

Recognizing sponge in *Spongiostroma* Gürich, 1906 from the Mississippian of Belgium

Jeong-Hyun Lee^{1*}  and Robert Riding²

¹Department of Geological Sciences, Chungnam National University, Daejeon 34134, South Korea <jeonghyunlee@cnu.ac.kr>

²Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, TN 37996, USA <rriding@utk.edu>

Abstract.—*Spongiostroma* Gürich, 1906 from the Mississippian of Belgium was initially provisionally placed in Foraminifera and subsequently compared with hydrozoans and microbial carbonates. For nearly 100 years, the term spongiostromate has been widely applied to clotted microbial fabrics in stromatolites and oncolites. Examination of the type material shows that *S. mæandrinum* Gürich, 1906, the type species of *Spongiostroma*, consists of numerous juxtaposed millimetric pillow-like masses permeated by thin anastomose sparry microscopic fibers (vermiform fabric) in fine-grained groundmass, locally traversed by millimetric rounded to elongate partly sediment-filled openings. Here we interpret *S. mæandrinum* to be a lobate sponge composed of mammiform papillae formed by calcified spongin network and traversed by canals and spongocoel. These are typical features of calcified remains of keratosan demosponges. We redescribe and revise *S. mæandrinum* and interpret it as a keratosan demosponge with papilliform morphology. This upholds Gürich's (1906) initial opinion that *Spongiostroma* could be a sponge and supports suggestions that keratosan vermiform fabric has long been confused with microbial carbonate. Since *S. mæandrinum* is not a stromatolite, it is inappropriate to use the term spongiostromate to describe microbial carbonate microfabric.

Introduction

Calcified fossil sponges and microbial carbonates are commonly closely associated in marine limestones (Pitcher, 1964; Albersstadt et al., 1974; Klappa and James, 1980; Fagerstrom, 1987; Desrochers and James, 1989; Wood, 1990; Brunton and Dixon, 1994; Reitner et al., 1995; Neuweiler et al., 1997; Liu et al., 2003; Li et al., 2017; Lee and Riding, 2018) and can be confused with one another (Luo and Reitner, 2016). In some examples, the similarities are superficial, as in the case of Paleozoic stromatoporoid sponges and stromatolites, both of which can form layered domes but are usually readily distinguished by their internal structure since stromatoporoids are characterized by complex calcified skeletons (Stearn, 2015a).

In other cases, distinguishing calcified sponges from microbial carbonates may not be so straightforward. Keratosan demosponges, which are widespread in marine environments at the present day (Maldonado and Young, 1998), provide an instructive example. They lack mineralized spicules and skeletons and rely for support on a flexible spongin network, widely familiar in the bath sponge, *Spongia*. So far as is currently known, the fossil record of calcified remains of keratosaurs appears to be due mainly to syndimentary replacement by CaCO₃ that preserves the delicate spongin framework as a microscopic anastomose network in fine-grained carbonate (Luo and Reitner, 2014). The identity of keratosan spongin preserved as mineralized microscopic sparry network was first recognized by Reitner et al. (2001). Using serial sectioning, Luo and Reitner (2014)

demonstrated the similarity of the three-dimensional architecture of present-day spongin network to that of “putative fossils of keratose demosponges” from the Devonian and Triassic. This led to the realization that Phanerozoic keratosan fossils had probably often been misinterpreted as microbial carbonate (Luo, 2015; Luo and Reitner, 2016) and to the recognition of well-preserved keratosan vermiform fabric (“keratolite”) intercalated within Cambrian–Ordovician stromatolites (Lee and Riding, 2021a, b) and occupying cavities in ~890 Ma reefs (Turner, 2021).

Spongiostroma Gürich, 1906 is one of a number of enigmatic structures, internally patterned by small but complex fabrics, that form layered and domical masses in the lower Carboniferous of Belgium. Despite their name, which refers to their spongy appearance in thin section, Gürich (1906, p. 5, 32) provisionally placed spongiostromides in protozoans (foraminifers). This suggestion was not adopted by subsequent workers who variously compared spongiostromides with hydrozoans (Rothpletz, 1908) and algae (cyanobacteria) (Garwood, 1914; Twenhofel, 1919, p. 340). This led Pia (1927, p. 36) to regard *Spongiostroma* as a stromatolite and to propose the name Spongiostromata to encompass stromatolites and oncolites in general. This approach was popularized by Johnson (1961, p. 204). The outcome was that “spongiostromate” became widely used to describe “laminated, poorly differentiated micritic and peloidal microfabric” in carbonate sediments (Flügel, 2004, p. 373). Consequently, for nearly 100 years, *Spongiostroma* has been widely regarded as a stromatolite.

Here we refigure and redescribe the type material of *Spongiostroma mæandrinum* Gürich, 1906, the type species of *Spongiostroma*. Its pillow-like mesostructure is permeated by

*Corresponding author.

vermiform fabric and contains canal- and spongocoel-like openings. We interpret *S. mæandrinum* as the calcified remains of keratosan demosponge. If so, then *S. mæandrinum* was the first fossil keratosan to be given a name. The second was *Vauxia gracilentia* Walcott, 1920 from the Burgess Shale, originally described as a glass sponge (hexactinellid) (Walcott, 1920) and subsequently reassigned as a keratosan sponge (Rigby, 1986). Vauxiidae includes seven species of *Vauxia* and one species of *Angulosus-pongia*, restricted to the Cambrian Burgess Shale-type fauna (Yang et al., 2017; Luo et al., 2020; Wei et al., 2021). Recently, Luo et al. (2021) suggested archaeocyaths to be hypercalcified keratosan sponges, similar to Recent *Vaceletia* (Wörheide, 2008). Recognition of *Spongiostroma* as a keratosan demosponge (1) enhances recognition of fossil sponges, (2) clarifies longstanding confusion between vermiform fabric and clotted microbial fabrics (Pia, 1927; Johnson, 1961; Flügel, 2004; Kershaw et al., 2021), and (3) qualifies the suggestion that *Spongiostroma* is not a sponge (Neuweiler et al., online preprint).

Materials and methods

Édouard-François Dupont, Director of the Musée royal d’Histoire naturelle in Brussels (currently the Museum of the Royal Belgian Institute of Natural Sciences), from 1868 to 1909, assembled a large collection of “sedimentary and constructed” limestones from the Devonian and Carboniferous of southern Belgium (Gürich, 1906, p. 5). These were prepared for display as large (mostly 20 × 20 cm, some 20 × 40 and 40 × 40 cm) thin sections on plate glass. In 1903 and 1904, Gürich (1906, p. 5), motivated by his discovery of what he thought were Carboniferous (later recognized to be Famennian; Wolniewicz, 2009) stromatoporoids near Krakow, Poland, visited Brussels to study the fabrics in the hundreds of “enormous transparent glass plates” displayed at the Museum. These “giant thin plates” were both a boon and a problem. They reveal large-scale structure, but due to their thickness, probably ~100 µm or more, the microstructure is often indistinct, as Rothpletz (1908, p. 3) noted when comparing them with Silurian fossils. In addition, in some cases (e.g., *Spongiostroma*), the thin sections were only made parallel to bedding.

