STUDIES ON OCTOCORALLIA OF THE FAMILIES BRIAREIDAE, PARAGORGIIDAE AND ANTHOTHELIDAE

PROEFSCHRIFT

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CONTENTS

INTRODUCTION

The object of these studies is a closer examination of the anatomy of the Octocorallian family Briareidae Gray. Our knowledge of the structure of different genera and species belonging to this family is unsatisfactory. Some authors pointed out this fact, e.g., Broch (1916), Hickson (1930) and Stiasny (1937). The latter complains more than once of the great uncertainty still prevailing with regard to the most important anatomical problems, even in apparently well-examined forms, such as *Anthothela grandiflora* (M. Sars) and *Paragorgia arborea* (L.).

A closer investigation of the canal system especially was desirable in view of the important place it occupies in taxonomical respect. Therefore, the principal part of the present paper treats of the canal system and the relation between this system and the coelenterons. I laid down the results in diagrams.

Meanwhile the examination has not been restricted to the canal system, but it has been extended to other important problems. The spicules, e.g., if necessary, were examined again and so was the occurrence of horny substance, mesogloeal cell-strings and cell-vessels, the medulla-chords, etc. Unfortunately the material, for the greater part collected during the "Siboga" Expedition, was not sufficiently preserved for accurate histological examination. Only occasionally cytological observations about ectoderm, endoderm and mesogloeal cells are recorded.

Dr. G. Stiasny, conservator of the Rijksmuseum van Natuurlijke Historie at Leiden, drew my attention to the many problems concerning the anatomy of the Briareidae Gray. In more than one respect I came to other results than Dr. Stiasny in his paper of 1937. This did not prevent him from assisting me by word and deed, and I tender my best thanks to him for his interest and support!

As regards the material, I want to express my gratitude to Prof. Dr. H. Boschma, Director of the Rijksmuseum van Natuurlijke Historie at Leiden, who placed at my disposal several specimens of Briareidae, which were present in the Rijksmuseum and to Prof. Dr. L. F. de Beaufort, Director of the Zoological Museum at Amsterdam for entrusting to me the splendid material of the "Siboga" Expedition. Moreover I received some material from Prof. Dr. S. J. Hickson at Cambridge (*Solenocaulon ramosum* Hickson), from Dr. Carl Dons at Trondheim (*Paragorgia arborea* (L.). *Anthothela grandiflora* (M. Sars)) and from Dr. T. Soot-Ryem at Tromsö (*Paragorgia arborea* (L.)); I am greatly indebted to them for sending these specimens.

The "Siboga"-material was described before by Nutting (1911) and Stiasny(1937). The latter also examined many specimens of another origin. Both authors, however, confined themselves in their taxonomic investigations to the enumeration of habitus, colour, size and shape of spicules, the occurrence of horny substance and the like.

Nutting in particular mentions very few anatomical facts. Stiasny made a more detailed examination of the Briareidae. However, it appeared to me, that there are many mistakes in the results of his investigations. This especially refers to the horny substance. Stiasny only made free-hand sections with a razor or scalpel, but he did not stain them. In this way the horny substance is not clearly observable. Moreover, Stiasny applied a wrong method of measuring, and owing to this the lengths of the spicules he gives are often 25—50 % too small. Further there are numerous mistakes in Stiasny's textfigures. For instance: the four drawings of textfig. F2 concerning transverse sections and diagram of *Anthothela grandiflora* are incorrect. Whenever I had occasion for it in the present paper, I pointed out the mistakes in the drawings. His figures of the spicules are good, but it is a pity that not all the spicules were represented on the same scale. This makes it very difficult to compare the spicules of the same species, but also those of the various species with each other, the more so, because the dimensions given in the text proved unreliable. In other respects also (canal system, e.g.) Stiasny's statements are disputable.

Technical comments. As regards the conservation of the material, see Stiasny (1937, p. 4). I did not use dry specimens, except for the examination of the spicules of *Briareum asbestinum* (Pall.).

Of some species I made longitudinal and transverse sections with a razor. Such sections often proved sufficient to get a good idea of the canal system

and particularly of the usually wide medullary canals. But such undecalcified and unstained sections were absolutely useless for examining horny substance. Therefore they were stained, sometimes after decalcification with a strongly diluted solution of nitric acid. There are different methods of staining horny substance. I tried especially the following methods:

1. Method of Martinotti (1924) with orange G-methyleosin-waterblue. With this method I obtained good results: the horny substance was stained red-brown, often in a very characteristic way.

2. Staining with methyleosin alone already gave good results. First the sections were a little overstained in an alcoholic solution of methyleosin, afterwards differentiated in 80 % alcohol. The horny substance proved to hold the stain better than the mesogloea did.

3. Staining with carbol-gentianviolet and afterwards with carbolfuchsin. Good results, horn purple. This method may also be recommended to make canals and cell-strings more clearly visible in free-hand sections.

To make microtome-sections, the fragments were first decalcified with nitric acid, afterwards embedded in paraffin in the usual way and cut to a thickness of 10—15 μ. I found once more that orange G was a good stain for horny substance. To obtain proof that it was really the horny substance that was stained, I made microtome sections of *Muricella umbraticoides* Stud. and of *Eumuricea squarrosa* Verr. (Holaxonia, with a horny axis!). Now this axis showed the same light-brown colour as the horny sheaths of the Scleraxonia examined. Therefore I stained many series with haematoxylin Ehrlich-orange G. A better and more contrasting result is obtained when they are afterwards stained with methyleosin; staining with haematoxylin Ehrlich-methyleosin alone gives entire satisfaction too.

Terminology. There are some technical terms having more than one meaning in literature. I point, e.g., to the different meanings which the words axis, coenenchyma, verruca, calyx, "Kelch", polyp, etc., may have. Therefore it is necessary to give a clear definition of the terms used, as Deichmann did (1936, p. 28). I copied some definitions of hers, here and there I made alterations.

Aggregate: the hard calcareous mass formed by the fusion of spicules (in *Solenocaulon*; more detailed discussion in chapter VIII).

Anthocodia (not: anthocodium, plural anthocodia, as Aurivillius always has it): the distal free part of the zooid having a thin wall and bearing the mouth and tentacles; cf. Hickson (1930, textfigs. 1 and 2).

Anthostele: the proximal rigid part of the zooid having a thick wall ("Polypenkelch" of Kükenthal).

Autozooid: individual with a complete circle of tentacles and long mesenteries.

Coelenteron, coelenteric cavity or gastral cavity: the body cavity of the zooid. In *Briareum asbestinum* and *Paragorgia arborea* the gastral cavities of the terminal zooids appear to consist of two portions, a spacious distal one and a narrow canal-shaped proximal one. These portions I name coelenteric cavity s. str. and coelenteric canal respectively. In fig. 51 I give a diagram of the species mentioned above. The terminal zooids are drawn entirely in black and now the distal coelenteric cavities s. str. and the proximal coelenteric canals are distinguishable.

Coenenchyma: the common colonial mesogloea with its spicules, mesogloeal cells, horny sheaths (vide Hickson, 1906) and consisting of cortex and medulla [1]).

Cortex: the outer layer of coenenchyma in which the coelenterons are embedded.

Crown: a ring of transversely placed, bow-shaped spindles in the anthocodia below the tentacles.

Front and back of a colony: if the zooids are gathered more densely on one side than on the other.

Medulla: the inner layer of the coenenchyma. In *Paragorgia arborea* the terms circumsolenial and intersolenial medulla are used.

Medulla-chord ("Markstrang" of Kükenthal): part of the medulla, more or less lying in the centre, consisting of homogeneous mesogloea without spicules or provided with spicules of a characteristic shape; the presence of cortical spicules is not at all typical.

Mesogloea: a substance, usually gelatinous in consistency, separating the coelenterons, surrounding solenia and spicules, and containing isolated cells, cell-strings and cell-vessels (vide vessels).

Mesogloeal chords: chords or strings of homogeneous mesogloea, occurring in the medulla of some Briareidae, devoid of spicules and horny substance.

Points: the eight rows of spicules on the aboral sides of the tentacles.

Siphonozooid: the reduced individual without tentacles; has a relatively large siphonoglyph, two long dorsal mesenterial filaments and two short ventral ones.

Solenium: canal lined by endoderm and connecting the gastral cavities

1) I have always avoided the term axis; see p. 60 sq.

or forming a network in cortex and medulla. The solenia may be divided into:

a. cortical solenia, occurring in the cortex,

b. medullary solenia, in the medulla,

c. boundary solenia, canals separating the cortex from the medulla,

d. boundary space, formed by the fusion of boundary canals into one space, separating cortex and medulla in a very distinct way.

Stalk: the steril basal part of a colony (*Solenocaulon*). Moreover eggs and spermaria may be provided with a stalk.

Ventral (sulcar) aspect of a zooid: the side of a zooid with the ciliated groove (siphonoglyph or sulcus); the muscle-banners are all situated on the ventral sides of the mesenteries. The opposite side is called asulcar or dorsal.

Verruca: more or less retracted anthostele, forming a low tubercle or hillock on the surface of the colony.

For the sake of distinction I will call the rough tubercle-shaped processes of the spicules warts.

Vessels or cell-vessels ("Zellkanäle" of Kükenthal): wide or narrower canal-shaped spaces occurring in the mesogloea, not lined by endoderm; in most cases mesogloeal cells are met with in the lumen of the vessels, sometimes they are devoid of cells. Such mesogloeal spaces I will call vessels to distinguish them from the canals (endodermal canals, solenia). Cell-strings and cell-vessels may pass into each other (cf. Kükenthal, 1919, p. 655).

Zooid: the individual animal, regardless of its anatomical features.

The spicules. To make preparations of the spicules I have tried the old method of boiling in potash, but the result was rather poor—it seemed as if the spicules became transparent. Later on I used "Milton", recommended by Hickson (1937, p. 83). This method gave excellent results. A fragment of the coral was laid in a concave slide and a few drops of "Milton" were added. The fragment having been entirely pulverized, the liquid is sucked up by filterpaper. After that clear water is added which has to be refreshed a few times. After being washed thoroughly in this way, the spicules are placed on a common slide and carefully dried over a spirit-flame and embedded in Canada-balsam. This method has the great advantage of enabling us to make preparations of the spicules of small objects (anthocodiae, fine scales of the cortex, etc), without spicules getting lost.

The variability of the spicules is very great: there are always aberrant forms. Still it is not difficult to trace the spicules, that are characteristic for any species, in the medulla, the cortex, the tentacles, etc. In the present

paper only typical spicules like these have been drawn, because they are of the greatest value for the taxonomy. Aberrant forms, however interesting ("Drillinge", "Vierlinge", abnormally long or short ones, etc.), but occurring sporadically or in a very small number, were omitted.

In order to be able to compare the spicules of the same species and of the different species more easily, all the spicules have been pictured on the same scale, viz., 200 ×.

