FURTHER STUDIES ON OCTOCORALLIA

by

J. VERSEVELDT

With 9 text-figures

INTRODUCTION

This paper is to be regarded as a continuation of my previous publication (Verseveldt, 1940[1]). Some three species, sufficient material of which for an anatomical examination was available, had then to remain undiscussed; they are: *Semperina rubra* Köll., *Anthothela macrocalyx* (Nutt.) (= *Suberia macrocalyx* Nutting (1911) = *Semperina macrocalyx* (Nutt.) Kükenthal (1919)) and *Sibogagorgia weberi* Stiasny, which species have been examined by me in the same way as formerly the others.

It has become clear to me that the second of the species mentioned cannot be considered as belonging either to the genus *Suberia* Studer or the genus *Semperina* Köll. A close relationship with *Anthothela grandiflora* (M. Sars) caused me to decide on the name *Anthothela macrocalyx* (Nutt.) (cf. chapter II, § 8).

The results of my investigations make it necessary to refer to my views previously mentioned (Verseveldt, 1940) with regard to the canal system and the taxonomy. For both in *Semperina rubra* and *Sibogagorgia weberi* the canal system differs in some degree from that of the species examined before. For we see that in the medulla in the tips of the branches of *Semperina rubra* there do occur many small and even a single large solenium, whereas for the family Anthothelidae Broch I rejected the presence of medullary canals in the terminal parts. So while in all the species examined up till now the medullary canals cease somewhere in apical direction, in *Semperina rubra* we find them even as far as in the ends of the branches. In my opinion this is not of radical importance, 1° because the larger medullary canals, which in the more basal parts occur in larger numbers, prove to be scarce in the terminal parts, and 2° because the medullary

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[1] In this publication of 1940 (contents and p. 90 sq.) instead of *Solenocaulon sterroclonium* is to be read *Solenocaulon sterroklonium*.

canals cannot be looked upon as continuations of the coelenterons (cf. diagram, fig. 1). Moreover the gastral cavities are short and wide, the circle of boundary canals forms a sharp boundary between cortex and medulla, so that also *Semperina rubra* must be considered as belonging to the family Anthothelidae. Indeed, *Semperina rubra* shows so much resemblance with *S. brunnea* as regards habitus, spicules, position of the zooids, relation between cortex and medulla, etc., that it would not be justified to separate the two species. The diagnosis given by me (Verseveldt, 1940, p. 137) of the family Anthothelidae Broch must then be emended as follows: "In the tips of the branches the medulla may be perforated by solenia, but in that case they are not continuations of the coelenterons".

Following in the tracks of Stiasny (1937) I had provisionally looked upon *Sibogagorgia weberi* as belonging to the family Paragorgiidae Auriv. Now that I have had the opportunity to examine this species too, my opinion is that it belongs to a new family, which I suggest to call the Sibogagorgiidae. In chapter III, § 8, I have explained my grounds for this opinion.

I received the material collected by the "Siboga" Expedition again from the Zoological Museum at Amsterdam; my heartfelt thanks to Prof. Dr. L. F. de Beaufort, Director of this Museum, for the trust put in me.

I. SEMPERINA RUBRA KÖLL.

Semperina rubra was first recorded by Kölliker (1870) as a new genus and species of the Briareacea. His description and figures give a very good picture of the characteristic features of this coral. From the enlargements it appears that the stem, a transverse section of which is represented in his fig. 6 on pl. III, is about 8 mm in diameter; in my material the thickest stem is 6 mm in diameter.

Nutting's (1911, p. 11), Kükenthal's (1919, p. 52 sq.; Kükenthal himself did not examine *S. rubra*) and Stiasny's (1937, p. 36 sq.) publications do not give rise to preliminary remarks.

§ 1. The material. The same material, already described by Nutting (l.c.) and Stiasny (l.c.) and which was collected by the "Siboga" Expedition, Station 258, was reexamined by the present writer. Series of longitudinal and transverse microtome sections were made of some fragments of a stem, 4 mm in thickness, and of the terminal part of a branch, and moreover series of free-hand sections of other parts.

§ 2. Cortex and medulla. One of the characteristics of the genus *Semperina* is, that the zooids only occur at the front and the lateral sides of the branches, whereas they are lacking at the back. Connected with this is the conspicuous difference in thickness of the cortex at the different sides of the branches: where the zooids are, the cortex is thick, for the rest it is thin. Thus, for instance, in a branch of 4 mm in diameter the cortex at the front was about 1.2 mm and at the back 0.3 mm; in the stem of 6 mm in diameter the cortex was still thinner (0.13 mm). Consequently the medulla is situated excentrically.

The boundary-line between medulla and cortex is rather clearly indicated by the difference in colour, for the cortex contains red spicules and those of the medulla are colourless, although here there are also red spicules in irregularly distributed strings and groups (cf. Kölliker, pl. III fig. 6). On the boundary of cortex and medulla there are boundary canals, but they are often so wide and so far between that they do not always exactly show the boundary between the two layers in microtome sections. There is horny substance in the medulla in the form of sheaths round the spicules, while in the cortex this substance is lacking; however, this difference does not show a clear boundary in the sections either, because the quantity of horny substance gradually decreases in the outer medulla-layer. Finally in the cortex we see a denser network of tiny canals, while the zooids also lie entirely in the cortex.

§ 3. The zooids. The anthosteles are hardly or not developed at all, so that the zooids do not protrude like hillocks, being totally drawn in. Thus Kükenthal (1919, p. 50) is not right in stating as one of the characteristics of the genus *Semperina*: "Polypenkelche sind stets vorhanden".

The anthocodiae may be entirely retracted into the gastral cavities; in a great many zooids, however, they still protrude and clearly contrast with the red cortex by their pale yellowish colour. They are strongly armed with spicules, as already stated by Nutting.

The coelenterons are large and reach as far as the medulla with a wide, flat base. This also holds good with regard to the terminal zooids which consequently do not continue into medullary solenia (cf. diagram, fig. 1). They are connected on all sides with the tiny cortical canals (to be discussed later on), not with the wide boundary canals or with the medullary solenia.

The median plane usually stands vertically with the ventral aspect turned towards the top, i.e., adaxially; occasionally its position is slanting.

§ 4. The canal system. Again we can distinguish between cortical, boundary and medullary canals.

1. The cortical canals. a. At the back of the branches, where the cortex is thin, comparatively wide canals occur. Most of them are 0.35-0.50 mm in breadth and 0.11-0.18 mm in height, some of them, however, are nar-

rower. From the dimensions it follows that they are strongly flattened. They are rather straight and run in a longitudinal direction with only an occasional bifurcation, so that they are scarcely connected with one another. There is not much connection with the boundary canals either. The cortex is divided by these solenia into two layers, an outer layer of only 0.08 mm thickness, in which small red spicules occur in not more than one or two layers, and an inner layer, which is thicker. In the very thin cortex of the stem the wide cortical solenia are lacking; only narrower solenia occur, mostly alternating with the much wider boundary canals.

In *Semperina brunnea* Nutt. the cortical solenia are lacking at the back (cf. Verseveldt, 1940, fig. 17).

b. At the front and the lateral sides, where the cortex is thick, a great many more canals occur, which, however, show a much more intricate course, so as to be difficult to represent in a simple diagram. It seems the best course to distinguish between wide and narrow solenia and to trace the course and the mutual connections between them in view of the diagrams, figs. 1 and 2. It appears that at a distance of approximately 0.13 mm under the ectodermal surface there are somewhat wider solenia (fig. 2, a), forming a more or less distinguishable wreath. They are 0.06-0.08 mm in diameter and run in a longitudinal direction, now and then bifurcating and sometimes connected by transverse canals; they may also run into the coelenterons through narrow canals. Deeper in the cortex these wider solenia are also met with.

The second type of canals is extremely narrow, the lumen varying from 0.01-0.03 mm (fig. 2, b). They run irregularly through the cortex like a dense network; they occur equally in the outer cortical layer of 0.13 mm, mentioned above. They are connected with the wide cortical solenia and frequently pass into the coelenterons. Other canals, on the other hand, run parallel with these wider solenia or with the coelenterons or with the boundary canals without passing into them, so the lumina remain separated by a very thin membrane.

2. The boundary canals. In transverse sections these are mostly oval, 0.10-0.65 mm in breadth and 0.08-0.40 mm in height. These figures are indicative of a great variation in lumen. Especially at the back of the branch large boundary canals occur. They are practically straight canals, occasionally bifurcating or connected by transverse canals (fig. 2, c). This system of boundary solenia is connected with the larger cortical canals both at the back and at the front and lateral sides on the one hand and with the large medullary canals on the other. But the boundary canals are never seen to be

passing into the coelenterons. Neither are they connected with the narrow cortical solenia.

