with patches of carbonaceous material.

A large portion of *M. moxi* is hidden in the matrix, therefore only a narrow segment can be observed and studied with classical methods without isolating the fossil from the surrounding rock and damaging the completeness of the specimen. Tomography has become an effective tool in palaeontology (Sutton 2008), allowing us to examine the three-dimensional structure of the entire skeleton, investigate its morphology and also see the internal structure of the rock matrix enclosing the specimen. The exterior of the entire specimen gives a hint that the matrix is composed of two types of rock - yellowish sediment surrounding the fossil most proximately, and greyish sediment distally. The tomograms (Fig. 7A-C) show the embedded tubiculous skeleton of M. moxi with root-like appendages extending from the open surface, but also reveal that the 'back side' is less pronounced and likely of worse preservation. The tomograms also show that at the adverse side, in places, the boundary between the two types of matrix is gradational.

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA Hatschek, 1888 Subphylum MEDUSOZOA Peterson, 1979 Class uncertain Genus *Martsaphyton* new genus

Type species. Martsaphyton moxi gen. et sp. nov.; by monotypy.

Diagnosis. As for the type species by monotypy.

Occurrence. Ordovician (Darriwilian; Aseri Regional Stage), Estonia.

Martsaphyton moxi new species Figures 3–7

Etymology. Genus name after Martsa quarry, where the fossil was found, species name after Aleksander Moks, the discoverer of the specimen.

Material. Holotype TUG 1301-1, nearly complete skeleton, though with the apical portion now missing.



Fig. 6. Elemental composition of the boundary between the proximal matrix ('tube') around the specimen (above) and the peripheral matrix (below). **A**, EDS view of the boundary region between two types of matrices; **B**, composite image of the EDS element distribution maps; **C–J**, EDS element distribution maps.

Type locality. Martsa quarry, northern Estonia.

Stratigraphic distribution. Aseri Regional Stage, middle Darriwilian, Middle Ordovician.

Diagnosis. Phosphatic tubiculous skeleton with oval cross section. Skeleton has a widened apertural chamber and narrow proximal part with root-like appendages. The regularly and asymmetrically located appendages are thin and almost perpendicular to the skeleton axis. Skeleton structure lamellar.

Description. Tubiculous skeleton, about 80 mm long, with strongly widened apertural chamber. Aperture oval (25 mm \times 15 mm wide), laterally asymmetrical with one side (convex side) protruding (10 mm) further than the other side. The apertural chamber is about 30 mm long.

Walls of the apertural chamber are externally smooth with poorly developed irregular growth lines.

The wall of the skeleton has lamellar structure; it is thin in the apertural part and somewhat thicker in the proximal part. In cross section, the skeleton wall seems to have equal thickness all around the proximal part. The walls of the skeleton are externally slightly concave at the transition from the narrow proximal part of the skeleton to the wide apertural chamber. The narrow proximal part of the skeleton is more than three times longer than the wide apertural chamber.

The skeleton has somewhat flattened cone shape with oval cross section in the narrow proximal part, where it shows root-like appendages. The apertural chamber is devoid of root-like appendages. The appendages are not preserved in full length; they are connected to the main



Fig. 7. Tomograms of *Martsaphyton moxi* gen. et sp. nov. **A**, front view of the specimen, with colour adjustment highlighting the skeleton and the adjacent surrounding yellow matrix; **B**, **C**, virtual longitudinal sections through the specimen demonstrating differential preservation of the back side of the skeleton: ambiguous boundary between the skeleton and the matrix due to dissolution (B), and normal preservation of the skeleton wall (C).

body via small bump-like swellings about 3 mm in diameter. The appendages are thin, 1–2 mm in diameter, oval in cross section, distally filled with crystalline material. The appendages are almost perpendicular to the longer axis of the skeleton, though gently proximally inclined. The locations of the root-like appendages on the proximal part of the skeleton are regular and asymmetrical, occurring consecutively at different levels, never on the same level together. Every successive appendage has usually more than 90° different orientation (on the plane perpendicular to the skeleton axis) as compared to the preceding appendage. The distance between consecutive appendages along the skeleton's axis is 8–9 mm. The walls of appendages show externally faint and fine longitudinal striation.

