SOLENOPORA IS A CHAETETID SPONGE, NOT AN ALGA

by ROBERT RIDING

ABSTRACT. For over one hundred years the Ordovician fossil *Solenopora* Dybowski has been widely considered to be a calcified red alga. The type species, *Solenopora spongioides*, consists of tubes with longitudinally flexuous walls, lobate-petaloid cross-sections 30–175 μm across with septal projections, and sporadic cross-partitions. This internal micromorphology is not characteristic of calcified red algae, but is consistent with the original interpretation of *Solenopora* as a chaetetid, and with subsequent recognition of chaetetids as sponges. *Solenopora* is widely misidentified in Silurian and younger rocks. Removal of *Solenopora* from the algae underscores the need to comprehensively reassess the palaeoecological and phylogenetic significance of numerous disparate Ordovician–Miocene fossils currently classed as solenoporaceans.

KEY WORDS: alga, chaetetid, coralline, *Solenopora*, sponge, Ordovician.

THE Solenoporaceae Pia, 1927 has long been regarded as an important family of calcified algae that appeared in the Ordovician and survived into the Miocene (Edwards *et al*. 1993, p. 36). *Solenopora* Dybowski itself was originally described as a chaetetid (Dybowski 1877), but its reinterpretation as a red alga (Brown 1894) was widely accepted. Pia (1927) created the family Solenoporaceae, and since then it has been generally assumed that in the course of their long history solenoporaceans gave rise to corallines: the widespread encrusting red algae that contribute significantly to reefs and form rhodolith nodules in present-day seas (Johnson 1961; Wray 1977). Coralline algae are now abundant and diverse (Aguirre *et al*. 2000), whereas solenoporaceans are extinct. Steneck (1983) suggested that solenoporaceans were less resistant to herbivory than corallines, and that Cenozoic decline and extinction of solenoporaceans coincided with coralline diversification.

When Pia (1927, p. 97) established the Solenoporaceae he formalized widespread recognition of not only *Solenopora* but also *Lithocaulon* Meneghini, *Metasolenopora* Yabe, *Petrophyton* Yabe, *Solenomeris* Douvillé and *Solenoporella* Rothpletz as red algae. However, this family he created is a broad morphological grouping of organisms of widely differing ages. Apart from *Solenopora* from the Ordovician, the five other genera that Pia (1927) firmly included in the Solenoporaceae are restricted to the Jurassic, Cretaceous and Palaeogene. Solenoporaceans typically occur as heavily calcified nodular skeletons, internally composed of juxtaposed radial space-filling filaments or tubes, with or without cross-partitions. Rather than facilitating comparisons, such morphological simplicity makes it difficult to establish taxonomic distinctions. This overall skeletal organization is shared by a variety of organisms, including sponges as well as algae.

Establishing the affinity of *Solenopora* is fundamental to understanding of the Solenoporaceae. Contrary to current opinion, micromorphology of the type species, *Solenopora spongioides*, does not support the view that it is an alga. Here I propose that Dybowski (1877, p. 124) was correct to classify *Solenopora* as a chaetetid and that, along with other chaetetids (Hartman and Goreau 1972), it is a sponge. Authentic *Solenopora* appears to be restricted to the Lower Palaeozoic. The numerous younger organisms ranging to the Cretaceous, to which the name *Solenopora* has been applied (Johnson 1961), need to be re-identified. Such revision is likely to radically alter understanding of the palaeoecology and significance of these fossils, and to demand comprehensive reassessment of the evolutionary history of calcareous red algae.