I examined the following species: *Erythropodium caribaeorum* (Duch. & Mich.), *Briareum asbestinum* (Pall.), *Paragorgia arborea* (L.), *Solenopodium excavatum* (Nutting), *Anthothela grandiflora* (M. Sars), *Semperina brunnea* Nutting, *Solenocaulon jedanense* Nutting, *S. grayi* (Studer), *S. ramosum* Hickson, *S. sterroclonium* Germ., *Diodogorgia ceratosa* Kükth. and *Iciligorgia orientalis* Ridley. All these species were formerly regarded as belonging to one family, the Briareidae Gray. Broch (1916), Aurivillius (1931) and Stiasny (1937), however, have divided this family into new families, and I have come to the conclusion that this is right. With Kinoshita (1913), Broch (l.c.), Molander (1929) and Aurivillius (l.c.) I am of the opinion that the canal system is of a great taxonomical value. On the strength of this system and furthermore on the strength of the monomorphous or dimorphous character of the zooids I divided the family Briareidae Gray into three families which for the greater part correspond with the families Briareidae Auriv., Paragorgiidae Auriv. and Anthothelidae Broch. The canal system of the two first-named families corresponds with the diagram of fig. 51; the canal system of the last-named family is represented diagrammatically in fig. 52. Of the species examined *Erythropodium caribaeorum* and *Briareum asbestinum* belong to the Briareidae Auriv., *Paragorgia arborea* to the Paragorgiidae Auriv. and all the other species to the Anthothelidae Broch. In chapter XV I will discuss this matter more fully.

At the beginning of each chapter I mention the chief authors who have examined or recorded the species dealt with in this chapter. If an author is named anywhere without date, the paper mentioned at the beginning of the chapter is referred to.

I. ERYTHROPODIUM CARIBAEORUM (DUCH. & MICH.)

Of this species I examined a fragment of the largest of the three type-specimens of Kükenthal, mentioned by Stiasny (1937, p. 8). Besides free-hand sections I also examined a series of microtome sections across the coenenchyma.

The structure of *Erythropodium caribaeorum* was elaborately described by Kükenthal (1916b) and Stiasny (1937). I need not add much to their descriptions.

Much has been written in course of time about the genus *Erythropodium* and in particular about the place to be occupied by this genus in taxonomical respect. Kükenthal (1919, p. 31 sq.) gave an outline of the literature. He himself regards *Erythropodium* as belonging to the Briareidae, on the following grounds:

a. The coenenchyma of *Erythropodium* consists of two layers.

b. *Erythropodium* has a mesogloeal horny skeleton in the basal layer of the coenenchyma.

According to Kükenthal especially the last character is of great importance. He noticed a few horny fibres in the upper layer running horizontally. Some of these were rather thick. They consisted of concentrical strata and were surrounded by isolated cells or cell-strings. In the basal layer these horn-formations were more abundant, especially as sheaths round spicules. Towards the base these sheaths form a meshwork that in its turn passes into the basal horny membrane. This membrane is rather thick, consists of several strata and is secreted by mesogloeal cells. According to Kükenthal the basal layer of the coenenchyma is to be compared with the "axis" (medulla) of Scleraxonia.

In my preparations the horny basal membrane is present. This membrane sends up numerous horny offshoots or branchlets in the coenenchyma. These offshoots envelop the undermost spicules and form sheaths connecting these spicules with one another. The thickness of the layer in which these horny sheaths are found, is only about 0.015 mm. So it is very thin and contains 1—2 strata of spicules.

I looked for horny sheaths everywhere else in the coenenchyma, but in vain. Here and there little masses of horny substance, irregular in shape, did occur, but horn-formation like that has nothing to do with spicule-sheaths. Nor could I find anything of a "meshwork of horny sheaths".

From Kükenthal's description one gets the impression that the horny substance occurs everywhere in the basal layer, but my results are quite different. In Kükenthal's fig. E (1916 b) it strikes me that the horny sheaths are rather small and that they are lying in the same places as the remains of organic matter in my own sections. A definite opinion could have been obtained only by reexamination of the preparations of Kükenthal, but I think that Kükenthal mistook the organic matter for horny substance. Anyhow, in my preparations I cannot find all these horny sheaths.

Now the question in how far the genus *Erythropodium* differs from the

genus *Parerythropodium* requires an answer. Kükenthal again and again pointed out that the difference consists in the presence or absence of a meshwork-like horny skeleton. To find an answer to this question I examined a few series of *Parerythropodium (Alcyonium) coralloides* (Pall.) and of membranous forms (juvenile stages) of *Alcyonium digitatum* L. In the first species I could not detect a basal membrane with certainty. In the second species there was a distinct basal membrane, but it did not possess offshoots running upwards into the coenenchyma. In *Erythropodium caribaeorum* the formation of horny substance clearly is in a more advanced stage. But is this rather small difference sufficient to refer these species to different orders, viz. Alcyonaria and Gorgonaria, as Kükenthal does? In my opinion this is going too far (vide chapter XIV, § 5).

In *Erythropodium caribaeorum* the spicules gradually change in colour from the surface to the base of the coenenchyma. In the surface layer (0.15 mm thick) all the spicules are colourless. But at a somewhat greater depth among the colourless spicules a few red ones are met with. Basalwards the number of red spicules continuously increases, so that the basal layer (0.6—0.8 mm thick) exclusively contains red spicules (the thickness of the whole coenenchyma on an average is 1.5 mm). Only the undermost very thin layer consists of one stratum of colourless spicules scattered among the more numerous red spicules; they remind one of those of the surface layer.

So, if one wants to divide the coenenchyma into two layers on account of the colour, this division must be arbitrary, because a natural dividing line is absolutely lacking.

In the mesogloea we find cell-strings and cell-vessels; the latter are up to 0.022 mm in diameter.

The canal system and the zooids (cf. diagram, fig. 1). In *Erythropodium caribaeorum* the narrowest endodermal canals lie in the uppermost layer of the coenenchyma. They are 0.03—0.06 mm in diameter and approach the surface of the coenenchyma to within a very small distance, often not more than 0.006 mm. Basalwards the width of the canals rapidly increases; the widest canals, measuring 0.20—0.25 mm in diameter, are situated at the height of the bases of the coelenterons. Close above the basal membrane the canals are mostly about half as narrow again. All the canals chiefly run in a horizontal direction and form a close network. As already has been stated by Kükenthal, the coelenterons are connected on all sides with the canal system through narrow canals.

The coelenteric cavities themselves still show something remarkable: on the dorsal side all of them have an excavation (vide diagram) pointing

obliquely downwards, in which dorsal mesenteries are found. Sometimes these dorsal mesenteries pass for a small distance into the fine canals entering into the coelenterons. By means of these excavations it is easy to recognize the dorsal side of the zooids. And now we observe that the position of the zooids is very changeable: the median planes of the zooids are not

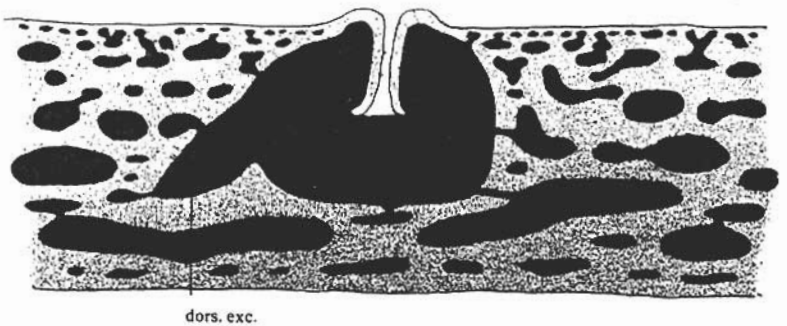

Fig. 1. *Erythropodium caribaeorum*. Diagram. dors. exc., dorsal excavation. The difference in dotting shows the gradual change in colour from the surface to the base. × 25.

parallel to each other (the terms abaxial and adaxial of course cannot be used in membranous forms like *Erythropodium*). The form of the coelenteron caused by the above-mentioned dorsal excavation remotely reminds one of the shape of some coelenterons of *Briareum asbestinum*; the continuation into a long coelenteric canal, however, is lacking.

II. BRIAREUM ASBESTINUM (PALLAS)

Of recent years this coral has been investigated by Kinoshita (1913), Kükenthal (1916b) and Stiasny (1935 and 1937). I also mention Duchassaing & Michelotti (1864), Studer (1887) and Deichmann (1936).

§ 1. The material.

Stiasny (1935) described the splendid and excellently preserved material of *Briareum asbestinum*, collected by Prof. Dr. H. Boschma at Tortugas. Of this material longitudinal and transverse sections were made, from the upper part as well as from the lower parts of the colony. Moreover, I examined some of the numerous fragments of dry material from the "American Sea" in the Rijksmuseum van Natuurlijke Historie, Leiden.

§ 2. Cortex and medulla.

In the coenenchyma of *Briareum asbestinum* Kinoshita distinguished two layers, cortex and medulla, both of them being sub-divided into two layers.

He based this division chiefly on differences in the canal system: in the cortex there is a meshwork of solenia, in the medulla we find longitudinal canals.

Kükenthal and Stiasny (1935) also distinguished two layers in the coenenchyma, but now especially on account of the colour. The cortical layer is light-yellow, the medulla is red or bluish-red (blue-violet). Both authors admit that a well-defined boundary does not exist. It is difficult indeed to define the boundary by means of this difference in colour caused by the spicules!

So the division of Kinoshita, based on the canal system, is to be preferred. But in this case, too, the separation between cortex and medulla is very indistinct. The best view is probably to let the separation coincide with the basal sides of the lateral coelenterons. In this case the horny substance and the longitudinal canals are confined to the medulla, and the coelenteric cavities belong to the cortex as in other Briareidae (cf. Kinoshita, fig. 5).

§ 3. The canal system and the coelenteric cavities.

Opinions differ about the canal system and the relation between this system and the body-cavities. Kinoshita (1913, p. 30) writes: "Die Magenhöhlen sind, von dem Niveau der Rindenoberfläche gemessen, 3 Mm tief, und sind etwas schräg nach unten gerichtet. Sie enden nicht am Boden blind abgerundet, sondern führen je zu einem schmalen Kanal, welcher, bald sich verschmälernd, gerade hinunter läuft und sich in das Netzwerk der Solenia verschwindet. Dieses Verhalten ist bei dem am Stammapex befindlichen Polypen viel stärker betont. Die Magenhöhlen bei diesen Polypen sind nämlich viel tiefer als bei den Lateralpolypen und gehen in den Kanalabschnitt, der den Stamm hinunter durchläuft, ganz allmählich über." Kinoshita (1913, p. 27) records the observation: "dass bei den Gattungen *Briareum* und *Paragorgia* die Terminalpolypen an ihrer Basis je zu einem Längskanal führen, welcher durch den Zentralstrang der Skeletachse hindurch bis zum Ausgangspunkt der betreffenden Zweige reicht...".

But Kükenthal's opinion is quite different. He writes (1916, p. 475): "Die Gastralräume der Polypen sind bis 3 mm tief und enden am Boden abgerundet. Ein Netzwerk von Solenia verbindet sie untereinander und mit den grösseren Solenia, welche in der Markschicht entlang ziehen. Gelegentlich treten die longitudinalen Solenia auch direkt in den Boden des Gastralraumes ein. Das lässt sich vereinzelt bei seitlichen Polypen beobachten, bei den am Ende des Stammes stehenden ist es sogar die Regel".

According to Kinoshita the zooids have long cavities and the longitudinal canals are to be considered as the direct continuations of these cavities.

Kükenthal, on the other hand, regards these canals as real solenia, because, firstly, the mesenteries do not continue into the longitudinal canals, and, secondly, similar large canals also occur in the membranous extensions, on which the stems arise.