3. The medullary canals. Here again we must distinguish between wide and narrow canals. The wide canals are round or oval in shape and are from 0.2-0.6 mm in diameter. They are only few in number: in a transverse section of a branch of 4 mm in diameter there usually occur only one or two of them, in the stem of 6 mm in diameter three or four. This is considerable fewer than Kölliker figured (1870, pl. III fig. 6), but this results probably from the fact that the stem he examined was thicker. They run either in a longitudinal direction and in that case may pass into the boundary canals basalwards as well as apicalwards, or they run more or less cross-wise through the stem and then connect a medullary canal with a boundary canal or two boundary canals mutually.

Stiasny (1937, p. 37) did not find wide canals in the medulla of the tips of the branches. This does not hold for a general rule. In my series of longitudinal sections through the tip of a branch I found a little canal of nearly 0.2 mm thickness in the place, where it is represented in my diagram (fig. 1), i.e., in the most apical part of the medulla. But for the rest I did not find a single large medullary canal in that twig along the distance of 12 mm. Of course it is quite possible that such medullary canals are lacking in other tip-parts or that they are found in other places. At any rate these medullary canals play a subordinate part in *Semperina rubra*. There is, however, no denying that there is some difference between the canal system in the terminal parts of *Semperina rubra* and that in the species, examined by me formerly (1940), for in those species such medullary canals were lacking. In the introduction I recorded already in which manner the diagnosis of the family Anthothelidae must be emended.

As regards their course, lumen, etc., the narrow medullary canals are very much like the narrow cortical canals; besides, they frequently pass into each other. They very often lie as flat oval canals against the boundary canals and the large medullary canals, but again we do not see anywhere here a transition from narrow to wide canals or any connection between them, for always there remains a thin membrane of partition. It would appear that the two canal types form a practically independent system.

The diagrams. The diagram of the canal system in the tip of a branch (fig. 1) shows the cortical layer containing the zooids, and the medulla (more darkly dotted). It is clearly visible that the terminal zooids in no way form a continuation with the medullary solenia, the shape of their coelenterons is similar to those of the lateral ones. In this respect there is a perfect analogy with *Semperina brunnea* (cf. Verseveldt, 1940, fig. 18). One zoid (in the middle, to the right) was drawn with projecting antho-

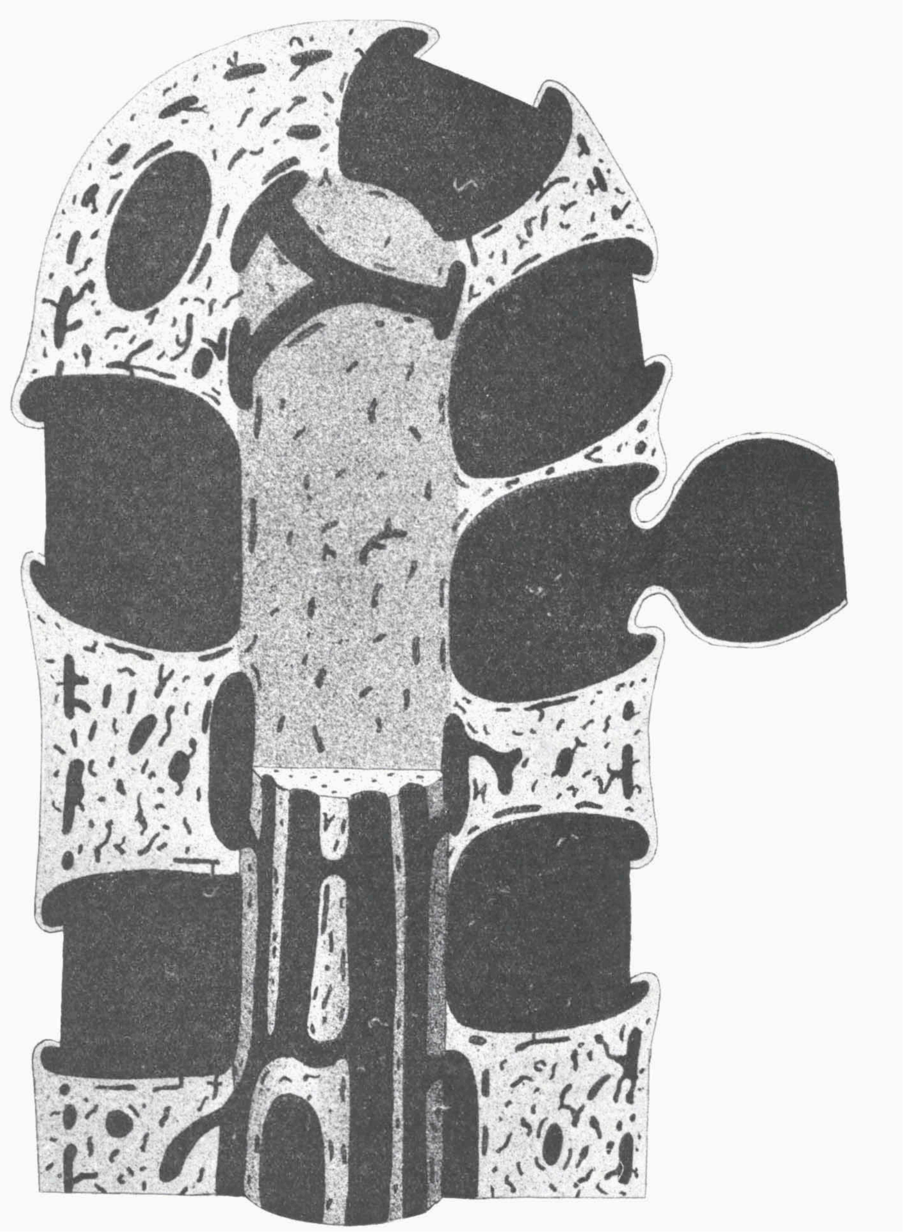

Fig. 1. *Semperina rubra*. Diagram of the canal system in the distal part of a branch. × 15.

codia, the zooids, which are withdrawn, are only slightly projecting above the surface of the colony (no anthosteles). In the cortex, close to the surface, the large canals are visible; also elsewhere they are met with; they pass into the boundary canals (below, to the left) and are connected with the numerous narrow solenia. To show the course of the boundary canals the more clearly, the medulla in the lower part of the figure was left intact. Now we see there the longitudinal boundary canals with here and there the wide transverse canals connecting them. In the upper part of the figure one half of the medulla was taken away. Large medullary canals are lacking, except the canal mentioned above, which runs close under the extremity of the medulla into a transverse direction and which bifurcates in the same way as drawn in the figure. Apart from that the narrow medullary solenia occur everywhere.

Fig. 2 is the diagram of the intricate canal system in a branch of approximately 4 mm in diameter. On the left there is the front of the branch, on the right the back; we see that the cortex is thin here. The medulla is again more darkly dotted. The diagram consists of four parts. In the undermost part we see in the undamaged cortex the wide apertures of the retracted zooids. In the next part on the left only the outer layer of the cortex has been removed, so that we can now follow the course of the outer large cortical solenia (a). On the right a larger part of the cortex has been removed so that the narrow cortical solenia (b) and moreover, quite to the right, the wide cortical solenia, as they are found at the back, are visible (cf. also the upper surface of the sectioned branch).

In the third part the whole of the cortex has been cut away to show the course of the boundary canals (c), which run into a longitudinal direction with transverse canals connecting them, so quite different from that of *Semperina brunnea* (cf. Verseveldt, 1940, fig. 17). In the upper part one half of the medulla was also cut away; one wide and numerous narrow medullary canals were drawn in it. Transverse canals connect the first with the boundary canals, apically the transverse canal itself passes into a boundary canal.

§ 5. The mesogloea. In *Semperina rubra* there is little to be seen concerning the presence of mesogloeal sheaths round the solenia. However, the partition-walls between the boundary canals and also between the large cortical solenia at the back are without spicules, but on their in- and outside the mesogloeal sheaths are not fully developed, just as this is the case round the medullary canals.

