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Well-preserved *Rothpletzella* microencruster on a brachiopod shell from the Upper Ordovician of Estonia

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Articles

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Abstract

A single shell of brachiopod *Porambonites wesenbergensis* Teichert, 1930 is encrusted in several places with thin sheets of *Rothpletzella*, tentatively assigned to *R. gotlandica* Wood, 1948, which are preserved as pyritized molds. The spheroidal shape of the pyrite is rare, as is its apparent nucleation on the calcitic walls of *Rothplezella*. Presumably, its calcareous sheaths were coated with organic films that provided substrate for heterogeneous nucleation. Comparable wall-directed nucleation was documented in the Ediacaran *Conotubus*, where pyritization initiates on the tube walls and progresses inward. The same brachiopod is also heavily encrusted by craniids and bryozoans. It is unclear whether the brachiopod *P. wesenbergensis* was encrusted postmortem or during its life.

Non-technical Summary

In a shallow Ordovician sea, the shell of a brachiopod called *Porambonites wesenbergensis* became a host for a variety of smaller organisms, creating a bustling, miniature ecosystem. Some areas of the shell were covered in thin layers of an ancient problematic organism called *Rothpletzella*, preserved as molds. This organism, which harnessed sunlight to produce energy, lived alongside other creatures such as craniid brachiopods and bryozoans, tiny colonial animals that filtered food from the water. In addition, tiny tube-like creatures resembling *Allonema* formed small clusters on the shell. This discovery sheds new light on how diverse life was in ancient communities that grew on hard surfaces, such as shells, during the Ordovician period. It suggests that these communities may have been more complex than scientists originally believed, with different organisms playing various ecological roles. It is still unclear whether these creatures settled on the brachiopod's shell while it was alive or after it died. The *Rothpletzella* and filter feeders did not seem to interfere with each other, as the algae did not compete for the same food as the filter feeders. Instead, the algae likely attracted grazers such as early snails, which may have left marks on the shell as they fed on the *Rothpletzella*.

Introduction

Hard substrates are commonly inhabited by various sclerobionts—organisms that live on or bore into hard surfaces, often using shells of other organisms as substrates (Taylor and Wilson, 2002, 2003). The most common hosts for sclerobionts are typically benthic suspension feeders with biomineralized skeletons, such as brachiopods, pteriomorph bivalves, crinoids, and hyolithids (e.g., Feldman and Brett, 1998; Galle and Parsley, 2005; Głuchowski, 2005; Barclay et al., 2013, 2015; Schneider, 2013; Freeman Peters et al., 2024), as well as stromatoporoids and corals (e.g., Kershaw, 1980; Baird and Brett, 1983; Lebold, 2000). Both living and dead substrates were encrusted with organisms. However, sclerobionts also often colonized mobile organisms, such as echinoids, trilobites, and cephalopods, although these records are less common than compared with immobile substrates (Baird et al., 1989; Brandt, 1996; Taylor and Brett, 1996; Key et al., 2010; Borszcz et al., 2013).

Sclerobionts serve as a valuable tool for paleoecological studies as the communities they form are almost always preserved in situ, providing a unique insight into ancient ecosystems (e.g., Freeman Peters et al., 2024). From the perspective of encrusting organisms, each host acts as a patch or "island," allowing the analysis of individual sclerobiont assemblages on a single host as a community (Brett, 1988). Although already present since the early Cambrian (Palmer, 1982; Brett et al., 1983), many common sclerobiont taxa originated during the Ordovician (Lescinsky, 1996; Ma et al., 2021), during or after the Great Ordovician Biodiversification Event (GOBE). It is essential to understand the evolutionary patterns and ecological distribution of sclerobiont communities during the Ordovician (Freeman Peters et al., 2024) to better comprehend their role in the GOBE. The fossilization potential of encrusting sclerobionts varies depending on whether they possessed mineral skeletons or were lightly mineralized or even entirely soft-bodied. The latter types of taxa were usually not preserved, and when soft-tissue sclerobionts are preserved, it is usually through bioimmuration (Taylor, 1990; Wilson et al., 1994).

One exceptional example concerns *Rothpletzella*. This calcareous microproblematicum has previously been considered either a cyanobacterium or a green alga, although its exact biological affinities remain uncertain (Riding, 1991). *Sphaerocodium*, first described by Rothpletz (1890) from the rocks of Wenlock age from Gotland Island (Sweden), was later identified by Wood (1948) as an intergrowth of *Rothpletzella* and *Wetheredella* (Riding and Fan, 2001, p. 804). During most of its research history, *Rothpletezella* was known exclusively from thin sections where it appeared as calcareous, bifurcating tubular filaments forming flat or undulose sheet-like layers (Zhou and Pratt, 2019; Zatoń and Jarochowska, 2020). Recently, well-preserved three-dimensional *Rothpletzella* sheets encrusting brachiopod shells were discovered from the Upper Devonian of Russia (Zatoń and Jarochowska, 2020). Since then, well-preserved epibiotic *Rothpletzella* have also been found on Middle Devonian corals (Zatoń and Wrzołek, 2020) and brachiopods (Brychcy et al., 2023) from Poland, as well as on Middle Devonian brachiopods from Morocco (Zatoń et al., 2022). These records suggest that *Rothpletzella* may, in fact, be more common as an encruster of different biogenic substrates than previously thought (Zatoń et al., 2022); however, it could have been easily overlooked earlier due to its faint appearance and minute size.