Hickson (1930) is of opinion that the only conclusive proof concerning the longitudinal canals can be given by the embryology. He writes (p. 243): "If they are derived from the system of endodermal canals connecting the body-cavities of the polyps they are solenia, but if they represent polyp-cavities which have lost their mesenteries in growth they are not solenia". I largely agree with Hickson in that the embryology can give the only conclusive proof. But something must be said about the above-mentioned quotation. "If they are derived from the system of endodermal canals ... they are solenia...", but surely new coelenteric cavities may arise from the endodermal canals? Hickson (1895, figs. 46 and 48) himself gave drawings, illustrating this (vide also the same work, p. 379). And as for the loss of mesenteries: I think it is quite possible that the mesenteries are only found in the distal part of a zooid, because for instance a stronger growth has begun in the proximal part. And when it is like this, Kükenthal's first argument falls through.

Stiasny (1935) made sections, only free-hand ones, however. Examining these sections, kindly put at my disposal by Dr. Stiasny, I got the impression that Kinoshita was right. Stiasny wrote (p. 189): "Alle Gastralräume sind gleichmässig gebaut, verschmälern sich allmählich und gehen direkt in die Längskanäle über. Der einzige Unterschied zwischen terminalen und lateralen Polypen wäre nur, dass die letzteren etwas kürzer und stärker abgebogen sind". In his opinion there is a great conformity between the condition of *Briareum* and that of *Alcyonium*.

So Kükenthal's opinion is opposed by that of Kinoshita and Stiasny. Broch (1916) and Hickson (1930), who apparently did not investigate *Briareum* themselves, hold with Kinoshita's opinion.

Now I am going to discuss the results of my own examination. In accordance with Kinoshita the canal system may be divided into an irregular meshwork of canals in the cortex and the more longitudinal canals in the medulla.

The cortical solenia have a lumen varying from 0.06—0.16 mm; on an average they are 0.11 mm in width. They form a close network between the coelenterons with which they are often connected by relatively small openings or narrow canals. Kinoshita moreover distinguished an outer cortex-layer of 0.5 mm in thickness with a fine meshwork of solenia. Kükenthal, too, noticed a close network of narrow solenia under the

epidermis. The outer solenia are indeed narrower (0.05—0.06 mm) than those lying more inward. But from these measurements it appears that the difference is not great; from the outside to the inside there is a gradual increase in width of the cortex-solenia. In the extremity of a branch I noticed still narrower solenia; the high endodermal epithelium allows there a lumen of only 0.015 mm. The existence of a separate layer, as Kinoshita says, is out of the question, and certainly one of 0.5 mm in thickness.

The endodermal epithelium lining the cortex-solenia is about 4 μ in height, but the superficial narrow solenia have a higher epithelium (15 μ) especially on the side turned outwards.

The medullary canals are not equal in width in all places. In the central part of the medulla they are narrower (0.15 mm and less) than in the thick outer layer of the medulla (mostly 0.25—0.30 mm, maximum nearly 0.50 mm). In longitudinal sections we see that the medulla-canals chiefly run in a longitudinal direction, but at the same time they frequently bifurcate and unite, so as to form a meshwork stretched lengthwise. For this reason it is already impossible to regard the medulla-canals as coelenteric cavities as Kinoshita c.s. do. In agreement with Kükenthal we must call them solenia.

From the fact that the medulla-canals form a network it follows that the number of canals will vary in different transverse sections. Now Stiasny (1935) thinks that, if his opinion about the canal system is right, the number of canals in transverse sections must increase in basal direction. And he states that he has found this to be true. In the light of what has been said above, it is quite possible that the number of canals increases in the basal direction. But if Stiasny's opinion were right, in any transverse section we must find as many medullary canals as there are zooids in the part above that section. And this is certainly not the case.

Let us now see what is the relation between the coelenterons and the medullary canals. It appears that different types of coelenterons are to be distinguished, chiefly depending on the place occupied by the zooids.

a. In the tips of the colony there are zooids, the coelenterons of which are gradually narrowing downwards and which pass into long medullary canals. These canals do not bifurcate for a long distance, but they are connected with each other directly by means of narrow anastomoses or indirectly by means of irregular solenia. In the most terminal zooids the coelenterons go downward in an almost straight line and then pass into the canals, but the farther from the tip, the more the coelenterons have to curve down when passing into the canals. I will call these canals coelenteric canals. They can be followed for a distance of 5 or 10 mm, but then they suddenly merge into an irregular meshwork of medullary solenia (cf. diagram, fig. 2, a).

b. In the tips there are also some zooids becoming narrower proximally, but terminating blindly cornet-shaped (diagram, fig. 2, b1); we cannot call this a "coelenteric canal". These coelenterons do not reach into the medulla either, but lie entirely in the cortex. At the blind extremity they are connected with ordinary cortical solenia.

c. The ordinary type, not occurring in the tips but for instance in the middle of a branch, is bag-shaped with a broad rounded or flat base (c in diagram). They are entirely lying in the cortex and are on all sides connected with the cortical solenia and at their base with the medullary canals.

Among these zooids, others are often met with which might be regarded as intermediate forms. In that case they are like type c, but the coelenteric cavity shows a downward turned point at the base (b2 in diagram).

d. Finally there are small zooids, varying in length but not reaching the boundary between medulla and cortex. They are narrower and shorter than the zooids belonging to type c, and are on all sides connected with cortical solenia, also at the proximal end. They occur in the tip parts of the branches to the number of 10 to 12, and are scattered among the larger zooids; very few occur a little farther from the tip (d in diagram). The stomodaeum of these zooids is short. The anthocodiae are entirely retracted inward, the tentacles are even turned inside out; anlages of pinnulae are present. Of genital organs nothing is to be seen. The eight mesenterial filaments are all present. Size and shape do not remind one of siphonozooids. There is no doubt that we must consider them to be young autozooids.

In looking over these results, we come to the conclusion, that the coelenteric cavities may terminate blindly (conform Kükenthal), but others may pass into long medullary canals (Kinoshita and Stiasny).

§ 4. The diagram.

I agree with Stiasny's statement that the diagram given by Kinoshita must be regarded as insufficient. The point is to show the transition especially of the terminal zooids into the medullary canals, but this does not appear from it at all.

Stiasny (1935) also has given a diagram. Although he did not represent the coelenteric cavities in black but used this colour for the coenenchyma, his meaning is quite clear. According to him, all the zooids are alike in their relation to the medullary canals, and according to my investigations this is incorrect. The real system is more complicated, and a diagram that may be in accordance with reality, must be more complicated than that given by Stiasny.

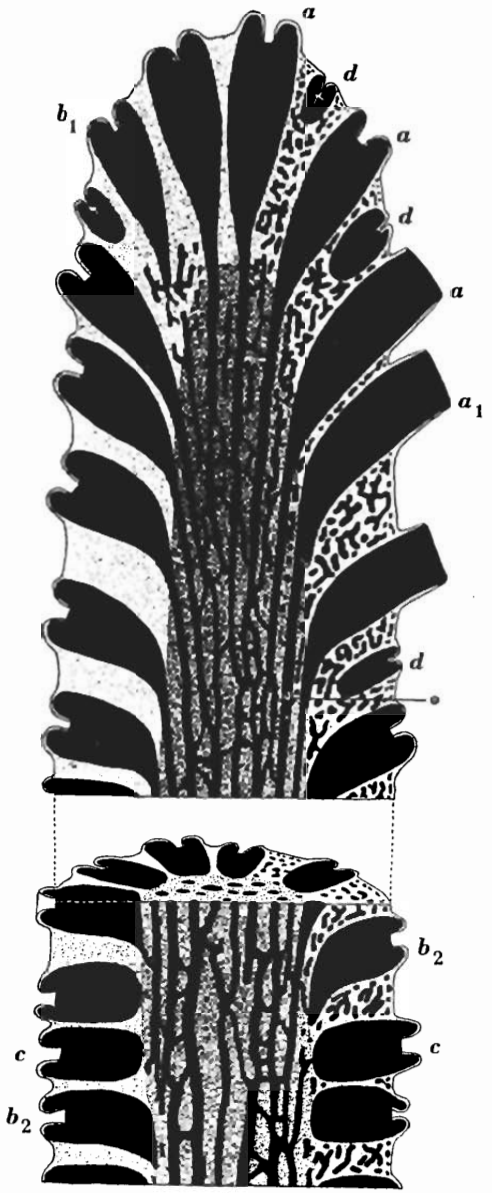

Fig. 2. *Briarcum asbestinum*. Diagram. × 6.

My diagram (fig. 2) consists of two parts belonging together; it represents the canal system in the tip of a branch.

The transverse section shows the distribution of the canals, etc. In order to make the diagram not too complicated, the cortical solenia in the left part of the drawing have been omitted. The medulla is more darkly dotted than the cortex. As for the signification of the letters a to d cf. § 3. In zooid a_1 an arrow indicates the place where the dorsal mesenteries terminate, and ⊙ the place, where I still have found a separate fragment of the dorsal mesenteries (see § 5). On the right side there are three zooids with expanded anthosteles. From the drawing it appears further that the medullary canals form a longitudinal meshwork, while in the cortex a close and irregular network of solenia is to be found.

§ 5. Where do the zooids terminate proximally?

It is unnecessary to put this question with regard to the types c and d. The limitation of the coelenteric cavities is clear enough in those cases. But with regard to the types a and b, occurring especially in the tips of the branches, this question has to be answered in connection with the controversy between Kinoshita c.s. and Kükenthal concerning the ending of the zooids.

From § 3 it appears that we may distinguish two kinds of longitudinal canals, viz., the coelenteric canals and the ordinary medullary solenia. In my opinion the coelenteric canals belong to the coelenterons of the zooids. The whole coelenteron consequently consists of a coelenteric cavity s. str. and a coelenteric canal. This opinion is supported by the following facts:

1. There is always a gradual transition from coelenteric cavity s. str. to coelenteric canal, especially in the most terminal zooids; there is no trace whatever of a sharp limit between both parts.

2. The mesenteries mostly are to be found in the coelenteric cavity s. str. only. In some cases, however, I saw that the mesenteries had continued for a small distance into the narrowing canal (cf. fig. 2, arrow in zooid a_1).In one coelenteric canal I have even found the remnant of a dorsal mesentery at a rather long distance from the coelenteric cavity s. str. (fig. 2, ⊙). From the structure it undoubtedly appears that we have to do with a dorsal mesentery. The small piece was not connected with the rest of the dorsal mesenteries and was apparently separated from it by a strong longitudinal growth. This discovery supports the possibility, suggested in § 3, that the origin of the coelenteric canal is due to a stronger growth of the proximal part of the young zooid. Furthermore the facts that the coelenteric canal runs on unbifurcated for a relatively long distance and that it arises in a meshwork of solenia, support the opinion that the coelenteric canal is a part of the coelenteron.

Summarizing we may say: all the medulla-canals are solenia, except the coelenteric canals (vide fig. 51).

§ 6. Endoderm, ectoderm and mesogloea.

The endoderm is always sharply separated from the mesogloea. I cannot distinguish cell-borders, so we have to do with a syncytium.

There is a difference between the endoderm lining the coelenterons and the one lining the solenia. The former is not only higher (the thickness of the epithelium is 11 μ and 4 μ respectively) but it is also more darkly stained. Where the cortical solenia pass into the coelenteric cavities the transition of the epithelia is visible. The cortex contains here and there minute endodermal canals (lumen 0.04 mm), connecting the larger cortical solenia. Only a few flattened cells are lining these small canals.

The endoderm of tentacles, coelenteric cavities and cortical solenia contains a great number of zooxanthellae. Farther inside the stem they

decrease in number; there are only few in the endoderm of the coelenteric canals and the outer medullary solenia.