Comparison. Martsaphyton moxi gen. et sp. nov. resembles most closely the tubes of *Sphenothallus* Hall, 1847 (Van Iten et al. 1992) in its phosphatic composition and lamellar skeleton structure, but it differs in having the root-like appendages, widened apertural chamber and in the lack of laterally thickened skeleton wall. *Martsaphyton moxi* was probably attached to a hard substrate via a small disc-like holdfast (lost in the fossil now, but previously photographed by A. Luha; Fig. 2A). The presence of a small holdfast also makes *M. moxi* similar to *Sphenothallus* (Van Iten et al. 1992) and conulariids (Vinn et al. 2019, p. 93, fig. 4A). Another phosphatic tubiculous fossil that slightly resembles *M. moxi* in its skeleton morphology and lamellar microstructure is *Torellella* Holm, 1893 (Vinn 2006). However, *Torellella* has no root-like appendages and widened apertural chamber (Vinn 2006).

DISCUSSION

Sphenothallus and other phosphatic tubular fossils such as *Torellella*, which likely are phylogenetically closely linked to *Martsaphyton*, were all hard substrate encrusters. It is possible that *Martsaphyton* was also attached to hard substrate with a holdfast similar to *Sphenothallus* (Van Iten

et al. 1992) and Torellella (Vinn 2006). If this was true, then Martsaphyton was attached to hard substrate either inside a burrow or on the seafloor. The original photograph of Martsaphyton (Fig. 2A) shows a holdfast-like structure in the proximal part of the animal attached to a possible skeleton. Unfortunately, this part of the fossil has been lost. The lateral root-like structures of Martsaphyton are also easier to interpret as indicating a sessile life mode. However, in asexual propagation in modern coronate scyphozoans stolons can be formed (Adler & Jarms 2009). These stolons are attached near the stalk of the polyp (Adler & Jarms 2009) and are somewhat similar to the appendages of Martsaphyton. Stalked echinoderms can attach to the substrate with root-like structures known as cirri (Ruppert et al. 2004, pp. 917-927). Further cirri may occur higher up the stem (Ruppert et al. 2004, pp. 917-927) similarly to the appendages in Martsaphyton. Kozłowski (1968) illustrated and described minute root-like structures near the apex of Conularia which slightly resemble the appendages of Martsaphyton, but are more chaotically arranged, increasing faster in diameter and more variably developed. Alternatively, one can hypothesize that the root-like appendages in Martsaphyton are not attachment structures, but lateral buds similar to those of Sphenothallus sica from the Devonian of Brazil (Van Iten et al. 1992, 2019). Possible lateral buds occur also in Sphenothallus from the Mississippian of Montana, USA (Van Iten et al. 1992). However, the lateral branches in Sphenothallus are oriented towards the aperture, but in Martsaphyton they are slightly tilted towards the apex. The latter orientation does not corroborate the idea that Martsaphyton had lateral buds. On the other hand, Martsaphyton has an apical attachment disc and had no need for additional attachment structures in the form of branches.

If *Martsaphyton* was a sessile invertebrate growing in upright position, it was likely feeding on suspension or plankton-size organisms. *Sphenothallus* and *Torellella* have been affiliated with cnidarians (Van Iten et al. 1992; Vinn 2006) and likely were predators. Both related cnidarians *Sphenothallus* and *Torellella* occur in the early Palaeozoic of Estonia (Öpik 1927; Vinn 2006; Vinn & Kirsimäe 2015). *Sphenothallus* is most common in the Sandbian oil shale and carbonate rocks of northern Estonia and *Torellella* occurs in the upper Cambrian siliciclastic rocks (Vinn 2006).

We interpret the phosphatic lamellae of *Martsaphyton* as an original tube structure. The varying thicknesses of the lamellae and their variable development can be explained by the partial recrystallization of the tube wall during diagenesis. The laterally changing sharpness of boundaries of lamellae suggests diagenetic alternation of the microstructure similarly to the microstructure of *Sphenothallus* (Vinn & Kirsimäe 2015). The diagenetically altered ultrastructure of the phylogenetically closely related *Sphenothallus* and *Torellella* is very similar to that of the

homogeneous ultrastructure of lamellae in Martsaphyton. Nevertheless, Vinn (2006) described unaltered laminae of Torellella as composed of fibres oriented parallel to the longitudinal axis of the tubes. Conulariids are the other phosphatic enidarians presumably related to Martsaphyton; their skeletons are also composed of thin lamellae (Van Iten 1991, 1992; Van Iten et al. 1992). The SEM imaging of sectioned specimens of Conularia and Paraconularia has revealed that their periderm consists of extremely thin (1-3 µm), alternating organic-rich and organic-poor microlamellae (Ford et al. 2016). This is similar to the periderm of Martsaphyton that consists of thin phosphatic lamellae, which are, in places, encrusted with thin carbonaceous material. One could speculate that biomineralization systems of phylogenetically closely related invertebrates were similar and it is likely that Martsaphyton, Sphenothallus, Torellella and conulariids shared a biomineralization system. However, while it is also possible that similar phosphatic skeletons evolved repeatedly, this issue needs a special study.

