

Problematic tubular fossils from the Portfjeld Formation (Ediacaran) of North Greenland

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Abstract.—Two rare, phosphatized, tubular microfossils of uncertain affinity, probably algal, are described from the Portfjeld biota (Ediacaran) of North Greenland. *Portfjeldia aestatis* n. gen. n. sp. preserves two tubules, one of which branches, within an annulated outer sheath. Its morphology can be compared to that of the much larger *Ramitubus* from the Weng’an biota of South China. An unnamed long, parallel-sided tubule occupied the postmortal cavity formed within diagenetically mineralized specimens of the cyanobacterium *Jiangispirellus*.

Introduction

The Ediacaran Portfjeld Formation in North Greenland (Fig. 1) contains a suite of phosphatized microfossils, including acritarchs and embryo-like forms, comparable to the Doushantuo biota from Weng’an, South China (Willman et al., 2020). The assemblage includes animal-like eggs, embryos, acritarchs, and cyanobacteria, many of which are extremely well preserved. Helically coiled threads assigned to cyanobacteria are conspicuous and were described by Peel (1988).

Simple cylindrical or tube-like fossils are common in the Proterozoic fossil record. Some of them are macroscopic, such as the carbonaceous *Tawuia* Hofmann in Hofmann and Aitken, 1979, and appear early in the Mesoproterozoic (Sun, 1987). Others, such as the mineralized *Cloudina* Germs, 1972, or the carbonaceous *Sabellidites* Yanishevsky, 1926, emerge later, in the Neoproterozoic (Cortijo et al., 2010; Moczyłowska et al., 2014). In addition to macrofossils, many types of rod-like or filamentous microfossils are also preserved in the Ediacaran as compressions (Arvestål and Willman, 2020), sedimentary casts and molds (Becker-Kerber et al., 2021), and silicified or phosphatized replicas (Muscente et al., 2015; Willman et al., 2020, respectively).

Due to their simple morphologies, the phylogenetic affinity of many of these fossils is controversial, with interpretations ranging from colonial bacteria to multicellular algae and to metazoans, often with annelid or cnidarian affinities (Butterfield et al., 1994; Butterfield, 2004; Sharma et al., 2009; Yang et al., 2020). Firm assessment, however, relies on preservation of specific and identifiable traits, and exceptional preservation is therefore the key to our understanding of these groups of simple fossils.

Peel (1988) described well-preserved, annulated, non-branching and helically coiled specimens with a parallel-sided,

sinistral helix as *Jiangispirellus groenlandicus* Peel, 1988 (Fig. 2.1–2.3). Although numerous in the Portfjeld biota, they are usually preserved as fragments, and were interpreted as prokaryotic cyanobacteria by Peel (1988). The spiral threads are naked trichomes and the annulation may be represented both by external molds of the trichome or internal molds showing the constituent cell walls; they lack a covering sheath (Peel, 1988; Peel and Willman, 2022; Fig. 2.1–2.3). *Jiangispirellus* specimens are associated with smooth, non-annulated filaments that were assigned to *Spirellus* Jiang in Luo et al., 1982, in which the enclosing sheath (Fig. 2.4–2.6) was often calcified prior to the diagenetic phosphatization that affects all specimens from the Portfjeld biota (Peel, 1988; Willman et al., 2020; Peel and Willman, 2022).

Here, we describe enigmatic specimens in which annulation comparable to that seen in *Jiangispirellus* is preserved together with prominent internal tubules. In one of these, two tubules are initially present within an outer annulated covering, and one of these subsequently branches such that all three tubules run along the preserved length of the arcuate specimen (Fig. 3.1–3.5; see Fig. 3.6–3.8 and Fig. 4 for poorly preserved specimens that show some, but not all, features described in the best-preserved specimen). In a second specimen, an inner tubule is continuous through several consecutive volutions of the embracing *Jiangispirellus* helix (Fig. 5.1, 5.2). Comparison of the two specimens raises questions concerning their interpretation—in particular if they represent distinct organisms or result from the postmortal occupation of diagenetically formed cavities within mineralized *Jiangispirellus* trichomes (Peel and Willman, 2022).

As far as we are aware, internal tubular structures of this kind have not been reported in known fossil or Recent cyanobacterial morphologies, and such structures are better interpreted as algae (Cunningham et al., 2015). However, Peel and Willman (2022) described numerous thread-like and branching cavity-dwelling organisms of uncertain, likely fungal, origin

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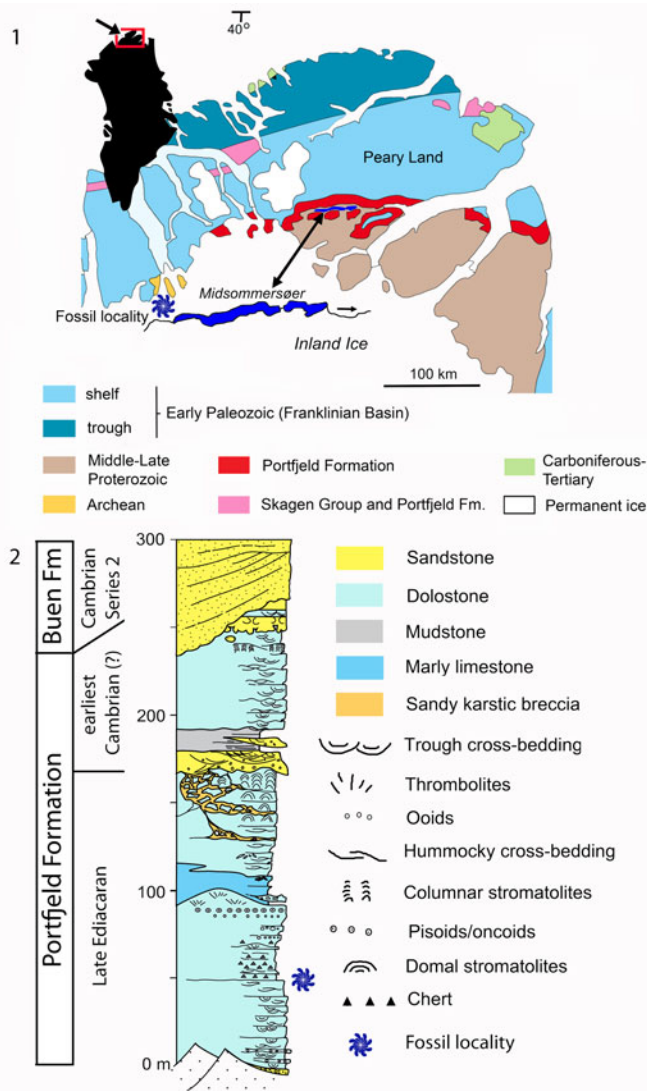