The ectoderm of *Briarcum asbestinum* consists of cover cells, which have the same shape as those, described by Chester (1913, p. 747) in *Pseudoplexaura crassa* Wright & Studer: conical cells united at their outwards turned bases, forming the external surface of the colony and extending with their apex into the mesogloea. Other cells are more column-shaped, with a thinner part in the middle. The nuclei are round; some of them are a little smaller and more darkly stainable than the others. The protoplasm is crowded with fine granulae. On the outer surface a cuticle has been secreted, in the tips of the branches the cuticle is much thicker than elsewhere. I could not notice any trace of cilia.

The ectoderm in the basal part of the anthocodiae shows the same structure as that of the branch itself. But distally the ectoderm has changed into a flat syncytium; the ectoderm of the tentacles exactly resembles this.

In the stomodaeum-wall high cylindrical cells with dark, spindle-shaped nuclei occur. Among them we find granular gland cells, which, according to Chester (p. 751) in *Pseudoplexaura crassa* were deeply stained with haematoxylin, but in *Briarcum asbestinum* they look clear orange-red, when stained with haematoxylin-eosin. So they show a striking contrast with the supporting cells. They seem not to occur in all zooids in the same number; in some zooids they are numerous, in others they only occur in a small number, or are lacking. The number of mucous gland cells (unstained and perfectly transparent) varies as well. The zooids possessing few granular gland cells, have more mucous gland cells.

The development of the siphonoglyph varies also, in some stomodaea being slightly developed and visible for a short distance. In the lowest part of the stomodaeum the siphonoglyph always seems to be lacking.

In the mesogloea we find numerous cells sometimes being oval or spindle-shaped or star-shaped. The latter are connected with one another by fine fibrillae forming a meshwork. The cells are often arranged closer together in cell-strings. It also occurs, especially round the coelenteric cavities, that the cells are situated in fairly spacious (15—25 μ) mesogloeal cavities; in this case they are lying close to the walls of these cavities or freely in their lumen. So here we have to do with cell-vessels.

Although the mesogloeal cells often lie close to the endoderm of coelenterons and solenia, I never saw them originate from the endoderm, as, for instance, Bock (1938, p. 22) described in *Bathyalcyon*. Moreover the staining and granulation is different in both kinds of cells: the endodermal cells have a basophilous not granulated substance (stained bluish-purple with haematoxylin-eosin), the mesogloeal cells are acidophilous (more reddish in colour) and granulated; it sometimes appears as if there were vacuoles in the cells last-mentioned. On the other hand, staining and granulation of mesogloeal cells correspond with that of the ectodermal cells; both types of cells last-mentioned hang together with each other and so it follows that in my opinion the mesogloeal cells are of ectodermal origin (as mentioned by Chester and Kükenthal).

In microtome sections the spicular cavities still contain the remains of organic matter of fibrous structure, stained blue with haematoxylin. In the walls of the cavities there are some dozens of nuclei of scleroblasts.

§ 7. The spicules and the "Markstrang" of Kükenthal.

The spicules were drawn by Kükenthal (1916b) and Stiasny (1935) in a satisfactory manner. Something must still be said about the distribution of the spicules in the coenenchyma according to shape and size, with regard to the so-called medulla-chord (Markstrang) of Kükenthal.

Kinoshita has noticed that the spicules in the central part of the axis are much smaller and for the greater part coloured deep purple, in comparison with spicules from the axis-cortex. They resemble, however, more the cortex-spicules and therefore Kinoshita supposes that the spicules of the central chord are nothing but cortex spicules. Kinoshita did not give measurements of the spicules. Kükenthal thought that he had found a similar likeness, but now between the spicules of the outer cortex-layer and the innermost medulla-layer. According to him this conformity consists in: 1. small size (0.25 mm), 2. the spindle-shape, and 3. the warts being more scattered. The spicules of the two intermediate layers are larger, often irregularly shaped, and more densely covered with warts.

The results of my investigations are as follows:

1. The size of the spicules. The minimum, maximum and average size of the spicules in the different layers of the coenenchyma of a branch were measured. A diagram was made of the results (fig. 3). The lengths of the spicules were marked on the ordinate, the layers of the coenenchyma on the abscis in accordance with the radial section drawn under the diagram. In the surface layer, close to the ectoderm, there are purple little rods, 0.08—0.13 mm in length, with rudimentary warts (a). Immediately under these smallest spicules there are longer ones (up to about 0.25 mm), also mostly purple coloured (b). Farther inward they increase in size (c), reaching their maximum in the outer medullary layer (d). The largest I

observed was 0.95 mm in length [1]). The average size varies from 0.5—0.7 mm.

In the centre of the medulla the spicules are smaller again as regards the average as well as the maximum dimensions (e). But in all the layers small spicules occur, mostly rod-shaped with short warts and always purple coloured. The minimum line in the diagram shows the measures of these smallest spicules. It further appears that, generally speaking, the purple spicules are smaller and more slender than the uncoloured ones.

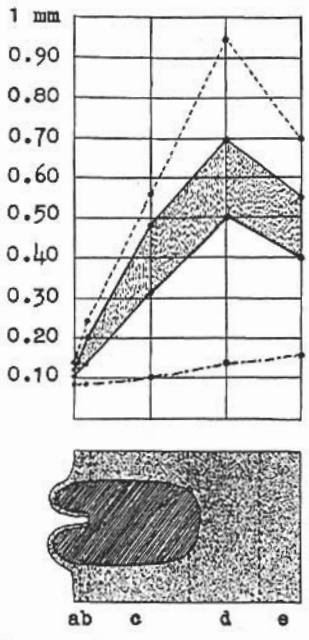

Fig. 3. *Briarcum asbestinum.* Graph of the proportion of the length of spicules in the different layers of the coenenchyma. -------, maximum measurements; - - - -, minimum measurements; dotted part, average measurements. Further explanation in text.

2. The shape of the spicules. It is very difficult to see that the spindle-shape should be the type of the spicules of the outermost cortex and the innermost medulla, so that it remains questionable; and on account of this, it appears to be impossible to tell by the size of the spicule to which part of the coenenchyma it belongs. The irregular forms, mentioned by Kükenthal as belonging to the inner cortex and outer medulla, occur everywhere in the coenenchyma. A difference in proportion between length and breadth of the spicules (8—10 : 1) is not to be found in the spicules of the different layers either.

3. The warts. As regards the warts there is no difference to be seen at all. Anywhere warts may be found varying in height and size from very minute to very conspicuous ones. Also the fact that the warts are more or less scattered is not a valid character.

From what has been said, it follows that the similarity between the outermost cortex and the innermost medulla is not at all so conspicuous as

1) Deichmann even has found one of 1 mm in length. She is right, if she does not want to establish a new species on account of this observation: the differences are too insignificant.

According to the text, the spicules drawn in fig. G by Kükenthal (1916 b) measure 0.25 mm in length, but according to the scale they are about 0.65 mm in length!

Kükenthal wants to make us believe. The presence of a distinct medulla-chord in *Briarcum asbestinum* is out of the question.

§ 8. The horny substance.

Kükenthal (1916 b, p. 475) writes: "Ein weites Netzwerk horniger Substanz durchzieht die Markschicht und fehlt auch der Rindenschicht nicht völlig. Besonders sind es an entkalkten Schnitten die Hohlräume, welche die Spicula in der Mesogloea zurücklassen, die von hornigen Ausscheidungen umgeben werden; hier und da kommt es auch zur Ausbildung dickerer Stränge". And in 1919 he writes (p. 681): "In den Stämmen ist das Hornskelett nur schwach als weitmaschiges Netz von Hornfasern entwickelt, welches die Markschicht durchzieht". He also speaks of "Hornfasern, welche die Spicula einscheiden", but only in the basal extension. From the diagnosis of *Briarcum asbestinum* (p. 47) it follows that these horn-sheaths also occur round the spicules of the stem.

I have found horny sheaths in the medulla only, and exclusively in its more central parts. These horny sheaths are chiefly restricted to the extremities of the spicules and to such places, where two spicules are lying side by side, so that they are connected by the horny substance. But I did not find anything like a "meshwork of horny substance", a "net of horny threads" or "horny fibres", expressions used by Kükenthal. Horny sheaths only occur enveloping spicules of the inner medulla.

§ 9. The genital organs.

a. Male genital organs. These occur in a large quantity in the zooids of one of the colonies. The mesenteries carry stalked testes. Each of these consists of a mass of spermatozoa covered by the endodermal epithelium. As contrasted with Kükenthal's statement (1919, p. 668), the tails of the spermatozoa of *Briarcum asbestinum* are not directed to one central cavity, but there are many cavities here in the sperm-mass, filled with the tails of spermatozoa (fig. 4). A sperm-sac therefore shows a chambered structure when sectioned.

In the centre of the testis another small cavity is to be observed, filled with spermatogonia, but frequently I saw several of such cavities scattered in the sperm-sac. In these cavities also little particles may be found, very different in size and shape, becoming deep-blue, almost black, when stained in haematoxylin Ehrlich-orange G. They appear like the nuclei of gigantic cells drawn by Kükenthal (1919, fig. 314), but I could not notice protoplasm and cell-walls around them. The largest testes in my sections were 0.33 mm in diameter.

b. Female genital organs. These also I have found in a large number in

the material. I agree with Kükenthal's statement (1919, p. 667) that the eggs in *Briarcum asbestinum* seem to be without stalks; I did not find any with a distinct stalk. Certainly the eggs were not yet ripe: the largest had a diameter of 0.135 mm, whereas Kükenthal records 0.8 mm.

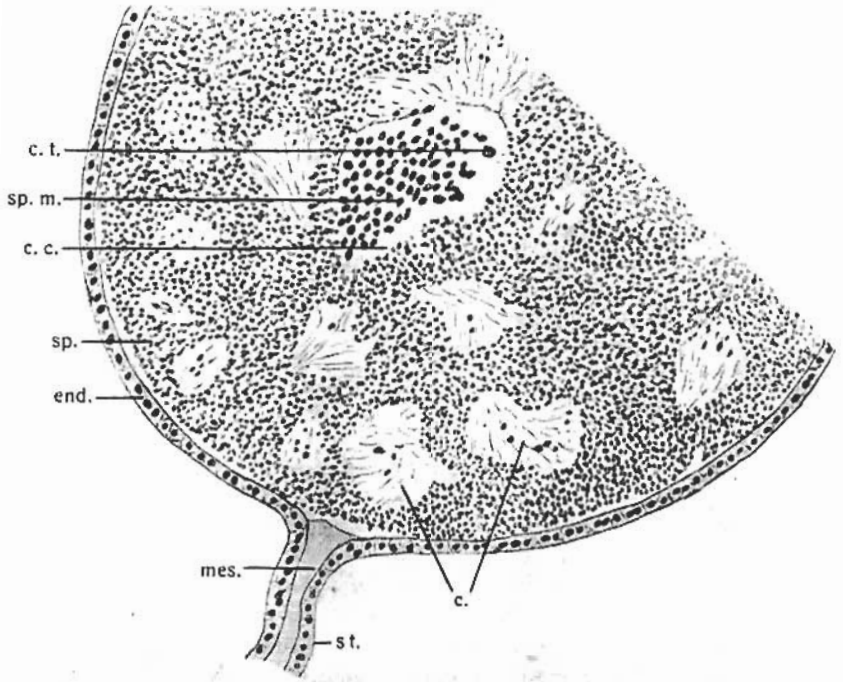

Fig. 4. *Briarcum asbestinum*. Part of a testis showing numerous cavities (c.) filled with the tails of the spermatozoa. c. c., central cavity; c. t., centrum of testis; end., endoderm; mes., mesogloea; sp., spermatozoa; sp. m., spermatogonia; st., stalk of the testis. × 360.

