

A REVIEW OF FAVOSITID AFFINITIES

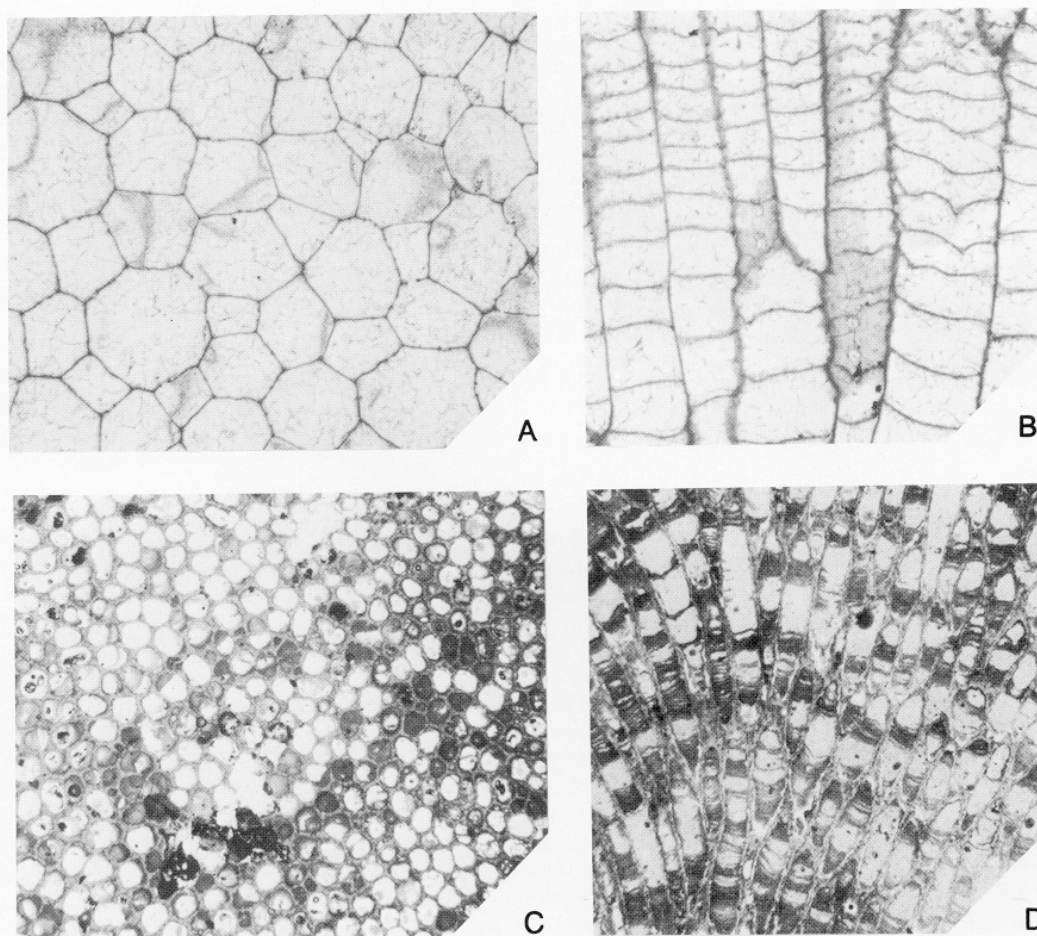
by COLIN T. SCRUTTON

ABSTRACT. Although the favositids have been traditionally interpreted as a group of Palaeozoic tabulate corals, there has been persistent speculation, particularly over the last decade, that they could be the massive basal skeletons of sponges and should be transferred to the Porifera. Two recent papers, claiming respectively the preservation of spicules and the fossilization of soft polyps, strongly focus the dispute. Here, all the evidence relating to the affinities of favositids, including these recent claims, is reviewed. It is concluded that this evidence strongly favours retention of the favositids within the Tabulata and assignment of the Tabulata to the Cnidaria Anthozoa.