Figure 1. Simplified geological map and lithostratigraphic column of the Portfjeld Formation. (1) Geological map showing the sampling site at the western end of Midsommersøer in North Greenland; (2) lithostratigraphic column through the Portfjeld Formation at eastern Midsommersøer where the fossiliferous horizon is located at a lower level than in the fossil locality at western Midsommersøer (see discussion in text; modified from Willman et al., 2020).

from within postmortal cavities formed within diagenetically mineralized specimens of *Jiangispirellus* derived from the same samples.

Geological setting

The carbonate-dominated Portfjeld Formation in southern areas of North Greenland unconformably overlies Mesoproterozoic sandstones of the Independence Fjord Group and outliers of Neoproterozoic tillites and associated carbonates inferred to be of Marinoan age (Higgins et al., 1991; Søndersholm and Jepsen, 1991; Ineson and Peel, 2011; Willman et al., 2020; Peel and Willman, 2022). The Portfjeld Formation is in turn overlain unconformably by the Buen Formation, consisting mainly of transgressive fluvial to marine-shelf siliciclastic sediments (Fig. 1). The sandstone-dominated lower member of the Buen

Formation yields trace fossils of early Cambrian age (Bryant and Pickerill, 1990), while the mudstone-dominated upper member contains rich faunas of Cambrian Series 2 (Stage 3–4) age (Peel and Willman, 2018; Wallet et al., 2021).

Lithologically, the Portfjeld Formation can be divided into two separate stratigraphic packages that are separated by a widely distributed karstic unconformity (Willman et al., 2020). The lower unit is ~170 m thick and dominated by dolostones. It represents two transgressive-regressive cycles of a carbonate ramp and consists of mid- to outer-ramp hummocky cross-stratified, intraclast-rich, grainstones and cherty dark dolostones and typical inner ramp ooid-pisoid grainstones, with varied microbial facies. The upper package (thickness 70–90 m) records a transgressive succession of fluvial sandstones and mudstones followed by high-energy shallow marine carbonate and siliciclastic facies, truncated upwards by dolines and karstic collapse structures at the boundary between the Portfjeld and Buen formations (Fig. 1).

During the Ediacaran, at the time of the deposition of the lower Portfjeld Formation, North Greenland was part of the geographically isolated paleocontinent Laurentia, estimated to have lain south of the Equator at paleolatitudes of 30–75°S (Li et al., 2013; Zhang et al., 2015; Willman et al., 2020).

Material and methods

Stromatolitic dolostone was collected by J.S. Peel and P. Frykman on 22 July 1978 from ~70 m above the base of the Portfjeld Formation on the north side of Wandel Dal, west of Øvre Midsommersø (82°14'N, 36°06'W; Peel, 1988). The original sample (GGU 271769) from this horizon, described by Peel (1988), and an identical split (GGU 271770), from which all current material was derived, were located by Willman et al. (2020, fig. 2) relative to a measured section to the east, overlooking Nedre Midsommersø, the easternmost of the two lakes comprising Midsommersøer (82°15'N, 33°25'W; Fig. 1.1), where the fossiliferous horizon lies at an equivalent stratigraphic level of ~50 m above the base of the formation where it transgressed the uneven surface beneath. The samples were macerated in weak acetic or formic acid and sieved in fractions down to 50 µm. The residues containing phosphatized microfossils were hand-picked under a binocular microscope. Specimens were mounted on aluminum stubs and imaged under high power using a Zeiss Supra 35VP scanning electron microscope. Images were cropped using Affinity Photo and Affinity Design.

Repositories and institutional abbreviations.—GGU prefix indicates a sample collected during regional mapping campaigns of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland, now Geological Survey of Denmark and Greenland; GEUS) in the Northeast Greenland National Park in compliance with operative conditions for access to, and activities within the park. MGUH indicates a specimen deposited in the paleontological type collection of the Natural History Museum of Denmark, Copenhagen. PMU indicates a specimen deposited in the paleontological type collection of the Museum of Evolution, Uppsala University, Sweden.

