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**TREMACYSTIA, BARROISIA, AND THE STATUS OF
SPHINCTOZOIDA (THALAMIDA) AS PORIFERA**

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ABSTRACT

The Sphinctozoida or Thalamida are extinct marine organisms, which have usually been identified as calcareous sponges. *Tremacystia dorbignyi* (HINDE) and *Barroisia anastomans* (MANTELL) have been studied because of a suggestion (ZHURAVLEVA & REZVOI, 1956) that spicules described from these species by HINDE (1882, 1883) and RAUFF (1913) are not genuine. Spicules found in both species are illustrated photographically; the spicules of *T. dorbignyi* are figured partly from separate mounts from which HINDE drew his figures. The supposed synonymy of *Barroisia* STEINMANN and *Tremacystia* HINDE is also considered; they are held to be separable genera, distinguished by structure of the chamber walls, and by *Tremacystia* being apparently pseudosiphonate when any central siphon is present.

INTRODUCTION

The Sphinctozoida (STEINMANN, 1882, as Sphinctozoa), or Thalamida (DE LAUBENFELS, 1955), are extinct marine organisms, found in rocks of Early Carboniferous to Late Cretaceous age. They are usually regarded as calcareous sponges, though their gross morphology is unlike that of any living Calcareous skeleton forms thin-walled hollow chambers, the walls of which are usually porous, though imperforate in some genera. The chambers are commonly arranged in linear series and then traversed by an axial passage, in the form of a series of simple foramina between successive chambers, or of a tubular axial siphon. Alternatively, some genera have the chambers arranged around an axial channel, or without regular order. Spicules like those of living Calcareous have been described from the Cretaceous species *Tremacystia dorbignyi* (HINDE) (HINDE, 1882, as *Verticillites dorbignyi*; 1883) and *Barroisia anastomans* (MANTELL) (CARTER, 1883, as *Verticillites anastomans*; RAUFF, 1913), though none are known from other genera.

The poriferan nature of Sphinctozoida recently has been rejected by Russian authors, who believe that the spicules of the two species cited are not genuine (ZHURAVLEVA & REZVOI, 1956). They wrote:

All the individual references to "spicules" in the Thalamida are rather antiquated (in recent studies they are not mentioned and photographs and drawings only confirm their absence). It is quite possible that HINDE and others mistook for spicules some of the structural formations which are obtained in the distinct concentrically-fibrous structure of the chamber walls. If the concentric stratifications of the wall around adjacent canals are in contact with one another, then between every three canals there will remain a space devoid of the concentric structure. Slightly coloured by organic material, and of a different crystalline structure, this space, when its contours are drawn, may present a figure very similar to a three-rayed spicule. This is how "spicules" were oriented in the Thalamida by Hinde, Rauff, and others. The fibres of the wall themselves have nothing in common with the true spicules of the Calcareous, including the Pharetrones.

Following this contention, they compared the Sphinctozoida with the older Archaeocyata, to

which they believed the former may prove to be related. A similar view was expressed in the *Osnovy Paleontologii* (ZHURAVLEVA, 1962), in which the Sphinctozoida (as Sphinctozoa) were placed outside the Porifera as a class *incertae sedis*.

This interpretation of species described by HINDE and RAUFF is not in accordance with the characters known to me from material which includes HINDE's original specimens and preparations of *Tremacystia dorbignyi*, and examples of *Barroisia anastomans* from the same locality as RAUFF's specimens. HINDE's figures of spicules of *T. dorbignyi* (1882, pl. 11, fig. 1-24; 1883, pl. 24, fig. 1c-o) were not based on gaps in the skeletal structure, but on preparations of individual spicules removed from the skeleton and mounted separately. The spicules are readily photographed, and are refigured here photographically from HINDE's specimens and other material. Those of *B. anastomans* are only seen in sections, but the structure described by CARTER and RAUFF is clearly present in the specimens examined.

The material studied also throws light on the question of whether *Barroisia* STEINMANN, 1882, and *Tremacystia* HINDE, 1883, should be regarded as separable (DE LAUBENFELS, 1955) or synonymous (SEILACHER, 1961), and on some new features of *Tremacystia dorbignyi* which are relevant in this context.

In preparing this paper, I have had the kind permission of the Trustees and Dr. H. BALL of the British Museum (Natural History) to study material in their charge, including HINDE's specimens and preparations which were found for me by Mr. S. WARE. Registration numbers cited in connection with HINDE's material refer to the catalogue of the Paleontology Department of the British Museum (Natural History). Mr. J. WENDLAND of this department provided the figured Cenomanian specimen of *Tremacystia dorbignyi*.