THE favositids are an important group of extinct organisms with a massive or branched calcareous coralline skeleton and are conventionally assigned to the Palaeozoic subclass Tabulata. Almost all specialists classify the Tabulata as corals in the anthozoan Cnidaria (Hill 1981). That the favositids might be sponges was first seriously suggested when the sclerosponges were discovered early in this century (Kirkpatrick 1912), an observation largely overlooked and ignored at the time. During the last twelve years, however, the rediscovery of the sclerosponges has promoted a long-running debate concerning the affinities of favositids and even of the Tabulata as a whole (Hartman and Goreau 1975; Flügel 1976; Stel 1978; Oliver 1979, 1986; Scrutton 1979; Oekentorp and Stel 1985). Two recent papers appear to polarize the argument: the claimed discovery of spicules in the favositid *Thamnopora* (Kazmierczak 1984), and the report of fossilized polyps in *Favosites* itself (Copper 1985). All specialists regard *Favosites* and *Thamnopora* as closely related so both presumably cannot be right. This paper sets these recent conflicting claims in context by reviewing all the evidence relating to the problem of affinity of these structurally simple fossils.

Some supposed tabulate corals variously homoeomorphic with favositids have been reclassified in the light of sclerosponge work. The Chaetetida, in whole or in part, are now widely considered to be sponges (Hartman and Goreau 1972; Fischer 1977; West and Clark 1984; Vacelet 1985; but see also Hill 1981) and some have yielded unquestionable spicules (Dieci *et al.* 1977; Gray 1981). However, Sokolov (1962) had already argued strongly against the inclusion of this group in the Tabulata before the new sclerosponge discoveries. In addition, a reassessment of *Nodulipora* and *Desmidopora*, formerly classified as Favositidae (Hill and Stumm 1956), has established a good case for their transfer to the sclerosponges (Hartman and Goreau 1975; Stel and Oekentorp 1981). It is possible that some further tabulate taxa may also eventually require reassignment, but generally it is considered less likely that tabulates other than favositids could be sponges (Hartman and Goreau 1975; Scrutton 1979), although transfer of the whole group to the Porifera has been proposed (Stel and de Coö 1977). The definition of the Tabulata taken here is that outlined by Scrutton (1984), who argued that the subclass essentially constitutes a monophyletic grouping. In this paper, discussion is limited to *Favosites* and its close relatives, collectively and informally termed favositids and equivalent in general terms to the Favositina of Hill (1981).

The sclerosponges are now considered to be a polyphyletic collection of various demosponges (Vacelet 1977, 1985). They are united only by the possession of a massive 'coralline' basal skeleton which in itself seems to be of little phylogenetic significance. Indeed, the basal skeleton in different sponges shows a wide range in macroscopic form, microstructure, and mineralogy. The term sclerosponge is retained here informally, as the group collectively represents the most coral-like representatives of the sponges. It includes the Tabulospongida of Hartman and Goreau (1975)