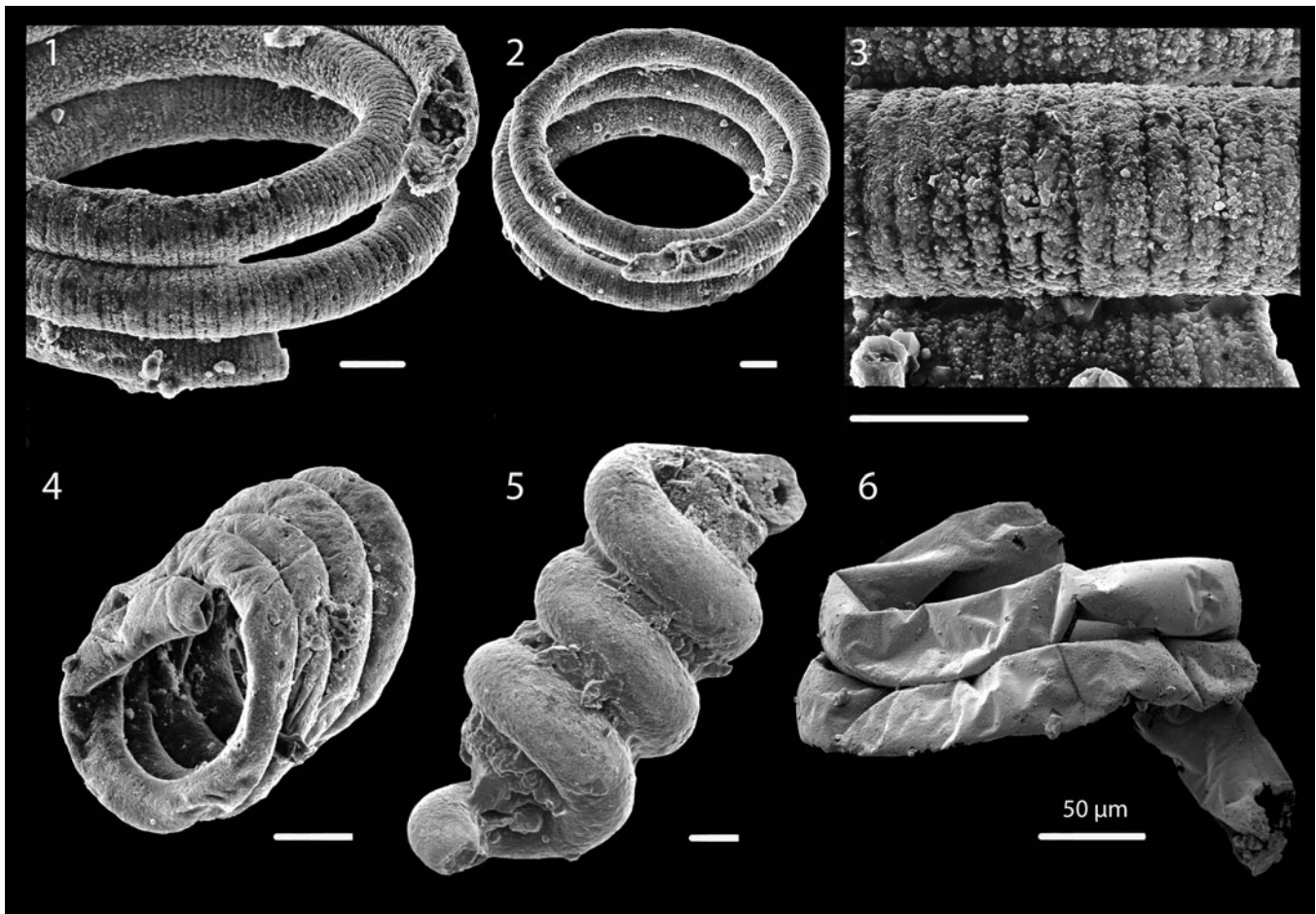


Figure 2. Examples of *Jiangispirellus* and *Spirellus*. (1–3) Holotype of *Jiangispirellus groenlandicus* trichome (MGUH 17.571) described in Peel (1988); (4–6) *Spirellus shankari* (Singh and Shukla, 1981); (4) un-mineralized sheath with slight deformation of the helix (MGUH 17.576); (5) with originally calcified sheath (MGUH 17.582); (6) with degraded un-mineralized sheath (PMU 39236/1). All specimens phosphatized and from GGU sample 271769, except (6), which is from 271770. Scale bar = 50 µm for all specimens.

Systematic paleontology

Incertae sedis

Genus *Portfjeldia* new genus

Type species.—*Portfjeldia aestatis* n. gen. n. sp., by monotypy, from the lower Portfjeld Formation (Ediacaran) of southern Peary Land, North Greenland.

Diagnosis.—As for the type species by monotypy.

Etymology.—After its derivation from the Portfjeld Formation.

Remarks.—*Portfjeldia* n. gen. is distinguished from the parallel-sided helix of *Jiangispirellus* by its shallow crescentic form and the presence of internal tubules. Thus, fragments of *Jiangispirellus* have a tighter curvature than those of *Portfjeldia* n. gen. *Jiangispirellus* is considered to be a trichome with internal transverse partitions interpreted as cell walls (Peel, 1988) that have not been observed in *Portfjeldia* n. gen. The two forms are similar in terms of the dimensions of the annulation on the outer surface.

Portfjeldia n. gen. is morphologically similar to a specimen of the much larger *Ramitubus decrescens* Liu et al., 2008, from the Weng'an biota of South China (Liu et al., 2008, text-fig. 4) where daughter tubules emerge from within an annulated mother tube. The mother tube in *Ramitubus* is compartmentalized by transverse cell walls, but this is neither seen in the illustrated specimen (Liu et al., 2008, text-fig. 4), nor in the tubules of the Chinese specimen or holotype of *Portfjeldia aestatis* n. gen. n. sp. from Greenland (Fig. 3.1). The presence of a compartmentalized mother tube is not demonstrated in the Greenland specimen, but is inferred from the comparison to *Ramitubus* and the addressed annulated outer covering.

Portfjeldia aestatis new species
Figures 3.1–3.5, ?4

Holotype.—PMU 36870/2 from GGU sample 271770, Portfjeld Formation, southern Peary Land.

Diagnosis.—Crescentic, seemingly with 1–3 slender, slowly expanding, tubules contained within an addressed annulated outer covering.