Here we describe older, Upper Ordovician fossils from Estonia, assigned to *Rothpletzella*, and discuss their preservation and paleoecology.

Geological background and locality

During the Late Ordovician, the region that is today northern Estonia was submerged beneath a broad, generally warm, and shallow epicontinental sea. The conodont-based $\delta^{18}O_{phos}$ studies suggest that the pre-Hirnantian Late Ordovician was characterized by a general cooling trend: a rapid climate cooling in the early Sandbian and a less intense cooling in the late Sandbian through the Katian (Männik et al., 2021). This extensive marine environment facilitated the deposition of a remarkably complete stratigraphic sequence, with all Ordovician stages well represented—predominantly by carbonate sedimentary rocks, which reflect the prevailing depositional conditions (Nõlvak, 1997). Throughout this time, the paleocontinent of Baltica experienced a profound climatic and paleogeographic transformation as it gradually migrated from the cool, high southern latitudes toward the equatorial belt (Torsvik and Cocks, 2013). This latitudinal drift ushered in a significant climatic warming, which in turn stimulated an upsurge in carbonate sedimentation—a response typical of tropical marine settings (Nestor and Einasto, 1997).

The onset of these tropical conditions became increasingly evident in the fossil record during the early Katian, marked by the emergence of warm-water faunal elements, such as tabulate corals and stromatoporoids, which are often found in non-reefal settings (Nestor and Einasto, 1997). In northeastern Estonia, the Oandu Regional Stage is particularly notable for its lithological composition, comprising clay-rich limestones and marls associated with the Hirmuse Formation (Hints and Meidla, 1997). These fine-grained sediments were deposited in a deeper part of the carbonate ramp—yet still within the sunlit, photic zone—suggesting a relatively tranquil depositional environment with adequate light penetration to support benthic life. It is within these layers that the large shells of the brachiopod *Porambonites* are found (Nestor and Einasto, 1997).

Rakvere swimming pool (59.34014°N, 26.361601°E) is currently a non-existing historical locality in the town of Rakvere (Fig. 1). The Rakvere outdoor swimming pools were built in 1937, adjacent to Soolikaoja. The swimming pool was excavated in the limestone of the Oandu Regional Stage. From the excavation site, Armin Öpik made a rich collection of fossils that included brachiopods, bryozoans, trilobites, rugosans, and gastropods (Rõõmusoks, 1970). The studied specimen originates from the historical collection of A. Öpik.

Material and methods

Teichert (1930) described the brachiopod *Porambonites wesenbergensis* from an unknown site located in the southeast part of Rakvere. The described specimen originates from the excavation of the Rakvere swimming pool. The Estonian collection material of *Porambonites wesenbergensis* (141 specimens housed at the Natural History Museum, University of Tartu, and 31 specimens housed at Tallinn University of Technology) demonstrates that the species is more common in the sediments of the Oandu Regional Stage (112 specimens). The whole collection was examined, and a single specimen with *Rothpletzella* was found. *P. wesenbergensis* (width 38–50 mm, length 35–50 mm) is a large brachiopod relative to other brachiopod species from the Oandu Regional Stage. They are often encrusted by bryozoans and craniids; their surface may also be bioeroded. Seventy percent of *P. wesenbergensis* specimens are encrusted. As pentamerids have very thin shells (Balthasar et al., 2020), the specimens of *P. wesenbergensis* are quite often damaged. A single, densely encrusted brachiopod specimen from the Oandu Regional Stage (the collection number TUG 1766-136) was selected for a detailed scanning electron microscopy (SEM) study of microencrustation patterns. The specimen was prepared for imaging by coating it with a thin conductive layer of gold and palladium, ensuring optimal surface conductivity and image resolution. SEM analyses were conducted using TESCAN VEGA II and TESCAN VEGA III instruments at the Palaeontological Institute of the Russian Academy of Sciences in Moscow. All micrographs were captured using a backscattered electron (BSE) detector, which enhances compositional contrast and facilitates the visualization of internal structural details. In addition to morphological observations, elemental composition data were obtained using energy dispersive X-ray spectroscopy (EDS/EDX), which utilized the

Figure 1. Locality map with Rakvere shown.

INCA energy system integrated with the SEM platform. This allowed for the qualitative and semi-quantitative analysis of the specimen's elemental constituents, providing essential insights into its mineralogical composition and diagenetic history. Before the SEM examinations, the brachiopod and encrusting faunas were photographed using a Canon EOS 5Dsr digital camera and an apochromatic zoom system (Leica Z16 APO) in the Department of Geology at Tallinn University of Technology.

For comparisons, we also analyzed similar fossils encrusting brachiopod shells from the Middle Devonian of Madéne el Mrakib, eastern Anti-Atlas, Morocco (for details, see Zatoń et al., 2022).