Separate cell-strings or cell-vessels were not observed. However, the narrow medullary canals, described in § 4, strongly reminded of the cell-

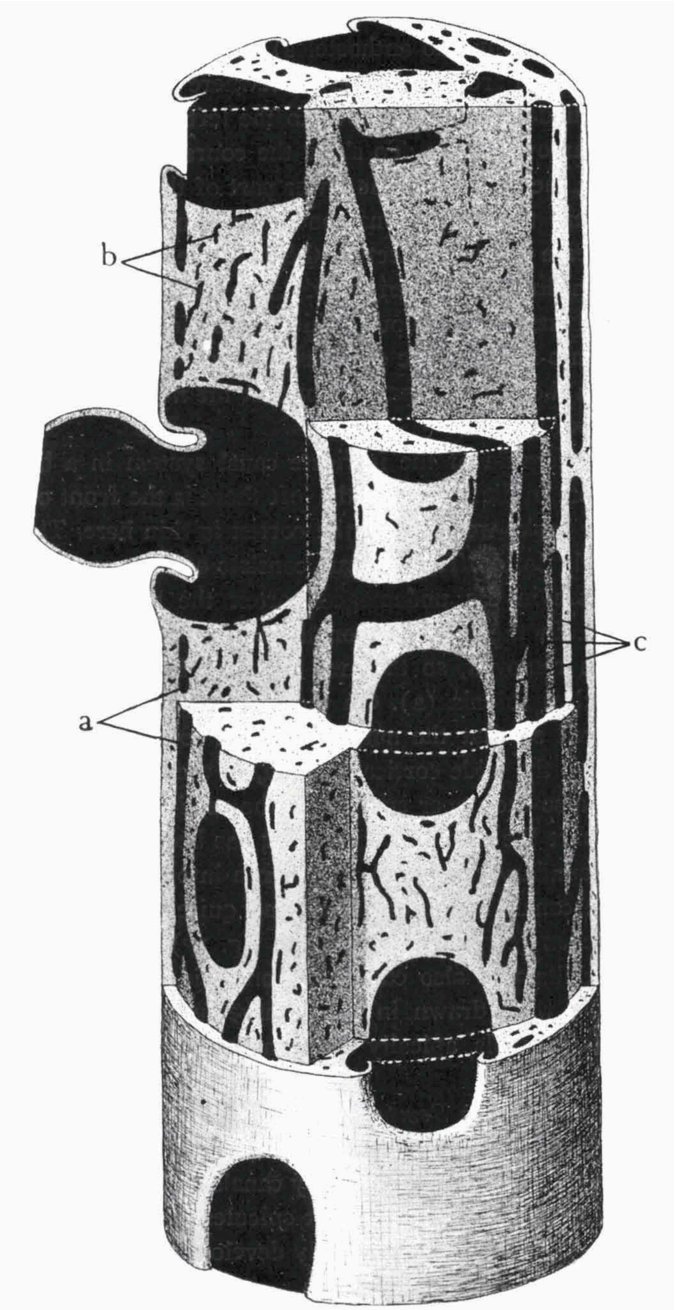

Fig. 2. *Semperina rubra.* Diagram of the canal system in a branch of about 4 mm in diameter. × 15.

vessels of corals, which I examined previously (1940), particularly by the fact that they are not connected with the wide endodermal canals anywhere, but I could not detect an essential difference between these narrow canals in the medulla and those in the cortex, whereas the epithelium of the last mentioned distinctly passes into the endoderm of the coelenterons. So, the endodermal nature of the narrow cortical solenia is indubitable; presumably the fine medullary canals are therefore endodermal, i.e., solenia. And for that reason I described them as such in § 4.

§ 6. The spicules. Although Kölliker (1870) already gave good figures of the spicules, it does not seem superfluous to give a systematic description of the various types of spicules and to draw them anew, in order to facilitate a better comparison with other *Semperina*-species and especially with *Anthothela* (= *Semperina*) *macrocalyx* (Nutt.), described in the next chapter.

a. The cortical spicules. These are rather small rod-shaped to spindle-shaped bodies, provided with warts. Here again we find quite a lot of transitional forms between the smallest spicules of a normal shape and the largest spicules. The smallest chiefly occur in the outermost cortical layer. They are 0.043-0.060 mm in length and 0.018 mm in thickness without warts or 0.030-0.040 mm, warts included. Often the warts are so dense that we hardly can see the actual surface of the spicule anymore (fig. 3a). A great many others, however, show the type, represented already by Kölliker (1870, pl. III fig. 8g). The warts stand more apart and not irregularly, but in two wreaths, while the tips are also provided with a wart (fig. 3b) or with a wreath of warts (fig. 3c), the "Achter" and "Zwölfer" Kükenthal's respectively.

In the outer cortical layer, however, there also occur already large spicules. Some of them are somewhat longer and thicker than type a, others are more like type c, the warts standing in more wreaths. Furthermore we find here, but especially further inward, transitional types (fig. 3d) to the longer, straight or slightly curved rod- or spindle-shaped spicules, which are up to 0.270 mm in length (fig. 3e). In some cases the warts are still crowded together, but in most cases they are more widely spread, sometimes irregularly, often, however, in wreaths. All cortical spicules are red.

b. The medullary spicules. Kölliker (1870) in fig. 6 of his pl. III quite correctly pointed out that there occur red patches in the white medulla. These irregularly distributed red parts contain spicules (fig. 3f), which are quite identical to type e (the same figure). On the whole they are a litlle larger, up to 0.35 mm in length; the types a, b and c are lacking in the medulla, type d is rare.

Among these red spicules there are fine, colourless, needle-shaped spicules, also filling up the white parts of the medulla and lying pell-mell. These are the typical medullary spicules (fig. 3g). Apart from a few small ones, most of the needles are 0.40-0.65 mm in length and 0.011-0.016 mm in thickness; the largest I measured was 0.85 mm in length and 0.020 mm in thickness. They are straight or slightly curved and covered with small protuberances, the number of which usually increases into the direction of the tips of the needles.

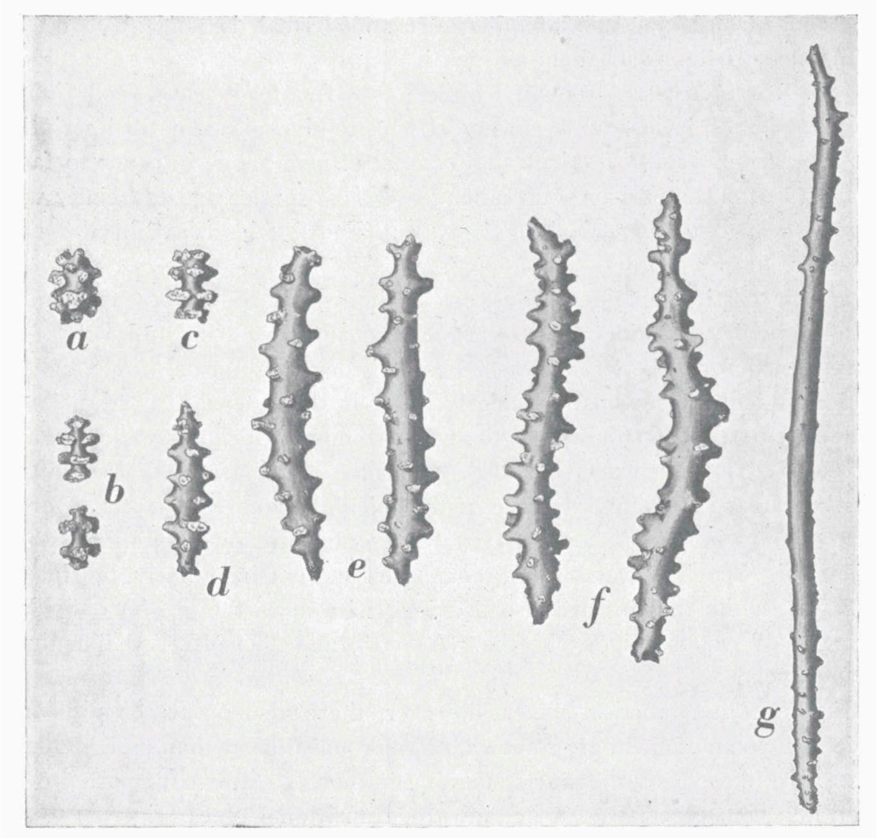

Fig. 3. *Semperina rubra*. a-e, cortical spicules; f and g, medullary spicules. × 200.

c. The anthocodial spicules. Nutting (1911, p. 11) described the situation of the spicules in the anthocodiae, but he did not give either figures or statements about their size. The "broad and heavy collaret of encrusting spindles" (Nutting, l.c.), i.e., the crown, mostly consists of spindle-shaped spicules, which are once, occasionally twice curved and densely set with small cone-shaped processes (fig. 4a). They are 0.30-0.50 mm, maximally 0.56 mm, in length and 0.028-0.052 mm in thickness (without processes). Presumably the spindle drawn by Kölliker in his fig. 8a does not belong to the medulla, but to an anthocodia!

The crown is not perfectly round but shows eight waves, turned outwards and the position of the spicules in these waves is such that they turn their curved side outwards. At the bases of the tentacles these spindles are arranged en chevron forming the points, and at the back the proximal part of the tentacles is armed with the same spicules in 4-5 rows. But the distal parts of the tentacles bear another type (fig. 4b, c): flattened spicules, strongly dentated at their tips and rather densely covered with warts at their sides. The shape is identical with the corresponding spicules of *Semperina brunnea* (Kükenthal, 1919, fig. 21, to the right).