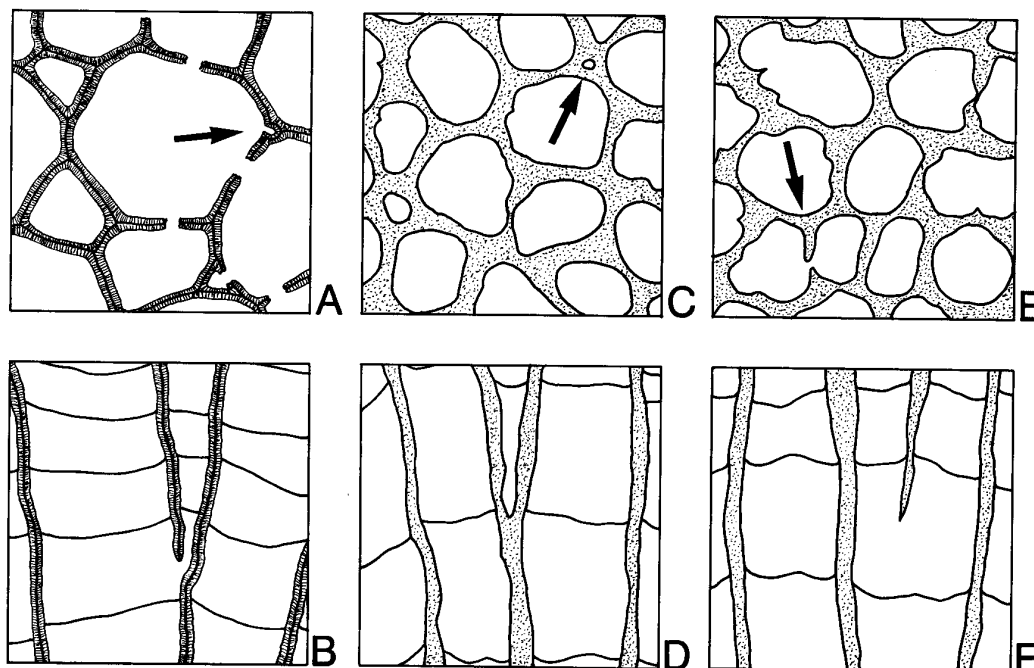


TEXT-FIG. 1. Comparison of basic morphology and characteristic corallite/calicle size in a favositid and a sclerosponge, in transverse and longitudinal sections. A, B, *Favosites multipora* Lonsdale, BM(NH) R51936; Silurian, Wenlock Series, Much Wenlock Limestone; road cut on B4378, 2.5 km north-north-east of Much Wenlock, Shropshire. C, D, *Tabulospongia japonica* Mori, BM(NH) 1986.7.7:1A; Recent; Ishigaki-shima, Ryukyu Islands, Japan. All $\times 8$.

as well as the morphologically very similar Chaetetida and these two orders together represent the sclerosponges most closely homoeomorphic with favositids (text-fig. 1).

ANALYSIS OF FAVOSITID STRUCTURE

Favosites is a colonial organism consisting of closely appressed polygonal tubes interconnected by mural pores (text-fig. 1A, B). Conventionally, the skeletal tubes in favositids are called corallites (as in corals generally) whilst those in sclerosponges are calicles; it will be convenient to use these terms here although I do so without prejudice. In favositids, corallite 'diameters' vary from c. 0.5–5.0 mm, comparable to corallite size in many other tabulate corals and some scleractinian corals, although



TEXT-FIG. 2. Three different methods of origin of new units within a colony. A, B, lateral increase in favositids; the point of communication with the parent corallite is so small that the critical stage is seldom seen in random sections; for this reason, increase in favositids was earlier thought to be intermural increase. C, D, intramural increase in sclerosponges; the new calicle arises within the wall with no communication with surrounding calicles. E, F, longitudinal fission in sclerosponges; an existing calicle is subdivided subsequently by the growth and fusion of pseudosepta from opposite walls; occasionally, subdivision may be effected by a single pseudoseptum growing from one wall across the calicle. A, C, E are cross-sections, with an arrow indicating the critical stage of increase; B, D, F are 'perfect' longitudinal sections through the corresponding critical stages.

to few rugose corals (most of which have larger corallites). Of the living sclerosponges so far known, none has calicle diameters in excess of 0.6 mm (text-fig. 1C, D), and those with the larger diameters have a functional relationship between the calicles and ostia in which the tissue enclosed by each calicle is the unit supported by a single ostium (Hartman and Goreau 1975). *Merlia*, however, with very small calicles (0.12–0.15 mm), has no such relationship. The fossil tabulosponges and the chaetetids have calicle diameters not exceeding *c.* 1.2 mm, with most in the range 0.15–0.50 mm, significantly smaller than the corallites in the majority of favositids.

New corallites in *Favosites* are now known always to arise by lateral increase (Oliver 1968; Stel 1978; Scrutton 1979), equivalent to the peripheral intracalicular increase of Hill (1981) (text-fig. 2A, B). The process is structurally comparable with lateral increase in other corals. In sclerosponges, however, new calicles arise either by longitudinal fission or by apparently true intramural increase (Hartman and Goreau 1972, 1975) (text-fig. 2C–F). There appears to be no overlap between the two groups.