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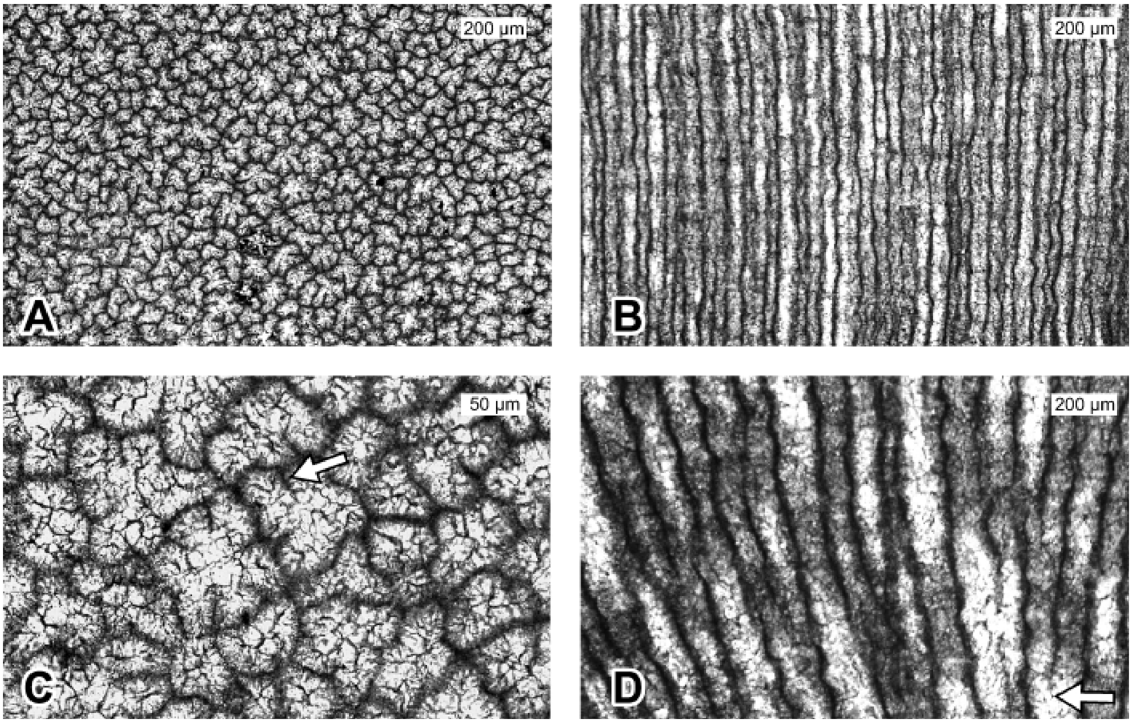


TEXT-FIG. 1. *Solenopora spongioides*, Saku Member, Vasalemma Formation (Caradoc, Late Ordovician), Estonia. Specimens of Öpik and Thomson (1933) in Museum of Geology collections, Tartu University, Estonia. A, TUG 1140–4, transverse section showing irregular lobate tube cross-sections; Saku lime-kiln, 16 km south-south-west of Tallinn. B, TUG 1140–1, longitudinal section showing flexuous walls. Delicate growth banding is visible, but tabulae are scarce; Üksnurme, 18 km south-south-west of Tallinn. C, TUG 1140–4, transverse section, showing septal projection (arrow); Saku lime-kiln, 16 km south-south-west of Tallinn. D, TUG 1140–2, longitudinal section, showing tube fission (arrow); Vasalemma, 33 km west-south-west of Tallinn.

SOLENOPORA SPONGIOIDES

Type material

Solenopora is based on Caradoc (Late Ordovician) specimens from northern Estonia, defined as: overall body spheroidal; polyps irregularly prismatic, of very small diameter; coenenchyme lacking; cross-partitions lacking (translated from Dybowski 1877, p. 124). The type material was from a Pleistocene glacial erratic at Härgla (German Herküll), 38 km south of Tallinn. It probably derived from outcrops of the Saku Member of the Vasalemma Formation that contain abundant *Solenopora*, 20 km to the north in the area of Üksnurme (Öpik and Thomson 1933). The type specimens are missing.

Dybowski's (1877, pl. 2, fig. 11) illustrations and the Üksnurme specimens show rounded calcareous nodules composed of radiating juxtaposed tubes with shared walls. Tube cross-sections are lobate-petaloid to irregular and rounded-polygonal, with septal projections (Text-fig. 1). Tubes increase in number by longitudinal fission caused by septal growth and union. Tube walls are longitudinally folded into minute undulations. Dybowski (1877, p. 125) reported tube diameters of 30–80 μm. In longitudinal section, Üksnurme specimens show tube widths of 40–175 μm; in transverse section maximum tube diameters have a range of 65–135 μm (Text-fig. 1). Flat to concave-up cross-partitions (tabulae) are only sporadically present and non-aligned.