This paper provides background information for the revised edition of *Treatise on Invertebrate Paleontology*, Part E, which is now in preparation.

DESCRIPTION OF MATERIAL

TREMACYSTIA DORBIGNYI (Hinde), 1882

Figures 1,1-11 and 2,1-6

The material studied comprises HINDE's figured types S.8785 (1882, pl. 10, fig. 2; 1883, pl. 34, fig. 1) and S.8786 (1882, pl. 10, fig. 1; 1883, pl. 34, fig. 2), slide preparations S.1420-1426, and other specimens S.8787 and S.8791-8800, from the Upper Greensand of Warminster, Wiltshire, England; additional specimens from this locality; and two specimens from the Cenomanian Wilmington Sand of Wilmington, Devonshire, England.

The skeleton of the chamber wall is certainly spicular in this species. The specimens studied show varying states of preservation, but all contain observable spicules. There are two main kinds of spicules, as described and figured by HINDE (1882, p. 192-195; pl. 11, fig. 1-24; 1883, p. 172, pl. 34, fig. 1c-o); both can be removed and mounted separately (Fig. 1,1-6, 2,1-6), as HINDE also stated (1882, p. 192). The main mass of the skeleton is formed by small densely matted "filiform" diactins or subtriactins (HINDE, 1882, pl. 11, fig. 14-15, 18-23; 1883, pl. 34, fig. 1m-o) (Fig. 2,3,4), arranged around the skeletal pores and commonly also curved around them. These spic-

ules are essentially sagittal triactins, with the unpaired ray reduced to a small rudiment or lacking altogether; among them typical triactins and linking intermediates can be found as occasional variants (Fig. 2,5). The spicules are arranged with the rudiment of the unpaired ray directed away from the skeletal pore whenever present. The external surface of the skeleton shows much larger sagittal triactins and tetractins (HINDE, 1882, pl. 10, fig. 7; pl. 11, fig. 1-8; 1883, pl. 34, fig. 1c-k) (Fig. 1,3-11; 2,1,6; 3; 4). These spicules occur with three rays at the surface, and the fourth directed inward when present. In some parts, single examples may occur in the center of a group of three pores, but this arrangement is not general; groups of spicules may be crowded together with no pores between them. In parts spicules are arranged with the paired rays aligned transversely and the third pointing downward, this arrangement being specially prevalent around the margins of terminal oscula or internal foramina (which originate as oscula) (Fig. 1,11). Spicules which are smaller than the main ones may also be seen, among or under them; in some of these smaller examples, the paired rays are

convex away from the third ray instead of toward it, producing a pickaxe-like spicule (HINDE, 1882, pl. 11, fig. 5; 1883, pl. 34, fig. 1i) (Fig. 2,2).

Other variations in the present structure of the skeleton affect the clarity with which spicules are seen. In the clearest state, both types of spicules are visible individually, and can be separated. No cementing material is apparent, though fine granular calcite adheres to the surfaces of spicules (Fig. 1,1-6, 2,1-6). In a modified condition, the filiform spicules are partly or completely replaced by coarser granular calcite, in which the larger spicules are imbedded. Lastly, the whole of the skeleton may now consist of granular calcite, without evident spicules. These variations can occur between different parts of a single specimen. They appear to mark progressive breakdown of the spicules, which is unlikely in life and therefore probably is diagenetic.

No other part of the skeleton was specially described by HINDE, but he noted the presence of an imperforate siphonal tube in one of his types (1882, p. 192). A siphon-like tube occurs in the terminal chamber of his fragmentary specimen S.8800; in addition, the underlying chamber, with no siphon, contains remains of a laterally placed vesicular diaphragm. Both of these structures show small sagittal triactins on their surfaces. Those of the outside of the "siphon" have the unpaired ray subequal to about half the length of the paired rays, and usually directed downward. The inside shows spicules with transversely aligned paired rays, and the unpaired ray a downward directed rudiment (Fig. 1,9). The vesicular diaphragm in the chamber below shows spicules like those of the outside of the "siphon," so far as its structure is observable.

BARROISIA ANASTOMANS (Mantell), 1848

Figure 2,7-9

The material studied consists of thin sections of samples of a calcareous lens in the Yellow Sponge Gravel of Faringdon Pit, Faringdon, Berkshire, England, showing portions of several *Barroisia* colonies (Fig. 2,7-9). This material was chosen for its favorable preservation and ease of sectioning compared with the normal loose gravel. The age of the deposit is latest Aptian.