Finally in the wall of the oesophagus there are very tiny spindles with relatively high processes (fig. 4d). They are only about 0.07 mm in length.

When we compare the spicules of *Semperina rubra* as a whole with those of *S. brunnea* (figures in Kükenthal, 1919, figs. 21-24 and in Verseveldt, 1940, fig. 20), it appears that there is a great deal of resemblance.

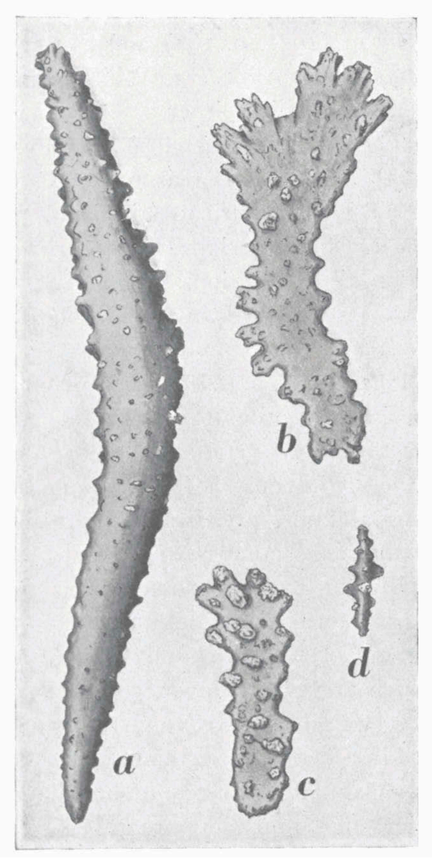

Fig. 4. *Semperina rubra.* a, spicule from the crown; b and c, spicules from the tentacles; d, spicule from the stomodaeum. × 200.

§ 7. The horny substance. Horny substance occurs everywhere in the medulla, even, in however little quantity, in the most apical parts. It forms rather thin sheaths round the spicules and is regularly distributed over the medulla. It may be beautifully reddened by methyleosin, also in the microtome sections.

Stiasny's statement (1937, p. 37) about the presence of yellowish horny substance in the lumen of many large longitudinal canals is incorrect again (cf. Verseveldt, 1940, p. 133).

II. ANTHOTHELA MACROCALYX (NUTTING)

Nutting (1911, p. 15) described this species under the name of *Suberia macrocalyx*. Following in the tracks of Kükenthal (1919, p. 57) who regarded this species as belonging to the genus *Semperina* Köll., Thomson & Dean (1931, p. 192) and Stiasny (1937, pp. 31 and 35) call this coral *Semperina macrocalyx*. While examining it, it became clearer and clearer to me that it is neither a *Suberia*-species nor a representative of the genus *Semperina*. I stated close relationship with *Anthothela grandiflora* (M. Sars), and for this reason I shall call this species *Anthothela macrocalyx*. In § 8 I will return to this point.

§ 1. The material. The material I have examined, was collected by the "Siboga" Expedition, Station 122, and was described previously by Nutting (l.c.) and Stiasny (l.c.). The fragment recorded by Thomson & Dean (l.c.) was not at my disposal.

I have laid myself out to make microtome sections of Nutting's type-specimen in order to be able to study the canal system in particular. But the results ever and again were so poor that I have been obliged to satisfy myself with only a few incomplete observations. Neither could the free-hand sections spread much light, the material being difficult to cut owing to the large number of big spicules. Yet the examination yielded results sufficient to state something about the anatomy of this coral and to discuss once more its taxonomical place.

§ 2. Cortex and medulla. The stem, 2.5 mm in diameter, and the branches, which are even thinner, consist of cortex and medulla. The cortical layer is very thin (0.06-0.08 mm) and contains only one layer of spicules. When making free-hand sections the cortex comes off easily. It is separated from the medulla by a circle of boundary canals (§ 4). The cortex is continued in the high, thin and more or less transparent anthosteles, which also contain one layer of spicules. This transition of the cortex into high anthosteles reminds strongly of that found in *Anthothela grandiflora* (cf. Verseveldt, 1940, fig. 13), but in the latter the cortex is thicker.

The medulla is crowded with spicules, which differ somewhat from the cortical ones (§ 6) and which, at least in the proximal parts, are surrounded by horny sheaths.

§ 3. The zooids. Nutting (1911, p. 15) wrote: "The calyces are irregularly distributed on three sides of the proximal parts of the stem and branches and on all sides of the distal parts of the colony". Stiasny, on the other hand, found in the same material no front side covered with zooids and a back without zooids. And in the fragment of Thomson & Dean the anthosteles stood, it is true, in proximal parts mainly on one side, leaving an almost bare back, but in the distal parts the zooids were closer and on all sides. "Die Stellung der Kelche scheint eben sehr variabel zu sein" (Stiasny, 1937, p. 35, foot-note). As I could ascertain, there is indeed nothing to be seen like a zooids-free back as it occurs in the proximal as well as in the distal parts of *Semperina brunnea* Nutt. and *S. rubra* Köll. And therefore Kükenthal may not use this as a ground to include this species in the genus *Semperina.*

Hardly any observations could be made about the structure of the zooids, the position of the median plane and the connections of the coelenterons with the canal system. But it was found that the coelenterons round their broad, flat base are connected with the boundary canals, so that a diagram of *A. macrocalyx,* at least with regard to the structure of the anthosteles and the relation to the boundary canals, shows much similarity with that of *Anthothela grandiflora.* The anthocodiae are retracted and protrude like small bulb-shaped bodies from the anthosteles (cf. Thomson & Dean, pl. XIV fig. 3).

§ 4. The canal system. In the very thin cortex no cortical solenia occur, so that two types of endodermal canals remain, viz., the boundary canals and the medullary canals.

a. The boundary canals. They lie in a wreath round the medulla and form a strongly marked separation between cortex and medulla. On transverse sections they are usually much flattened, on the cortex-side they are flat, on the medulla-side they are rounder. Their height in a radial direction amounts to 0.05-0.11 mm, sometimes to 0.16 mm; the breadth is 0.18-0.20 mm.

b. The medullary canals. In the centre of the stem, which is 2.5 mm thick, there are three or four large canals, which are 0.3-0.5 mm wide and in transverse sections round, oval or angular. The course of these canals in a longitudinal direction, the mutual connections, etc., could only insufficiently be examined, but this much is sure that the mutual connection is only slight and that they run rather straight through the stem. Besides these central large solenia there are numerous narrower canals scattered in the medulla, measuring 0.05-0.15 mm in diameter. These also run in a longitudinal direction, but bifurcate repeatedly, while they are also often connected with the boundary canals.

I regret very much that I could not find anything about the relation between these medullary solenia and the terminal zooids and that it is therefore impossible to give a diagram of the canal system.

§ 5. The mesogloea. In the medulla the spicules are so crowded that the mesogloea has been reduced to extremely thin layers between the spicules. Cell-strings and (or) cell-vessels occur, but special points could not be observed. On the medulla-side of the boundary canals there is a somewhat thicker layer of homogeneous mesogloea.

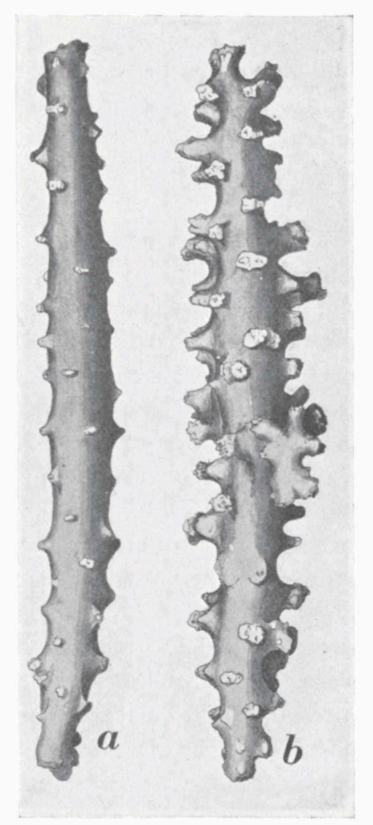

Fig. 5. *Anthothela macrocalyx*. Cortical spicules from the stem. × 200.