The male as well as the female genital cells only occur in the zooids, lying at a distance of 12 mm and more from the tips of the branches. Consequently, closer to the tips the zooids have not yet gonads.

III. PARAGORGIA ARBOREA (L.)

The principal literature concerning *Paragorgia arborea* is to be found in Broch (1912), Kinoshita (1913), Schimbke (1914), Kükenthal (1919), Hickson (1930) and Stiasny (1937). The records of Kölliker (1864), Studer (1882 and 1887), Nutting (1908 and 1913), Hickson (1915), Verrill (1922) and Deichmann (1936) are of little importance. Notwithstanding this large number of authors a good many questions are still waiting for an answer, especially those regarding the canal system, the presence or absence of a horny skeleton, the production of genital cells, etc.

§ 1. The material.

1. Fragments of dark red, light red (pink) and white (pale red) specimens. Trondheims fjord, depth 150—200 m. Collected by Dr. Carl Dons, May 30, 1937.

2. Large fragments of dark red specimens, Rijksmuseum van Natuurlijke Historie, Leiden, collected at Tromsö by Dr. T. Soot-Ryen.

The longitudinal free-hand sections excellently show the course of the longitudinal canals in the medulla, but an immediate transition of these canals into the terminal body-cavities could not be observed with absolute certainty in such sections; for that purpose microtome-sections were made. Situation and distribution of spicules may be very nicely studied in undecalcified free-hand sections.

§ 2. Medulla and cortex.

Just as in *Briarcum asbestinum*, Kinoshita distinguishes four layers in the coenenchyma of *Paragorgia arborea*, viz., an outer and an inner cortical layer, an axis-cortex and a central chord.

I have no objection to the division of the cortex into an outer and an inner layer, especially on account of the shape and the distribution of the spicules. But, like Stiasny, I can find no central chord in the medulla. Consequently a subdivision of the medulla into two layers is wrong.

The boundary between medulla and cortex is more distinct than in *Briarcum asbestinum*, though also in this case a well-defined medulla is out of the question. Points of difference between cortex and medulla are:

1. The coelenteric cavities s. str. are only found in the cortex and reach as far as the medulla.

2. Apart from the outer cortical layer (thickness 0.1—0.2 mm), there are very few spicules in the cortex (see § 6); in the medulla there are a great many, but only in the intersolenial medulla (§ 5), packed closely.

3. In the cortex the horny substance is lacking; in the medulla it occurs abundantly (§ 7).

4. In the inner cortical layer there is an irregular, close meshwork of rather spacious solenia, somewhat stretched in a longitudinal direction; in the medulla the mostly wider medulla-canals are more scattered (§ 4).

5. Round the cortical solenia the "Schwammgewebe" is lacking, whereas in the medulla it envelopes all the canals, large and small.

Especially the points 2 and 3 are important, because they always enable us to indicate where, in the sections, the cortex ends and the medulla begins.

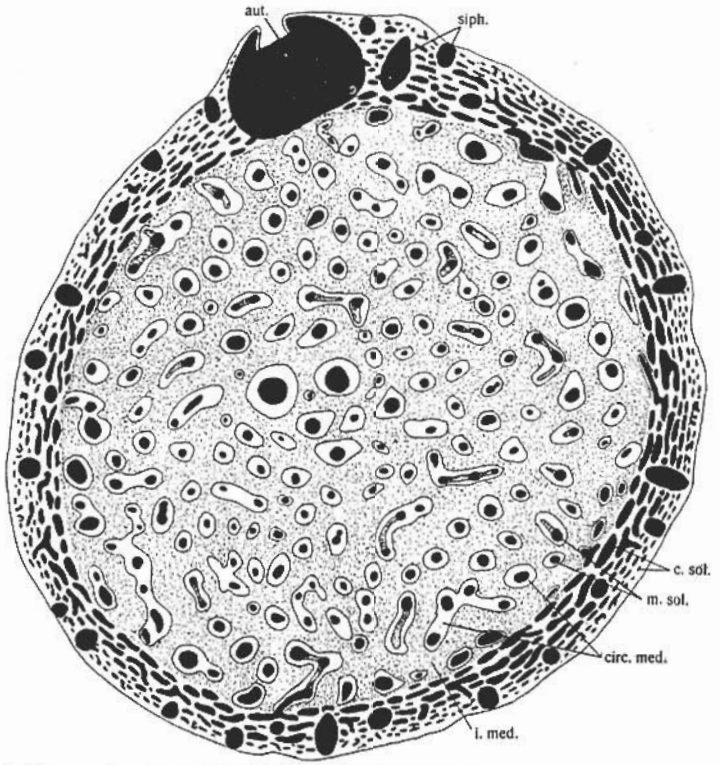

Fig. 5. *Paragorgia arborea*. Transverse section through the stem. aut., autozoid; c. sol., cortical solenia; circ. med., circumsolenial medulla; i. med., intersolenial medulla; m. sol., medullary solenia; siph., siphonozooid. × 7.

§ 3. The zooids.

It is well known that *Paragorgia* shows a dimorphism of the zooids: autozooids and siphonozooids.

a. Autozooids. According to their place we may distinguish lateral and terminal autozooids. Difference in place is always accompanied by difference in form of the coelenteron. The coelenterons of the first-named zooids terminate blindly with a more or less flat or rounded base. They

reach as far as the medulla; there is, however, often a layer of cortical solenia between the base of the coelenteron and the medulla. The terminal solenia are gradually narrowing in an aboral direction and pass into a medullary canal (further discussed in the next §).

The coelenterons of autozooids are on all sides and in many places connected with the cortex-solenia. The thin partition-walls between two adjacent zooids are frequently perforated, and by this means there is a direct connection between the coelenterons. A meshwork of solenia, however, is lacking in these partition-walls and so it is incorrect, when Kükenthal writes (1919, p. 80), that in the rather thin walls the network of canals proceeds in a radial direction.

According to Broch (1912, p. 13) only the siphonozooids produce genital cells. Schimbke (1914, p. 59), on the other hand, writes that he has observed genital products in the autozooids, viz., sperm-sacs, and in the siphonozooids sometimes small bodies resembling unripe sperm-sacs. But he is not quite sure of it. Kükenthal (1919, p. 79—80) says the genital cells develop in the siphonozooids. Now in my microtome-sections I have found genital cells (oocytes) in the autozooids as well as in the siphonozooids. So both kinds of zooids may produce genital cells, but in the siphonozooids they are certainly found in a larger number.

b. Siphonozooids. These occur all over the colony, irregularly scattered, but chiefly in the vicinity of the autozooids. The coelenterons of the terminal siphonozooids differ among themselves in length and run straight inwards. The lateral ones, especially those along the branches, in places where autozooids are lacking, are strongly bent in a basal direction. They penetrate far into the cortex, but never do they reach to the medulla. They are long and narrow (proportion up to 15 × 1) and are gradually becoming narrower in an aboral direction. All the siphonozooids are mutually and with the autozooids connected by means of cortical solenia.

Schimbke gave a description of the siphonozooids, with which I can wholly agree. As regards the gonads and the mesenteries his description wants some amplification. The stomodaeum is connected with the body-wall by eight mesenteries. Four of them pass into mesenterial filaments, viz., the two ventral and the two dorsal ones (fig. 6). The dorsal mesenteries run on to the base of the coelenteric cavities, the ventral ones are short and soon become thicker. On this thickened part the ova are formed. (I did not happen to find sperm-sacs in any specimen). The ova are stalked, the probably unripe ones are not. In the aboral direction the siphonozooids are gradually continuous with the cortical solenia; sometimes I even noticed a direct continuity with a medullary canal (diagram, fig. 7 in the middle,

left side). So, generally speaking, we cannot say that the siphonozooids terminate blindly, as Stiasny (1937, p. 77) remarks.

In textfig. Z, x of Stiasny (1937, p. 76) we see five autozooids, sectioned at different heights and not two autozooids and three siphonozooids, for the latter are much smaller than the autozooids.

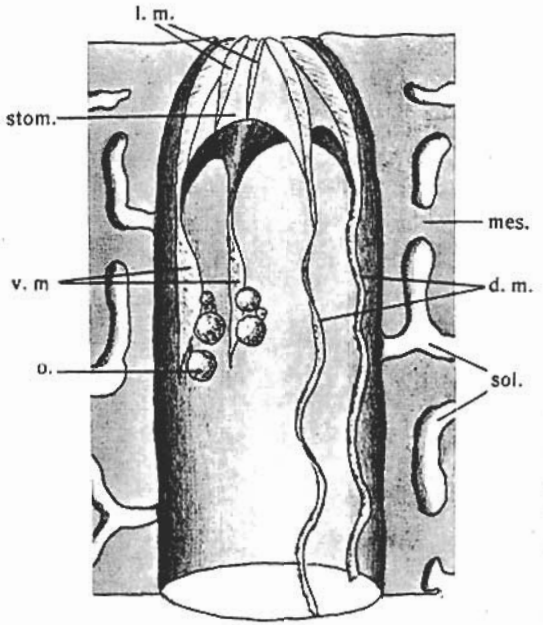

Fig. 6. *Paragorgia arborea*. Diagram of the oral part of a siphonozooid. d. m., dorsal mesenteries; l. m., lateral mesenteries; mes., mesogloea; o., ovum; sol., solenia; stom., stomodaeum; v. m., ventral mesenteries. × 80.

§ 4. The canal system and the coelenterons.

Like the canal system of *Briarcum asbestinum*, that of *Paragorgia arborea* is a subject of discussion between Kinoshita, Hickson and Stiasny on the one hand and Kükenthal on the other. Kinoshita c.s. are of opinion that the medulla-canals are directly continuous with the coelenteric cavities and consequently they are part of these cavities, whereas Kükenthal regards the medulla-canals as solenia. In this case the solenia of the inner medulla-layer would pass "directly" into the terminal coelenterons, whereas the

lateral coelenterons would be connected with the medullary solenia by means of a network of narrower solenia. According to Kükenthal the lateral as well as the terminal zooids have short body-cavities, being round at the aboral termination.

The results of my investigation are as follows. The medulla-canals run chiefly in a longitudinal direction, but ramify and anastomose repeatedly, so that we must qualify them as solenia, forming a meshwork strongly stretched longitudinally. Moreover they are connected with each other by numerous narrower transversal anastomoses. The most peripheral medulla-canals are connected with the cortical solenia by radial canals. A medulla-canal may even gradually leave the medulla and distally pass into the meshwork of cortex-solenia (see diagram, fig. 7).

What about the relation between the autozooids and this system of medulla-canals? It appears that the lateral and the terminal zooids proceed differently in this respect. Along the branches the lateral zooids are situated separately or they are united in little groups. These groups often form lateral tubercles, into which also the medulla with the medulla-canals proceeds (fig. 7, rightside, bottom). A direct passing into the medulla-canals is observable neither in the isolated zooids nor in those which are grouped together. A meshwork of cortical solenia occurs between medulla-canals and autozooids, which are relatively short and terminate with a flat base as far as the medulla. Sometimes the coelenteron passes into a short canal, curved downwards; it soon becomes lost in the many cortex-solenia.

At the tips of the branches we must distinguish between the latero-terminal and the true terminal zooids. The former are in the apex too, but more towards the sides, the latter are on the middle of the tip. The latero-terminal zooids basally pass gradually into a canal, which lies entirely in the cortex and which is perhaps only distinguishable from the cortical solenia by its wider lumen. The proper terminal zooids, on the other hand, being about funnel-shaped, gradually narrow into medullary canals. In tracing the course of these canals we see that most of them soon pass into an irregular meshwork of somewhat narrower solenia. Only occasionally can such a canal be followed for a larger distance, but there is no difference whatever between this and any other medullary canal, except that it apically straightway passes into a coelenteron.