According to CARTER (1883, p. 26), the skeleton of the chamber wall contains an internal layer of triactinal spicules, and an external crust

with pinlike monaxons, arranged in a "funnel-like" manner around the perforating radial canals with their tylote ends outward. This structure was subsequently verified by RAUFF (1913, p. 109, fig. 12). Both types of spicules can be seen in the material studied, though they cannot be isolated like those of *Tremacystia dorbignyi*. As shown by RAUFF, the spicules are imbedded in a finely fibrous groundmass, which extends on both sides of the triactin layer though it is thicker externally. The triactins lie more or less tangentially, with their rays extending between adjacent radial perforations (*see* RAUFF, 1913, pl. 2, fig. 9); their arrangement is, however, less regular than in RAUFF's idealized figure (1913, fig. 12), and in part they appear to form simply an irregular feltwork. The monaxial spicules were seen in all sections examined, though RAUFF's diagram is idealized as regards their arrangement. Occurrence of filiform spicules like those of *T. dorbignyi*, claimed by HINDE (1883, p. 182), was not confirmed.

VACELET (1964, p. 108) has recently suggested that the pinlike monaxons may be really siliceous tylostyles, whose presence is due to boring of the skeleton by the demosponge *Cliona* GRANT. If these spicules were those of a *Cliona*, it ought to be possible to recognize the presence of borings, and of a difference between aspicular skeletal material and secondary fillings, with the spicules restricted to the latter. The material studied shows neither recognizable borings, nor restriction of the monaxons to parts which could be regarded as filled borings; the only perforations are the radial canals, and the "tylostyles" occur through the whole of the intervals between canals. One would also expect *Cliona* borings to extend through the whole chamber wall, not just an external part of it. Moreover the arrangement of the spicules, with the tylote end outward, is opposite to that usual with demosponge tylostyles, including those of *Cliona* when they show any special arrangement. It, therefore, seems best to treat these spicules as produced by *Barroisia anastomans* itself. A further possibility is that loose *Cliona* spicules might be taken up and used by *B. anastomans*, in the way that some modern sponges may take up and employ foreign spicules; but this is a speculation only, and the fact that the spicules show a generally constant arrangement could be counted against it.