§ 6. The spicules. a. The cortical spicules. In the thin cortex there is only one layer of spicules, which almost all lie in a longitudinal direction. They are of a drawn-out spindle shape or bar-shaped and mostly somewhat curved. There is much variation in length, from 0.30 to 0.83 mm, most of them are 0.40-0.60 mm long. The thickness without processes amounts to 0.035-0.065 mm, mostly about 0.050 mm. Generally speaking, the thickest spicules have also higher (up to 0.021 mm) and broader warts than the thin, slender ones where the processes are narrower and lower (up to 0.012 mm). Thus we may distinguish between two extreme forms, which are drawn in fig. 5. Spicules, which are longer and thicker than those I have drawn in fig. 5b are not rare. The processes may be cleft and even bifurcated like short antlers; sometimes they grow together.

b. The spicules of the anthosteles exactly resemble those of the cortex. They lie in one layer lengthwise of the anthostele, near the edge they are arranged en chevron; owing to this the edge has eight points, which are slightly developed.

c. In the anthocodiae we find again the same spicules. They lie in numerous (6-10) horizontal rows, apically they are arranged en chevron again, but now the spicules are strong and club-shaped. I have not succeeded in finding the curious, thick and club-shaped spicules drawn by Thomson & Dean (1931, pl. XXIV fig. 6) and by Stiasny (1937, textfig.

J, a and b) anywhere either in cortex or medulla, they only occur in the anthocodiae. They lie with their thick blunt ends to the top of the tentacles. In the state of retraction of the anthocodiae these thick ends offer strong protection. Most of them are 0.50-0.65 mm long, but shorter ones also occur (0.30 mm); the club-shaped end is 0.085-0.120 mm thick, without processes.

d. The medullary spicules lie almost all of them parallel to each other in a longitudinal direction. They are exactly like the cortical spicules of type a (fig. 5), but there are many spicules whose processes are somewhat higher and closer together than in the type drawn, but which do not reach the height and breadth of type b. As a matter of fact the rugged-looking spicules of type b hardly occur here.

If we compare the above mentioned spicules of *A. macrocalyx* with those of the principal species certae of the genus *Semperina*, viz., *S. rubra* Köll. and *S. brunnea* Nutt., we find the following important differences:

1. In the cortex of *A. macrocalyx* only large, bar-shaped and spindle-shaped spicules are met with, in *S. rubra* and *S. brunnea* small, oval "Gürtelstäbe" occur, especially in the outer layers of the cortex.
2. In the medulla of *A. macrocalyx* there is the same spindle-shaped type as in the cortex, in *S. rubra* and *S. brunnea* long, needle-shaped spicules occur.
3. In the tentacles of *A. macrocalyx* we find club-shaped spicules, in *S. rubra* and *S. brunnea* flat, deeply indented spicules.

In § 8 I will make further remarks on the taxonomical importance of these differences.

§ 7. The horny substance. It only occurs in the medulla and especially in the innermost part of it round the large medullary canals. It forms sheaths round the spicules, on account of which these are glued together, so that in "Milton" they are difficult to separate. It is curious that the horny substance only occurs in the thick proximal parts and not in the thin tips.

§ 8. Taxonomy. Kükenthal (1919, p. 51) thought that it was hardly possible to separate "*Suberia*" *macrocalyx* (as it was called by Nutting) from the genus *Semperina*. "Gemeinsam ist ihnen der Aufbau der Kolonie, das Fehlen der Polypen auf einer Fläche, das Vorhandensein von Polypenkelchen und die Gestalt der Spicula. Von Unterschieden treten folgende auf: Die Polypenkelche sind bei beiden Suberiaarten (viz., *S. köllikeri* and *S. macrocalyx*) höher als bei Semperina, und bei Semperina wiegen Gürtelstäbe vor, bei Suberia Spindeln". But Kükenthal adds in the same breath that this distinction is "nicht durchgreifend".

With regard to the points of agreement mentioned by Kükenthal I have explained in § 3 that in *A. macrocalyx* a distinctly visible zooid-less back is not to be found. But in other respects too, there is a great difference between *A. macrocalyx* and the principal species of the genus *Semperina.* In the following table they are summed up:

Anthothela macrocalyx	*Semperina rubra* and *S. brunnea*
1. Thin, slender branches.	1. Strong, cylindrical branches.
2. Cortex everywhere equally thin (0.07 mm), so medulla lying central.	2. Cortex at the back thin (though much thicker than in *A. macrocalyx*), at the front and lateral sides much thicker, so medulla excentric.
3. Zooids irregularly scattered, back not clearly distinguishable or lacking.	3. Front and back clearly developed.
4. Anthosteles very high, not retractile.	4. Anthosteles low, forming verrucae.
5. In the cortex only long fusiform spindles.	5. In the outmost layers of the cortex only small, oval "Gürtelstäbe".
6. In the medulla no needles.	6. In the medulla needles occur.
7. In the tentacles club-shaped spicules.	7. In the tentacles flat, deeply indented spicules.
8. No cortical solenia.	8. Cortical solenia are present.
9. In the centre of the medulla some large longitudinal canals.	9. Such canals are lacking.

From this summary it appears that none of the four arguments mentioned by Kükenthal to include *macrocalyx* in the genus *Semperina* cuts ice.

Nor can *macrocalyx* be referred to the genus *Suberia* for the following reasons:

1. The habitus is quite different from that of *Suberia clavaria* Th. Studer.
2. In *macrocalyx* the ends of the branches are not club-shaped, only are the zooids closer together (Nutting: clumps or clusters).
3. The anthosteles are not retractile.
4. In the anthocodiae there occur spicules.
5. The cortex is very thin instead of very thick.
6. No small "Gürtelstäbe".
7. Medullary canals occur.

It appears to me, however, that with *Anthothela grandiflora* (M. Sars) there are important points of agreement. They are:

1. Resemblance in habitus, though *macrocalyx* is of a somewhat more delicate structure and though there are no anastomoses. It is not known whether a membraneous or basal enlargement occurs, as the basal part of the stem is wanting.
2. In *A. grandiflora*, too, the zooids are often one-sided (cf. Stiasny, 1937, p. 20).
3. The terminal zooids form clusters.
4. The anthosteles are not retractile.
5. The anthocodial spicules are club-shaped.
6. The cortex is thin (in *A. grandiflora* 0.2 mm).
7. In *macrocalyx* there are many boundary canals, which are so often connected with each other that they may be looked upon as a transition to the boundary space of *A. grandiflora.*
8. Much resemblance in the shape of the cortical and especially in the medullary spicules, though in *macrocalyx* the small cortical spicules are lacking (cf. Verseveldt, 1940, fig. 15a).
9. A diagram of *macrocalyx* would look just like that of *A. grandiflora* as regards the relation between the zooids and the boundary canals.
10. The light, almost white colour.

Of course there are also points of difference. Thus in *A. grandiflora* the large central medullary canals are lacking. In *A. grandiflora* and in *A. macrocalyx* cortical solenia are lacking, but in *A. grandiflora* they are met with in the neighbourhood of the terminal zooids; I suppose they will be lacking round the terminal zooids of *macrocalyx,* though further investigation must confirm this.

There are therefore many grounds for the conclusion that *macrocalyx* for the present must be looked upon as belonging to the genus *Anthothela.* Anyhow it is no *Suberia-* or *Semperina-*species. It is to be regretted that I could not look into an important point, the canal system in the distal parts. In my opinion it will depend on the behaviour of the medullary canals with regard to the terminal zooids, whether for *macrocalyx* quite a new genus must be assumed. For the present it remains *Anthothela macrocalyx* (Nutting).

III. SIBOGAGORGIA WEBERI STIASNY

§ 1. The material. I have reexamined the specimen collected by the "Siboga" Expedition, Station 297. It was first described by Nutting (1911, p. 13) under the name of *Suberia kölliker* Studer and afterwards by Stiasny (1937, p. 80) as the new species *Sibogagorgia weberi*. Quite rightly Stiasny qualified Nutting's determination as incorrect, especially on the ground of the dimorphism of the zooids.

Nutting did not give any figure either of the habitus or of the spicules. His description of the habitus, of the length and the thickness of stem and branches, etc., is substantially in accordance with that of Stiasny. In his pl. IV figs. 26 and 27 Stiasny has represented the colony in natural size. But the enlargement of his figures 28 and 29 (same plate) does not amount to 5 ×, but only 2.7-3.0 ×; a simple remeasuring of the figs. 26 and 29 will suffice to prove this, for the fragment drawn in fig. 29 represents the middlemost part of fig. 26.

I had the opportunity to examine the different parts of the colony minutely. First of all the basal part of the stem with its base of attachment, represented by Stiasny in pl. IV fig. 27. As in this part the zooids seem to be lacking, it might be taken for a stalk, such a one as also occurs in *Solenocaulon*. On closer investigation, however, there appear to be many siphonozooids on it, so that in accordance with the nomenclature that I suggested (Verseveldt, 1940, p. 5), this part should not be called stalk but stem. Of this basal part of the stem and of a part from the middle of the stem transverse and longitudinal sections were made both by hand and with the microtome. To spare the material only one club-shaped terminal branch could be examined: of one half of it longitudinal sections were made by hand, of the other half longitudinal and transverse sections with the microtome.