Repository and institutional abbreviation. The specimen is housed at the Natural History Museum, University of Tartu (TUG).

Results

Characteristics of Rothpletzella. The study specimen of *Porambonites wesenbergensis* (Fig. 2) is encrusted in several places with thin sheets that exhibit a fan-shaped morphology (Figs. 3, 4). These fossils form either a single fan or several lobes that usually grow in the same general direction, forming a structure that is several millimeters in diameter. The fans are small, with a maximum width of 0.5 mm, and each individual lobe is typically around 0.2 mm wide. The surface of the lobes displays distinct longitudinal boundaries, which are slightly diverging and run almost parallel to each other, separating them into wider, closely spaced, branch-like structures. The branches are regularly split via bifurcation, creating secondary branches that further divide into two separate structures. These branches are either straight or gently curved, and they gradually widen until the bifurcation point, with maximal widths ranging from 18 to 38 µm. After bifurcation, the width of each branch ranges from 8 to 20 µm. The width of both the bifurcated branches and the single branches that follow the bifurcation shows considerable variation within the same specimen. The angle at which secondary branches emerge from the main branch ranges from 10° to 15°. The fossils are preserved as pyritized replacements of calcite. The EDS analysis reveals a high concentration of iron and sulfur in the branches of the studied specimens (Fig. 5). Pyrite is present in the form of small spheroids (Fig. 3.4).

Other encrusters and bioerosional traces. The large shell of *P. wesenbergensis* hosting *Rothpletzella* is also encrusted by three trepostome bryozoan colonies with sheet-like morphology (Fig. 6.1). In addition, 12 small craniid brachiopods are attached to the host's shell. Eleven of them closely resemble specimens of the genus *Petrocrania* (Fig. 6.2). The surface of the brachiopod shell also contains a single *Trypanites* boring. Several small tubes with a smooth external surface and almost constant diameter form tiny aggregations (Fig. 6.3), somewhat resembling the ascodictyid *Allonema* (see, e.g., Jarochowska et al., 2016). The surface of the *P. wesenbergensis* shell also exhibits multiple tiny and shallow linear scratch marks, tentatively identified as *Radulichnus* (0.4–1.7 mm long and up to 0.26 mm wide; Fig. 6.4). These scratch marks were not observed on the surface of *Rothpletzella.*

Discussion

Affinity of the fossil. The studied fossils closely resemble those previously described from the Upper Devonian and interpreted as *Rothpletzella* (Zatoń and Jarochowska, 2020; Fig. 7). They are also similar to those reported from the Middle Devonian of Poland and Morocco (Zatoń and Wrzołek, 2020; Zatoń et al., 2022; Brychcy et al., 2023). The studied fossils match *Rothpletzella* in terms of size and the general architecture of sheets seen in thin section (i.e., fan shapes, branching; see, e.g., Zhou and Pratt, 2019; Zatoń and Jarochowska, 2020). Like two-dimensional preservations of *Rothpletzella*, its branches are tightly packed, forming a coherent structure rather than loosely arranged filaments or filose growth. The main difference between the Upper Devonian, three-dimensionally preserved specimens and our material is the size of the branches, which are markedly larger in the Devonian specimens (the width of a single branch ranges from 37 to 88 µm). Although the width of the branches in the Middle Devonian specimens from Morocco is also larger (32 to 40 µm), the differences are smaller.

Johnson (1964) systematically compiled morphometric data used to delineate four distinct species within *Rothpletzella.* Among these, a maximum filament diameter of 40 µm was reported for both *R. straeleni* Lecompte, 1936 and *R. gotlandica* Wood, 1948. However, this species-level differentiation based on filament dimensions was later challenged by Riding and Soja (1993), who