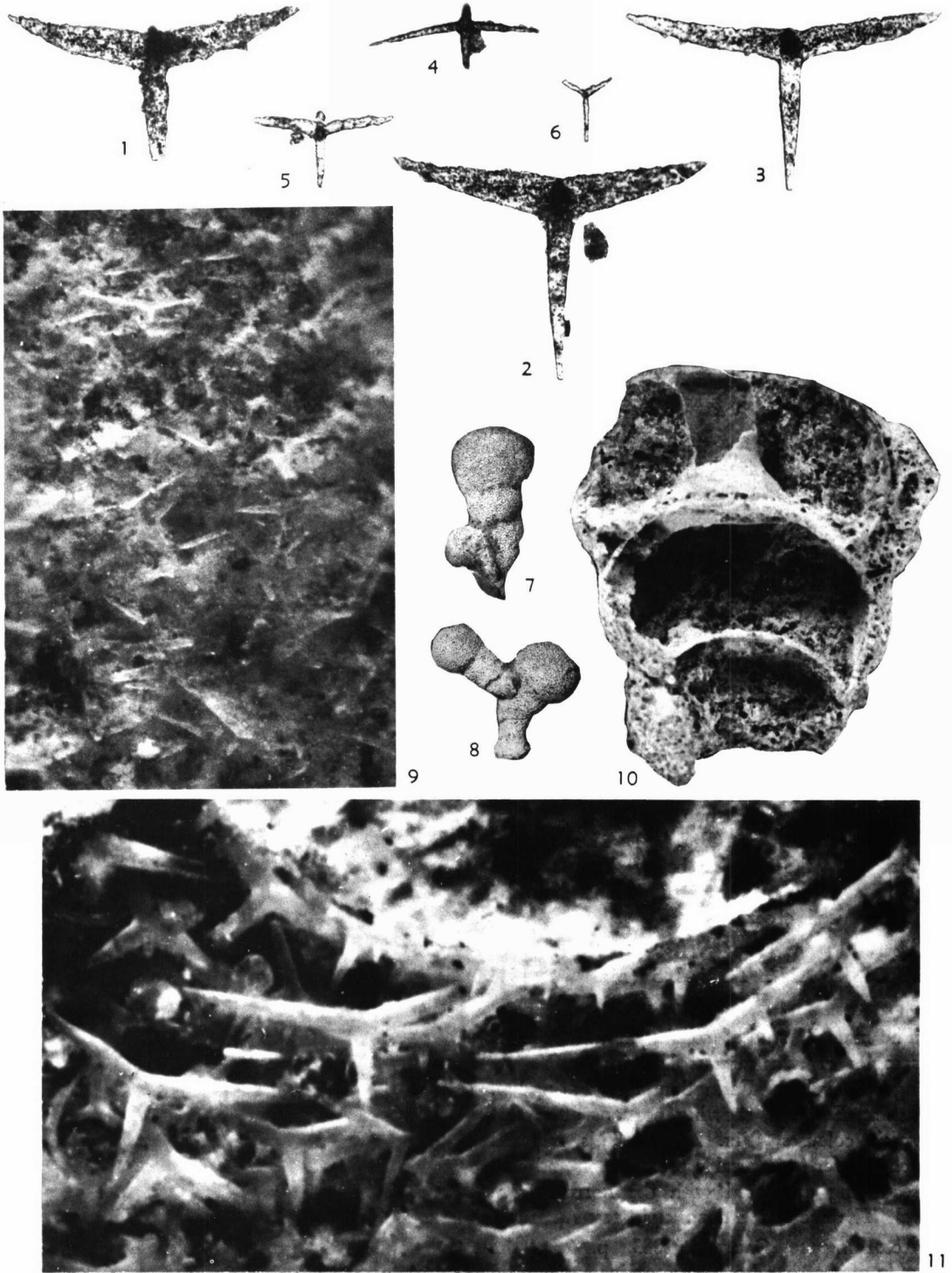


FIG. 1. *Tremacystia dorbignyi* (HINDE). [Explanation on facing page.]

DISCUSSION

First, the specimens described above show clearly that the spicules described by HINDE and by RAUFF in *Tremacystia dorbignyi* and *Barroisia anastomans* are not imaginary. There are no grounds for ZHURAVLEVA and REZVOI's suggestion that HINDE mistook spaces in a fibrous structure for spicules in *T. dorbignyi*. HINDE himself stated that the spicules could be removed and mounted separately (1882, p. 192), and that his figures showed detached examples (1882, p. 204; 1883, caption of pl. 34). The examples here figured (Fig. 1,1-6, 2,1-6) are from HINDE's slides, with his handwritten label giving the original (HINDE, 1882) name "*Verticillites d'orbignyi*." Even the supposed concentrically fibrous structure consists of separable spicules (Fig. 2,2-4). The siphon-like structure and diaphragm in HINDE's S.8800 also contain spicules, though he does not mention them specially. The spicules of *B. anastomans* might be thought to be less certainly genuine, if only this species were studied, since they cannot be extracted and seen separately; but comparison with *T. dorbignyi* leaves no reasonable doubt of their existence. Their preservation is also identical to that of spicules of accompanying Pharetronida (e.g., *Raphidonema* HINDE) whose status as sponges is not doubted. The triactinal spicules may form an irregular feltwork, in which their form is clearly not determined by the arrangement of canal spaces (Fig. 5). The monaxons also seem to be genuine spicules, not fibers; they are well defined parallel-sided needles, with the distal end tylote in at least some examples. There are no good reasons for thinking them foreign.

The character of the skeleton thus provides no grounds for claiming that *Tremacystia dorbignyi* and *Barroisia anastomans* are not calcareous sponges. Their status as sponges is entirely acceptable, except that it cannot be certain without knowledge of the soft parts. The same must apply

to the other *Sphinctozoida*, unless one can believe that the group has included both sponges and homeomorphic forms of different origin. Considering its general uniformity, this does not seem likely.

To explain the seeming absence of spicules in other *Sphinctozoida*, there are several possibilities.

1) The spicules may be destroyed by recrystallization, except in unusual circumstances. Specimens of *Tremacystia dorbignyi* show gradational passage from a state in which all spicules are preserved to conditions in which the smaller spicules or all spicules are replaced by granular calcite.

2) The large spicules of *Tremacystia dorbignyi* are exposed on the surface, but those of *Barroisia anastomans* are covered by the external sclerosome, and only seen in sections, without which their presence is not detectable.

3) The spicules may have normally been smaller than the large spicules of *Tremacystia dorbignyi*, and, therefore, less readily preserved. When poorly preserved, a skeleton composed of small matted filiform spicules like those of *T. dorbignyi* might also show a concentrically fibrous structure (see ZHURAVLEVA & REZVOI, 1956), without possibility of recognition that the fibers were spicules.

4) As a speculation only, if the spicules were secreted as aragonite (instead of calcite, as in normal Calcarea), they would be specially susceptible to destruction by recrystallization.