§ 2. Cortex and medulla. Stiasny (1937, p. 80) asserts that the surface between the calyces is not smooth, but "mit feinen, mehr/minder parallelen Längsrunzeln bedeckt". This sculpture reminded him of that of *Suberogorgia ornata* (p. 82). This observation of Stiasny's is incorrect— Stiasny's own transverse sections, which were at my disposal, might have convinced him of this (cf. his text-fig. BB, r and s). What Stiasny saw, and drew in his text-fig. BB, q, are nothing but partition walls between the peripheral cortical solenia (to be discussed later on), which are clearly visible in a thin section of the surface layers. These cortical solenia run into a more or less longitudinal direction. Hence Stiasny also mentions this direction for his "Längsrunzeln". Looking at the undamaged (!) cortex of the colony through a pocket lens, we can clearly see the dim outlines of the little canals through the extremely thin cortical layer. Thus, in reality, the surface is smooth.

On a transverse section of the stem and the branches it appears that there is a marked difference in colour between the outer layer of the coenenchyma, the cortex, and the central part, the medulla, for the cortex is white and the medulla light brown. This difference in colour is caused by the large amount of horny substance heaped up in the medulla (§ 7). On closer examination a wreath of boundary canals appears to be present on the boundary of cortex and medulla. Also with regard to the spicules there is a clear difference between the two parts of the coenenchyma.

The cortex is not everywhere of the same thickness. In the basal part of the stem the cortex is about 0.6 mm thick, upwards it increases in thickness (about 1 mm). Round the autozooids the cortex still thickens gradually, up to 2.5-3.0 mm, while on the tip of the club-shaped branch it appeared to be 6 mm in thickness (cf. figs. 6-8).

§ 3. The zooids. The dimorphism of the zooids, overlooked by Nutting, was rightly ascertained by Stiasny. A more elaborate description of the zooids, particularly of the shape of the gastral cavities and their relation to the canal system is to follow now.

a. The autozooids. These are lacking on the base of attachment and on the basal part of the stem. Outwardly they are recognizable as hillocks. Eight sharp points stand round the opening. According to place we may distinguish terminal and lateral zooids. The terminal and termino-lateral zooids are united in the club-shaped ends of the branches (fig. 6). The gastral cavities of the real terminal zooids (fig. 6, a_1) are long. Proximally they are gradually narrowing and end up with a flat base against the top of the medulla. The termino-lateral zooids (a_2, a_3) have the same long coelenterons, which are curved now; they run along the medulla for some way to finish up with a somewhat rounded base; the dorsal mesenteries reach the same point.

The lateral autozooids (fig. 7, a) as we find them on the middle of the stem have coelenterons, which are much shorter, up to 3 mm in length, measured from the aperture to the rounded base. These lateral zooids are also curved downwards, presumably there is a gradual transition from the long terminal zooids into the short lateral ones. The latter nearly reach to the medulla, not quite though, for between coelenteron and medulla we find an extremely thin layer of cortical spicules, while there are also boundary canals.

All coelenterons are on all sides connected with the intracortical solenia (§ 4) and at their base with the boundary canals.

b. The siphonozooids. These occur everywhere, except, probably, on the foot. They do occur on the basal part of the stem, where the autozooids are lacking. Outwardly their presence is not betrayed by small processes; so, there are no "kleine, runde „Erhöhungen"", as incorrectly stated by

Stiasny (1937, p. 80). Still, even by means of a strong lens, they are easy to find, because the coelenterons are dimly visible through the thin surface layer. On the basal part of the stem they are rather sparse, so that their number is not large here; further upwards they are far more numerous.

The gastral cavities appear to be very variable in shape. Sometimes the cavity runs in a practically radial direction medulla-wards (figs. 7, b and 8); then again the cavity shows a more or less strong curve downwards (fig. 7, to the right, under the autozooid). There is variation in length as well: if the cortex is thin, the coelenterons are short, if it is thick (i.e., round the autozooids), they are long. There appear also to be great differences as regards the length of the siphonozooids in the extremity of the branch, for there are some, which by no means reach to the medulla (fig. 6, s_1, s_2, s_4), whereas, on the other hand, some of them (s_3) do reach as far as the medulla, just as the autozooids by which they are surrounded.

In transverse section the coelenterons are round and 0.4-0.7 mm in width. On all sides they are frequently connected with the intracortical solenia. Where they reach to the medulla we also see the boundary canals pass into them. The peripheral cortical canals (§ 4), however, are hardly ever or not at all connected with them.

The stomodaeum is invariably very short, the siphonoglyph is clearly developed. The mesenteries are short, except the dorsal, which are strongly developed and continue as far as the base of the coelenterons. Eggs occur in great numbers in the siphonozooids; the largest having a diameter of 0.46 mm; also in the autozooids an egg was occasionally found.

§ 4. The canal system. In *Sibogagorgia weberi* the endodermal canals occur in the cortex, in the medulla and on the boundary of both. The cortical solenia may be subdivided into peripheral and intracortical ones.

a. Peripheral cortical solenia (fig. 6, p.c.s.). Under an extremely thin cortical layer of only 0.1 mm in thickness there is a network of narrow canals, extended longitudinally (fig. 8, at the bottom). In a transverse section they are of oval shape. In the basal part of the stem they measure 0.05-0.10 mm in height and 0.11-0.16 mm in breadth, in the higher parts of the stem they are wider, viz. 0.10-0.15 × 0.13-0.22 mm. As stated above, they are dimly visible through the thin surface layer by means of a lens. There is no connection whatever either with the intracortical solenia or with the gastral cavities of the autozooids. Only occasionally a connecting little canal was found between a solenium of the peripheral system and the gastral cavity of a siphonozooid. Consequently it appears that the peripheral cortical canals form a rather independent system.

b. Intracortical solenia (fig. 6, i.s.). In the cortical layer, which remains between the network of peripheral solenia and the boundary solenia we meet numerous, mostly very narrow solenia. Most of them are only 0.05 mm thick, although there are also some, which are wider, up to 0.15 mm, especially higher up in the stem. Where the cortex is thin they are lying in one layer in the middle of the cortex; where the cortex is thicker, e.g., round the autozooids and in the tips of the branches, they are scattered about all through the cortex. Radial little canals of the same lumen are connecting these intracortical solenia with the boundary canals; there is no connection between them and the peripheral solenia.

c. Boundary canals (fig. 6, b.s.). As we saw before, the boundary solenia form a circle round the medulla. They are wider than those mentioned sub a and b. In transverse section they are oval in shape, 0.10-0.15 mm in height and 0.15-0.30 mm in breadth. They form a close network (fig. 8, in the middle), not unlike the peripheral solenia, but larger. They are connected with or pass into the gastral cavities of the zooids.

d. Medullary solenia. They occur everywhere in the medulla even in the most apical parts (fig. 6). They show a longitudinal course, with many branches and are connected by slanting or cross solenia. They are round in shape, with a rather strongly varying lumen: the largest are 0.05-0.10 mm in diameter; most of them, however, are narrower, even so much that there is hardly any lumen left. They may gradually pass into the boundary solenia or are connected with them by transverse canals. The same phenomenon is also seen in the tip of the branch. As appears from fig. 6 they certainly cannot be considered here to be direct continuations of gastral cavities. So in this respect there is a fundamental difference with *Briareum asbestinum* (Pallas) and especially with *Paragorgia arborea* (L.)„ the last mentioned in many points (e.g. in habitus, dimorphism of the zooids) resembling *Sibogagorgia weberi.* When we compare fig. 6 of this paper with fig. 7 of my former (1940), the difference is conspicuous.

The diagrams. Fig. 6 represents the canal system in a club-shaped tip of a branch. In the middle of the top part there is an autozooid (a_1), which continues to the medulla (darkly dotted); to the right and the left of it two short siphonozooids have been drawn (s_1 and s_2); still further to the left there is a siphonozooid (s_3) that does reach the medulla. Then, to the left as well as to the right, we see autozooids (a_2 and a_3) running along the medulla for some way to end up in a somewhat rounded base. Finally two more types of siphonozooids (s_4 and s_5) have been drawn, as they were met with in this place, and also the half of an autozooid (a_4). Everywhere on the outside of the branch we find the peripheral cortical solenia (p.c.s.), which are not connected with the underlying intracortical solenia (i.s.) or with the coelenterons. The intracortical solenia and the boundary solenia (b.s.) pass into the zooids indeed. The course of the medullary canals and the character of their connection with the boundary canals is clearly visible in the drawing.