So we see that the autozooids may penetrate into the coenenchyma to a different distance. Moreover we may state that there are various kinds of intermediate forms between short, blindly ending lateral zooids and terminal zooids, narrowing in a funnel-shaped way into long canals. Just

as in *Briarcum asbestinum*, we will call these canals coelenteric canals. They vary considerably in length, from 3.5 mm and shorter to more than 15 mm.

Now the question is, whether these coelenteric canals really must be regarded as long body-cavities or not. Kükenthal thinks they are not, because mesenteries or mesenterial filaments are lacking. I noticed, however, in a long coelenteric canal in two places peculiar long narrow bodies, fused with the endoderm and by their size immediately reminding one of fragments of dorsal mesenteries. On closer examination the tissue, however, appeared to be different from that of ordinary mesenteries. The nuclei are indistinct and less numerous. They made the impression of more or less degenerated fragments of mesenterial filaments. Another explanation I could not find. If this is right, it supports Kinoshita's opinion.

So some medulla-canals, viz., the coelenteric canals, might be considered as parts of coelenterons. All the other medulla-canals have to be considered as true solenia. By no means this complex meshwork may be regarded as coelenteric cavities!

In the cortex the solenia form a close network of oval canals, varying in height from 0.1—0.2 mm. The nearer to the surface the narrower they become: close under the ectoderm they are so narrow that the lumen is almost filled up with the endodermal cells. Consequently it is incorrect to assert (Kükenthal, 1919, p. 79, Stiasny, 1937, p. 75) that the canals are lacking in the outer layer of the cortex. At the boundary between medulla and cortex there is nothing to be observed of a crown of canals (pace Kükenthal, diagnosis p. 98), see fig. 5.

Kinoshita and Stiasny each gave a diagram showing the relation between coelenteric cavities and medulla-canals. Stiasny rightly pointed out the indistinctness in Kinoshita's diagram. But I cannot agree with Stiasny's diagram either. It is too schematic, too simple and therefore not in accordance with reality, which is much more complicated. For, firstly, it is only a few terminal autozooids that pass into long medullary canals, but most of them pass into a shorter "coelenteric canal"; and, secondly, the ordinary medulla-canals form a meshwork; and this is not visible in Stiasny's diagram.

I give a new diagram, which is more in accordance with reality, but simplified for the sake of distinctness; especially the cortical solenia have been drawn fragmentarily. In this diagram (fig. 7) the following facts are represented:

1. The three middle-most terminal autozooids penetrate the stem for a different distance. The left one passes into a wide medulla-canal, which is traceable far basally. The two others soon terminate into a meshwork of solenia, which is frequently connected with the meshwork of the cortical solenia.

2. The two latero-terminal autozooids in the tip of the branch show the transition-type to ordinary lateral zooids, because their coelenteric canals do not reach the medulla, but entirely lie in the cortex.

3. On the left side two lateral autozooids, which, at their base, still pass into a short coelenteric canal.

4. On the right three autozooids without such a canal; they are situated on a lateral tubercle of the stem.

5. Between the coelenteric cavities there are thin partition-walls, without solenia.

6. The autozooids are, just as the siphonozooids, frequently connected with each other as well as with solenia.

7. The siphonozooids are long and narrow, especially in the vicinity of the autozooids. All of them are more or less curved downwards.

Fig. 7. *Paragorgia arborea*. Diagram. × 6.

8. The medullary canals in the more basal part of the diagram form a meshwork; a few bend off into the tubercle.

9. Between the wide medulla-canals there is a fine network of endodermal canals in the intersolenial medulla.

§ 5. The mesogloea and the "Schwammgewebe" of Kükenthal.

Some investigators have noticed that the medullary canals, especially the most central, are enveloped by a zone of more or less transparent tissue. Broch and Kinoshita do not mention this tissue. Kükenthal gives some details; he states that the horny substance is lacking and that, just as in *Anthothela*, radial threads run through the mesogloea. He obviously thinks that this tissue appears in its typical form in *Anthothela grandiflora* and therefore he says that in *Paragorgia arborea* there is no formation of "ausgeprägter Schwammsubstanz". On p. 685 Kükenthal still records the lack of spicules in the "Schwammsubstanz", which he describes here as "gallertartiger Mesogloea", grown "blasig" by the formation of large vacuoles.

Contradictory to this is Stiasny's description. He found (1937, p. 75) "in den breiteren Längsgefässen der Markschicht die Lumina erfüllt von einer dicken Lage gelblicher, ganz durchsichtiger Hornsubstanz, die im Querschnitt diaphragma-artig vorspringt und nur ein ganz dünnes Lumen in der Mitte freilässt". So, according to Stiasny it has all become horny substance!

Now, what is this "Schwammgewebe"? In *Paragorgia arborea* it appears to consist of a special mesogloeal tissue, enveloping every solenium like a zone. This zone varies in width, the average being equal to that of the canals occurring in it. I call this tissue circumsolenial medulla and the rest of the medulla I call intersolenial medulla (dotted in fig. 5). As a matter of fact the spicules are lacking in the circumsolenial medulla and the horny substance is lacking too; in the intersolenial medulla both occur in great quantities. The circumsolenial medulla consists of a hyalin mass, in which a close meshwork of narrow canals (average diameter 25—30 μ), without epithelial cells. But in the lumen there are mesogloeal cells, either separated or in groups. So, what Kükenthal took for vacuoles, are in reality mesogloeal vessels.

Sometimes the circumsolenial medulla shows this typical vesicular structure far less distinctly. The vessels are narrower then and completely filled with mesogloeal cells. In this case they are fairly well like the mesogloeal vessels in the cortex.

Round the endodermal canals and running parallel to them, there is

already a meshwork of these vessels. But there is no communication between the lumina of the vessels and the solenia, a thin layer of mesogloea forming the partition-wall between them. Other vessels arise from those running parallel to the solenia. They run in a more radial direction through

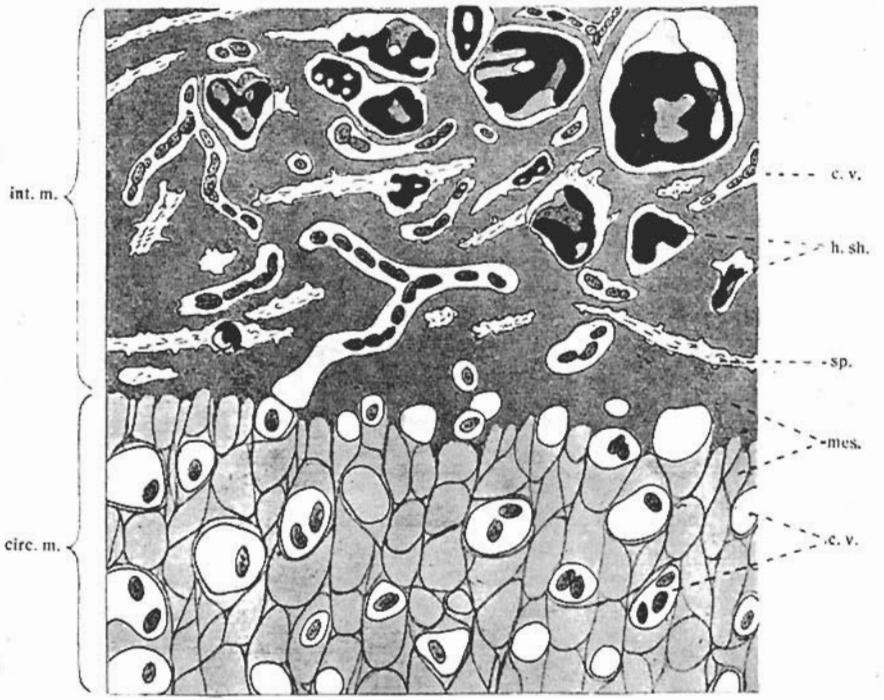

Fig. 8. *Paragorgia arborea*. Section through the circumsolenial medulla (circ. m.) and the intersolenial medulla (int. m.). c.v., cell-vessels; h. sh., horny sheaths; mes., mesogloea; sp., cavities left by spicules. × 300.

the circumsolenial medulla, so that this tissue seems to have a radial structure. This impression is backed by the fact, that there are dark-coloured lines and bands, likewise running in a radial direction which seems to arise from the intersolenial medulla (cf. fig. 8). They make the impression to consist of compact mesogloeal substance and not of connective tissue-like threads. Fig. 9 may give an idea of the meshwork of vessels. The greater the distance from the solenia, the more numerous and wider (30—45 μ) the vessels become. At the boundary between circumsolenial and inter-

solenial medulla they pass into the less close meshwork of narrow vessels, lying in the intersolenial medulla (fig. 8). Here they occur between the numerous spicules, and are often not distinguishable from cell-strings.

As the circumsolenial medulla consists of hyalin mesogloea, in which numerous vessels occur and in which spicules, etc., are lacking, this matter is very transparent. When studying a sufficiently thin transverse section of a branch, one may easily overlook the circumsolenial medulla, with the solenia lying in it. Only thus the bad textfig. 31 of Kükenthal (1919) is to be accounted for.

In microtome-sections the circumsolenial medulla is often hardly stained.

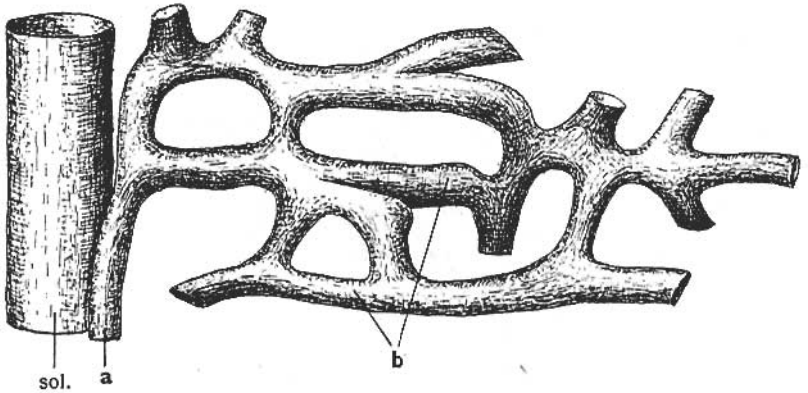

Fig. 9. *Paragorgia arborea*. Diagram of the mesogloeal canals in the circumsolenial medulla. a, vessel running parallel to the solenium; b, radial vessels; sol., solenium. × 300.

After staining with haematoxylin Ehrlich-orange G, they show a fine contrast between the circumsolenial medulla, which is stained light-blue and the intersolenial medulla, the mesogloea of which becomes yellow-brown.

All the medullary solenia are surrounded by a circumsolenial zone. This layer, however, is often very thin round the narrow anastomoses and the outer medullary solenia, and only observable after close examination. Consequently, textfig. Z. x, given by Stiasny is incorrect: he draws the circumsolenial medulla round four medulla-canals only.

In the cortex there are also mesogloeal vessels. They form a close meshwork, the lumen being narrow (9—12 μ) and closely filled with cells. There are further numerous connective tissue-like threads, running in various directions.

§ 6. The spicules.