The specimens described by Gürich (1906) were collected in the area of the river Meuse, ~60 km southeast of Brussels, between Namur and Huy, and south of Huy, and the locations are indicated only very generally by Gürich (1906, p. 10). The type specimen of *S. mæandrinum* was collected from the V2d (uppermost Viséan; see Groessens, 1989, table 2) near Namêche, 9 km east of Namur (Gürich, 1906, p. 41). We were unable to locate *Spongiostroma* in outcrops in this area in 2019. Due to their large size (20 × 20 cm), it is not possible to observe the thin sections of the type material with conventional petrographic microscopes. We photographed thin sections at the museum with a digital camera and microscope (Dino-Lite), using a light box for illumination. Our focus here is *S. mæandrinum*. We have not examined other Spongiostromidae. So far as we are aware, this is the first time the type material of *Spongiostroma* has been refigured.

Repository and institutional abbreviation.—Type material examined in this study is deposited in the Museum of the

Royal Belgian Institute of Natural Sciences (IRSNB), Brussels, Belgium.

Systematic paleontology

Class Demospongiae Sollas, 1885

Order unknown

Family Spongiostromidae Gürich, 1906

Remarks.—Gürich (1906, p. 5) based the Spongiostromidae on samples from the Viséan near Namur, Belgium. He regarded them as “encrusting organisms” that were neither stromatoporoids nor “stromatactides” even though they contained features he regarded as very similar to stromatoporoids. He suggested they might be protozoans (foraminifers): order Spongiostromaceae, family Spongiostromidae (Gürich, 1906, p. 35, 53) and recognized five genera: *Aphrostroma*, *Chondrostroma*, *Malacostroma*, *Pycnostroma* and *Spongiostroma*.

Two groups of present-day sponge are nonspicular (i.e., lacking mineralized spicules) and supported by spongin fibers. These are the subclass Keratosa (orders Dictyoceratida and Dendroceratida) and the order Verongida in the subclass Myxospongiae (Wörheide et al., 2012). Since “most of the taxonomically important features of nonspicular sponges, such as the microscopic structure of the skeletal fibers and the type of choanocyte chambers, are obscured or obliterated by the fossilization process” (Luo and Reitner, 2014, p. 468), it is not possible to confidently assign Spongiostromidae to a specific order within Demospongiae, and we here regard *Spongiostroma*, the type genus of the family Spongiostromidae, as a nonspiculate demosponge (phylum Porifera, class Demospongiae). Luo and Reitner (2014) used “Keratosa” or “keratose sponges” for fossil sponges in the sense of Minchin (1900, p. 153–154), who defined the group as “Demospongiae in which the skeleton consists of fibers of spongin, without ‘proper’ spicules.” In this sense, most verongids could be included in “Keratosa.” Accordingly, we also use Keratosa to indicate the presence of a supportive spongin network. We therefore regard *Spongiostroma* as a keratosan demosponge sensu Minchin (1900).

S. mæandrinum is the type genus and species of the Spongiostromidae. It remains to be seen whether other genera such as *Aphrostroma*, *Chondrostroma*, *Malacostroma*, and *Pycnostroma*, as well as other species of the genus *Spongiostroma*, including *S. bacilliferum* Gürich, 1906, *S. ovuliferum* Gürich, 1906, *S. granulatum* Gürich, 1906, *S. balticum* Rothpletz, 1908, and *S. Holmi* Rothpletz, 1908, are spongiostromides. Some of these fossils in Gürich’s (1906) illustrations resemble imperfectly preserved microbial carbonate.

Genus *Spongiostroma* Gürich, 1906

Type species.—*Spongiostroma mæandrinum* Gürich, 1906

Diagnosis.—As for the type species by monotypy.

Spongiostroma mæandrinum Gürich, 1906
 Figures 1–3

1906 *Spongiostroma mæandrinum* Gürich, p. 41, pl. 6, fig. 1.

Holotype.—Museum of the Royal Belgian Institute of Natural Sciences (plaque 229) (IRSNB a 11037).

Diagnosis.—Millimetric, irregularly rounded, pillow-shaped juxtaposed papillae, consisting of thin anastomose sparry microscopic network in fine-grained groundmass (vermiform fabric); with sporadic round to stellate canals and locally traversed by rounded elongate curved spongocoels.

Occurrence.—Uppermost Visean (V2d), Namêche, Belgium. Exact locality unknown.

Description.—Horizontal section of clusters of irregularly rounded to amalgamate lobes (~5–15 cm) in peloidal to intraclastic micritic matrix. Each lobe consists of numerous juxtaposed subrounded polygonal to irregular rounded pillow-shaped papillae, ~1–10 mm (typically ~3–5 mm) across, outlined and bounded by diffuse sinuous, locally discontinuous, borders of darker micritic peloidal sediment up to ~200–500 µm wide. Papillae consist of a sparry network of irregularly anastomose fibers (vermiform fabric), mainly 25–45 µm wide and with branch internode distances mainly between 50–120 µm (Fig. 4) in generally micritic groundmass, locally patterned by faint and irregularly diffuse 30–50 µm size darker micritic bodies. Papillae locally contain rounded to stellate, locally branched, sparite-filled canals, 200–800 µm across, and are occasionally traversed by larger rounded curvilinear areas (spongocoel) ~1 mm wide, filled by peloidal sediment.

Remarks.—Gürich (1906, p. 41) described *Spongiostroma mæandrinum* as follows: “Le tissu est relativement homogène et compact. Les granulations descendent jusqu’à 1/20 m et mesurent, en moyenne, 1/15 mm. Les canaux du tissu ont environ 1/40 mm. de diamètre. Dans le plan de la coupe, ils forment des dessins allongés ou ramifiés, en forme de couronnes ou de lignes brisées, constituant, en certains endroits, un réseau à mailles plus serrées et rappelant le tissu des Éponges. Les canaux coloniaux ne sont, ni nombreux, ni grands; très souvent des canaux coloniaux, d’environ 1/15 mm de diamètre, montrent une disposition circulaire.” (The fabric is relatively homogeneous and compact. The granules go down to about 1/20 m [authors’ comment: this appears to be a mistake for mm] and measure, on average, 1/15 mm. The tissue canals are about 1/40 mm in diameter. In the plane of the section, they form elongated or branched patterns, in the form of crowns or broken lines, constituting, in certain places, a tight network reminiscent of the fabric of sponges. The colonial canals are neither numerous nor large; very often the colonial canals, about 1/15 mm in diameter, show a circular arrangement.) Gürich (1906, p. 41, 54) emphasized that the type specimen of *S. mæandrinum* is a horizontal section.