The determination of original composition and microstructure in fossil material is a more debatable area but the favositid skeleton was most probably originally calcitic (Richter 1972; Sandberg 1975). Corallite walls are considered to have had a fibronormal microstructure, although some argue that lamellar microstructure was primary in certain genera (Lafuste 1962). More critically,

there is no doubt that this fabric is based on an epithecal surface bounding individual corallites which is expressed as a median dense band when corallite walls are fused back to back (Oekentorp and Sorauf 1970; Schouppé and Oekentorp 1974; Stel 1978; Hill 1981) (text-fig. 3A-C). Precisely similar walls are known in cerioid rugose corals such as *Actinocyathus*, *Hexagonaria*, *Lithostrotion*, and many others (Hill 1981), as well as in other tabulate corals (Flower 1961). This indication of the individuality of the component corallites within the favositid colony is buttressed by two additional features. First, by the occurrence of subcerioid growth, in which irregular intercorallite cavities are formed within an otherwise cerioid morphology (Philip 1960). Secondly, by the manner of formation of pseudopericulae, plates with concentric growth lines, often with an excentric origin, that individually close off abandoned calices in some specimens (Dunbar 1927; Swann 1947). The presence of intermural spaces (Swann 1947; Ross 1953) would represent further evidence, although some structures so described are due to commensal organisms and others are at least enhanced diagenetically if not wholly of diagenetic origin (Oekentorp 1969). Even so, the distribution of the commensal structures themselves often follows a pattern related to the corallite walls which suggests that the latter defined individual units of soft tissue.

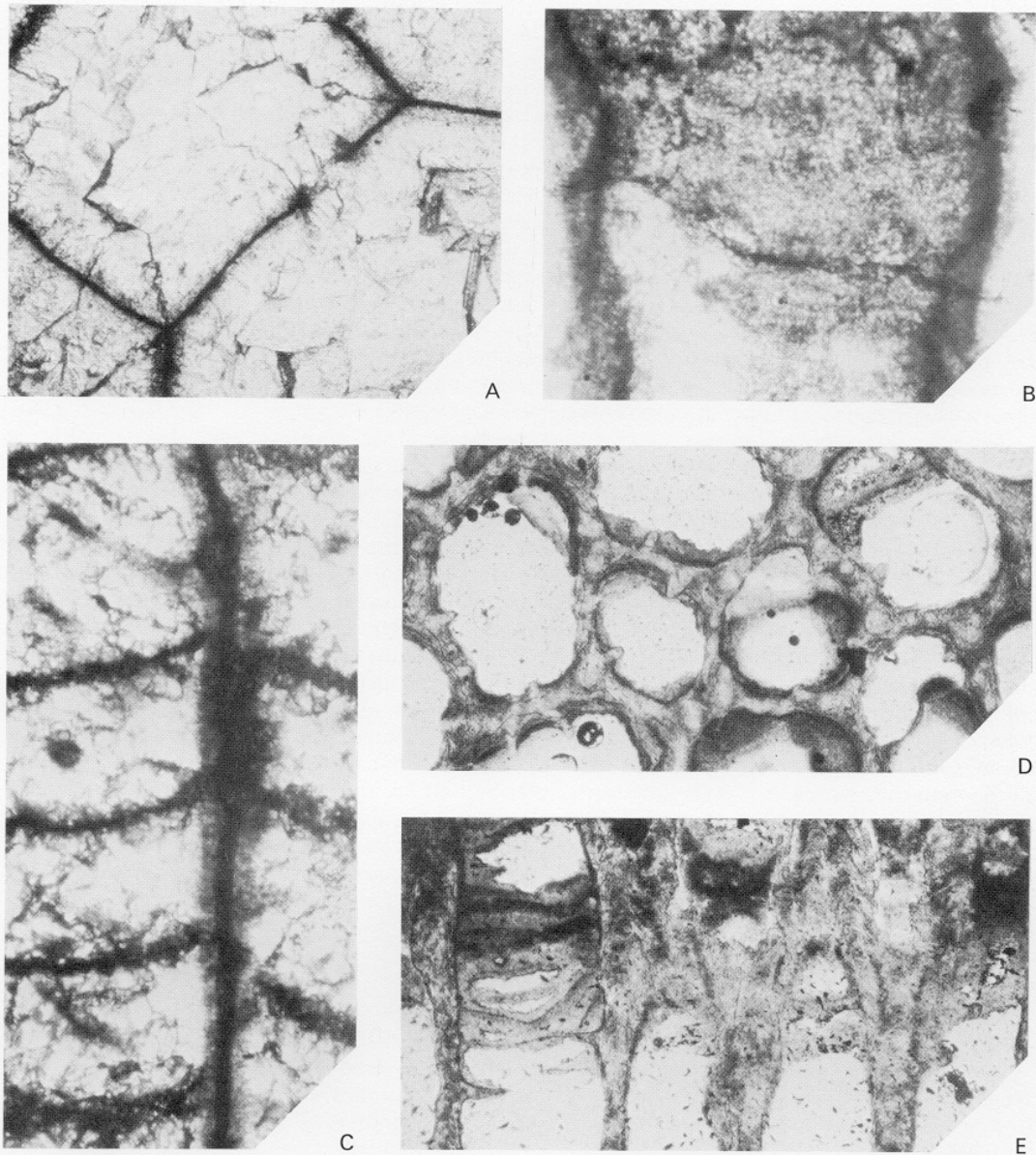
Sclerosponges are mainly aragonitic with spherulitic or trabecular structure, although calcitic lamellar skeletons are known in tabulosponges (Hartman and Goreau 1972, 1975; Vacelet 1985) (text-fig. 3D, E). In neither, however, is there any indication of an axial zone in the wall representing fused epitheca, or of any individuality of the component calices (Hartman and Goreau 1975). Intercalicular walls have a unitary microstructure. The 'epitheca' of sclerosponges (Hartman and Goreau 1972, 1975) is equivalent to the holotheca of non-cerioid tabulate and massive rugose corals (Hill 1981). In most, if not all, cerioid tabulates and rugosans the outer wall of the colony is the sum of the free epithecal walls of adjacent, peripheral corallites.