5) The rigid skeleton may sometimes have been wholly aspicular, as in the living Pharetronida *Murrayona* KIRKPATRICK and *Petrobiona* LÉVI & VACELET. VACELET (1964, p. 108-109) suggests this for all *Sphinctozoida*; but both *Tremacystia dorbignyi* and *Barroisia anastomans* had spicules in their rigid parts, and this is still the case in *B. anastomans* if only the triactins are counted. The spicules of *B. anastomans* are, how-

Specimens are from Cretaceous Upper Greensand of Warminster, Wiltshire (1-10), and Wilmington Sands, Devonshire (11), England.

1-6. Detached spicules, from two of HINDE's slide preparations (BMNH S.1245, S.1246), $\times 100$, comprising (1-3) large sagittal tetractins, photographed with the unpaired proximal ray toward the camera; (4) small sagittal tetractin with the paired rays reflected; (5, 6) other small tetractins.

7-8. Specimens (BMNH S.8785, S.8786) figured by HINDE, $\times 1$.

9-10. HINDE's specimen (BMNH S.8800) showing (9) siphon-like tube in top chamber and part of vesicular diaphragm attached to left side and roof of second chamber, $\times 4$, and (10) interior of siphon-like tube showing spicules, $\times 100$.

11. Oscular margin of specimen from Wilmington Sands, Devonshire, showing orientation of sagittal triactins and tetractins, $\times 60$.