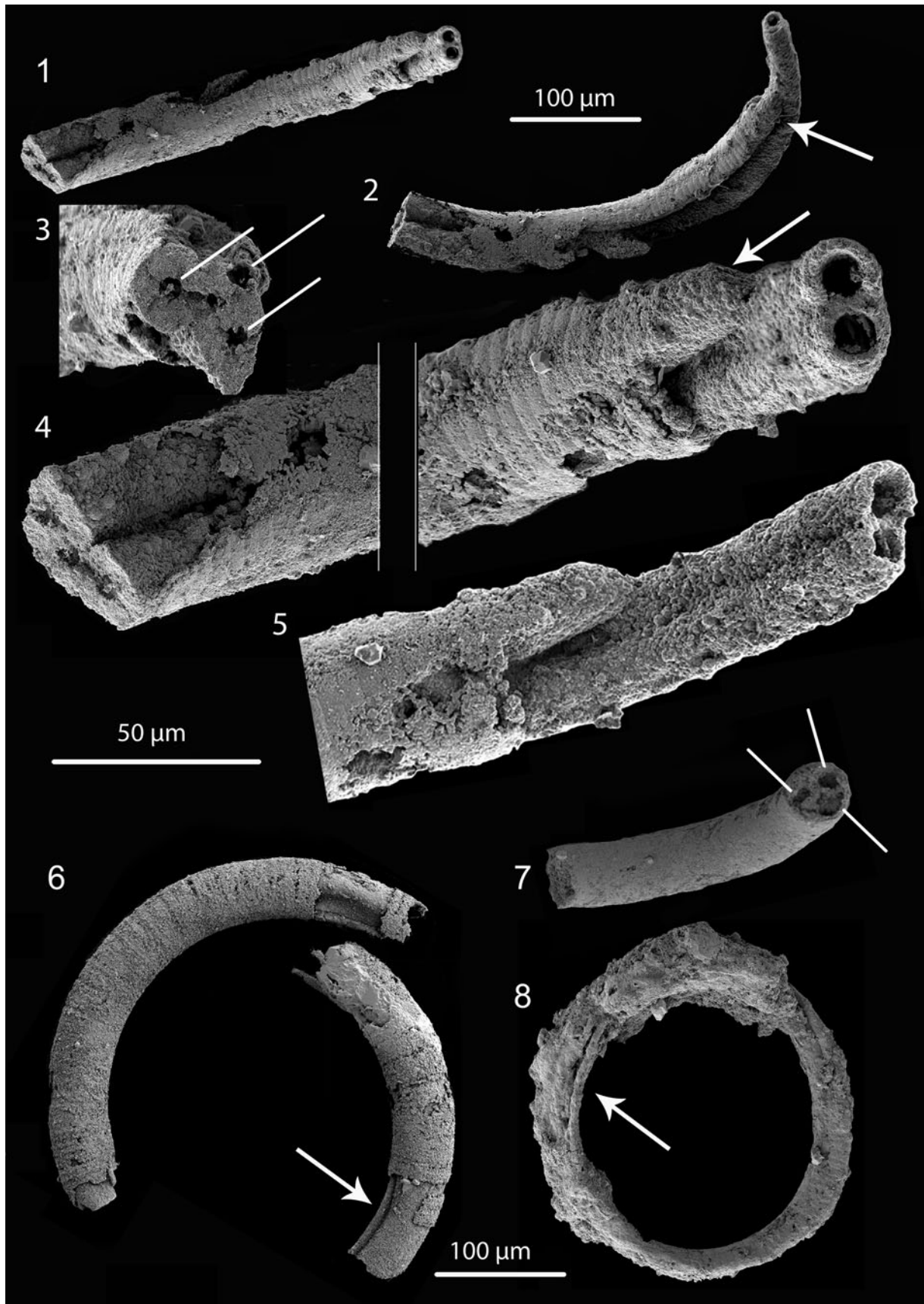


Figure 3. Holotype of *Portfjeldia aestatis* n. gen. n. sp. and other unnamed tubular fossils showing various types of similar internal structures: (1–5) *Portfjeldia aestatis* n. gen. n. sp. (PMU 36870/2) from various viewpoints displaying two tubules interpreted as being originally enclosed by a now partly degraded external sheath; (3) enlargement of lower left of (4) with lines indicating three tubes rather than two, indicating a possible triradial symmetry; arrows in (2) and (4) show possible branching and development of daughter tube; (5) possible third tubule originating as a ridge near the other extremity. (6) Broken tube (PMU 39237/1), possibly related to the problematic spiral tube also described; arrow indicates internal groove also visible in (4). (7) Broken tube (PMU 38168/2) showing three possible tubules indicating a triradial structure (white lines). (8) Single whorl of a degraded, annulated helix with internal tubular structure (arrow) (PMU 36876/4). Scale bar 100 µm for (1, 2, 6–8) and 50 µm for (3–5).

Description.—The holotype and best preserved specimen (Fig. 3.1–3.5) is crescent shaped and consists of an outer tubular covering with a well-developed, annulated, outer surface, but without demonstrated internal compartmentalization. In cross-section the annulated tube is not circular, but shows longitudinal grooves and folds because it is adpressed against the emerging inner tubules (Fig. 3.1), which may indicate it was originally flexible. Inside the tube, two smaller tubules run side by side along the length of the specimen. The two tubules are circular and share a common, now mineralized, wall, creating an external longitudinal groove between them (Fig. 3.2). The presence of a third tubule is suggested by the triradial cross-section at one specimen extremity (Figs. 3.3, 3.4 left), with the tubule originating as a ridge near the other extremity (Fig. 3.4, 3.5). This ridge originates close to the extremity and appears to represent a branch from the adjacent tubule. The specimen as preserved is a fragment ~400 µm long and 45 µm wide. The outer diameter of each tubule is ~20 µm and the internal cavity is 10 µm, but the thickness of the tubule walls reflects diagenetic mineralization rather than the original dimensions. The tubules lack preserved internal structures.

Etymology.—From the Latin *aestas*, meaning summer, reflecting the occurrence near Midsommersøer, the mid-summer lakes.

Remarks.—Several fragments of possible *Jiangispirellus* appear to have some features that are present in *Portfjeldia aestatis*, including similar tubes preserved as a channel impressed into an inner phosphatized layer (Fig. 3.6), possible triradial symmetry (Fig. 3.7), or internal tubules (Fig. 3.8). In addition to the holotype, in which the outer annulated covering is only partly phosphatized, four poorly preserved specimens (Fig. 4.1–4.4) show two tubules that appear to be branched and slightly separated from each other; an outer annulated covering is recognized in only one of these (Fig. 4.4). A single, slightly curved, slender tube, with poorly preserved annulation at its narrow end (Fig. 4.5) may be in place here, leading to the tentative interpretation that 1–3 tubules may be present in *Portfjeldia aestatis* n. gen. n. sp. The shallowly arcuate form of *Portfjeldia aestatis* n. gen. n. sp. is distinct from the parallel-sided, tight, sinistrally coiled helix of *Jiangispirellus groenlandicus*, but evidence of degradation from the helical form characteristic of *Jiangispirellus groenlandicus* is lacking. Furthermore, the external annulated layer in *Portfjeldia aestatis* n. gen. n. sp. is closely molded to the form of the inner tubules (Fig. 3.1), unlike the circular cross-section of *Jiangispirellus groenlandicus*.