The septal spines and tabulae of *Favosites* can be matched by both other corals and some sclerosponges in gross morphology and possibly microstructure, although if favositid septal spines are trabecular, as Hill (1981) speculated, then they are uniquely cnidarian (text-fig. 3C, E). Although favositid spines may be arranged in regular vertical rows and there may be twelve such rows, other configurations may occur and their distribution may also be irregular (Schouppé and Oekentorp 1974; Oekentorp 1976; Oekentorp and Stel 1985). A very similar range of variation appears to be possible in some sclerosponges. However, some favositids, the Agetolitidae, have unusually well-developed septa for which rugosan septal insertion has been claimed (Kim 1974), thus strongly supporting anthozoan affinities.

The mural pores of favositids (text-figs. 2A, B, 3A, B) are structurally comparable with, and were presumably identical in function to, the horizontal tubules of syringoporoids. There is no difference between the appearance of syringoporoid intercommunication when the corallites become compressed and contiguous and the mural pores of favositids (see, for example, Hill 1981). Some other tabulate coral groups also possess mural pores of supposed similar function to those of favositids, if of different structure in detail, but pores are not present in all tabulate corals. No similar structures are known in living sclerosponges and the chaetetids, although they are present in the probable fossil sclerosponges *Nodulipora* and *Desmidopora*. Stel and Oekentorp (1981) suggested a relationship between the presence of pores and larger calicle size in sclerosponges, although they noted an exception to this themselves. Flügel's (1976) suggested analogy between mural pores in favositids and astrorhizal systems in sclerosponges is ingenious but unconvincing (Scrutton 1979; Stel and Oekentorp 1981).

Mural pores are as equally unknown among rugose and scleractinian corals as among the bulk of sclerosponges. However, in favositids they can be interpreted most convincingly as a device allowing interpolypal communication and thus a higher level of integration of the colony than in unmodified cerioid morphologies (Coates and Oliver 1973). In other corals this is achieved by the wholesale loss of the epithecal barrier to integration, or by pervasively and finely perforate walls in some Scleractinia. It is clear, however, that the presence or absence of mural pores cannot be taken as a criterion of great significance in determining the affinity of the favositids.

