Calcareous algae

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Calcareous algae can be recognised in the field in Gotland as porcelaneous white nodules and masses of *Solenopora* and as laminated balls which have been termed *Sphaerocodium* and *Spongiostroma*. *Solenopora* is usually found in the reefal sediments but the balls form distinctive horizons in several parts of the sequence, notably the Tofta Beds and Eke Beds, and have commonly been mentioned in the descriptions and correlation of various stratigraphic units. Only Rothpletz (1908, 1913) has made a comprehensive study of the systematics of these fossils but several subsequent workers (Hadding 1941, 1950, 1959, and others) have emphasized the sedimentological importance of calcareous algae in both reef and shallow-water, probably restricted, environments throughout the sequence. But many questions remain, especially concerning the volumetric importance and roles of algae in reefal deposits and their systematics.

The material examined comprises 39 thin sections, 102 peels and some 50 hand specimens collected by Liljevall. It includes also thin sections from Vattenfallet of syntype and other material decribed by Rothpletz (1913). The information in the log (Fig. 20) on most algae is based on thin sections and peels made from the standard series of rock samples (the level of these samples is shown by black rectangles along the left column). The data on large algae, such as *Solenopora*, are mostly based on Liljevall's collection.

Annotated floral list

Solenopora gotlandica Rothpletz, S. compacta Billings

The diagnosis of *Solenopora* relies primarily upon the poor or irregular development of "tabula-like" cross-partitions in the vertical tubes in order to distinguish it from *Pseudochaetes* and *Parachaetes*. Definition of species has mainly been made on the basis of the dimensions of the resulting "cells". The cross-sectional shape of the tubes has also been used to define species. But all these features: cross-partitions, cell-size, cross-sectional shape, can vary considerably within a single specimen (see also Johnson & Konishi 1959:30). Possibly because of this, numerous species have been erected with characters which overlap, particularly in cell dimensions (see Johnson 1960, table 1). Consequently, the Solenoporaceae require thorough revision. For convenience here, and to prevent further confusion, I have followed Rothpletz and



Fig. 20.

have distinguished S. gotlandica and S. compacta. But it is important to note that Johnson & Konishi (1959:33) placed both these species in Parachaetes and also that Sinclair (1956) suggested that S. compacta is a stromatoporoid. Nevertheless, the S. compacta described from Vattenfallet is not a stromatoporoid and both species can reasonably be retained in Solenopora for the present. S. gotlandica is readily distinguished in thin section by its very fine "cells" with diameters of approx. 25–30 μ m. S. compacta has distinctly larger "cells" with diameters of approx. 80–120 μ m. Nearly half the specimens of Solenopora are so affected by recrystallization that the species is indeterminate. There is some scope for confusion between the coarser species of Solenopora, such as S. compacta, and Hedstroemia (see below), and it is possible that Rothpletz (1913, Pl.2:6) mistakenly referred S. compacta to H. bifilosa. Pseudostylodictyon simplex Mori, 1969, is not a stromatoporoid (Heldur Nestor and Kei Mori, personal communications) and specimens close to the holotype belong to S. gotlandica.

Girvanella sp.

This is a very small sinuous tube. Sometimes it forms nodules but without microscopic examination the presence of *Girvanella* cannot be confirmed. There are numerous species of *Girvanella* (see Fournie 1967) primarily characterised by the tube diameter. As in the case of *Solenopora* species the degree of overlap is considerable and confident application of species names is not possible without extensive revision. No specific names have yet, so far as I know, been applied to *Girvanella* from Gotland and I prefer here to leave the species open. The range of the diameter of the tube is 13–20 μ m and this is within, although slightly below the average for, the range of variation shown by *G. problematica*, the type species, at the type locality (Wood 1957, text–fig. 1a).