When the Portfjeld biota was first described (Peel, 1988), another filamentous fossil, *Spirellus shankari* (Singh and Shukla, 1981), was found co-occurring with *Jiangispirellus*

groenlandicus in the same sample. *Jiangispirellus groenlandicus* is distinguished from *Spirellus shankari* in that the latter has a smooth outer surface considered to represent a filament with an outer sheath (Fig. 2). Peel (1988) considered that the two types were not taphonomic variants. Thus, *Jiangispirellus* was not a *Spirellus* that had lost its external sheath but a separate species, primarily due to the fact that *Spirellus* filaments from the Portfjeld Formation generally have smaller dimensions than *Jiangispirellus groenlandicus*, although these may be greatly increased by carbonate mineralization of the sheath. The integrity of *Jiangispirellus* was recognized by Knoll (1992) and Mankiewicz (1992).

Problematic spiral tube Figure 5.1, 5.2

Description.—A robust parallel-sided, currently phosphatized, un-ornamented tube up to almost 2 mm in length, is of uniform width with an outer diameter of ~20 µm and an internal diameter of ~10 µm. The fossil is located within the parallel-sided sinistrally helix of a postmortally phosphatized specimen of *Jiangispirellus groenlandicus* and can be traced, with a slight interruption due to breakage, through three or four consecutive coils of the helix that are recognized from traces of the inner (adaxial) surface (Fig. 5.1). The tubule is coiled obliquely within the *Jiangispirellus* helical coil such that it translates from the upper part of the first coil (uppermost, as oriented in Fig. 5.1) to the lower part of the final preserved coil (lowermost, as oriented in Fig. 5.1). In the first coil (Fig. 5.2), the annulation of the *Jiangispirellus* trichome persists, and is imposed on the surface of the tubule, while traces of compartmentalization (mineralized cell walls) are retained within the *Jiangispirellus* trichome. The tubule is broken at each end and displays no evidence of branching or internal structure.

Materials.—One well-preserved specimen (PMU 36870/3) and several fragments from GGU sample 271770, Portfjeld Formation, southern Peary Land.

Remarks.—Several fragments of *Jiangispirellus* appear to show similar tubes preserved as a channel impressed into an inner phosphatized layer (Fig. 3.6, see also Fig. 4.1).

The problematic spiral tube differs from *Portfjeldia aestatis* n. gen. n. sp. in being unequivocally located within the tightly coiled, parallel-sided helix of a diagenetically phosphatized specimen of *Jiangispirellus groenlandicus*, although the association with the host is interpreted as being postmortal—a consequence of the nature of the coiling of the tubes within *Jiangispirellus*. Tubules of *Portfjeldia aestatis* n. gen. n. sp. differ in having a low rate of expansion while the problematic tube is

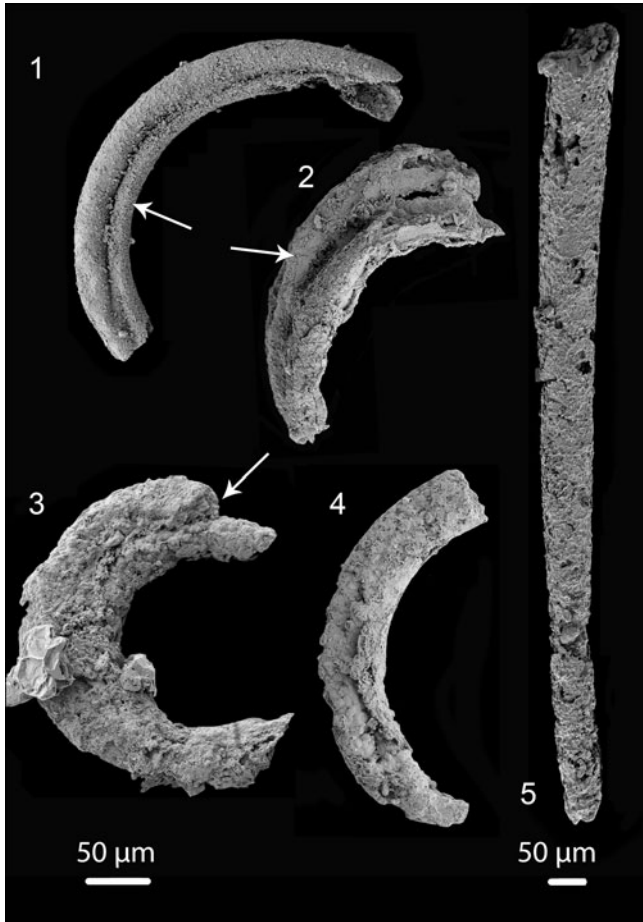


Figure 4. Tentative *Portfjeldia aestatis* n. gen. n. sp. in different states of preservation: (1–3) showing two tubules that appear to be branched and slightly separated from each other (arrows) (1) (PMU 36865/3), (2) (PMU 38169/2); (3) (PMU 36873/3); (4) outer annulated cover casing two tubes (PMU 39238/1); (5) slender slightly curved tube, with poorly preserved annulation at its narrow end (PMU 39239/1). Tentatively this single tube may be placed within *Portfjeldia aestatis* n. gen. n. sp., leading to the suggestion that 1–3 tubules may be present in *Portfjeldia* n. gen. Left scale bar 50 μm for (1–4), right scale bar 50 μm for (5).

parallel-sided. *Portfjeldia aestatis* n. gen. n. sp. has an outer annular covering similar to that of circular coils of the trichome in *Jiangispirellus groenlandicus*, but this is closely adpressed to the tubules (Fig. 3.1), a feature also seen in some specimens of *Ramitubus decrescens* (illustrated by Liu et al., 2008, text-fig. 4). Furthermore, *Portfjeldia aestatis* n. gen. n. sp. differs in its shallow arcuate form from the tight helix of *Jiangispirellus* that accommodates the problematic tube. A taphonomic variant of a problematic, branching, inner tube is seen in Figure 5.3. Secondary phosphatization of a *Jiangispirellus groenlandicus* (Fig. 5.4) shows no internal septa, indicating that the “trichome” might have been hollow, which is similar to the preservation of the problematic spiral tube.