Neither favositids nor any other tabulate corals show any sign of astrorhizal structures like those



TEXT-FIG. 3. Microstructural characteristics of a favositid and a sclerosponge. A-C, *Favosites multipora* Lonsdale (specimen details as for text-fig. 1A, B). The dark mid-line of the wall, representing fused epithecae of adjacent corallites, and its fibro-normal coating is clear in A and C, and growth lines on the epithecal surface in section can be distinguished in B; mural pores are present in A and B and septal spines are sectioned (particularly top left) in C. D, E, *Tabulopongia japonica* Mori (specimen details as for text-fig. 1C, D). The skeleton is high-Mg calcite with lamellar microstructure, clearly seen in E; the undulose surfaces of the lamellae are responsible for the concentric patterns in the wall in cross-section D; calical spines are well developed, formed of sharply peaked extensions of lamellar tissue, but spicules are not incorporated into the calcitic skeleton. All $\times 50$.

of sclerosponges and stromatoporoids. As many sponges do not reflect the system of exhalant canals in their skeletons, this may not be particularly significant. However, the individuality of favositid corallites strongly argues against the former presence of continuously integrated tissue across the colony surface as in sponges. Under these circumstances, some skeletal reflection would be expected of a sponge-scale exhalant current system—hence Flügel's interpretation of mural pores (Flügel 1976). Mural pore distribution, however, seems to have no pattern to it that would support such an interpretation. Indeed, *Nodulipora* may possess both astrophorae and mural pores with no specific relationship between them (Stel and Oekentorp 1981).

Turning now to recent developments: first, Kazmierczak (1984) has claimed the preservation of desma-like spicules in a Devonian *Thamnopora*. These are rare, approximately parallel-sided, irregularly branched structures preserved in the peripheral part of the skeleton in microgranular low-Mg calcite and lined with micrite. They do not have a convincing spicular morphology. Their appearance, location, and mode of occurrence, however, strongly suggests that they are endolithic borings (Oekentorp 1985; Finks 1986). No convincing records of spicules in favositids are known. On the other hand, this is not a strong argument in itself *against* sponge affinities as several sclerosponges, particularly tabulosponges (Hartman and Goreau 1975; Mori 1976, 1977), do not incorporate spicules into their calcareous skeletons (text-fig. 3D, E).

The second recent development is the report by Copper (1985) of presumed polyps of cnidarian character preserved in Silurian *Favosites* from Anticosti Island. Six well-preserved colonies show small dome-like structures in the centres of calices, with axial pits surrounded by normally twelve concentrically wrinkled radiating segments. In the specimen figured, their development is strikingly wide and uniform. A possible diagenetic origin for the structures has been suggested by Oekentorp and Stel (1985); their reference to a *Protrochiscolithus* figured by Flower (1961, pls. 14 and 16) is misleading, however, as the polypoid appearance of the silicified surface in that case is a direct reflection of the septal structure of the genus. No such interpretation seems possible with Copper's *Favosites*. Oliver (1986) tentatively suggested an origin related to pseudoperculae; this may be important in understanding how calcification might have occurred, but the 'polyps' are most unlike known pseudoperculae in detailed form and regularity. It is a remarkable case of preservation and one not easy to explain, but it is difficult to avoid the conclusion that the structures seen are indeed the remains of polyps. The twelve tentacles of Copper's favositid polyps are intriguing in view of the frequency with which twelvefold septal distributions occur in tabulates (taken here to include the heliolitids: Hill 1981; Scrutton 1979, 1984). However, septal layouts and patterns of insertion in tabulates require further study (Oliver 1986) and it is premature at the moment to set aside the Tabulata as a group characterized by dodecal symmetry (Copper 1985; Oekentorp and Stel 1985).