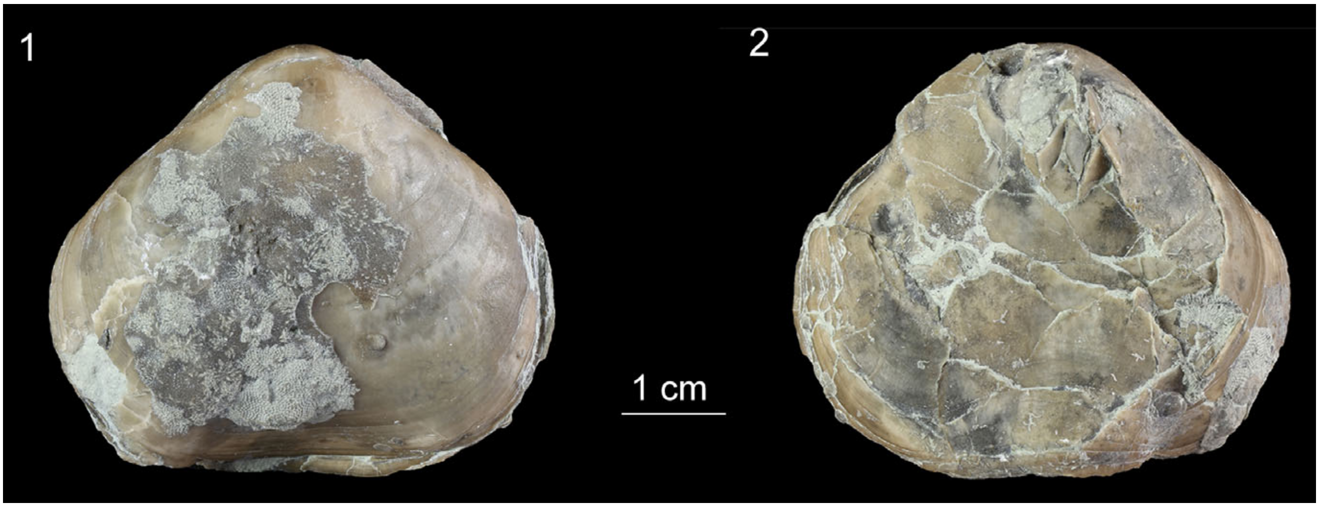

Figure 2. Encrusted *Porambonites wesenbergensis* from the Oandu Regional Stage (lower Katian), Rakvere, northern Estonia (TUG 1766-136). (**1**) Ventral valve with sulcus. (**2**) Dorsal valve with fold.

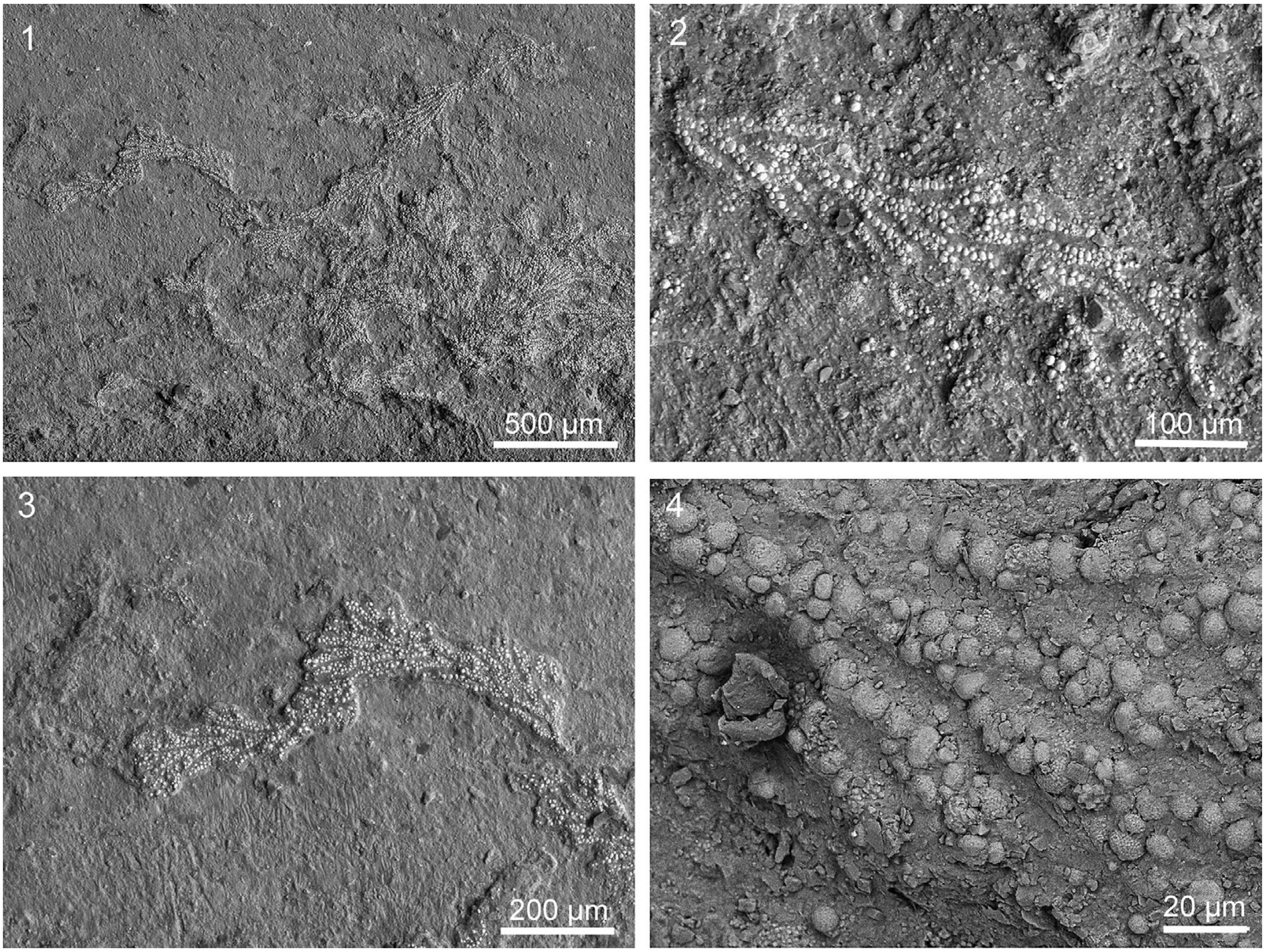

Figure 3. *Rothpletzella gotlandica* from the Oandu Regional Stage (lower Katian), Rakvere, northern Estonia (TUG 1766-136-21). (**1**) General view of the sheet-like encruster. (**2-3**) Detail views of single branches. (**4**) Detail of a branch showing pyrite granules.

analyzed *Rothpletzella* specimens from Silurian deposits in Alaska. Their observations revealed a continuous range of filament widths, spanning from 13 to 37 µm, across specimens previously ascribed to multiple species. As a result, they advocated taxonomic consolidation, assigning all examined material to the type species *R. gotlandica.* Given that the dimensions of our specimens fall comfortably within this range, a tentative assignment to *R. gotlandica* appears justifiable.