Interpretation of the tubes

Various problematic tube-like structures of micro- to macroscopic size have been reported from different Ediacaran and older terranes worldwide. The phylogenetic affinities of most of these morphologically simple structures are debated, but the

majority of the macroscopic tubes are considered to be metazoan (Liu et al., 2008; but see Cunningham et al., 2017). Some macroscopic tubes (e.g., *Cloudina* Germs, 1972, *Shaanxilithes* Xing, Yue, and Zhang in Xing et al., 1984, and *Sinotubulites* Chen et al., 1981) also may represent the earliest biomineralizing organisms, whereas others, such as *Conotubus* Zhang and Lin in Lin et al., 1986, may be only weakly mineralized (Hua et al., 2007). As a consequence of their novel construction, some of these early tubular organisms are important in our understanding of the earliest metazoans. Generally, however, these stacked, cone-in-cone structures have a diameter normally reaching several millimeters in length (Germs, 1972; Yang et al., 2020), considerably larger than the tubular fossils reported herein. The slightly curved or sinuous, and sometimes branching morphology (Cortijo et al., 2015; Wang et al., 2021) seen in many of the macroscopic tubes is shared with the specimens described here. However, the size differences and overall differences in morphology mean that the biological affinities of the organisms described here should not be directly compared with this group of macroscopic, tubular, and probably mineralized fossils.

Interpretation of the paleobiological affinity of microscopic filamentous structures offers several phylogenetic alternatives. Depending on size and shape, microscopic filaments are usually interpreted as cyanobacteria, algae, or fungi, but it is often challenging to even distinguish between prokaryotic and eukaryotic organisms due to overlap in size and morphology (Knoll et al., 2006). In an attempt to describe different grades of filamentous organisms Butterfield (2009) proposed a set of morphological groups, or body plans: simple uniseriate filaments; simple multi-seriate filaments; simple coenocytic/semi-coenocytic filaments; branched coenocytic/semi-coenocytic filaments; and complex multicellular filaments. These grades represent everything from prokaryotes to multicellular eukaryotes. Consequently, the morphology of the fossils described here must therefore be compared with several different groups before attempting to interpret their affinity.

Affinity to cyanobacteria

Bundled filaments of similar size to the specimens described here, enclosed in a sheath, are known from various fossil cyanobacteria, such as *Microcoleus* Gomont, 1892, and *Schizothrix* Gomont, 1892 (Lee and Golubic, 1998; Castenholz, 2001), and even in sulfur-oxidizing bacteria such as *Thioploca* Lauterborn, 1907 (Teske and Nelson, 2006). Other cyanobacteria, such as *Trichodesmium* Gomont, 1892, or *Subtifloria* Maslov, 1956, a Cambrian calcareous tubular filament with cable-like bundled filaments, can be compared morphologically to our specimen. The bundled filaments in those mentioned are, however, not enclosed within a sheath (Maslov, 1956; Riding, 1991a, b), and therefore not closely related to our specimens.

A collection of three-dimensionally preserved phosphatized fossils described from the latest Ediacaran in Shaanxi Province, China (Min et al., 2020) includes *Subtifloria*. The assemblage was identified as a mixture of (originally calcified) oscillatoriaceans and rivulariaceans, the latter being among the most complex cyanobacteria at the present day. The larger assemblage described from China is similar to the Portfjeld

biota in containing *Obruchevella* Reitlinger, 1948 (Min et al., 2020, fig. 4A, E), which occurs in North Greenland together with the other helical forms, *Jiangispirellus* and *Spirellus* (Peel, 1988), but contains nothing resembling *Portfjeldia aestatis* n. gen. n. sp. More importantly, however, the combination of biomineralized skeletons, algae, cyanobacteria, and possible metazoans in the Chinese and Greenland Ediacaran biotas shows that considerable diversity remains to be discovered in the phosphatized micro-remains.

Modern, more diversified and complex cyanobacteria, such as the Order Nostocales, develop resting cells, called akinetes, from solitary cells towards the end of the vegetative growth period. The akinetes can germinate to form new filaments when conditions improve (Komárek and Johansen, 2015), but unlike the individual structures here, these are often associated with microbial mats. Although complexity is an undefined term, our specimens undoubtedly have a more complex grade of organization than any standard photoautotrophic cyanobacteria, which rules out a relationship with filamentous cyanobacteria. Consequently, if the tubules are part of an integrated organism, the organism does not belong within the cyanobacteria.

Another Recent cyanobacterium, *Blennothrix geneshi* Watanabe and Komárek, 1989 (Oscillatoriaceae), is characterized by the presence of several trichomes in a lamellated sheath in which the trichomes can branch or, rarely, false branch (Jiménez et al., 2005). This construction is similar to that seen in *Portfjeldia aestatis* n. gen. n. sp. However, false branching has annulated filaments within the outer sheath whereas *Portfjeldia* n. gen. displays branching within an outer annulated sheath.

Without the internal problematic spiral tubule, the specimen presented here (Fig. 5.1, 5.2) would be interpreted as a typical fragment of the cyanobacterium *Jiangispirellus groenlandicus* due to the presence of the clear annulations and traces of compartmentalization (Fig. 5.1, 5.2). The problematic spiral tube is, however, clearly a cavity-dwelling organism within the postmortal diagenetic cavity formed by a phosphatized specimen of *Jiangispirellus* (similar to other cavity-dwellers described by Peel and Willman, 2022). While the shape of the problematic spiral tube is comparable to many cyanobacteria, its occurrence within such a closed cavity may hinder its interpretation as a photoautotrophic cyanobacterium.