Comparisons with coralline algae

In some corallines, such as the melobesioids *Lithothamnion* and *Mesophyllum*, fusion due to wall resorption results in filaments being lobate in cross-section (Aguirre *et al.* 1996, pl. 1, fig. 2), and longitudinally irregular. In contrast, in *Solenopora* the tubes show good longitudinal continuity (Text-fig. 1B) and their lobate cross-sections are not due to fusion (Steneck 1983) but to the septal projections that cause tube fission. Fission is unknown in corallines, but occurs in chaetetids. Furthermore, *Solenopora spongioides*, as Nicholson and Etheridge (1885) noted, lacks both the well-defined cellularity and small filament size typical of corallines. *Solenopora* tube diameters are in the range 30–175 μm, whereas coralline filaments are generally 5–30 μm wide (Juan Carlos Braga, pers. comm. 2002). In corallines, apart from exceptions such as in protuberant growth (e.g. Woelkerling 1988, fig. 40), cell length:width ratios generally are four or less (Juan Carlos Braga, pers. comm. 2002). In contrast, in the type material of *Solenopora spongioides* tabulae are so sporadic that they are not present in every tube and distinct cells are not developed (Dybowski, 1877, pl. 2, fig. 11). Reproductive organs reported in *Solenopora spongioides* in support of a red algal affinity (Öpik and Thomson, 1933) have not been confirmed (Poignant, 1991) and appear to be borings.

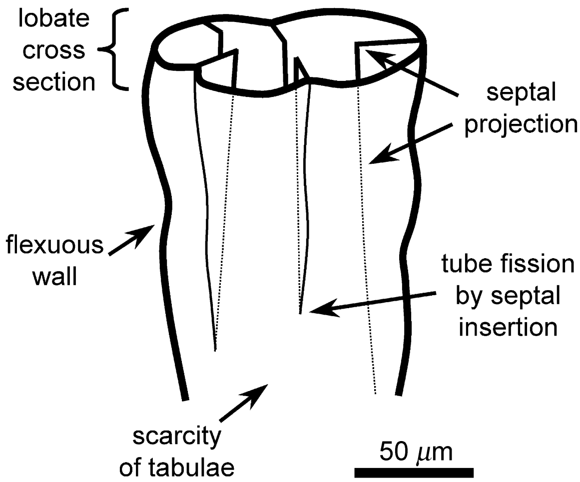
Comparisons with chaetetids

Hartman and Goreau's (1972) revival of Kirkpatrick's (1912) view that chaetetids are sponges has gained wide support, and they have been suggested to represent an organizational grade of demosponge (Vacelet 1985). In addition to spicules, extant tetractinomorph demosponges such as *Spirastrella* (*Acanthochaetetes*, *Tabulospongia*) (Basile *et al.* 1984, fig. 3; Reitner 1991, p. 203) exhibit calcareous chaetetid 'basal' skeletons with tabulate tubes (calicles) (Vacelet 1985; Reitner *et al.* 1997). Chaetetid features (West and Clark 1984) shared by *Solenopora* include lobate-petaloid to irregular-polygonal tube cross-sections, septal projections, and tube increase by fission produced by vertical merging of septa (Text-fig. 1). Wide variability in tube diameter, seen in *Solenopora spongioides* (Text-fig. 1B, D), is also shown by Carboniferous *Chaetetes* (West 1994). The relationship in some chaetetids between fission and formation of irregular tube cross-sections (Gray 1980, p. 809, pl. 102, fig. 5), occurs in *Solenopora* (Text-fig. 1C–D). Chaetetids characteristically have tabulae, but these can be very thin (e.g. Reitner 1991, fig. 6B) and poorly developed (Cremer 1995), and may be 'rarely visible' in fossils (Gray 1980, p. 809). *Solenopora* similarly shows variable tabula development. Chaetetid tube (calicle) diameters have a range of 150–500 μm, and are even smaller in some present-day *Merlia* (120–150 μm; Scrutton 1987, p. 487). Thus, although the 30–175 μm tube diameter observed in *Solenopora* is on average much less than in most chaetetids, it overlaps the lower size range of chaetetids.