Two fabric features emphasized by Gürich (1906) are “granulations” and “canaux du tissu.” The faintly patterned groundmass (“granulations” of Gürich, 1906, p. 40), barely

discernible in Figure 3.5, 3.6, might reflect initial soft-tissue degradation by bacteria such as sulfate reducers (Luo and Reitner, 2014). They could also be an artifact of the relatively thick (maybe >100 µm) section that likely contains superimposed sparitic fibers. Further work is required to resolve this question. Here we consider the “canaux du tissu” (tissue canals) to be vermiform fabric and interpret them as calcified remains of keratosan spongin network (Luo and Reitner, 2014). Opaque material prominent between lobes and along their margins in the type specimen (Fig. 1), and locally between papillae (Figs. 2.1, 2.3, 2.4, 3.3), is probably diagenetic kerogen. Yellow areas (Fig. 1) are aged resin used in section preparation.

In *S. mæandrinum*, in addition to “canaux du tissu,” Gürich (1906, p. 41) described “canaux coloniaux,” respectively ~25 and ~67 µm in diameter. Our measurements of the type specimen do not distinguish these and instead indicate that these vermiform fabric fibers are mainly 25–45 µm in width, within an overall size range of 10–110 µm (Fig. 4.1). These data can be compared with fibers that display more consistent width in other Mississippian examples, ~20 µm (Luo and Reitner, 2016), and in Ordovician examples, 35–50 µm (Park et al., 2015). Fibers with similarly uneven diameters occur in earliest Triassic examples (Wu et al., 2022, fig. 7). We therefore suggest that there is only a single population of “canals” in *S. mæandrinum*, representing vermiform fabric that was locally influenced by diagenetic enlargement, as Walter (1972, p. 12) observed. Nonetheless, we cannot exclude the possibility that these fibers might also reflect the size and shape of the original spongin network.

Gürich (1906) did not mention the pillow-shaped mammiform papillae, and his single illustration (Gürich, 1906, pl. 6, fig. 1; Fig. 2.2) does not show them clearly, but they are evident elsewhere in the same section of the type specimen (Figs. 1, 2). We interpret *S. mæandrinum* as a lobate keratosan sponge composed of juxtaposed mammiform papillae in which adjacent papillae merge or are separated by diffuse and discontinuous peloidal micrite borders. We therefore regard the pervasive vermiform fabric of the papillae, evident in the type specimen (Figs. 2.2, 3.1, 3.5), as the calcified remains of spongin network; papillae are locally traversed by sediment-filled spongocoel (central cavities) (Figs. 2.5, 2.6, 3.2) and possibly by smaller canal systems preserved as rounded to stellate and branched spar-filled tubes (Figs. 2.4, 2.5, 3.2, 3.4). We infer that sediment-filled spongocoels were probably open to the exterior, whereas spar-filled canals were more isolated within the interior of the papillae.

Since the type specimen of *S. mæandrinum* is a horizontal thin section (Gürich, 1906, p. 41, 54), it does not show layering, and it is unclear whether the original sample was layered. The specimens assembled and prepared by Dupont were examined as thin sections by Gürich in the Museum (Gürich, 1906, p. 2). During a brief visit to Namur, Gürich (1906, p. 10) noted that he “found Spongiostromides in the quarries immediately to the north of Namur, at many points, from Saint-Antoine, above Herbatte, to Grands-Malades station.” There is no indication that he visited the type locality of *S. mæandrinum* at Namêche.

Discussion

There is a long history of confusion between fossil calcified sponges and microbial carbonates. Stromatoporoids provide a