The biological affinity of *Rothpletzella* has long been debated (Liu et al., 2016, 2021; Päßler et al., 2018). It is frequently found within cyanobacteria (Zhou and Pratt, 2019; Zatoń and Jarochowska, 2020), yet such classification raises contradictions, especially considering Devonian-aged specimens assigned to the genus. A comparison of the studied material with *Girvanella* is relevant as this calcified microfossil is widely regarded as a filamentous cyanobacterium and is commonly found in Paleozoic carbonates (e.g., Zhou and Pratt, 2019). The filaments of *Girvanella* generally range from 10 to 40 µm in diameter, with most clustered around 20–30 µm (Riding, 1991; Pratt, 2001), which is similar than the dimensions of the studied specimens. To analyze the phylogenetic affinities of *Rothplezella*, one should establish constraints on cyanobacterial cell size. While the upper limit for cyanobacterial cell diameter is observed in *Oscillatoria*—a free-living, non-branching freshwater genus reaching up to 100 µm—most large cyanobacteria, including *Stigonema*, do not exceed 60 µm in diameter (Nielsen, 2006; Schulz-Vogt et al., 2007). Although the dimensions of our specimens are consistent with cyanobacterial limits, their close morphological resemblance to larger forms from the Devonian makes the cyanobacterial affinities problematic. However, the size question cannot be separated from the temporal context. Microbial body sizes in the Ediacaran have often been significantly larger than their Phanerozoic counterparts, reflecting ecological and physiological differences across the Proterozoic–Phanerozoic transition (Knoll et al., 2006; Javaux, 2019). Thus, while Ediacaran microbial fossils include unusually large tubular and spheroidal forms, most Phanerozoic cyanobacteria, including calcified types, exhibit more constrained and typically smaller dimensions.

To address this discrepancy, Zatoń and Jarochowska (2020) proposed that *Rothpletzella* was more plausibly a eukaryotic alga with a phototrophic lifestyle, possibly affiliated with the order Bryopsidales. This hypothesis accommodates both the filament size and the morphological complexity observed across different stratigraphic levels. Intriguingly, a temporal trend emerges in the size of *Rothpletzella* branches: the smallest forms are documented in Upper Ordovician and Silurian deposits (Johnson, 1964; Zatoń and Jarochowska, 2020), while progressively larger sizes are seen in Middle Devonian specimens, culminating in the largest dimensions during the Upper Devonian. By three-dimensional preservation similar to that of the