CONCLUSIONS

There appears to be no single item of evidence in favour of the favositids being sponges, other than a very gross morphological similarity with the tabulosponges. Mural pores and septal structures in favositids both show features more strongly related to other tabulates and to the Rugosa respectively, whilst neither in the broadest sense is exclusively cnidarian. On the other hand, corallite size, and particularly mode of increase and evidence of corallite individuality are all positive cnidarian features. The polyps described by Copper (1985) appear to represent one additional, if spectacular, item on the cnidarian side. The weight of evidence is strongly in favour of favositids being cnidarians and a subgroup of the monophyletic subclass Tabulata (as defined by Scrutton 1984). To maintain any claim for sponge affinities for these extinct organisms, not only must Copper's polyps be explained away, but some new and convincing positive evidence must be forthcoming.

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REFERENCES

- COATES, A. G. and OLIVER, W. A., JR. 1973. Coloniality in zoantharian corals. In BOARDMAN, R. S., CHEETHAM, A. H. and OLIVER, W. A., JR. (eds.). *Animal colonies*, 3-27. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.
- COPPER, P. 1985. Fossilized polyps in 430-Myr-old *Favosites* corals. *Nature, Lond.* **316**, 142-144.
- DIECI, G., RUSSO, A., RUSSO, F. and MARCHI, M. S. 1977. Occurrence of spicules in Triassic chaetetids and ceratoporellids. *Boll. Soc. paleont. ital.* **16**, 229-238.
- DUNBAR, C. O. 1927. Pseudopercula in the tabulate coral *Favosites*. *Am. J. Sci.* **13**, 101-114.
- FINKS, R. M. 1986. 'Spicules' in *Thamnopora*. *Fossil Cnidaria*, **15** (1.2), 22.
- FISCHER, J.-C. 1977. Biogéographie des Chaetetida et des Tabulospongida post-paléozoïques. *Mém. Bur. Rech. géol. minier.* **89**, 530-534.
- FLOWER, R. H. 1961. Montoya and related colonial corals. *Mem. Inst. Min. Technol. New Mex.* **7**, 1-97.
- FLÜGEL, H. W. 1976. Ein Spongienmodell für die Favositidae. *Lethaia*, **9**, 405-419.
- GRAY, D. I. 1981. Spicule pseudomorphs in a new Palaeozoic chaetetid, and its sclerosponge affinities. *Palaeontology*, **23**, 803-820.
- HARTMAN, W. D. and GOREAU, T. F. 1972. *Ceratoporella* (Porifera: Sclerospongiae) and the chaetetid 'corals'. *Trans. Conn. Acad. Arts Sci.* **44**, 133-148.
- 1975. A Pacific tabulate sponge, living representative of a new order of sclerosponges. *Postilla*, **167**, 1-13.
- HILL, D. 1981. Rugosa and Tabulata. In TEICHERT, C. (ed.). *Treatise on invertebrate paleontology, Part F (Suppl. I)*, xi + 762 pp. Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas.
- and STUMM, E. C. 1956. Tabulata. In MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part F*, 444-477. Geological Society of America and University of Kansas Press, New York and Lawrence, Kansas.
- KAZMIERCZAK, J. 1984. Favositid tabulates: evidence for poriferan affinity. *Science*, **225**, 835-837.
- KIM, A. I. 1974. O filogenii i položzenii v sisteme nekotorykh tabulyatomorfnykh koralllov. In SOKOLOV, B. S. (ed.). *Drevnie Cnidaria*, **1**, 118-122. Nauka, Moscow. [In Russian.]
- KIRKPATRICK, R. 1912. On the nature of stromatoporoids. *Nature, Lond.* **89**, 607.
- LAFUSTE, J. 1962. Note préliminaire sur la microstructure de la muraille chez *Favosites* Lamarck (Coelenterata, Tabulata). *C. somm. Séanc. Soc. géol. Fr.* **1962**, 105-106.
- MORI, K. 1976. A new recent sclerosponge from Ngargol, Palau Islands and its fossil relatives. *Sci. Rep. Tohoku Univ.*, 2nd ser. (Geol.), **46**, 1-9.
- 1977. A calcitic sclerosponge from the Ishigaki-shima coast, Ryukyu Islands, Japan. *Ibid.* **47**, 1-5.
- OEKENTORP, K. 1969. Kommensalismus bei Favositiden. *Münst. Forsch. Geol. Paläont.* **12**, 165-216.
- 1976. Beschreibung und Systematik devonischer Favositidae asturiens und Betrachtungen zur Biogeographie nord-spanischer Korallenfaunen. *Ibid.* **37**, 1-129.
- 1985. Spicules in favositid Tabulata—remarks to J. Kazmierczak's interpretation. *Fossil Cnidaria*, **14** (1), 34-35.
- and SORAUF, J. E. 1970. Über Wandporen bei *Favosites* (Fav.) *gothlandicus* Lamarck, 1816 (Coelenterata, Tabulata). *Neues Jb. Geol. Paläont. Abh.* **134**, 283-298.
- and STEL, J. H. 1985. *Favosites*—a true coral. Remarks to P. Copper's discoveries of fossilized polyps. *Fossil Cnidaria*, **14** (2), 28-29.
- OLIVER, W. A., JR. 1968. Some aspects of colony development in corals. *J. Paleont.* **42** (5) (Paleont. Soc. Mem. 2), 16-34.
- 1979. Review: Sponges they are not. *Paleobiology*, **5**, 188-190.
- 1986. Favositids are corals—further remarks. *Fossil Cnidaria*, **15** (1.2), 19-21.
- PHILIP, G. M. 1960. The Middle Palaeozoic squamulate favositids of Victoria. *Palaeontology*, **3**, 186-207.
- RICHTER, D. K. 1972. Authigenic quartz preserving skeletal material. *Sedimentology*, **19**, 211-218.
- ROSS, M. H. 1953. The Favositidae of the Hamilton Group (Middle Devonian of New York). *Bull. Buffalo Soc. nat. Sci.* **21**, 37-89.
- SANDBERG, P. A. 1975. Bryozoan diagenesis: bearing on the nature of the original skeleton of rugose corals. *J. Paleont.* **49**, 587-606.
- SCHOUPPE, A. VON and OEKENTORP, K. 1974. Morphogenese und Bau der Tabulata unter besonderer Berücksichtigung der Favositida. *Palaeontographica*, **A145**, 79-194.
- SCRUTTON, C. T. 1979. Early fossil cnidarians. In HOUSE, M. R. (ed.). *The origin of major invertebrate groups*, 161-207. Academic Press, London and New York.