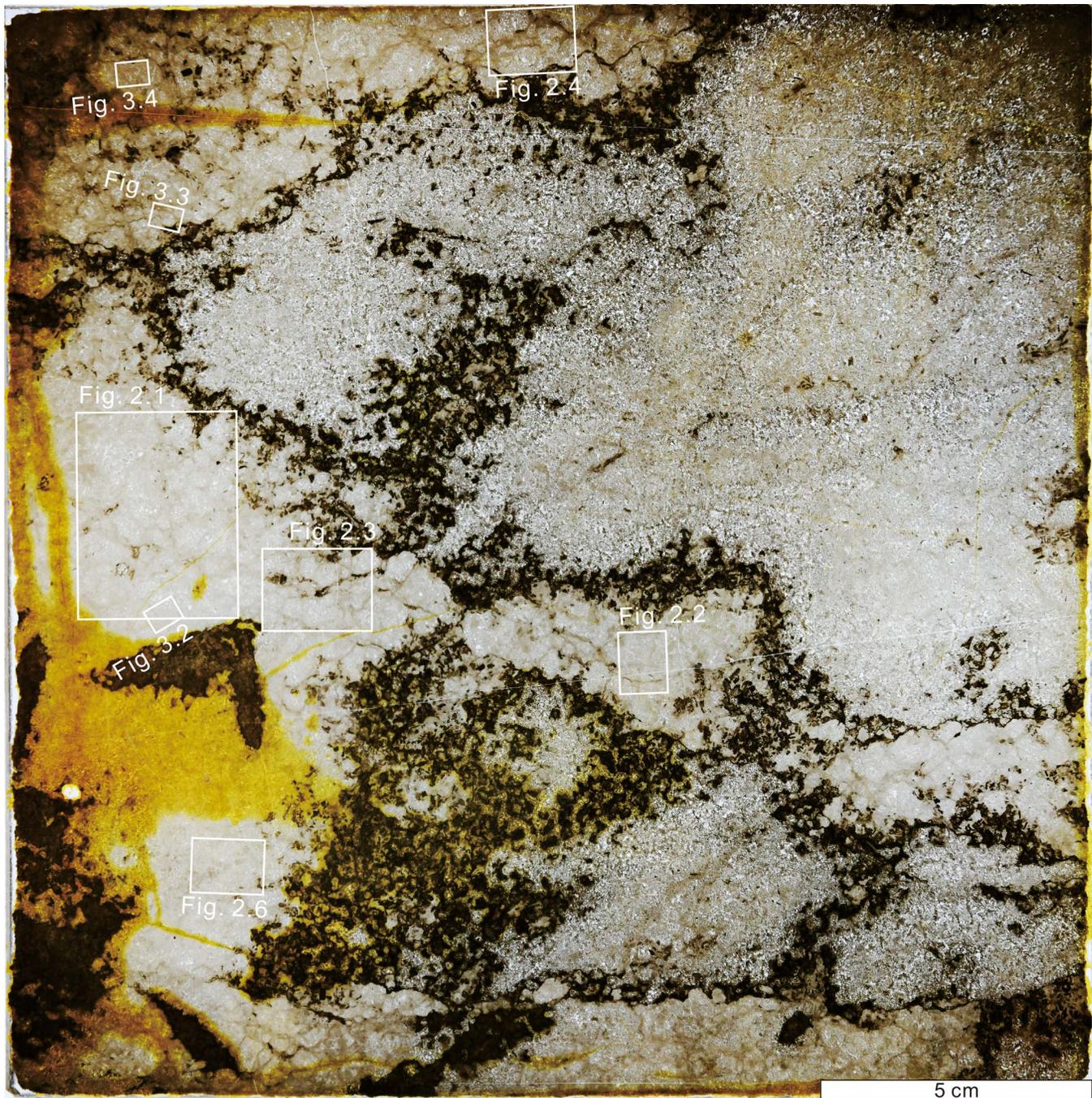
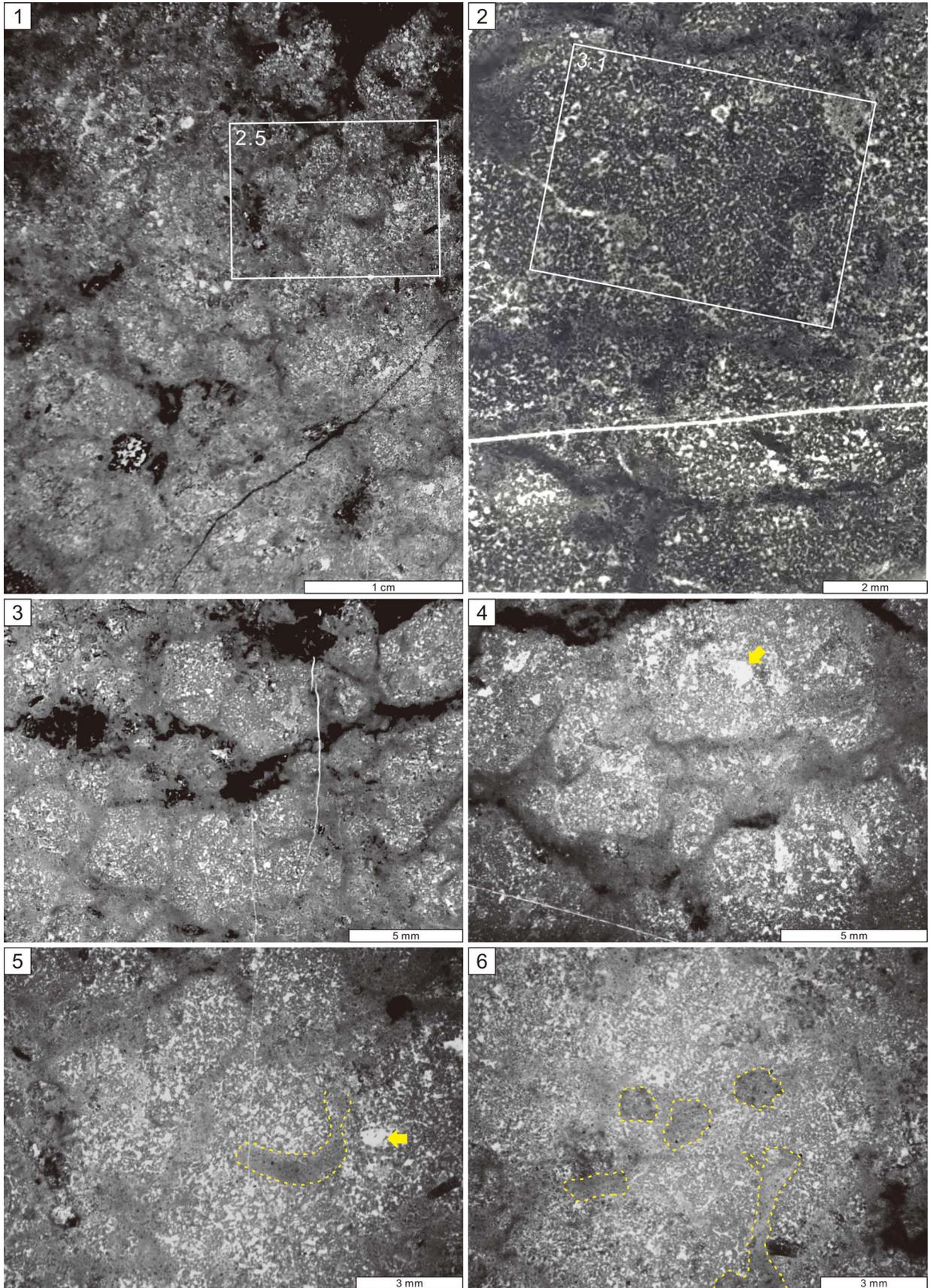


Figure 1. Type specimen of *Spongiostroma maendrinum* (stored at the Museum of Natural Sciences of Belgium, IRSNB a 11037). The lighter areas, bounded by opaque material (possibly diagenetic kerogen), are locally sufficiently well preserved (e.g., top left, center left) to reveal the rounded to ovoid outlines of numerous juxtaposed millimetric pillow-like masses (interpreted as papillae) that constitute larger (≥ 5 cm) sponge lobes within carbonate sediment. Yellow areas are aged resin used in section preparation. White boxes indicate the areas shown in subsequent figures.

classic example. These major components of mid-Paleozoic reefs are now widely regarded as calcified sponges comparable to coralline sponges (Stearn, 1972, 2015b). However, their ability to form laminated calcareous layers and domes led to early comparisons with stromatolites (Fenton and Fenton, 1937; Galloway and St. Jean, 1955; Kaźmierczak, 1980). In some cases, sponge versus stromatolite affinities of Ordovician domical fossils continue to be debated (Keller and Flügel, 1996; Stearn et al., 1999, p. 23), but these uncertainties are usually resolved

by distinct differences in internal structure since stromatoporoids often preserve skeletal elements such as laminae and pillars (Stearn et al., 1999; Stearn, 2015a), whereas stromatolite microfabrics are largely characterized by clotted and porostromate fabrics and trapped grains (Pia, 1927; Flügel, 2004, p. 373). By contrast, the differences between calcified remains of keratosan sponge fossils and microbial carbonates have taken much longer to recognize. Calcified keratosaurs are characterized by microscopic anastomose fibers that represent the outlines of



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Figure 2. Photomicrographs of *Spongiostroma mæandrinum*. (1, 2) General views showing numerous juxtaposed millimetric pillow-like masses (interpreted as papillae). (2) Reproduction of Gürich (1906, pl. 6, fig. 1). (3, 4) Closely juxtaposed papillae of differing size and shape, with darker interspaces occupied by micritic sediment, locally with opaque material. Contacts between papillae range from arcuate to linear. (5, 6) Details of papillae containing round to elongate areas filled with peloidal packstone (yellow dotted lines), interpreted as possible spongocoels. Rounded spar-filled areas (arrowed) in (4, 5) may represent canals.