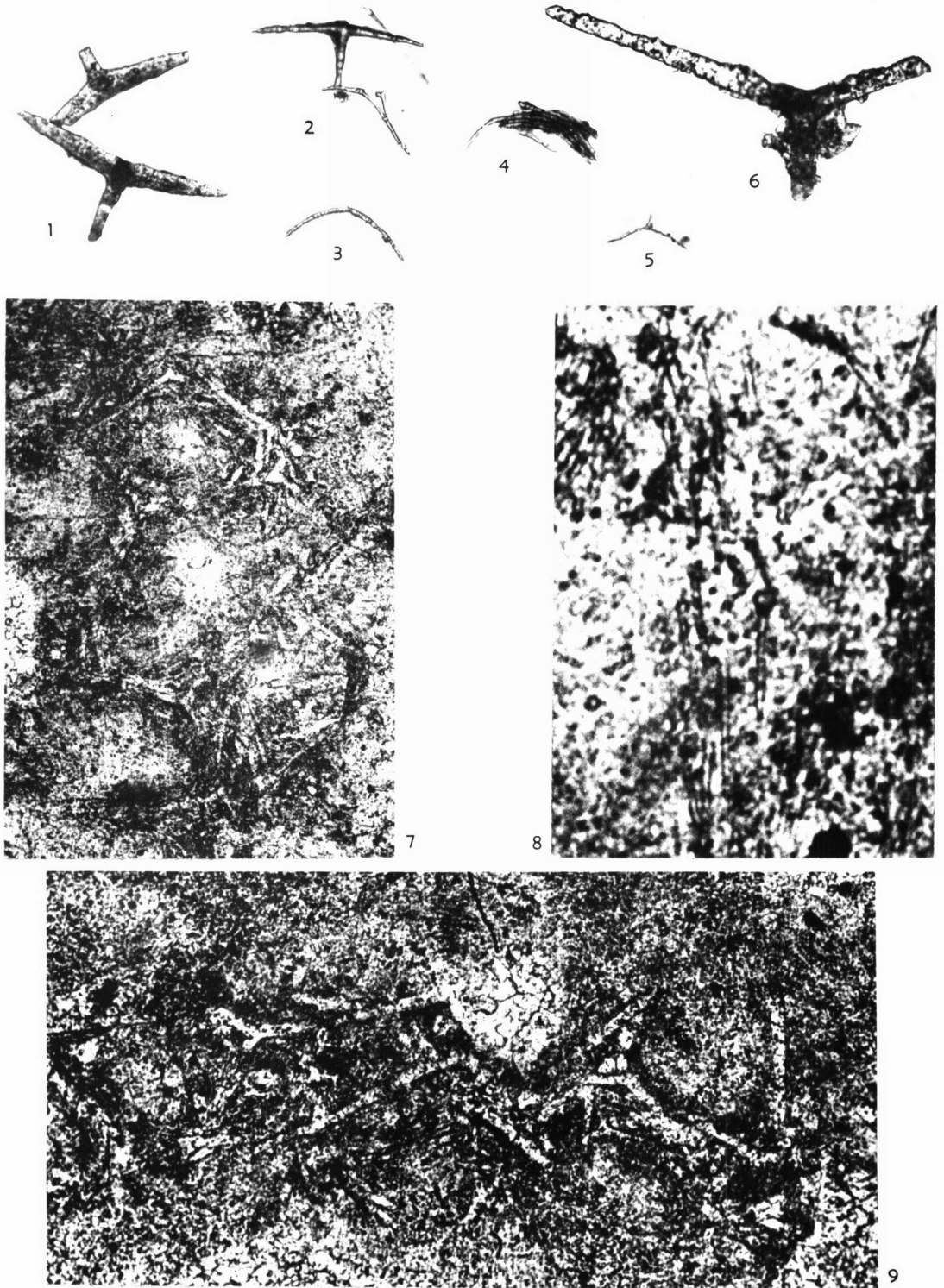


FIG. 2. *Tremacystia dorbignyi* (HINDE) (1-6) and *Barroisia anastomans* (MANTELL) (7-9). [Explanation on facing page.]

ever, enclosed in a calcareous groundmass, or "sclerosome," which implies the secretion of aspicular material around them. It is certainly possible that such material formed the whole rigid skeleton in some genera.

A possible relationship of the Sphinctozoida to the Archaeocyatha is a separate problem, which is outside the scope of this paper. In brief, it is by no means ruled out by the presence of spicules in some Sphinctozoida; and any demonstrable connection would be evidence that the Archaeocyatha were Porifera. In any case, the presence of rigid aspicular structures in *Murrayona* and *Petrobiona* (VACELET, 1964) shows certainly that comparable aspicular structures may belong to calcareous sponges.

BARROISIA AND TREMACYSTIA AS GENERA

HINDE's genus *Tremacystia* was proposed one year later than STEINMANN's *Barroisia*, with *Barroisia* STEINMANN (1882) listed as a synonym (HINDE, 1883, p. 171), and with the name *Barroisia anastomans* listed in synonymy under HINDE's name *Tremacystia anastomans* HINDE, 1883, p. 175). Hence *Tremacystia* HINDE can be regarded as a junior synonym of *Barroisia* STEINMANN, though HINDE named no type species. This view is followed by SEILACHER (1961, p. 749-750). DE LAUBENFELS (1955, p. E101), however, listed both genera separately, with *Verticillites d'orbignyi* HINDE, 1882, selected as type species of *Tremacystia* HINDE, 1883. This leaves both names available, since the type of *Barroisia* is *B. anastomans*.

DE LAUBENFELS gave no reason for thinking that the two genera are separate, defining *Tremacystia* by "Resembles *Barroisia*"; but he may have relied on the different spiculations described by HINDE and RAUFF, to define which involves

too much detail for the style of diagnosis he adopted. These differences, and another (see below), support separation of the two genera.

1) In *Tremacystia dorbignyi*, the large triactins and tetractins are exposed on the surface of the skeleton. In *Barroisia anastomans*, they occur at about two thirds of the depth of the skeletal wall, and are covered externally by calcareous material containing bundles of monaxons. There is no trace of this stratum in *T. dorbignyi*, even in material showing external molds of the skeletal surface.

2) In *Tremacystia dorbignyi*, the large spicules are mainly tetractinal; in *Barroisia anastomans*, they appear to be all triactinal.

3) In *Tremacystia dorbignyi*, the large spicules are typically sagittal; those of *Barroisia anastomans* appear to be simply equiradiate where their character can be recognized.

4) In *Tremacystia dorbignyi*, the main thickness of the skeleton is formed by matted filiform spicules, which underly the large forms. This stratum appears to be lacking in *Barroisia anastomans*; it was not found by RAUFF, nor seen in any of the specimens now examined though monaxons of the external zone were clearly seen.

5) *Barroisia anastomans* has a well developed siphon, which is normally present in all chambers but early ones, or the first few in lateral branches which have budded from the surface of an older part. The development of the siphon is ambisiphonate, with the segments growing upward and downward from the foraminal margins of the chamber walls. A ring of large holes is left centrally, where the two halves grow together. *Tremacystia dorbignyi* appears to be basically cryptosiphonate, with a siphon-like tube (but not a true siphon) present in some specimens. Where the fossils are broken across chambers, no central tube is seen except in the last chamber of HINDE'S S.8800. This tube is very thin-walled, by com-

Specimens of *Tremacystia dorbignyi* (1-6) are from Cretaceous Greensand at Warminster, Wiltshire, England; those of *Barroisia anastomans* (7-9) are from Yellow Sponge Gravel (late Aptian (Lower Cretaceous) at Farlington, Berkshire, England.