Affinity to algae

In modern ecosystems, algae are important and diverse components of both marine and terrestrial ecosystems (Stevenson, 2014), and thallus structures can vary from simple and unbranched to complex branching, and from non-motile to motile. Precambrian filamentous eukaryotic algae are usually identified by showing evidence of branching or heteromorphic cells (Butterfield, 2004; Tang et al., 2020) whereas organisms that are small (generally <50 µm, but there is overlap between large cyanobacteria and small algae) and do not show evidence for eukaryotic or multicellular construction are considered to be prokaryotes (cyanobacteria) (Butterfield et al., 1994). Filamentous red algae are probably the most ancient group of algae (1.6 Ga old, sensu Bengtson et al., 2017), but other forms, including the filamentous green algae *Proterocladus* Butterfield

in Butterfield et al., 1994, appear shortly after (1.0 Ga, sensu Tang et al., 2020) and the group diversifies throughout the Neoproterozoic (Butterfield and Rainbird, 1998). It is likely that algae played an important role in the metazoan radiation during the Ediacaran-Cambrian transition primarily due to large primary productivity in shallow epeiric seas, and establishing new ecological tiering (LoDuca et al., 2017).

An algal affinity for the organisms described here is possible, even likely. The possible budding/branching structure in *Portfjeldia aestatis* n. gen. n. sp. (Fig. 3.4) is a typical algal trait, as is the curved, generally tubiform morphology. Filamentous algae can also show annulations similar to the outer structure of the Portfjeld organisms. However, as far as we are aware, structures comparable to the continuous internal tubules within an annulated outer wall are not known from any algal groups. Similarly, the single problematic spiral tube is readily interpreted as an alga.

Affinity to Metazoa

The presence of metazoans in the Ediacaran can be deduced from various complex trace fossils (Budd and Jensen, 2000) or from body fossils, such as the bilaterian *Kimberella* Glaessner and Wade, 1966, although it is well understood that many other components of the biota are difficult to interpret (Seilacher, 1992; Peterson et al., 2003). Nevertheless, mineralized tubular organisms, a construction facilitated by high levels of carbonate saturation, are common in the Ediacaran (Wood et al., 2017). For example, the anabaritids, a group of early skeletal fossils, are globally distributed in strata of Late Precambrian–Cambrian age (Kouchinsky et al., 2009; Zhuravlev et al., 2012). Anabaritids are tubular organisms that grew by apertural accretion and their main morphological feature is a triradial symmetry seen as lobes and grooves (Kouchinsky and Bengtson, 2002). Their biological affinity is uncertain, but points to Cnidaria. A triradial symmetry reminiscent of anabaritids is seen in Figure 3.3, but the triradial symmetry in *Portfjeldia* n. gen. represents three conjoined tubes whereas that in anabaritids is developed within a single tube. Other anabaritids are curved and display transverse sections comparable to our specimen (compare with Devaere et al., 2021, fig. 11G, P).

Wutubus annularis Chen et al., 2014, from the Denying Formation of the Yangtze Gorges area of South China, is an annulated tubular or narrowly conical fossil in which annulae are arranged uniseriably to form an erect benthic organism of unknown phylogenetic affinity (Chen et al., 2014). *Wutubus* is much larger (length 20–180 mm) than the microscopic Portfjeld specimens described here.

Sinocyclocyclicus guizhouensis Xue, Tang, and Yu, 1992, is another tube interpreted as a possible stem cnidarian (Liu et al., 2008), although Cunningham et al. (2015) considered it to be an alga. Some *Sinocyclocyclicus* (Xiao et al., 2000, fig. 2 H, I) are morphologically similar to the fossils described herein.

As with *Ramitubus* Liu et al., 2008, and other forms reviewed by Cunningham et al. (2015), the original probably organic tubes show cross-wall compartmentalization and may be branched but are generally a size order larger than the present