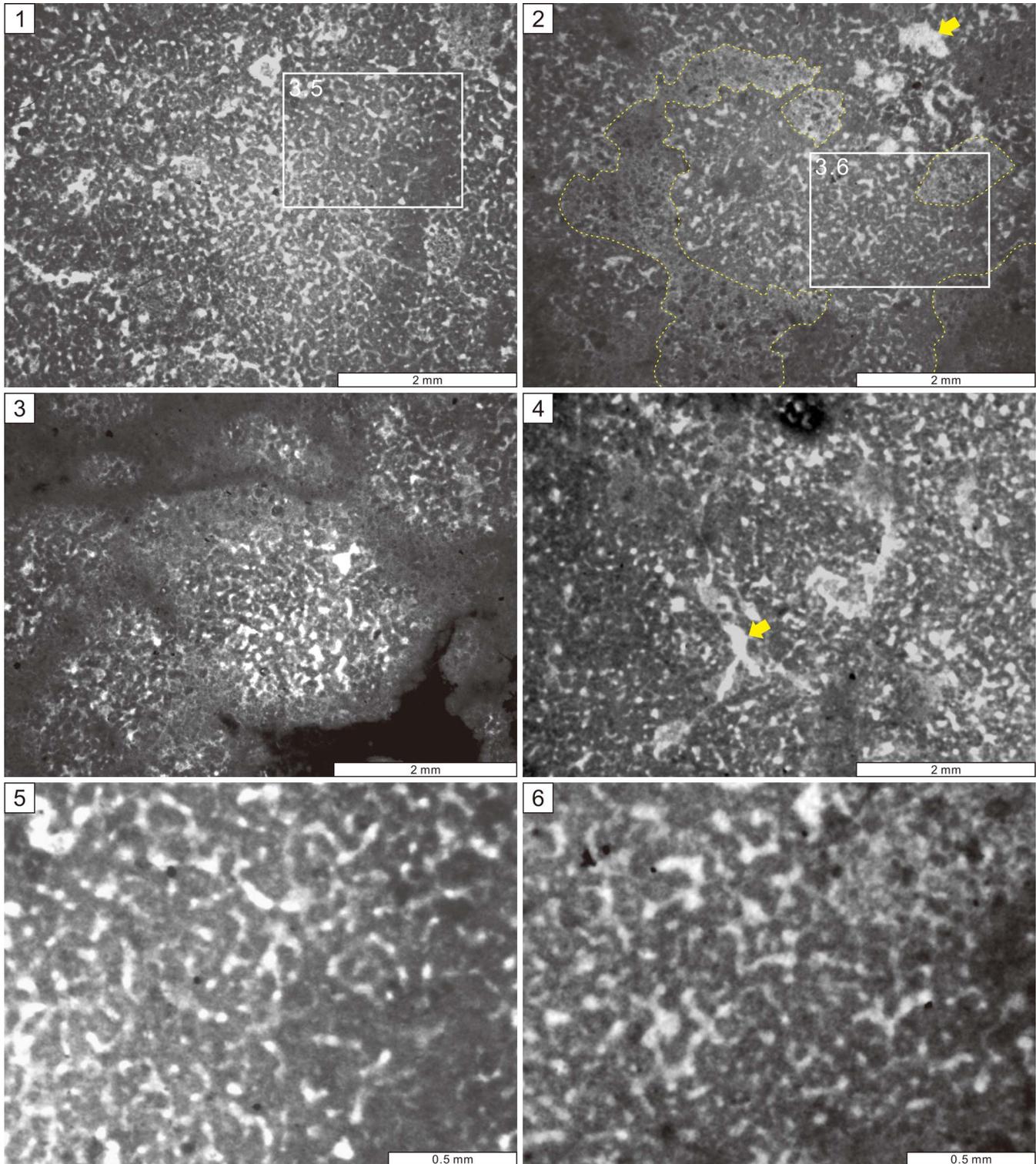


Figure 3. (1) Detail of Figure 2.2 showing that the area figured by Gürich (1906, pl. 6, fig. 1) is dominated by coarse (probably neomorphically enlarged) vermiform fabric. (2) Sediment-filled areas interpreted as possible spongocoels are outlined by yellow lines. Arrow indicates spar-filled area interpreted as a canal. (3) Examples of small papillae of varied size and shape bounded by thin darker micritic areas. (4) Branching structure (arrowed), possibly a canal, traversing vermiform fabric. (5, 6) Details of vermiform fabric, showing characteristic network. The fibers are variably, probably neomorphically, enlarged.

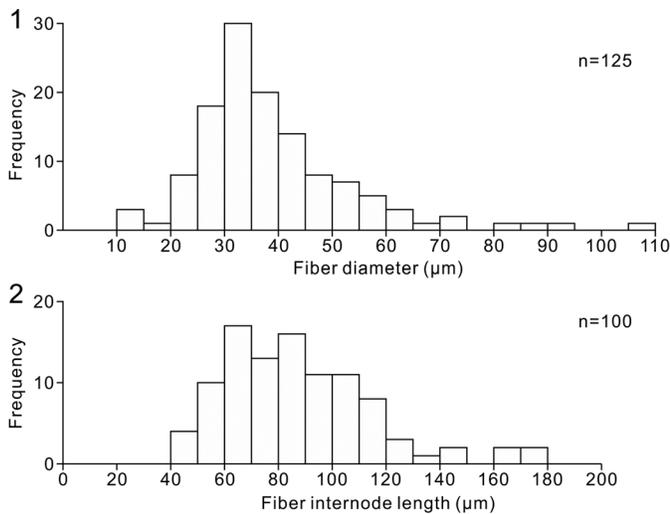


Figure 4. Vermiform fiber dimensions measured from Figure 3.6. (1) Histogram of vermiform fiber widths. (2) Histogram of vermiform fiber network internode distance.

original spongin skeletal network. This “vermiform” fabric was initially interpreted as algal in origin (Walter, 1972), and keratosan sponges were often misidentified as microbial until this fabric was recognized as spongin network (Reitner et al., 2001; Luo and Reitner, 2014).