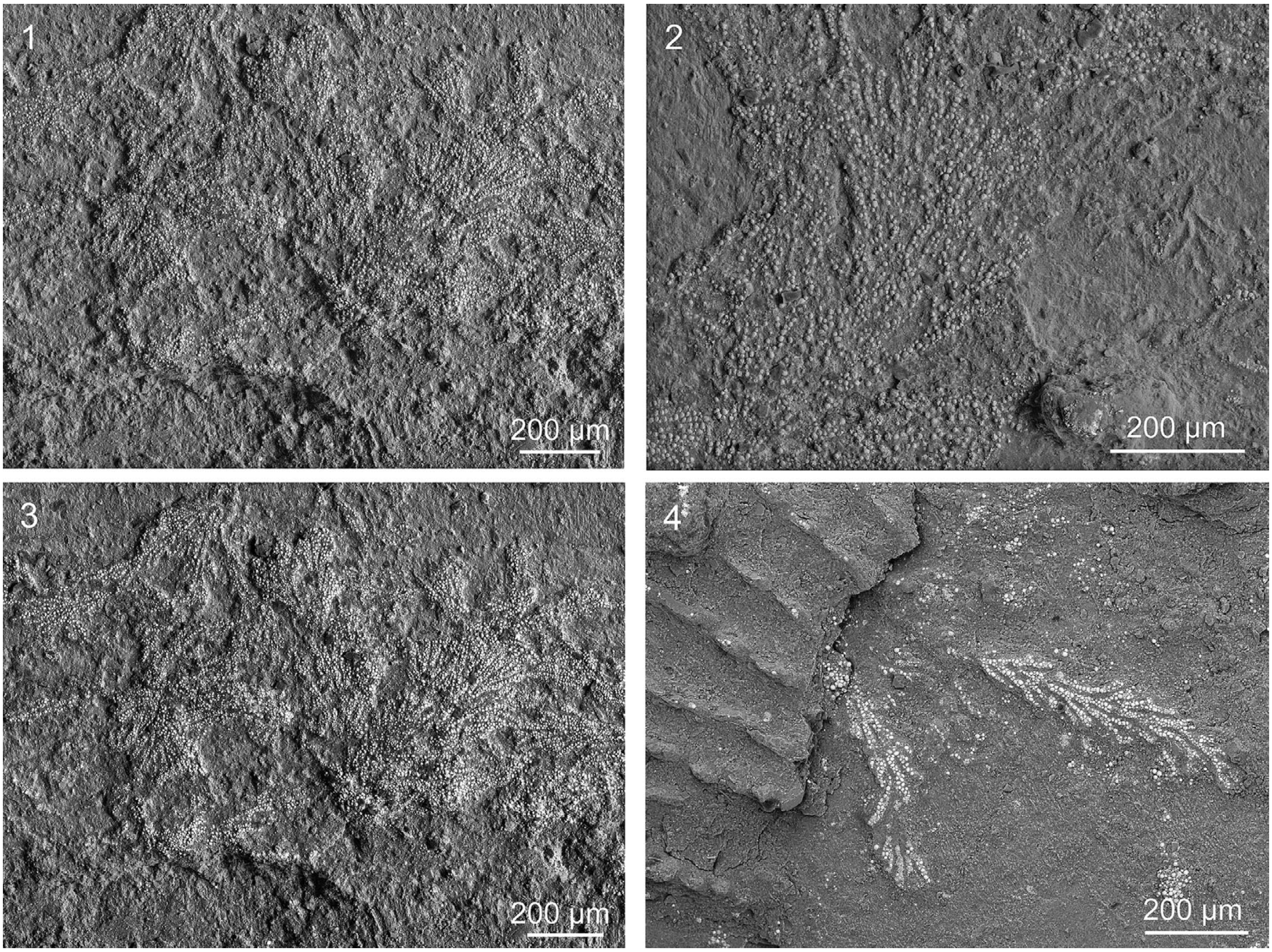

Figure 4. *Rothpletzella gotlandica* from the Oandu Regional Stage (lower Katian), Rakvere, northern Estonia (TUG 1766-136-21). (**1-3**) General views of the sheet-like encrusters. (**4**) Detail view of a single branch.

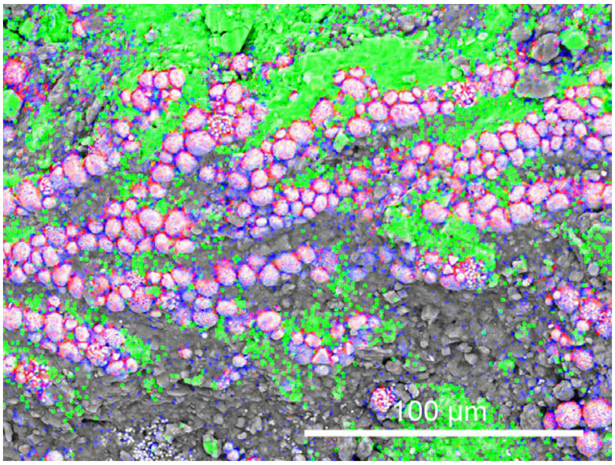

Figure 5. Elemental composition of *Rothpletzella gotlandica* from the Oandu Regional Stage (lower Katian), Rakvere, northern Estonia (TUG 1766-136-21). Green = calcium; red = sulfur; blue = iron.

Upper Devonian large forms, combined with dimensions like those of smaller Ordovician/Silurian representatives of *Rothpletzella*, the studied material provides additional evidence to support the identification of large Upper Devonian forms as *Rothpletzella*. This stratigraphic increase in branch diameter provides further support for the idea that these forms may represent a continuum or a series of closely related but distinct species that have evolved over time (Zatoń and Jarochowska, 2020). Moreover, one would expect the size evolution to proceed in the opposite direction, from larger to smaller, in the case of cyanobacterial affinities of *Rothpletzella*, to fit it into the general evolution of cyanobacteria from large Ediacaran forms to smaller forms in the Phanerozoic.

In conclusion, we admit that since the fossils consist only of the calcareous skeleton, or of pyrite coatings or infillings of this calcareous sheath, they do not provide any definitive information about cellular-level organization. Considering this, available evidence is broadly permissive of either a bacterial or algal affinity, without specifying any group of algae for the latter.

Preservation. Much like the specimens analyzed in this study, previously described *Rothpletzella* specimens from the Upper Devonian strata of Russia exhibit pyritization, as documented by Zatoń and Jarochowska (2020). By contrast, related encrusting forms associated with Middle Devonian rugose corals from Poland are preserved in a distinctly different manner—manifesting as calcareous, thin laminae (Zatoń and Wrzołek, 2020). Similarly, *Rothpletzella*-like encrustations found on Middle Devonian brachiopods from Morocco