However, septal projections are more common in *Solenopora* than is usual in most chaetetids, and tube walls in chaetetids are generally relatively straight or gently curved in longitudinal section (R. R. West, pers. comm. 2002). Flexuous walls and common septal projections liken *Solenopora* to some tetradiids (Graham Young, pers. comm. 2002), although tetradiids generally have larger tubes, commonly 400–1700 μm across (Moore *et al.* 1952, p. 113). Tetradiids, exemplified by *Tetradium* Dana, are Ordovician fossils characteristically with four septa. Overall, *Solenopora* resembles chaetetids in tube size and overall morphology. It resembles tetradiids in having flexuous walls and abundant septal projections, but is much smaller than most tetradiids and lacks their distinctive fourfold septation. Tetradiids have generally been regarded as tabulate corals (Hill and Stumm 1956). However, Scrutton (1997, p. 189) noted that tetradiids 'are not closely related to the rest of the Tabulata and should be excluded from that group. Similarities between tetradiid longitudinal fission and that of chaetetids suggest a possible relationship with the sponges . . .'.

DISCUSSION

Nicholson and Etheridge (1885, pp. 531–532) considered that tube size alone distinguished *Solenopora* from *Chaetetes*. They suggested that *Solenopora* might be a coralline alga, but doubted that it possessed the necessary cellular structure. Brown (1894) concluded that *Solenopora* is cellular in organization, but



TEXT-FIG. 2. Characteristic micromorphological features of the tube in *Solenopora spongioides*.

his broad examination of *Solenopora* included species not congeneric with the type species, *Solenopora spongioides*. This confusion escaped notice, and Brown's (1894) opinion that *Solenopora* probably is a coralline alga ultimately led Pia (1927) to create the family Solenoporaceae for diverse Ordovician–Miocene fossils believed to include ancestors of modern corallines. Even as he did this, however, Pia (1927, 1930) expressed doubts concerning solenoporacean affinities and suggested that some might be hydrozoans. Despite this uncertainty, the view of the Solenoporaceae as a homogeneous group of red algae became firmly entrenched (Johnson 1961).

The key to liberating *Solenopora* from the straitjacket of supposed algal affinity is recognition that the Solenoporaceae is heterogeneous (Riding 1993) and that contemporaneous Early Palaeozoic algal solenoporaceans are not congeneric with *Solenopora spongioides* (Brooke and Riding 1998). Micromorphological features distinguishing *Solenopora spongioides* from coralline algae (septal projections, tube fission, poor cellularity, larger 'filament' size; Text-fig. 2) uphold Dybowski's (1877) assignment of *Solenopora* to chaetetids. Furthermore, and contrary to Nicholson and Etheridge's (1885) view, *Solenopora* tube-size overlaps with that of calicles (tubes) in recognized chaetetids. It is proposed here that *Solenopora* is a small chaetetid. Possibly it provides a link between tetradiids and chaetetids. Confirmation of a sponge affinity would require recognition of features, such as spicules and astrorhizal canal systems, that remain scarce in Palaeozoic chaetetids (West and Clark 1894), and have not yet been reported in *Solenopora spongioides*.

So far as other solenoporaceans are concerned, some of them, such as *Marinella* Pfender (Barattolo and del Re 1985; Leinfelder and Werner 1993), *Metasolenopora* and *Petrophyton* (Yabe 1912), as well as *Solenoporella* (Riding 1993), resemble red algae and may belong with or be related to corallines. On the other hand, *Parachaetetes* Deninger and *Pseudochaetetes* Haug are likely to be chaetetids, *Goldsonia* Shrock and Twenhofel appears to be a receptaculitid, and forms such as *Solenopora paquettiana* Ami remain problematic.

CONCLUSIONS

Reassignment of *Solenopora* to chaetetids excludes it from being the basis for an algal group. *Solenopora*, as originally defined, is known only from the Ordovician and possibly Lower Silurian, yet more than 80 per cent of records of *Solenopora* are from younger successions up to and including the Miocene (GeoRef, 2002). These identifications are almost certainly incorrect. It is no longer possible to support the concept of the Solenoporaceae as a coherent group by reference to its Early Palaeozoic antecedents, and other fossils hitherto attributed to the Solenoporaceae require comprehensive review. They appear to include chaetetids, receptaculitids and Problematica, as well as red algae. This transforms our perception of the family. However, despite this challenge to the long-established view of the Solenoporaceae as a homogeneous group ancestral to modern corallines, it is likely that a number of these genera remain a key to understanding the evolution of coralline and coralline-like red algae. Their elucidation is an important goal for future research.

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