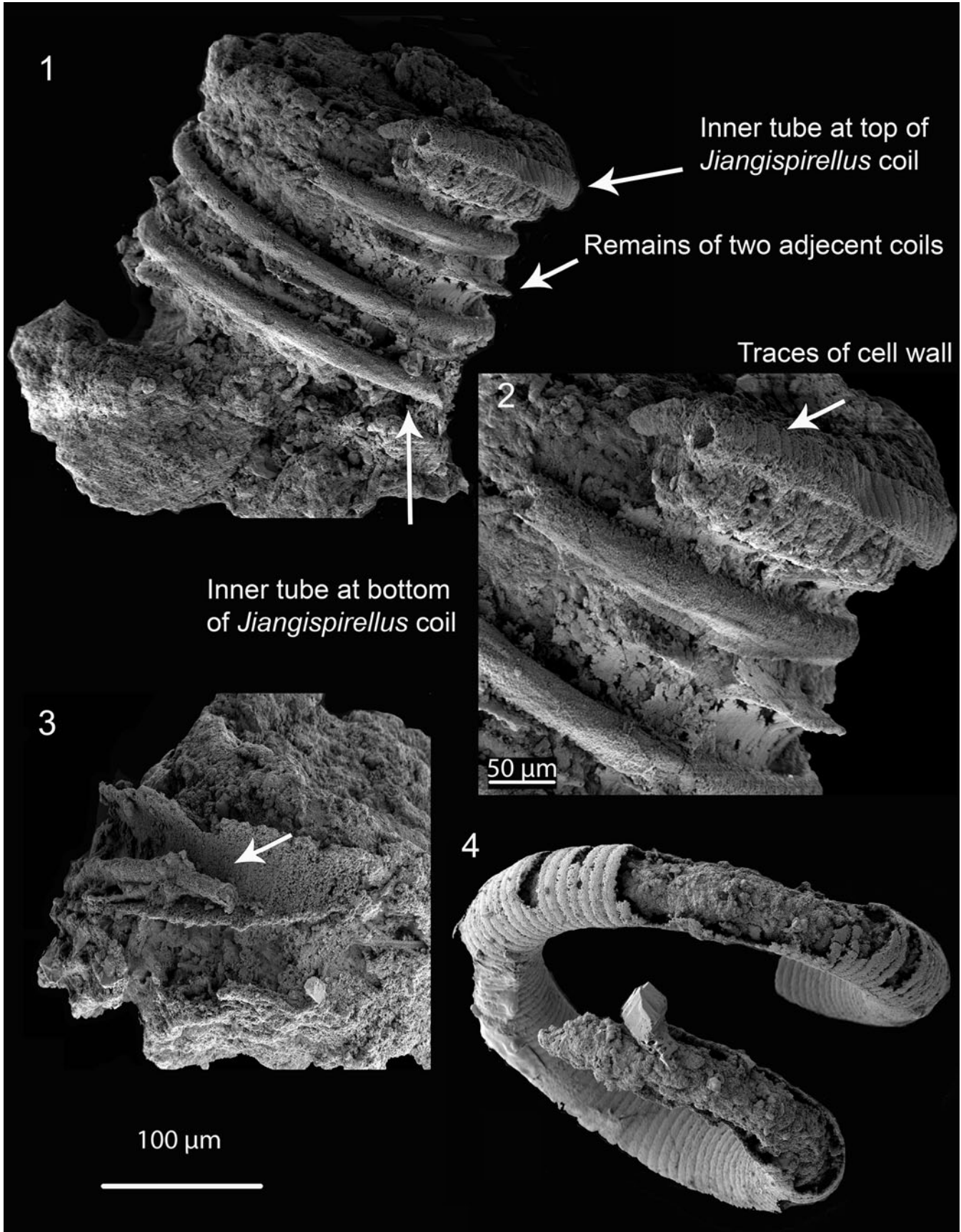


Figure 5. Problematic helically spiraled tubular organism. (1, 2) Preserved as an internal tube inside an outer *Jiangispirellus* “trichome,” showing traces of cell wall (PMU 36870/3); (3) remains of a possible branching organism (arrow) within a “trichome” (PMU 36868/4); (4) preserved “trichome” of *Jiangispirellus groenlandicus* with internal secondary phosphatization (PMU 36874/5). Note that no internal septa are preserved, indicating that the phosphatized “trichome” covered a hollow chamber. Scale bar 100 μm for (1, 3, 4) and 50 μm for (2).

material. However, specimens of *Ramitubus decrescens* (illustrated by Liu et al., 2008, text-fig. 4) show several tubules and an associated outer annulated covering similar to that also present in *Portfjeldia aestatis* n. gen. n. sp. (Fig. 3.4). As mentioned, the metazoan affinities have been questioned and alternative explanations, such as cyanobacteria (*Sinocyclocyclicus*) or algae (*Ramitubus*), are considered more likely (Sun et al., 2019).

Our specimens do not show any evidence of flexible bending or compression, which might indicate that they are actually originally mineralized rather than organic. However, while specimens of *Spirellus* in the Portfjeld biota were often degraded prior to phosphatization (Fig. 2), the co-occurring helices of the naked trichomes of *Jiangispirellus* usually display only minimal deformation.

Other alternatives

The single problematic, spiral, hollow tube is associated with traces of cell walls preserved on the inner surface of the *Jiangispirellus* helix (Fig. 5.2), but there is no direct evidence that it penetrated these walls in life. On the contrary, its migration in consecutive revolutions from the top of the first coil to the bottom in the final coil would not be possible if there were septa separating the cells unless the septa were penetrated. The problematic spiral tube is therefore interpreted as a cavity-dwelling organism occupying the postmortally formed cavity formed within a partially mineralized specimen of *Jiangispirellus groenlandicus*.

If the tubules of *Portfjeldia aestatis* n. gen. n. sp. are not part of an integrated organism such as an alga, they could be interpreted as a cavity-dwelling microorganism (cryptoendolith, sensu Stockfors and Peel, 2005; see discussion of terminology in Peel and Willman, 2022) like the problematic spiral tube, akin to other forms described by Peel and Willman (2022). These organisms inhabit the postmortally formed empty spaces within mineralized skeletons of other organisms or hard substrates. Cavity-dwelling organisms can be representatives of different phyla, such as bacteria, algae, or fungi (Campbell, 1982; Gan et al., 2021; Peel and Willman, 2022), but described cavity-dwelling organisms do not show the level organization seen here. A complex of tubular structures within a specimen of *Jiangispirellus* (Fig. 3.8) is closely similar to cavity-dwelling organisms from the same sample illustrated by Peel and Willman (2022, fig. 3.14). However, unlike most cryptoendoliths, the tubules in the holotype of *Portfjeldia aestatis* n. gen. n. sp. are not thread-like, irregular, or part of a meshwork, but more robust, forming an arcuate bundle of semi-parallel tubules. Their form is therefore interpreted as an original morphological feature, similar to the branching *Ramitubus* illustrated by Liu et al. (2008), and not the result of cavity-dwelling behavior.

The possibility that the tubules of *Portfjeldia aestatis* n. gen. n. sp. and the problematic spiral tube may represent a parasitic infestation, or even some kind of symbiotic relationship, is considered unlikely.

Conclusions

Portfjeldia aestatis n. gen. n. sp. is probably an alga, although its diagenetically mineralized tubules do not preserve internal structures that might indicate a cellular compartmentalization. *Portfjeldia aestatis* n. gen. n. sp. can be compared morphologically with the larger *Ramitubus*, originally described from the Weng’an biota of South China, and may be related, in particular if one accepts the alternative suggestion that *Ramitubus* is an alga. The problematic long, single, slender tubule also lacks preserved internal structures. It occurs in diagenetic cavities formed within postmortally phosphatized specimens of the cyanobacterium *Jiangispirellus groenlandicus*, an environment that likely favors interpretation as an alga rather than a phototrophic cyanobacteria.

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