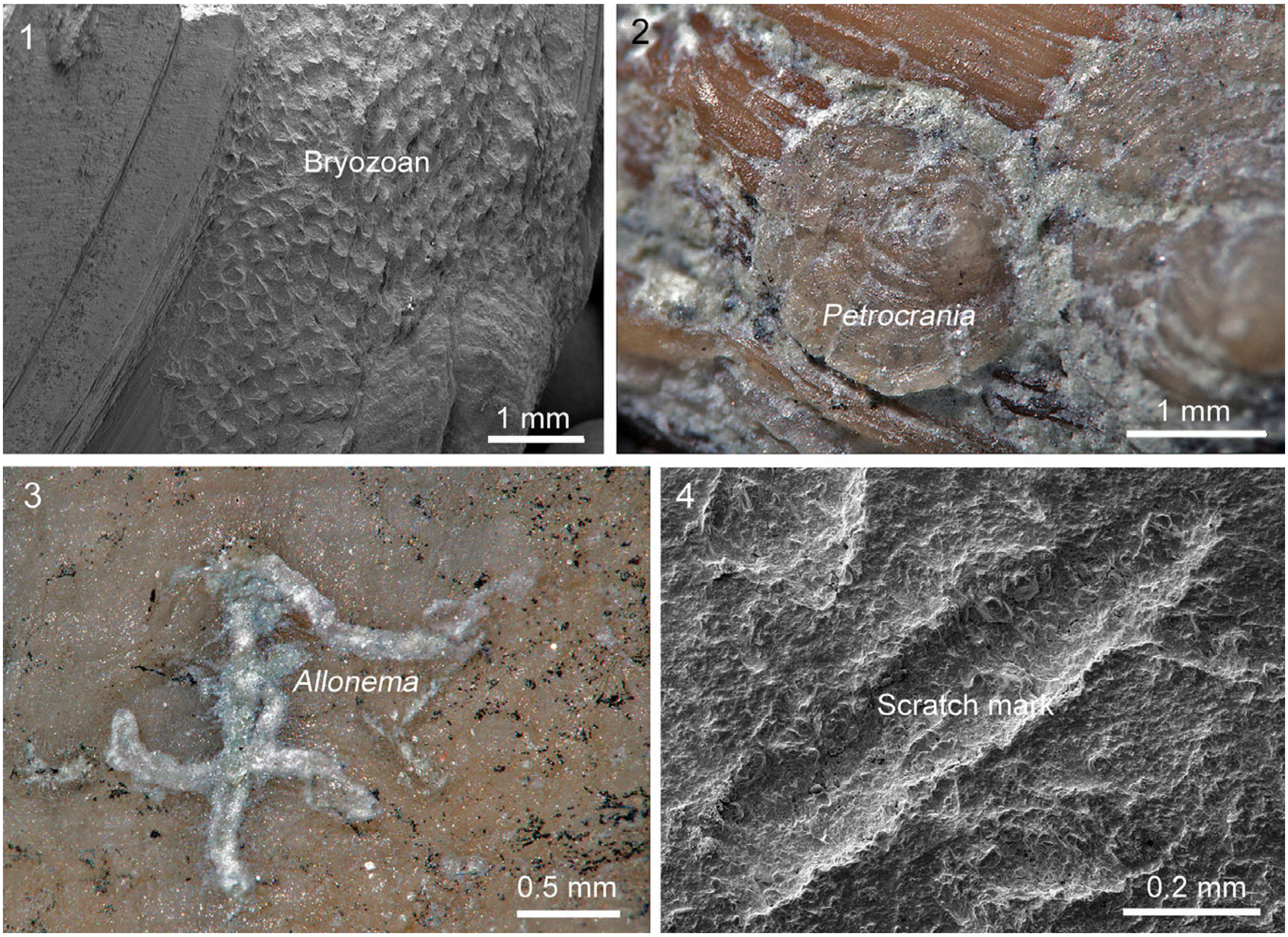

Figure 6. Encrusters on *Porambonites wesenbergensis.* (**1**) Trepostome bryozoan (TUG 1766-136). (**2**) Small *Petrocrania* sp. near a larger *Petrocrania* specimen (TUG 1766-136-4). (**3**) Tubes of *Allonema* sp.(TUG 1766-136-17). (**4**) Scratch marks on the brachiopod exterior (TUG 1766-136).