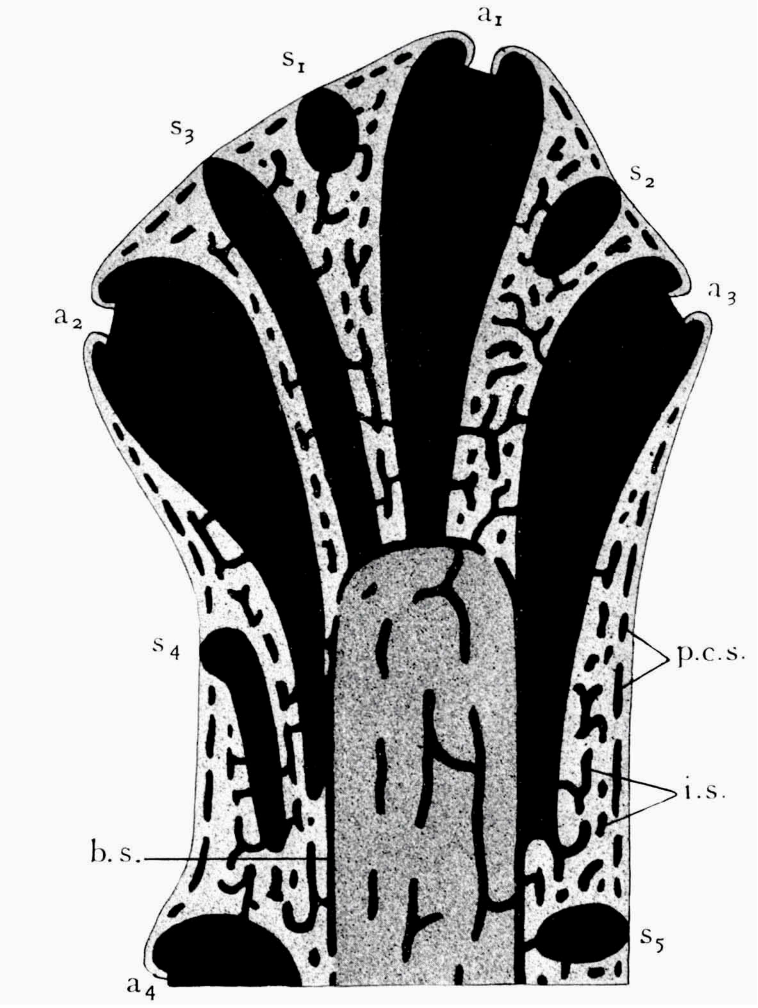

Fig. 6. *Sibogagorgia weberi*. Diagram of the canal system in the distal part of a branch. a, autozooids; b.s., boundary solenia; i.s., intracortical solenia; p.c.s., peripheral cortical solenia; s, siphonozooids. × 11.

In fig. 7 the canal system in the central part of the stem has been drawn. Both autozooids and siphonozooids occur in it. The coelenterons of the two large autozooids are much shorter than those of the terminal autozooids; they do not reach to the medulla: the boundary solenia run behind them. The siphonozooids vary much as regards length and direction of the coelenterons.

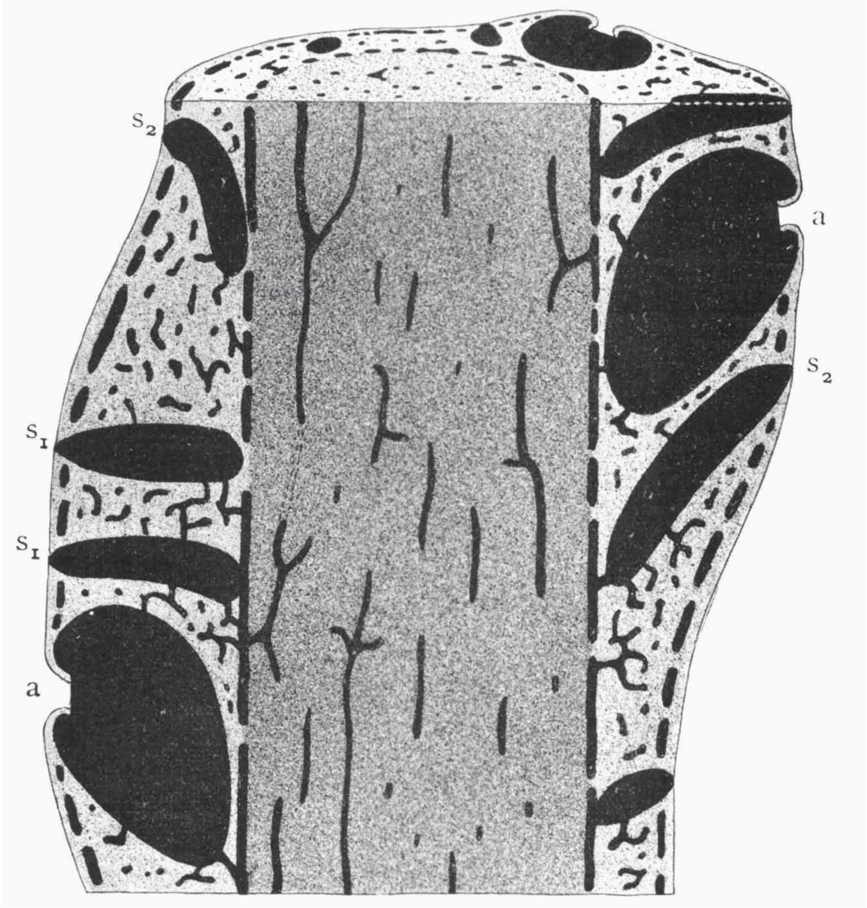

Fig. 7. *Sibogagorgia weberi.* Diagram of the canal system in the middle part of a branch. a, autozooids; s, siphonozooids. × 11.

Fig. 8 represents the diagram of the canal system in the basal part of a stem, where the autozooids are lacking. The cortex is thin everywhere; here and there siphonozooids (s) occur. In the lower part of the figure a fragment of the outermost cortical layer has been removed, just as far as the peripheral cortical solenia, so that the network of these small canals has become visible. Here we also find a transverse section of a siphonozooid. In the next part the whole cortex has been removed: the network of boundary canals is now visible. In the top the front part of the medulla has also been taken away, so that the course of the medullary canals becomes visible.

§ 5. The mesogloea. All the canals are surrounded by a layer of homogeneous mesogloea; there are no spicules in it. It is extremely thin round the peripheral cortical solenia, the same as round the intracortical solenia. Round the boundary canals and the medullary canals the mesogloeal sheaths are more clearly developed: they are here 0.03-0.08 mm in thickness.

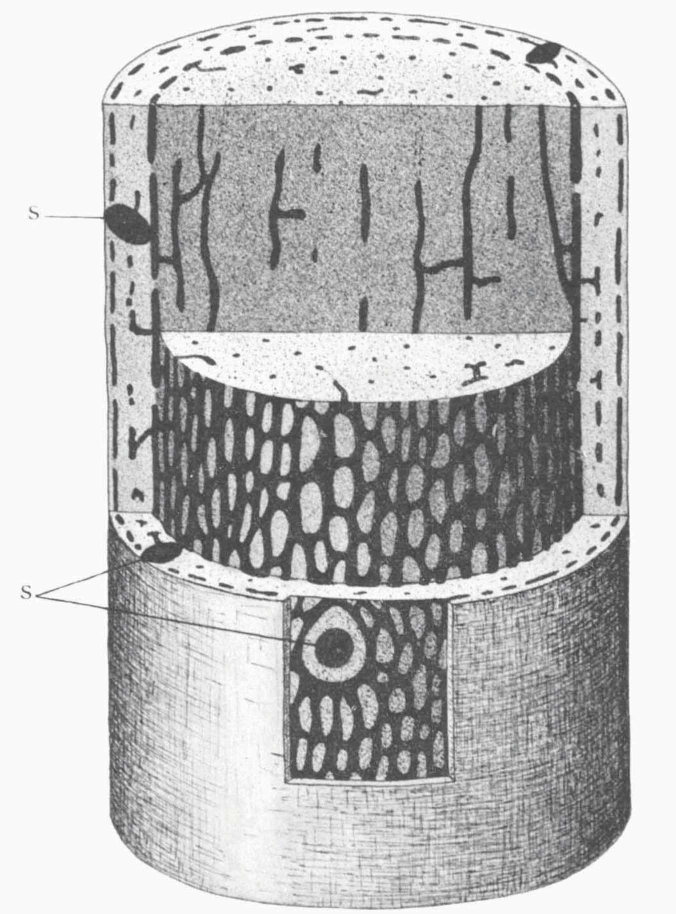

Fig. 8. *Sibogagorgia weberi.* Diagram of the canal system in the basal part of the stem. s, siphonozooids. × 11.