1-6. Detached spicules of *Tremacystia dorbignyi* (HINDE), from HINDE's slide preparations BMNH S.1245 and S.1246, comprising 1) two medium-sized sagittal tetractins, with proximal rays towards the camera; 2)

a "pickaxe-like" triactin, with the paired rays reflexed, and two filiform spicules; 3) a single filiform diactin; 4) a group of adherent filiform spicules; 5) filiform triactin; and 6) a large sagittal triactin, incomplete, $\times 100$.

7-9. Sections of *Barroisia anastomans* (MANTELL) comprising (7) tangential section showing traces of spicules in middle skeletal layer, $\times 100$; (8) monaxons of outer skeletal layer, $\times 300$; and (9) transverse section showing traces of irregularly felted spicules, $\times 170$.

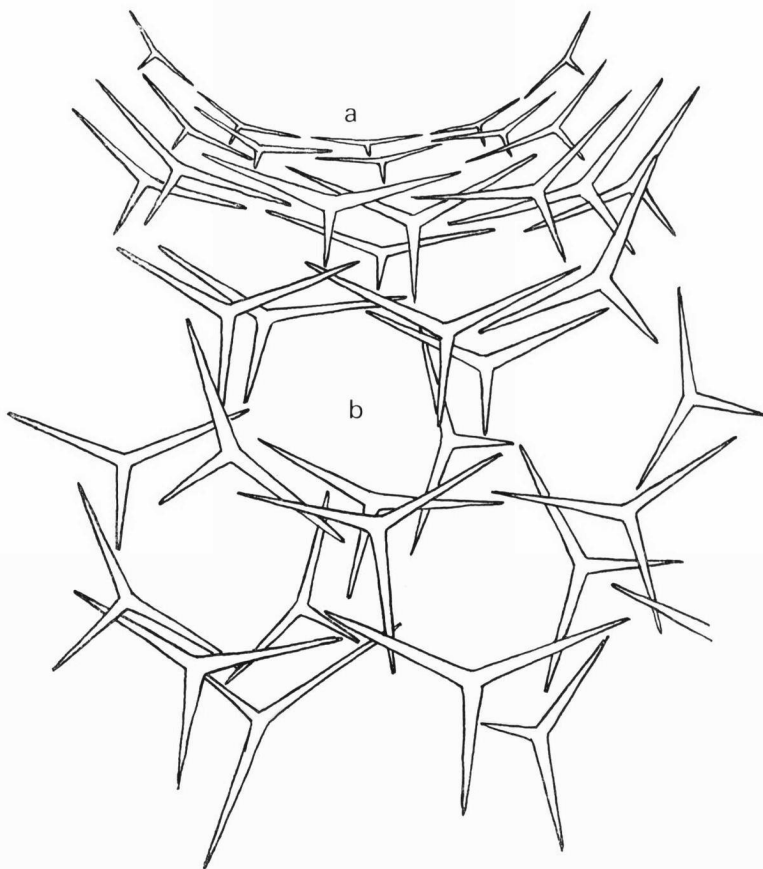


FIG. 3. Diagram showing arrangement of large spicules on external surface in *Tremacystia dorbignyi* (HINDE); *a*, oscular margin; *b*, position of radial canal.

parison with the rest of the skeleton and with a normal *Barroisia* siphon, and is completely imperforate. The top is attached to the roof of the chamber, just outside the foraminal margin; the lower end spreads out as a sheet on the wall of the underlying chamber, covering over the pores, and has clearly not grown from the foraminal margin. The underlying chamber has no central tube, but contains parts of a vesicular lateral diaphragm. The spicules seen in these structures are similar, and unlike those of the external wall; hence the two appear homologous. From this it seems likely that both are essentially vesicular structures (see SEILACHER, 1961, p. 742, fig. 4), of which one has happened to grow in a siphon-like form.

Some of these differences could be only apparent; in particular, lack of the external stratum in *Tremacystia dorbignyi* could be due to its hav-

ing been lost, or not hardened during life. At present, however, the two species should not be referred to one genus.

A further possibility is that *Tremacystia* HINDE should be identified with *Sphaerocoelia* STEINMANN (1882, p. 162), as is done by ZHURAVLEVA (1962, p. 78). *Sphaerocoelia* [*Thalamopora*] *michelini* (SIMONOWITSCH), Cenomanian type species of *Sphaerocoelia*, agrees with *T. dorbignyi* in habitus, in chamber size, in having the chamber walls perforate, and in being cryptosiphonate if the siphon-like structure described from *T. dorbignyi* above is interpreted correctly. A Cenomanian sponge called *S. incrassata* (D'ORBIGNY) by DOUVILLÉ (1914, pl. 12, fig. 1-3) is also similar in appearance, and was found to show vesicular tissue in certain chambers (*ibid.*, p. 400). It seems clearly possible that these nominal species