These have been described and drawn satisfactorily by Stiasny and Broch. Their records concerning the distribution of the spicules, however, need amplification. They are right in stating that in the surface layer of the cortex the very small red spicules are present "lückenlos angestaut" (Broch, 1912, p. 14) and "massenhaft" (Stiasny, 1937, p. 76). About the distribution of the colourless spicules in the inner cortical layer, Broch says (p. 16): "Die farblosen Spicula der Rinde... liegen kreuz und quer in den Geweben dicht angestaut". The last remark is incorrect, for there are relatively few spicules in the inner cortical layer. This fact is the more conspicuous, when attention is paid to the very dense crowd of spicules in the intersolenial medulla. Only round the autozooids the colourless (sometimes slightly pink-coloured) cortical spicules are more numerous again.

As already remarked the spicules are wholly lacking in the circumsolenial medulla and a central medulla-chord does not occur either.

§ 7. The horny substance.

About the presence or absence of horny substance, the authors do not agree. Broch (1912, p. 16) only speaks casually of a horny axis-tissue. Kinoshita does not mention the horny matter in *Paragorgia* at all. Nutting (1911) denies the presence of horn-sheaths round the spicules of Briareidae in general. Hickson (1930) examined *Paragorgia nodosa* (syn. with *P. arborea*) and found nothing like a horny skeleton, even in the thicker stems. That Stiasny mistook the circumsolenial medulla for horny substance, has been stated already in § 5. Kükenthal, however, states (1919, p. 80): „Das Hornskelett von *Paragorgia* ist nur schwach entwickelt; es finden sich in der Markschicht Hornstränge aus konzentrischen Lagen bestehend und miteinander verbunden. Vielfach sind diese Hornbildungen als Umwandungen der Spicula zu erkennen". And on p. 683, he also speaks of concentric wreaths of horny chords round the central part of the medulla.

I observed that in *Paragorgia arborea* the horny substance exclusively occurs in the intersolenial medulla. It occurs here more abundantly than in the medulla of *Briarcum asbestinum*, but just as in this species it only forms horny sheaths round the extremities or the middle parts of the spicules. Adjacent spicules are very often connected with each other by these horn-sheaths. The mostly smooth processes of the spicules often pierce out through the horny sheaths (fig. 10).

Consequently my observations partly agree with Kükenthal's. Only I

cannot discover anything like wreaths of horny chords round the central part of the medulla. For the solenia are irregularly scattered and therefore the intersolenial medulla also shows an irregular distribution. A wreath-shaped arrangement does not exist and horny chords are not to be found either.

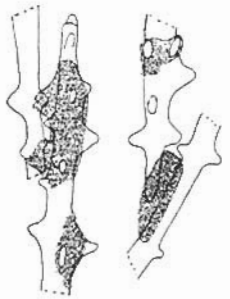

Fig. 10. *Paragorgia arborea*. Medullary spicules, surrounded and connected by horny substance (dotted). × 200.

IV. SOLENOPODIUM EXCAVATUM (NUTTING)

Nutting's investigation (1911) of this species was very insufficient. Stiasny (1937) reexamined the same "Siboga"-material and he gave decent drawings of the spicules. But the measures given by Stiasny are too small.

I investigated a branch (6—7 mm in thickness) of the type-specimen of Nutting. Besides free-hand sections, some microtome sections were made, viz., a series of longitudinal sections through the tip of a branch and some series of transverse sections.

This coenenchyma round the central channel has not everywhere the same thickness (fig. 11). On the back of the branch the coenenchyma is thinnest (about 0.5 mm). The branch may also be split on the back; at the tips the branches are perforated. On the frontal and lateral sides, where the zooids are met with, the coenenchyma is thicker, up to about 2 mm.

The coenenchyma consists of two layers, which are, as contrasted with *Erythropodium caribaeorum*, very well defined. The cortex consists of colourless spicules only; the medulla, on the other hand, exclusively contains bright red spicules. The medulla is thinnest on the back (about 0.2 mm in thickness); in all the other places it is thicker, up to about 0.4 mm. The cortex varies greatly in thickness, viz., from 0.3 mm (on the back) to upwards of 1.5 mm (on the front).

In trying to cut a thin transverse section of a branch by means of a razor, one observes that the surface layer of the cortex offers much resistance. This is caused by the numerous spicules, densely packed in a practically longitudinal direction, and lying in two strata; the total thickness is about 0.08 mm. I further noticed that the subjacent cortical layer could be compressed like a sponge. Especially in microtome sections I found that the whole cortex—except the above-mentioned surface layer—

contains a close and irregular meshwork of spacious solenia. The coenenchyma between the solenia has been strongly reduced and contains spicules, which occur here in a smaller number than in the surface layer. If we try

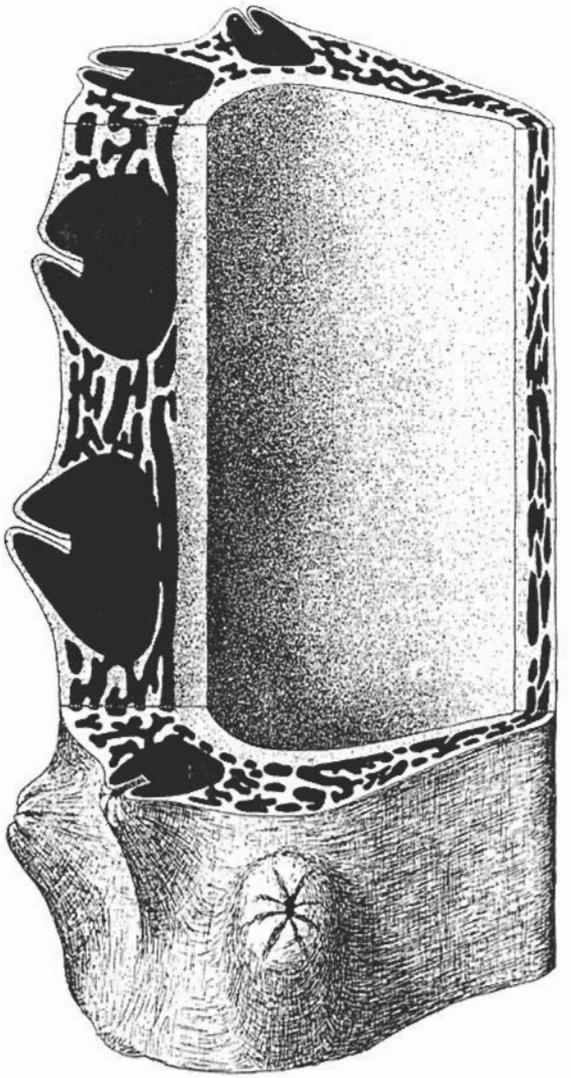

Fig. 11. *Solenopodium excavatum*. Diagram of a branch. × 12.

to cut further through the red medulla, the latter also offers more resistance, which is again caused by the numerous red spicules lying close together in a longitudinal direction.

The medullary layer is devoid of solenia. Stiasny (1937, p. 14) recorded them; perhaps they do occur in the medulla of the more basal parts of the colony. The cortex-solenia generally are 0.20—0.25 mm in diameter (some up to 0.35 mm) and they form a meshwork, elongated longitudinally. The boundary canals form an elongated meshwork too; they are not distinguishable from the other solenia.

The coelenterons are connected on all sides with the solenia. Direct connections between the coelenterons do not occur: they are too widely spread for that and the meshwork of solenia is too irregular in form. The bottom of the coelenteric cavity is not flat but convex. In the middle of the bottom the cavity just reaches the medulla, but for the rest we still find a few solenia between the cavity and the medulla.

In a longitudinal section we see that many coelenterons are more or less enlarged in a basal direction, whereas the anthosteles often stand in an oblique upward direction. All this reminds one of a similar condition in the lateral zooids of *Briareum asbestinum* (cf. fig. 2). The ventral aspect of the zooids is often turned adaxial; sometimes the median plane has an oblique position with respect to the longitudinal axis of the branch.

Special attention should be paid to the distribution of the different types of spicules. I must state emphatically that only the spicules of one branch of 6—7 mm in thickness were examined. As was stated above, the outer cortical spicules occur densely crowded in two strata, arranged longitudinally; only in the anthosteles they change their course into a direction, rectangular to the entrance of the zooid. There is another difference between the spicules of these two strata: those of the outermost stratum measure 0.028—0.040 mm in diameter (fig. 12a); those of the second stratum are thicker (0.040—0.055 mm; max. 0.068 mm; fig. 12b) [1]. But all the spicules are alike in length (0.30—0.50 mm, max. 0.55 mm). The warts, provided with very small spines, are 0.011—0.019 mm in height and as a rule are arranged in transverse rows ("*Briareum*-type").

In the thick subjacent cortical layer the spicules occur in a much smaller number, consequently more isolated. They are as long as the spicules of the surface layer, but they vary from 0.030—0.080 mm in breadth, so here we find still broader spindles. The processes are quite different in form. Besides

1) All dimensions of thickness without warts!

spindles similar in form, etc., with those in fig. 12b, we find others with processes reduced to low, cone-shaped tubercles (fig. 12c; cf. Stiasny, 1937, textfig. C, e). Moreover, other spicules exist, which have remained thin, but which are provided with high, well-developed warts (fig. 12d). All

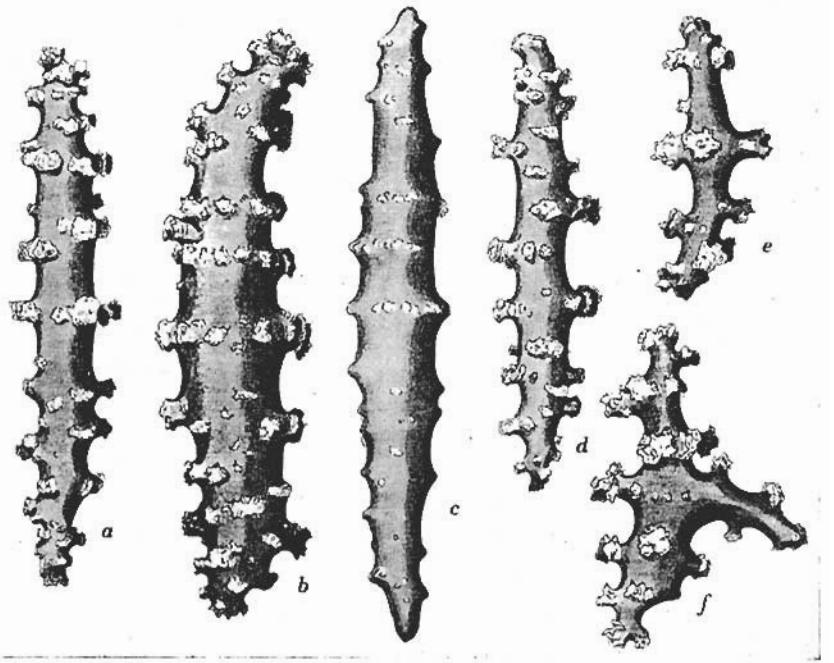

Fig. 12. *Solenopodium excavatum*. a—d, cortical spicules; a, spicule of the outermost stratum; b, spicule of the second stratum; c and d, spicules of the thick subjacent layer; e and f, spicules of the interior stratum of the medulla. × 200.

the cortical spicules are colourless—here and there I noticed a red spicule, but they are rare.