Spongiostroma as a foraminifer or hydrozoan.—*Spongiostroma*, together with other encrusting, locally domical, genera (*Aphrostroma*, *Pycnostroma*, *Chondrostroma*, *Malacostroma*), was described by Gürich (1906, 1907) from Mississippian limestones of Belgium. Gürich (1906, p. 35) emphasized their layered spongy fabrics “traversé, sans aucune régularité, par des canaux plus fins ... et par des canaux plus larges” (traversed without any regularity by narrow and wider canals). He realized that they were neither stromatoporoids nor “stromatactides” and placed them in new taxa: the family Spongiostromidæ under the order Spongiostromaceae (Gürich, 1906, p. 32). He recognized spicule-like structures in *Pycnostroma* (Gürich, 1906, pl. 6, fig. 2) (we note that these resemble originally siliceous demosponge spicules that are now disarticulated) but decided that they were canals. Gürich (1906, 1907) seriously considered the possibility that *Spongiostroma* could be a sponge, but he was unable to identify the body cavity. Consequently, he provisionally referred the Spongiostromaceae as a whole to the Protozoa (foraminifers). He explained his reasoning as follows: “D’autre part, le système général des canaux clairs du tissu montre, en certains endroits, un aspect rappelant la structure des Spongiaires. La masse claire de calcite serait, alors, le squelette de l’éponge, et la masse trouble, les indications de la substance organique. Mais, alors, les espaces pour la cavité du corps manqueraient. Ce n’est que chez les Protozoaires qu’on peut attendre aussi peu de régularité dans la distribution du squelette, et je propose, à cause de cela, de placer, provisoirement, le groupe entier des Spongiostromacés parmi les Protozoaires, ou ils représenteraient un ordre special” (On the other hand, the general system of the clear canals of the tissue shows, in certain places, an aspect reminiscent of the structure of sponges. The mass of clear calcite

would then be the skeleton of the sponge, and the cloudy mass an indication of the organic material. But, then, the spaces for the cavity of the body would be missing. It is only in the Protozoa that one can expect so little regularity in the distribution of the skeleton, and because of this, I propose to provisionally place the entire group of Spongiostromaceae among the Protozoa, where they represent a special order) (Gürich, 1906, p. 32). This comparison may have been encouraged by Dawson’s (1865, 1876) foraminifer interpretation of Neoproterozoic *Eozoön* from Québec, Canada, most specimens of which have since been interpreted as inorganic (O’Brien, 1970; Hofmann, 1971; Adelman, 2007).

Gürich’s (1906) comparison of Spongiostromidæ with protozoans was not accepted by subsequent researchers. Rothpletz (1908, p. 3–4) described oncolid-like nodules from the Silurian of Gotland, Sweden. In addition to *Girvanella* and *Solenopora*, he observed a fossil broadly resembling calcareous algae, sponges, and hydrozoans that he was unable to identify until he read Gürich (1906). Consequently, in addition to *Solenopora* and *Sphaerocodium*, Rothpletz (1908, p. 17) recognized two new species of *Spongiostroma*. He placed them in the hydrozoans, noting that the nodules they form are “easily confused with those of *Sphaerocodium* and *Solenopora*” but that in detail they lack both the radial-fibrous structure of *Solenopora* and the delicate filaments typical of *Sphaerocodium*. Rothpletz’s (1908, pls. 5, 6) illustrations of these fossils (*Spongiostroma balticum* and *S. holmi*) show complex chambered and/or tubiform fabrics. These fabrics do not closely resemble those of *S. mæandrinum*, although they could be similar to some of the other spongiostromides described by Gürich (1906). Rothpletz (1913, pl. 7, fig. 3) again figured *Spongiostroma* with *Sphaerocodium* (*Rothpletzella*) from the Silurian of Gotland and continued to regard it as a hydrozoan. The magnification of this illustration is too low to resolve the details.

Spongiostromata as cyanobacteria.—Garwood (1914, p. 269) described Gürich’s (1906) suggestion of a protozoan (foraminifer) affinity for *Spongiostroma* as “decidedly speculative,” adding “the features which he selects for the subdivision of the different forms into genera and species are very indefinite.” Garwood (1914) broadly compared “*Spongiostroma*” with fabrics in crusts and nodules associated with *Aphralysia* and *Ortonella* in a lower Carboniferous “Algal Layer” in northern England. He figured a specimen attributed to *Spongiostroma* cf. *Malacostroma concentricum* (Garwood, 1914, pl. 21, fig. 1) that he suggested (Garwood, 1914, p. 271) could be “a flocculent precipitate of carbonate of lime.” Similarly, Twenhofel (1919, p. 3439) considered *Spongiostroma*, together with *Cryptozoön*, to be algal (cyanobacterial).

Pia (1927, p. 36–37) regarded *Spongiostroma* as a stromatolite and created the Spongiostromata as an overarching term to encompass “Stromatolithi” and “Oncolithi.” He categorized Spongiostromata as calcified cyanobacterial (thallophyte) deposits that in general “show no clear organic structure, but often characteristic growth-forms.” This approach was adopted by Johnson (1942, 1946, 1951, 1961, 1963), who placed stromatolite-like forms in the family or “section” Spongiostromata under Cyanophyta. Johnson (1951, p. 29) wrote: “Pia erected this family to include the great number of fossils

which form spongy colonies of molds of algal threads.” Commenting on Spongiostromata and stromatolites, Johnson (1961, p. 204) noted that “the two terms have become more or less synonymous.” adding “These fossils show no clear or usable microstructure.” Monty (1977, p. 16) regarded spongiostromids as stromatolitic, and “spongiostromate microstructures” as “cryptalgal” (Monty, 1981, p. 2).

Spongiostromate and clotted fabric.—Stromatolites (Kalkowsky, 1908) can be described according to their internal layering and external shape (“form genera and form-species,” Fenton and Fenton, 1933; Semikhatov and Raaben, 2000), as well as with respect to their microfibrils (Pia, 1927). Both approaches have long been employed in stromatolite description, with “spongiostromate” (Johnson, 1963) widely used to broadly describe common microfibrils. Hofmann (1978, p. 572) wrote: “The two independent and fundamentally different concepts associated with stromatoliteology since the beginning of this century are the spongiostrome concept of Gürich (1906) and the stromatolite concept of Kalkowsky (1908). Spongiostromid ‘genera’ (and ‘species’) were defined on the basis of microstructure (see Gürich (1906), pp. 53–55; (1907), pp. 137, 138), whereas stromatolite ‘genera’ (Pia, 1927, p. 37) were based on gross morphology and lamina shape.” Pratt (1982, p. 1216) described “clotted, spongiiform microstructure consisting of often indistinct, silt-sized micrite peloids separated by interparticle and tiny fenestral pores.” Flügel (2004, p. 373) stated: “Spongiostromate refers to a laminated, poorly differentiated micritic and peloidal microfabric.” Spongiostromate continues to be used in this sense (e.g., Martindale et al., 2015; Vennin et al., 2019; Bosence and Gallois, 2022; Claussen et al., 2022), although “grumous” has been recommended as the preferred term (Grey and Awramik, 2020, p. 213, 224). This latter term, derived from “structure grumeleuse” (clotted structure), was originally used to describe Mississippian limestones by Cayeux (1935, p. 271) as “many little clots of an extremely finely crystalline calcite, standing out as dark grey in a matrix of colourless granular calcite” (Bathurst, 1976, p. 511). Cayeux (1935, p. 271) suggested that it was a product of incomplete recrystallization. However, as noted by Bathurst (1976, p. 512–513), other interpretations are possible and need to consider that “Structure grumeleuse is common in algal stromatolites.”