Rothpletzella munthei (Rothpletz)

Rothpletz's error in recognizing Sphaerocodium in Gotland was corrected by Wood (1948) who referred Rothpletz's species S. gotlandicum and S. munthei to a new genus Rothpletzella. Wood also distinguished another new genus, Wetheredella, in the material which Rothpletz had previously referred to as Sphaerocodium. Wood's revision of Sphaerocodium was justified but he perhaps did not make it sufficiently clear that the type material of Sphaerocodium from the Alps is quite different from the Gotland material described by Rothpletz. Because of this Wray (1967:37) mistakenly assumed that Wood had simply split the genus Sphaerocodium and that this name had to be conserved for part of the material from Gotland. Consequently, Wray emended Wood's revision and replaced Rothpletzella (1967) bv Sphaerocodium. But this is not warranted and Rothpletzella is valid. Hadding

(1941) used the name *Pilotrix* for laminar or encrusting growths of "Sphaerocodium" and Girvanella in the Gotland reefs. Consequently, it is possible that *Pilotrix* is a senior synonym of *Rothpletzella* or *Wetheredella*. Rothpletzella from Vattenfallet mainly ranges in external tube diameter from 15–25 μ m and corresponds approximately to the dimensions of *R. munthei* (20–25 μ m) as revised by Wood (1948:19). These are small specimens when compared with the other Gotland species, *R. gotlandicum* (30–35 μ m), and Devonian species described by Wray (1967:37–40) are even larger.

Wetheredella silurica Wood

W. silurica has tubes of approx. 100 μ m external diameter (Wood 1948:20). Specimens from Vattenfallet are in the range 40–120 μ m. Copper (1976:277) has erected W. tumulus, on the basis of Ordovician material, which has diameters in the range of 30–140 μ m. The validity of this species is questionable and I regard it as a junior synonym of W. silurica (Riding 1977d).

Hedstroemia halimedoidea Rothpletz

It can be difficult to separate *Hedstroemia* from some of the larger *Solenopora* species, especially *S. spongioides* (see above, *Solenopora*), and its species are not very well defined. Specimens from Vattenfallet appear to be referable to *H. halimedoidea*.

Rhabdoporella stolleyi Rothpletz

Rothpletz's species *R. pachyderma* and *R. stolleyi* are distinguished mainly by the thickness of the wall. Only the thin-walled form, *R. stolleyi*, has been observed in the Vattenfallet material. The tubes are $60-100 \mu m$ in diameter.

Oncolites

Fenestral non-skeletal oncolites, which in the past have been referred to as *Spongiostroma*, occur at Vattenfallet. Rothpletz (1913:36–37) noted *S. holmi* from the Vattenfallet section above 29 m. I prefer not to use Linnean nomenclature for these structures.

Affinity

The systematic position of many Palaeozoic fossils commonly regarded as calcareous algae is uncertain. This is especially true in the Silurian. Only a few of the taxa mentioned here can confidently be regarded as algae, but they cannot, without controversy, be placed in other groups at present. Since they have traditionally been included together it is convenient to consider them here as a group, but their probable heterogeneity places constraints on their environmental significance. Care should be exercised in using these fossils to interpret the Vattenfallet sequence.

General problems regarding the nature of *Solenopora* and *Girvanella* are discussed elsewhere (Riding 1977c). *Solenopora* shows morphological similarities to some bryozoans and tabulate corals. In the past it has also been regarded as a hydrozoan. But because of its resemblance to crustose Corallinaceae it has usually been regarded as a related red alga. The essential problem of its affinity is that it appears to lack positive criteria for placing it in one group rather than another. *Girvanella* represents the calcified sheaths of filamentous cyanophytes (Riding 1977a).

Hedstroemia and Rothpletzella consist of densely packed branching tubes. Those of Hedstroemia are erect and radiating, with diameters of 50–180 μ m. The tubes of Rothpletzella are smaller (20–40 μ m in Gotland species) and prostrate. Both genera have been placed in the Porostromata by Pia (1927:38–39, Rothpletzella being called Sphaerocodium) and both cyanophyte and green algal affinities have been proposed for them (Rothpletz 1913:16–17; Wood 1948:18).