In examining a transverse section of the stem, we see very clearly numerous light, transparent spots in the medulla, where spicules are lacking. It is only in very thin free-hand sections or better still in microtome sections that in these spots the mostly very narrow medullary canals can be detected. Only in few of these light spots we immediately see a solenium, but then we have before us one of the wide medullary canals! Consequently the transparent spots are mesogloeal sheaths round medullary solenia, they are not the canals themselves. It follows that what Stiasny (1937) drew in his text-fig. BB, s as medullary canals (the lumen is far too wide!) are actually the mesogloeal sheaths round the much narrower canals.

In the sheaths, but also in the other mesogloea we find numerous irregular cell-strings forming a network. These strings are often some cells in thickness; here and there these cells are diverging so as to form cell-vessels.

§ 6. The spicules. The cortex and the medulla appear to contain spicules, characteristic for any of these layers. However, among these typical spicules we observe remarkable intermediate forms, so that it was possible to arrange quite a series of types of spicules, beginning with the very small bodies from the outer cortical layer and ending up with the long rod-shaped medullary spicules.

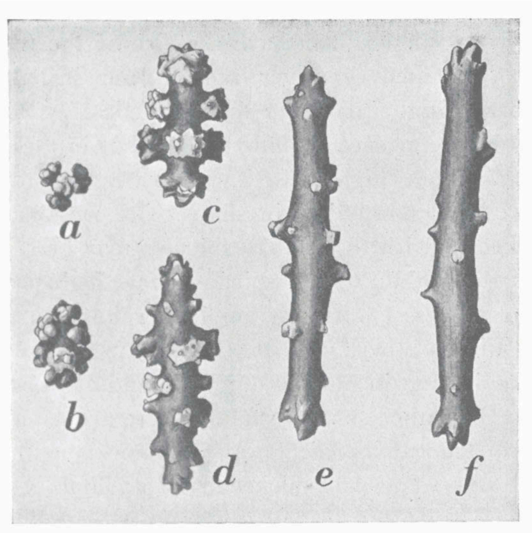

Fig. 9. *Sibogagorgia weberi.* a-c, cortical spicules; d-f, medullary spicules. × 200.

a. In the outer cortical layer there are small, more or less spherical bodies with four warts (fig. 9 a), 0.043 mm in diameter, and also small rods with each a wart at the end, but their number is not large. By far most of the spicules are short, thick rods with a wart at the poles and two wreaths with three stalked warts, the wreaths being arranged alternately (fig. 9 b). The warts are large and dense, and are themselves composed again of numerous blunt conical processes. The length of these spicules varies from 0.055-0.070 mm, most of them being 0.060 mm in length. The same spicules also occur in the basal, retracted part of the anthocodiae.

b. In the subjacent cortical layer the spicules show the same type of "Gürtelstäbe", but they are larger, mostly 0.055-0.085 mm in length, the maximum length amounting to 0.130 mm (fig. 9 c). They again have a wart on each end and moreover two alternating wreaths of three warts each, being more scattered now. This type was already made mention of by Nutting (1911) and Stiasny (1937). Besides this type we find, however, already a few forms, which may be considered as transitions to the more rod-shaped medullary spicules; they are 0.140 mm in length.

c. In the inner cortical layer, close to the boundary canals, and apart from the typical cortical spicules, a few ordinary medullary spicules make their appearance.

d. In the medulla the rodlike or spindle-shaped spicules are prevailing. Still we find everywhere spicules in it, perfectly identical with the cortical ones. Some of them have the size of the real cortical spicules (0.07 mm), most of them, however, are 0.12 mm in length. Then we find transitional forms (fig. 9 d) from these "cortical" forms to the real medullary ones. They are already spindle-shaped, but in the middle of the spicule there are still a few high-stalked warts, whereas towards the ends the processes are low and conical in shape. The length amounts to 0.16-0.21 mm. The likeness with the rodlike spicules may be still more striking; then we find in the middle of the spicule a few high processes, it is true, but they do not possess a warty top any longer, but a smooth, more or less truncated top.

Finally there are the medullary spicules proper, which are by far dominating in number (fig. 9 e and f). They are fusiform or rodlike, and on the rather smooth surface there are comparatively few processes, which are truncated-conical or volcano-shaped. The ends of the spicules are always somewhat thickened on account of some processes. Nearly all of these spicules are 0.25-0.29 mm in length, only a few being 0.33 mm in length.

All the medullary spicules are lying in a more or less longitudinal direction; like the cortical spicules, they are transparent and very brittle.

§ 7. The horny substance. This substance is only found in the medulla and in large quantities; it forms horny sheaths round the spicules. By staining with methyleosin it may be given a fine red colour. On account of the presence of homogeneous mesogloeal layers round the medullary canals the horny substance together with the spicules are accumulated in the spaces between these mesogloeal layers.

§ 8. Taxonomy. In my former paper (Verseveldt, 1940, p. 137) I classified the genus *Sibogagorgia* Stiasny in the family Paragorgiidae Auriv. In doing so I followed Stiasny's example, as his statements about the presence of medullary canals seemed to favour such a classification. Besides, I secretly hoped, it would appear on closer examination that the canal system of *Sibogagorgia* would be similar to that of *Paragorgia*, i.e., to my fig. 51 (l.c.). However, this is not the actual state of affairs. It is true, medullary canals occur everywhere, also in the extreme parts of the tips, but these may not be considered as continuations of gastral cavities. Moreover, medulla and cortex are always clearly separated by boundary canals. Accordingly the similarity with my fig. 52 (l.c.) is much greater. Compare for instance also fig. 6 in the present paper with fig. 40 in my former, regarding *Diodogorgia ceratosa*. Consequently on the ground of the canal system *Sibogagorgia weberi* cannot be classified in the family Paragorgiidae.

But neither does it belong to the family Anthothelidae Broch on account of the dimorphism of the zooids. The reason, why *Paragorgia* was separated from the Anthothelidae, also holds good for the separation of *Sibogagorgia*, although, on account of the canal system, the latter might be classified in that family. So, seeing that *Sibogagorgia* can be classified neither in the Paragorgiidae nor in the Anthothelidae, there is nothing for it but to create a new family, the SIBOGAGORGIIDAE.

In some respects this family is closely related to the Paragorgiidae. In both families we see:

1. Dimorphism of the zooids.
2. A striking similarity in habitus (club-shaped extremities of the branches).
3. Numerous medullary canals with mesogloeal sheaths.
4. The spicules, especially those of the medulla, show some resemblance.
5. Also in *Paragorgia arborea* there occur nearly white specimens.

But there are also important differences:

1. In *Paragorgia* the coelenterons of the terminal zooids pass into the medulla, in *Sibogagorgia* they do not.
2. In *Paragorgia* there is no clear separation between cortex and medulla, there are no boundary canals; in *Sibogagorgia* both are present.
3. In *Paragorgia* there is no separate independent network of peripheral cortical solenia, in *Sibogagorgia* there is.

On the other hand, however, there is also a great resemblance to the Anthothelidae, especially as regards the canal system. In my opinion this is decisive. Consequently, like the Anthothelidae, the family Sibogagorgiidae should be classified in the Scleraxonia.

The diagnosis of the family Sibogagorgiidae should run as follows:

Scleraxonia with coenenchyma consisting of a cortical and a medullary layer separated from each other by a circle of boundary canals. In the tips of the branches the medulla may be perforated by solenia, it is true, but these are not direct continuations of the coelenterons. The last mentioned reach as far as the medulla and are connected with each other by boundary and cortical solenia. Medulla consisting of free spicules, many of them surrounded by horny sheaths. Zooids dimorphous. — One genus with one species, *Sibogagorgia weberi* Stiasny.

LITERATURE

KÖLLIKER, A., 1870. Beiträge zur Kenntniss der Polypen. Verh. d. Phys. Med. Ges. in Würzburg (N. F.), vol. 2.

KÜKENTHAL, W., 1919. Gorgonaria. Wissensch. Ergebn. d. Deutschen Tiefsee-Expedition a. d. Dampfer „Valdivia" 1898-1899, vol. 13, Teil 2.

——, 1924. Gorgonaria. Das Tierreich, vol. 47. Berlin und Leipzig.

NUTTING, C. C., 1911. The Gorgonacea of the Siboga Expedition. VIII, The Scleraxonia. Siboga-Expeditie, Monogr. 13, b5.

STIASNY, G., 1937. Die Gorgonacea der Siboga-Expedition. Suppl. II, Revision der Scleraxonia mit Ausschluss der Melitodidae und Coralliidae. Siboga-Expeditie, Monogr. 13, b8.

THOMSON, A. J. & L. M. I. DEAN, 1931. The Alcyonacea of the Siboga Expedition with an addendum to the Gorgonacea. Siboga-Expeditie, Monogr. 13, d.

VERSEVELDT, J., 1940. Studies on Octocorallia of the families Briareidae, Paragorgiidae and Anthothelidae. Temminckia, vol. 5. Also as thesis, Leiden.