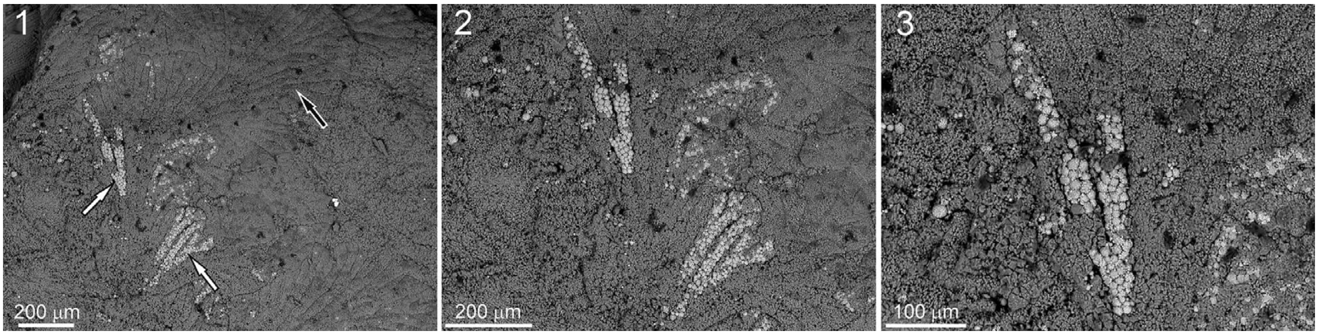

Figure 7. SEM microphotograph of *Rothpletzella* encrusting the Middle Devonian brachiopod shell from Morocco: (**1**) Fan-shaped colony with distinct bifurcation pattern. Some parts are pyritized (white arrows), while the rest of the thalli occur in the form of a calcareous sheath (black arrow). (**2, 3**) Magnified parts of the same colony showing pyritized bifurcating parts within the calcareous sheath.

show a mixed mode of preservation, with both calcareous and pyritized components present within the same specimens (Zatoń et al., 2022; Fig. 6). These variations in taphonomic pathways offer insights into the original biomineralization and post-depositional diagenetic history of these encrusting microorganisms. *Rothpletzella* possessed an originally thin, calcareous sheath, which was susceptible to early diagenetic dissolution, suggesting an original aragonitic or high-magnesium calcitic composition. However, the latter usually loses magnesium during diagenesis rather than suffer dissolution. In depositional settings where early mineralization did not occur or conditions favored dissolution—particularly in environments lacking rapid pyrite formation—these delicate thalli would likely have been poorly preserved or vanished from the fossil record altogether (Zatoń and Jarochowska, 2020).

Pyritization appears to have had a role in the preservation of *Rothpletzella* in certain sedimentary contexts. What is unusual is the spheroidal shape of the pyrite "crystals" and their apparent nucleation on the calcitic walls of *Rothplezella* (Brown, 1996). After the burial of *Rothplezella*, sulfate-reducing bacteria respired organic matter and generated H_2S. Where dissolved Fe^{2+} was available, FeS was formed first and later converted into pyrite (FeS_2) via polysulfide or H_2S pathways (Thiel et al., 2019; Duverger et al., 2020). High supersaturation presumably caused the rapid nucleation of numerous microcrystals, which aggregated into raspberry-like spheroids. Extracellular polymeric substances (EPS) and microbial biofilms likely provided a template that promoted pyrite clustering (Borkow and Babcock, 2003; MacLean et al., 2008). The main question is why the pyrite nucleated on the walls of *Rothpletzella.* Presumably, its calcareous sheaths were coated with organic films that provided substrate for heterogeneous nucleation. Comparable wall-directed nucleation has been documented in the Ediacaran *Conotubus*, where pyritization initiates on the tube walls and progresses inward (Schiffbauer et al., 2014). In semi-closed cavities (i.e., shell interiors), sulfide diffuses outward from decaying organics, while Fe^{2+} diffuses inward from pore waters. Their meeting zone at the wall produces FeS and eventually pyrite. This diffusion–precipitation behavior explains the rim-first mineralization observed in tube fossils and carbonate concretions (Schiffbauer et al., 2014). The seawater was rich in sulfate and reactive iron (Thiel et al., 2019). Moreover, microenvironments within carbonate shells often create reducing "mini-reactors" lined with pyrite (Tomasovych et al., 2021). A high abundance of pyrite-lined shells in the present-day northern Adriatic Sea has been interpreted as limited net exposure of labile tissues to O_2 even when the seafloor is inhabited by abundant burrowing infauna (Tomasovych et al., 2021). There is a similarity between our material and pyrite-lined shells, and we hypothesize that the fossilization of *Rothpletzella* and the formation of pyrite-lined shells took place under similar geochemical conditions. Pyrite spheres have been described from the Devonian black shales of North America (Schieber and Baird, 2001), although the dimensions of these spheres as well as their paleoenvironment differ from those of *Rothpletzella.*

Paleoecology and environment. As mentioned, similarly preserved encrusting *Rothpletzella* specimens as described here have previously been reported so far only from a few Middle and Upper Devonian localities; in the Upper Ordovician, they are described for the first time. However, it is likely that they were not that rare; apart from their low fossilization potential, the fossils were simply overlooked due to their small size. Future studies should investigate the frequency of these encrusters in the Upper Ordovician. The paleoenvironment of our specimens was a shallow epicontinental sea with a soft carbonate mud bottom and depth range within the photic zone. The heavily encrusted shell of the *Porambonites wesenbergensis* reveals a high taxonomic diversity of epibionts. However, it is not clear whether the *P. wesenbergensis* was encrusted postmortem or during its life. The encrusters could represent a co-existing association, but the lack of spatial competition between the organisms makes it impossible to say that all the encrusters were alive at the same time. The phototrophic *Rothpletzella* did not compete with the filter feeders (i.e., brachiopods and bryozoans) for the food, although they may have preoccupied some surfaces. These, however, attracted possible grazers, which likely fed on *Rothpletzella* and left scratch marks on the shell surface, although the direct evidence in the form of *Radulichnus* crossing *Rothpletzella* is lacking.

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Competing interests. The authors declare none.

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