Whereas vermiform fabric is relatively uniform, clotted fabric can show more variation. Clotted structure (structure grumeleuse) and clotted peloidal fabric are characterized by merging of micrite patches (Bathurst, 1976, fig. 350) and can be described as “irregular micritic peloidal aggregates surrounded and traversed by microspar” (Riding and Tomás, 2006, p. 23, fig. 7). These “peloidal aggregates” are characterized by a wide size range (~5–70 µm) and varied density of peloid spacing (Riding and Tomás, 2006), in contrast to vermiform fabric with spar-filled areas of more regular width (Figs. 3.5, 3.6, 4). Clotted fabric has long broadly been suggested to be a product of bacterial calcification (Kaisin, 1925; Chafetz, 1986, fig. 3; Riding, 2000, p. 187). Our recognition of vermiform fabric, canals, and other openings in the type specimen support recent suggestions (Lee and Hong, 2019, fig. 6a; Lee and Riding, 2021b, table 1) that *Spongiostroma* could be a keratosan sponge. If this is correct, then it would be inappropriate and confusing to

continue to use “spongiostromate” to describe clotted-peloidal fabrics in stromatolites and other microbial carbonates.

Vermiform fabric and keratosan spongin network.—Describing Cambrian fossils that he considered to be the stromatolites *Madiganites mawsoni* and *Ilicta composita*, Walter (1972, p. 82) noted a distinctive microfabric that he named vermiform microstructure: “It consists of narrow, sinuous areas of sparry carbonate surrounded by darker, usually finer-grained, carbonate. In the known examples the sparry patches are less than 100 µ wide and reach a millimetre or more in length” (Walter, 1972, p. 24). He interpreted vermiform fabric as the remains of filamentous algae: “The filaments responsible for the vermiform microstructure were coarse, about 30–60 µ wide. Although the vermiform structures are unusually coarse for blue-green algae, they are finer than the coarsest extant blue-greens. They are comparable in size to the small filamentous red and green algae” (Walter, 1972, p. 87). Vermiform fabric has since been recognized as the calcified outlines of the originally proteinaceous spongin network of keratosan sponges (Reitner et al., 2001; Luo and Reitner, 2014, 2016, p. 565; Lee and Riding, 2021a, b). Well-preserved examples of vermiform fabric show that, unlike algal filaments, it is anastomose, i.e., interconnected (Luo and Reitner, 2014; Lee and Riding, 2021b, fig. 8c). Further work is required to discover whether *Madiganites* and *Ilicta* are keratosan sponges or, perhaps, as in the example of *Cryptozoön* (Lee and Riding, 2021a), interlayered keratosan and microbial carbonate.

Walter (1972, p. 12) noted that vermiform microstructure is readily obscured by recrystallization: “With slight alteration it forms a grumous microstructure.” This could help account for Pia’s (1927) creation of the term “Spongiostromata” to encompass stromatolites and oncolites composed of a wide range of micritic–sparitic fabrics that he described as showing “no clear organic structure” (Pia, 1927, p. 36). As observed in *Spongiostroma*, enlargement—presumably diagenetic—of vermiform fabric fibers is likely to have increased their width (Fig. 4). This may have contributed to the development of micritic areas that locally appear to be surrounded by interconnected sparry fenestrae (Fig. 3.5, 3.6). This supports Walter’s (1972) observation that diagenetic alteration can both modify and obscure vermiform fabric.

Fossil keratosan macrostructure.—Recognition of well-preserved vermiform fabric is a testament to the ability of the outlines of delicate organic fabrics to be preserved in carbonate sediments throughout the Phanerozoic and longer (Luo and Reitner, 2016; Turner, 2021). However, for a long time, failure to recognize other macro-features of fossil calcified keratosaurs hindered their identification, and reliance on vermiform fabric alone has led to uncertainty (Kershaw et al., 2021; Neuweiler et al., online preprint).

Spongiostroma exemplifies the difficulties encountered by early researchers in endeavoring to distinguish calcified fossils of sponges from foraminifers, hydrozoans, and microbial carbonates, even though—as we show here—*S. mæandrinum* appears to preserve not only vermiform microfabric but also macrostructural sponge features such as canals and spongocoel, as well as