There were also other phosphatic cnidarians in the early Palaeozoic of Estonia. Conulariids are relatively common in the Upper Ordovician carbonate rocks of northern Estonia (Estonian geocollections database at https://geocollections.info; Vinn et al. 2019). In addition to conulariids, a phosphatic problematicum *Palaenigma wrangeli* (Schmidt 1874) has been described from the Ordovician carbonate rocks of northern Estonia. However, the phylogenetic affinities of the latter fossil have not been recently studied and its relationships to the other tubiculous phosphatic cnidarians are unresolved.

The tubular structure around M. moxi comprises material with elevated levels of certain chemical elements that are not common in carbonate rocks in Estonia, like silica, aluminium, potassium and sodium. This suggests the possible involvement of material of volcanic origin. According to Sturesson & Bauert (1994), volcanic ash layers have been recorded at the same stratigraphical level in Sweden, but no visible indications of contemporaneous volcanic material have been observed in Estonia. The reverse side of the fossil, which is more poorly preserved than the open side, has probably been dissolved/decomposed due to chemical reactions (Figs 6, 7). The tubular structure around the specimen could be interpreted as a zone of diagenetic concentration and crystallization of mobile compounds, which are derived from dissolved volcanogenic components from the surrounding carbonate sediment.

CONCLUSIONS

Martsaphyton moxi gen. et sp. nov. is here identified as a member of the phylum Cnidaria and subphylum Medusozoa, with the class position unspecified. In the O. Tinn et al.: Martsaphyton moxi from the Darriwilian of Estonia

chemical composition and morphology, *M. moxi* can be compared to two other genera of phosphatic cnidarians – *Sphenothallus* Hall 1847 and *Torellella* Holm 1893, which also show tubiculous morphology and lamellar skeleton structure. From the latter, *M. moxi* differs in its unique root-like appendages, widened apertural chamber and lack of the laterally thickened skeleton wall.

The phosphatic lamellae of *Martsaphyton* are interpreted as an original tube structure. The laterally changing sharpness of boundaries of lamellae suggests some diagenetic alternation of the microstructure. *Martsaphyton* was sessile, attached to a hard substrate with a holdfast, probably also assisted by lateral root-like structures.

The rock matrix around the specimen shows a high content of silica, iron, aluminium, potassium and sodium. This suggests the possible involvement of material of volcanic origin.

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Mõistatuslik kõrverakne Martsaphyton moxi gen. et sp. nov. Eesti Darriwilist (Kesk-Ordoviitsium)

Oive Tinn, Olev Vinn ja Leho Ainsaar

Martsaphyton moxi ainsa eksemplari leidis 1925. aastal Põhja-Eestist Martsa paemurrust Viljandi kooliõpetaja Aleksander Moks. Ta andis selle edasi Artur Luhale, kes interpreteeris kummalise kujuga fossiili kui varajast maismaataime. Oma algsel kujul (praeguseks on tükike sellest kaduma läinud) on fossiili kujutatud vaid populaarteaduslikus ajakirjas Eesti Loodus 1967. aastal ilmunud fotol.

Osaliselt on *M. moxi* peidus ümbriskivimis, tervikpildi selle morfoloogiast andis tomograafiskaneering. *M. moxi*'l on õhukestest apatiitsetest lamellidest koosnev kooniline, 8 cm pikkune ja laiemas otsas 25 mm laiune skelett, millest eri kõrgustel harunevad lühikesed juuretaolised jätked. Morfoloogialt ja keemiliselt koostiselt sarnaneb *M. moxi* kõige enam kõrveraksete hulka kuuluvate *Sphenothallus*'e ning *Torellella*'ga, peamiseks erinevuseks on viimastel puuduvad lühikesed juurjad jätked. Eluviisilt võis *M. moxi* olla põhjale kinnituv suspensiooni- või planktonitoiduline.

*M. mox*i eksemplari ümbritsev kivim on ebahariliku keemilise koostisega: suurenenud on Si, Al, K ja Na sisaldus, mis võib viidata vulkaanilise päritoluga materjalile juurdekandele Aseri eal.