are identical biologically, but different authors give different accounts of the spicules. STEINMANN (1882, p. 162) found monaxons only, and he was followed (copied?) by DE LAUBENFELS (1955, p. 102, diagnosis of Sphaerocoelidae STEINMANN). DUNIKOWSKI (1883, p. 38) listed triactins, tetractins, and monaxons, but gave no indication of the form and arrangement of the monaxons, which need to be known for comparison with *T. dorbignyi*. Most recently, SEILACHER (1961, p. 775) men-

tioned triactins only. In view of this, one cannot be sure that the nominal type species are identical, without reference to the holotype of *S. michelini*. This holotype has not been available to the writer, and in any case may not show the spicules. It therefore seems better to retain *Tremacystia* HINDE as a separate genus for the present.

The following diagnoses of *Barroisia* and *Tremacystia* are suggested.

Order SPHINCTOZOIDA Steinmann, 1882

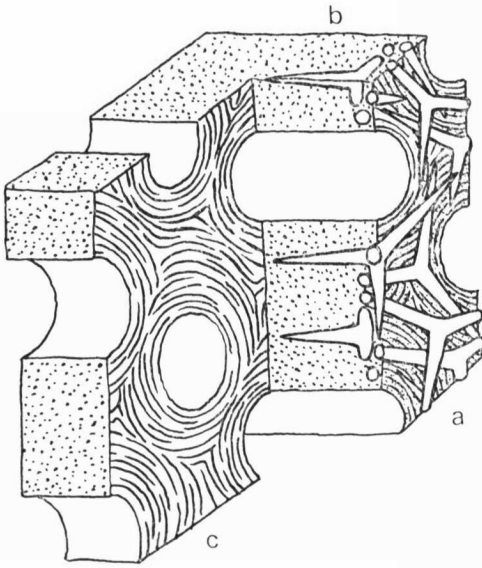


FIG. 4. Diagram of structure of chamber walls in *Tremacystia dorbignyi* (HINDE); *a*, external surface; *b*, outer zone with proximal rays of external tetractins surrounded by "filiform" spicules; *c*, inner zone composed of "filiform" spicules only. [Compare with Fig. 1 (external surface of *T. dorbignyi*) and Fig. 3 (structure of chamber wall in *Barroisia anastomans*).]

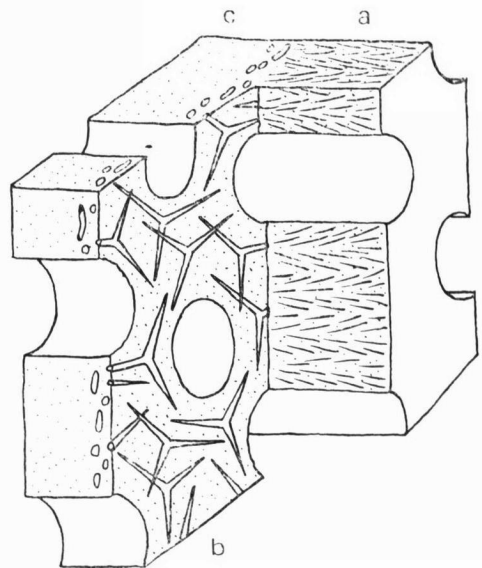


FIG. 5. Diagram of structure of chamber wall in *Barroisia anastomans* (MANTELL); *a*, external zone with pinlike monaxons in aspicular cement; *b*, median zone with felted triactins in aspicular cement; *c*, aspicular internal zone. [Compare with Fig. 4 (*Tremacystia dorbignyi*).]

Family SPHAEROCOELIDAE Steinmann, 1882

Genus BARROISIA Steinmann, 1882

Diagnosis.—Sponge, simple or forming branched colonies; chambers subglobular to discoidal; ambisiphonate, each siphonal segment with central ring of perforations. Chamber wall three-layered: outer layer with small pin-headed monaxons in calcareous cement, arranged in radiating groups with their tylote ends outward; middle

layer with larger triactins, arranged tangentially; inner layer without evident spicules (Fig. 5). *Cret.*, Eng.

Genus TREMACYSTIA Hinde, 1883

Diagnosis.—Sponge, simple or branching; chambers subglobular; single intercameral foramina, but no true siphon; some chambers may contain vesicular diaphragms, or similar structure

forming local siphon-like tube. Large sagittal triactins or tetractins on outside of chamber wall, tetractins with one ray running inward; these

spicules underlain by densely matted filiform diactins or subtriactins, which encircle radial canals (Fig. 3, 4). *Cret.*, Eng.

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