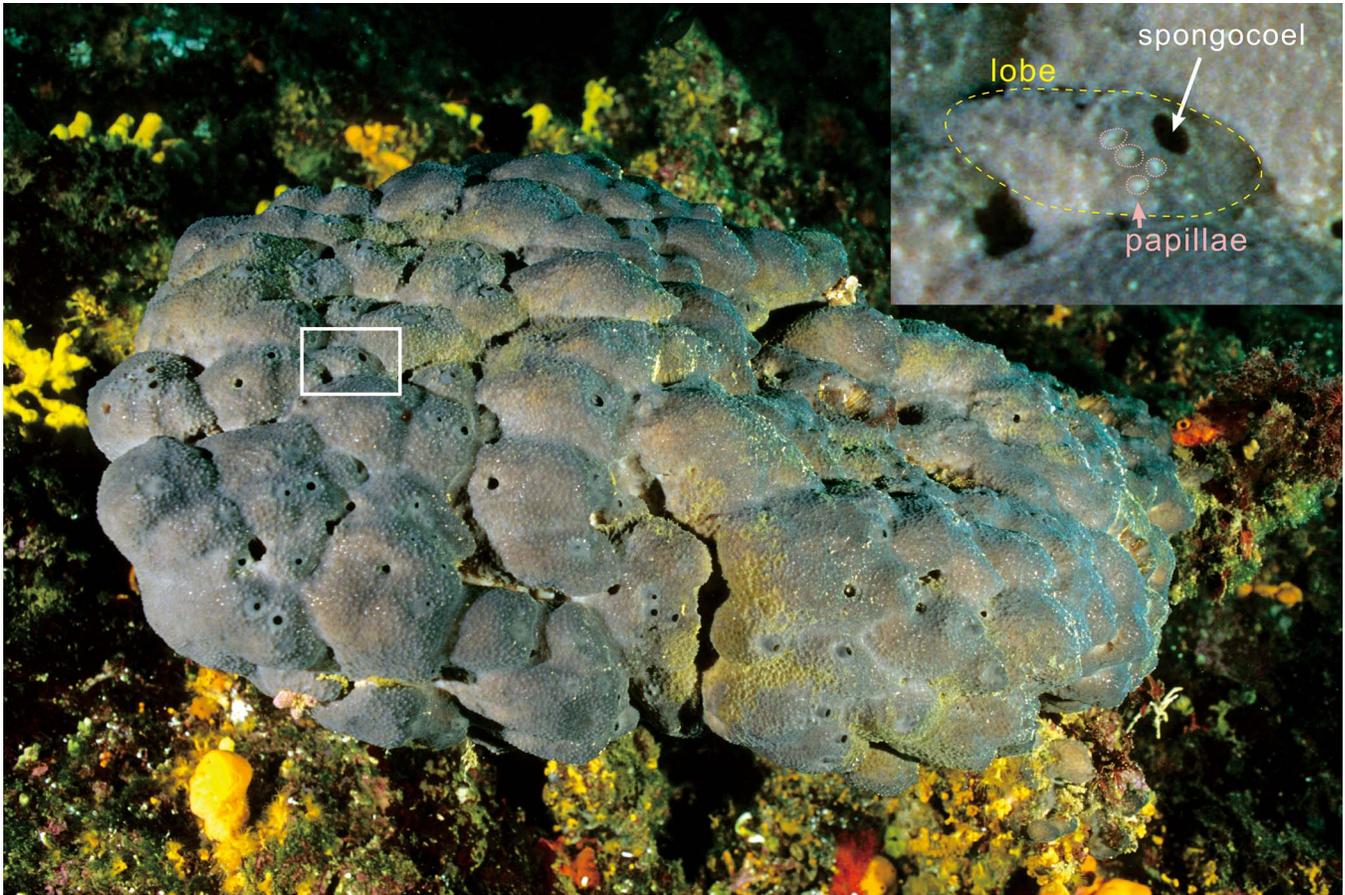


Figure 5. Present-day keratosan sponge (*Spongia officinalis* Linnaeus, 1759) (from WILDLIFE GmbH, 2002; location and scale unknown), organized into multiple juxtaposed lobes with spongocoel openings and patterned by innumerable papillae. We envisage that this morphology could approximate that of *Spongiostroma maendrinum*.

lobate outlines with mammiform papillae similar to some modern sponges (Fig. 5). In hindsight, it appears that, in addition to vermiform fabric (Luo and Reitner, 2016), a variety of additional morphological evidence supporting keratosan recognition is already available. In the following, we summarize some reported examples of macrofabrics that have been interpreted as remains of calcified fossil keratosan sponges, other than *Spongiostroma*.

Vermiform fabric in cavities and interspaces.—Vermiform fabric has been reported as cavity fill within reefs or shells (e.g., Reitner et al., 2001; Hong et al., 2014; J.-H. Lee et al., 2014, 2016, 2019; Park et al., 2017; M. Lee et al., 2019; Turner, 2021). Within the shells, it often fills the lower part of the cavity. In this situation it can create “geopetal” structures overlain by peloidal cavity fills that are again overlain by spar-filled areas (e.g., Lee et al., 2016, figs. 4c, 5b; Park et al., 2017, fig. 3e; M. Lee et al., 2019, fig. 5b, f). Vermiform fabric also occurs between Early Triassic crystal fans and dendrolites (e.g., Friesenbichler et al., 2018; Heindel et al., 2018; Pei et al., 2021; Wu et al., 2022).

Millimetric layers intercalated with microbial carbonate.—Vermiform fabric has been recognized forming very thin layers alternating with microbial carbonate (Luo and Reitner, 2016; Stock and Sandberg, 2019; Lee and Riding, 2021a, b; Pei

et al., 2021, 2022). Lee and Riding (2021a) suggested that steep margins observed in late Cambrian *Cryptozoön* could reflect the ability of keratosan sponges to encrust steep overhanging surfaces.

External morphology.—Distinctive lenticular outlines of keratosaurs (often initially described as non-lithistid demosponges) on millimetric–centimetric scales have been illustrated within fine-grained carbonates from both shallow- and relatively deep-water environments, e.g., upper Cambrian, Korea (Lee et al., 2021, fig. 6), Upper Ordovician of South China (Park et al., 2015, figs. 4, 6), Permian/Triassic boundary of Iran (Luo, 2015, fig. 5.6). External morphology is also locally visible in keratosaurs in reef cavities, e.g., Lower Ordovician of Korea (Hong et al., 2014, figs. 2, 3) and upper Cambrian of Nevada (J.-H. Lee et al., 2019, fig. 7a, f).

Canals.—In addition to the canal-like structures reported here in *Spongiostroma*, cylindrical microspar-filled branching structures about 10 times larger than the vermiform fabric have also been described as canals (Luo and Reitner, 2016, fig. 5b, e, h).

Spongocoel.—The presence of spongocoel, filled by micrite, has been reported in Cambrian reef framework in Shandong, China (Lee et al., 2014, fig. 7b; Lee and Hong, 2019, fig. 3e).

Conclusions

Gürich (1906) compared Mississippian *Spongiostroma* with sponges but was unable to identify canal-like openings, and provisionally assigned it to Foraminifera. Here we show that the type species, *S. mæandrinum*, is organized into papillae-like structures ~2–10 mm across that are pervasively composed of vermiform fabric and are traversed by narrow canals and contain larger spongocoel openings. We therefore interpret *Spongiostroma* as the calcified remains of a keratosan demosponge that originally had a fibrous spongin network.

Recognition of the poriferan nature of *Spongiostroma*, based on macrostructural features as well as its vermiform microfabric, provides criteria to assist discrimination between keratosan demosponges and stromatolite. Vermiform fabric is interpreted as calcified remains of spongin network. Changes to its size and regularity caused by neomorphic diagenesis can produce fabrics somewhat resembling microbial clotted peloidal fabric. This has resulted in a century of confusion during which time the term “spongiostromate” became a synonym for clotted-peloidal microbial fabrics. However, since *S. mæandrinum*, the type species of the family Spongiostromidae and of the genus, is not a stromatolite, it is inappropriate to use the term “spongiostromate” to describe microbial microfabrics.

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Competing Interests

The authors declare none.

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