Wood (1948:20) regarded *Wetheredella* as a foraminifer, but Loeblich & Tappan (1964:C787) and Copper (1976) suggest that it is an alga. I incline toward Wood's opinion but diagnostic criteria to clarify the nature of *Wetheredella* have still to be obtained. *Rhabdoporella* is regarded as a dasycladacean (Rothpletz 1913:27; Pia 1927:62), a view which is consistent with its porebearing tubiform skeleton.

Stratigraphical remarks

Rothpletzella, Girvanella and Wetheredella range throughout the section and Rothpletzella and Wetheredella commonly show close mutual association. Solenopora is markedly more abundant in the upper half of the section above 18 m. Rhabdoporella is commonest near the base, below 4 m. Hedstroemia and oncolites ("Spongiostroma") are virtually restricted to the uppermost part of the section, above 29 m, where they are closely associated.

Rhabdoporella occurs as very small tubular segments or fragments, approximately 0.5 mm long, in fine grained calcilutites. *Rothpletzella*, *Girvanella* and *Wetheredella* occur as small (up to 3 mm across, but often much less) flat or irregular aggregates in calcarenites. Sometimes they are attached to bioclasts but commonly they are loose and either represent crusts broken from a firm substrate, or original discrete masses. *Solenopora*, *Hedstroemia* and oncolites occur as nodules up to several centimetres across in coarse grainstones. Those of *Hedstroemia* are the smallest, being round or ovoid masses 1–2 mm across. The oncolites are smooth round, ovoid or bean-shaped bodies 2–10 mm in size. Solenopora nodules are normally very smooth and round, and range from 0.4-3.3 cm in size mostly being between 1-3 cm. Very occasionally irregularly branched or abraded specimens occur.

Discussion

The two principal modes of occurrence of macroscopic fossils generally regarded as "calcareous algae" on Gotland are both seen in the Vattenfallet section. *Solenopora* nodules are common between 18-30 m and "algal balls" are common above 29 m. However, these balls are "*Spongiostroma*" non-skeletal oncolites, and the "*Sphaerocodium*" skeletal oncolites (for definition of this term see Riding 1977b) constructed by *Rothpletzella* and *Wetheredella* are not seen. The relative environmental significance of skeletal and nonskeletal oncolites and stromatolites has yet to be determined.

The distribution of these macroscopic fossils, together with smaller genera, allows three assemblages to be distinguished within the section:

(1) a lower Rhabdoporella assemblage below 4 m,

(2) a middle Solenopora, Rothpletzella, Girvanella, Wetheredella assemblage between 4-29 m, and

(3) an upper *Hedstroemia*, non-skeletal oncolite assemblage above 29 m. *Rhabdoporella* is a small delicate fossil. It probably lived in relatively quietwater subtidal environments. Assemblage 2 probably reflects a more agitated shallow subtidal environment with free-living *Solenopora* forming rhodolitelike nodules in a lime sand substrate and with the *Rothpletzella*, *Girvanella*, *Wetheredella* crusts perhaps being derived from abrasion of adjacent reef surfaces. Assemblage 3 is a pebbly deposit of rolled calcified and uncalcified algal balls, probably indicative of very shallow subtidal conditions.

Most of these fossils are broken and transported to some degree. Rhabdoporella is entirely fragmented and the Rothpletzella, Girvanella, Wetheredella crusts are usually detached and broken. The oncolites and Hedstroemia bodies do not appear to have been stabilized. The Solenopora nodules are possibly closest to their sites of growth and many show asymmetry of their growth layers which suggests stabilization in the substrate.

The uncertain affinities of many of these taxa (see above) make it difficult to use them as specific environmental indicators and prevent any discussion of diversity levels. However, the presence of *Rhabdoporella*, a probable dasycladacean, in what is likely to be the deepest environment in the sequence, can be used to infer a maximum depth for all the environments represented. Calcareous green algae, provided they have not been transported into deeper water after death, are generally restricted to depths above 100 m in the Recent (Riding 1975). Dasycladaceae are usually considered to be commonest in much shallower water still, but it is not possible to confidently state a general maximum depth of less than 100 m at present.

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