- SCRUTTON, C. T. 1984. Origin and early evolution of tabulate corals. *Palaeontogr. am.* **54**, 110–118.
- SOKOLOV, B. S. 1962. Gruppa Chaetetida. In ORLOV, U. A. (ed.). *Osnovy paleontologii*, 2. Gubki, Arkheotsiaty, Kishhechnopolostnye, Chervy, 169–176. Izdatel'stvo Akademii Nauk, Moscow. [In Russian.]
- STEL, J. H. 1978. *Studies on the palaeobiology of favositids*, viii + 247 pp. Stabo-All Round B. V., Groningen.
- and DE COO, J. C. M. 1977. The Silurian Upper Burgsvik and Lower Hamra-Sundre Beds, Gotland. *Scripta Geol.* **44**, 1–43.
- and OEKENTORP, K. 1981. *Desmidopora* and *Nodulipora*: misfits in the coral world. *Acta palaeont. pol.* **25**, 403–417.
- SWANN, D. H. 1947. The *Favosites alpenensis* lineage in the Middle Devonian Traverse Group of Michigan. *Contr. Mus. Paleont. Univ. Mich.* **6**, 235–318.
- VACELET, J. 1977. Éponges Pharétronides actuelles et Sclérosponges de Polynésie française, de Madagascar et de la Réunion. *Bull. Mus. natn. Hist. nat. Paris* (3^e sér.), **444**, Zool. 307, 345–368.
- 1985. Coralline sponges and the evolution of the Porifera. In CONWAY MORRIS, S., GEORGE, J. D., GIBSON, R. and PLATT, H. M. (eds.). *The origin and relationships of lower invertebrates*, 1–13. Clarendon Press, Oxford.
- WEST, R. R. and CLARK, G. R., II. 1984. Palaeobiology and biological affinities of Palaeozoic chaetetids. *Palaeontogr. am.* **54**, 337–348.

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