The red medullary spicules show a sharp contrast with the colourless cortical ones. I found that in the medulla also two strata could be distinguished. For there is an important difference between the spicules lying close to the cortex and those of the interior strata lining the central channel. The spicules first-mentioned are straight or curved spindles; but they are often irregular in form, sickle-shaped or Y-shaped. The length is the same again as that of the cortical spicules, and so is the thickness (0.040—

0.055 mm). The processes of some spicules are as low as those of fig. 12c, but of many other spicules they have developed into high warts (0.025—0.035 mm)—so the processes show all kinds of differences. But spicules of the "*Briareum*-type" are scanty in the medulla.

Finally, on the interior side of the medulla I noticed a stratum, densely packed with spicules, in some respects different from the former (fig. 12e and f; cf. Stiasny, 1937, textfig. C, f, g, and h). The spicules of this stratum are shorter (0.20—0.30 mm) and thinner (0.025—0.035 mm), provided with very high warts (0.025—0.035 mm), which may grow into irregularly shaped processes. In that way the spicules may assume all kinds of phantastic forms.

All the medulla-spicules lie again in a more or less longitudinal direction but not so neatly as the spicules of the surface layer of the cortex.

Are there in the medullary strata spicules to be detected, which remind one of the outer cortical ones? Not at all! There is a considerable difference in colour, shape, size, etc. Consequently a "Markstrang" (sensu Kükenthal) is absolutely absent in *Solenopodium excavatum*.

In the mesogloea of the cortex many cell-strings and cell-vessels occur, often up to 0.03 mm in width. The cells are rather large and mostly lie against the walls of the vessels. In the medulla I found the vessels only close to the boundary canals; in the rest of the medulla they are lacking. The horny substance scantily occurs in the medulla and then as very fine sheaths round the spicules. The central channel of the branch is covered with a horny membrane, which is connected with some of the horny sheaths. Here and there some isolated sheaths occur too. In the cortex no horny substance is to be found.

Kükenthal (1919, p. 42) regarded *Solenopodium excavatum* (= *Suberia excavata* Nutting) as a species incerta; perhaps it might be identical with *Solenopodium stechei* (Kükth.). Aurivillius (1931, p. 8—10) went still further and considered *S. excavatum* as synonymous with *S. stechei*. His description, however, of the two specimens from Semau Strait, Timor, is quite in accordance with my description of the type specimen of *S. excavatum*. The measures of the spicules are also well in accordance with each other. Only the medulla-spicules, occurring in the interior layer are larger but thinner in my specimen than in the specimens of Aurivillius.

Anyway the dimensions given by Aurivillius are more in accordance with my statements than with Kükenthal's as regards *S. stechei*. Therefore I think that the specimen described by Aurivillius should be regarded as belonging to *S. excavatum* and not to *S. stechei*.

For I agree with Stiasny (1937, p. 14) that *S. excavatum* is a bona species. There are distinct differences between *S. excavatum* and *S. stechei*, partly mentioned already by Stiasny (l.c.). These are:

1. In *S. excavatum* no small, red spicules in the octodentate ridge of the verruca; Aurivillius does not mention them either.

2. In *S. excavatum* no spicules in the anthocodiae (vide Aurivillius).

3. The verrucae of *S. excavatum* are laterally compressed and turned obliquely upwards.

4. In *S. stechei* the exterior cortical spicules and the interior medullary spicules are equal in length and have the same shape (Kükenthal, 1919, figs. 10 and 14); in *S. excavatum* they do not show the least resemblance.

5. In *S. stechei* the exterior cortical spicules are 0.15 mm in length, in *S. excavatum* about 0.30—0.40 mm (Aurivillius: 0.25—0.35 mm!). In *S. stechei* the interior medulla-spicules measure 0.15 mm in length; they are partly red-coloured (Kükenthal); in *S. excavatum* they are at least as long again and carmine-coloured all of them.

6. In *S. stechei* the outermost solenia are narrow, farther inside they increase in width; in *S. excavatum* they are of the same width.

V. ANTHOTHELA GRANDIFLORA (M. SARS)

The structure of *Anthothela grandiflora* was described by many authors, of whom the principal are: Verrill (1883, 1922), Studer (1887), Wright & Studer (1889), Broch (1912, 1916), Molander (1918a), Kükenthal (1919), Thomson (1927), Deichmann (1936), Pax (1936) and Stiasny (1937).

§ 1. The material.

I had at my disposal the material, recorded and described by Stiasny (1937, p. 20: two specimens, Frank, 1895, Northern Atlantic Ocean). Moreover I received some large fragments from Dr. Carl Dons at Trondheim. Especially to study the occurrence of medullary canals and of the "Schwammgewebe", as Kükenthal calls it, I made transverse and longitudinal microtome-sections of different stems; the thickest measured 5 mm in diameter. Longitudinal and transverse sections of the basal extension and of the topmost part of a branch were also made.

§ 2. Medulla and cortex; boundary space.

Stiasny says (1937, p. 21) that the outer thin layer of the coenenchyma can easily be removed from the subjacent, more compact layers. I found that this is due to the fact that under the outer thin layer, a space is to

be found, which is very narrow in a radial direction, but very extensive in longitudinal and tangential direction. I propose to call this space the boundary space (see next §). The outer thin layer is the cortex and all the rest is the medulla.

The cortex is perfectly homologous with that of the other Anthothelidae; the differences between medulla and cortex in *Anthothela* are much the same as those of the other Anthothelidae. In the case of *Anthothela* we find:

1. The coelenterons reach as far as the medulla.

2. In the cortex solenia are met with; in the medulla they are absent with the exception of the basal parts of the stem and the membranous extension.

3. The spicules, which characterize the cortex, and of which there are a great many in it, are clearly distinguished from the usual type of medullary spicules.

4. Horny sheaths only occur round the medullary spicules.

The cortex is only about 0.2 mm thick. The boundary space which is separating the cortex from the medulla, is not higher than 0.08 mm. Consequently this space is hardly more than a narrow chink. The cortex, however, is connected everywhere with the medulla by thin and short columellae, about 0.05 mm thick. In my experience, after removing the cortex carefully from the medulla, the columellae stick to the medulla. In the basal extension, too, the boundary space separates a thin upper layer of cortex (0.2 mm again) from a thicker subjacent layer of medulla (text-fig. F2, r, of Stiasny is printed upside down).

In the case of *Anthothela* the boundary space makes a very distinct partition between medulla and cortex and therefore I agree with, e. g., Wright & Studer (who speak of "distinct axis") and Verrill (1922, p. 18: "well differentiated" axis). Consequently I do not agree with Broch (1912, p. 6), Molander (1918 a, p. 8), and Kükenthal (1919, p. 44), who write of a not distinctly separated medulla-layer. Nor can I agree with Stiasny's division of layers. He divides the "coenenchyma" (= cortex) into an outer thin layer and a deeper lying one; farther inside the stem a "nicht scharf vom Coenenchym abgegrenzte Markschicht, die excentrisch gelagert ist" follows. This division is not right. The deeper lying layer of the coenenchyma and this "Markschicht" together form the medulla. An "excentrisch gelagerte Markschicht" does not exist.

§ 3. The zooids and the endodermal canal system.

The zooids of *Anthothela grandiflora* stand separately either on the membranous extension or on the stems growing upwards. At the tips of

the stems and the branches they may also be united into little groups; in that case there remain only very thin (0.06 mm) partition-walls between the zooids.

The median plane of the zooids may have a different position in respect to the longitudinal axis of the stem: the ventral aspect may be abaxial, adaxial, or the median plane is standing obliquely.

The body wall of the zooids is nothing but the direct continuation of the cortex. The anthostele is 3—5 mm high. At the transition of the anthostele into the anthocodia the coenenchyma is twice narrowed; along the undermost narrowing the contracted anthocodia is apt to break off.

The way in which the coelenterons proximally end is dependent upon the place of the zooids. The coelenterons of the terminal zooids continue for some distance between medulla and cortex, but suddenly they end in a more or less rounded, sack-shaped extremity (see diagram, fig. 13, the three terminal zooids). The thin partition-walls in several places show small holes, so that there is a direct connection between the coelenterons.

The lateral zooids, however, have an almost cylindrical coelenteron, ending with a flat basis against the medulla; so these do not continue between medulla and cortex. Sometimes the medulla slightly protuberates into the coelenteron (vide fig. 13, right-hand lateral zooid). The shape, etc., of the zooids occurring on the membranous extension, is like that of the lateral zooids.

At their bases all the coelenterons are connected with the boundary space (see preceding §). This space lies in the place, where, in many other genera, the boundary canals are met with. The boundary space is homologous with these canals and we can deduce the situation in *Anthothela* from that of other genera by imagining the partition-walls between the canals as reduced to the numerous columellae. It seems that somewhat larger fragments of partition-walls occur here and there. Isolated canals are neither to be found. And so it is incorrect to speak of "longitudinal canals" as Kükenthal does (1919, p. 673 and fig. 315). As a matter of course, it is impossible to consider the boundary space or some parts of it as coelenterons. They are solenia, fused together into one space.

Besides the boundary space we can distinguish cortical and medullary solenia. The cortical solenia are almost exclusively found in the vicinity of the zooids. Here the cortex often is a little thicker and the solenia form a network, usually consisting of one layer and connected both with the boundary space and with the coelenterons. The width of cortical solenia is equal to the height of the boundary space, i.e. about 0.08 mm.

In *Anthothela grandiflora* the medullary canals occur solely in the mem-

branous extension and the basal portions of the stem. They are round or oval; the lumen varies from about 0.08 mm to 0.15 mm, so that the width does not differ much from that of the cortical solenia. In irregular windings the few canals run through the medulla; in fact, it cannot be called a "network".

These observations are for the greater part in accordance with those of Kükenthal (1919, p. 673). The medullary canals, however, are not narrower than the cortical solenia. It is right that the medullary canals are lacking in the upper part of the stem. This is also Stiasny's opinion (1937, p. 22). Nevertheless he draws them in his diagram! It is clear that his figure is wrong: the zooid-cavities do not continue at all into medullary canals. The "choked up"-canals, which Stiasny thought he had seen in the medulla, do not exist. The lighter spots, drawn by Stiasny, are perhaps places where the spicules are lying a little less close together. For the rest, the drawings of Stiasny should be looked upon with all reserve.

The diagram I made of *Anthothela grandiflora* (fig. 13) is utterly dissimilar from that given by Stiasny (textfig. F2, u). In comparing it furthermore with the diagrams of *Briareum asbestinum* and *Paragorgia arborea* we see that in *Anthothela grandiflora* the canal system is not only much simpler, but also principally unlike them, because the terminal zooids do not continue into medullary canals now, but terminate blindly. There are no medullary canals except in the basal parts of the colony. In the diagram three terminal zooids have been drawn, separated from each other by thin walls, but connected by numerous solenia, running round the medulla. Between the three terminal zooids the medulla has been left intact; in this manner we can see the course of the solenia. The border of the medulla has been indicated by the dotted line in the middle-most zooid. The left and the right terminal zooids have been drawn according to a median section, whereas the middle one gives an idea of the extension of the coelenteric cavities between medulla and cortex.

Under the left terminal zooid the cortex has been drawn with some solenia. The latter also occur in other places, but always in the vicinity of the zooids; so, e.g., in the cortex under the right-hand terminal zooid. At the upper end of the diagram, under the terminal zooids, we can observe, on the surface of the medulla, the boundary space entirely drawn in black, the white dots are the columellae.

The middle part of the stem, which bears the two lateral zooids, has been sectioned longitudinally and exactly through the centre of the medulla: the darkly dotted part is the medulla, the light dotted region is the cortex. In the part lower down only the cortex has been removed, so here the

boundary space with the columellae is visible again. Finally in the undermost part the cortex has been left intact. Cortex-solenia are missing here.

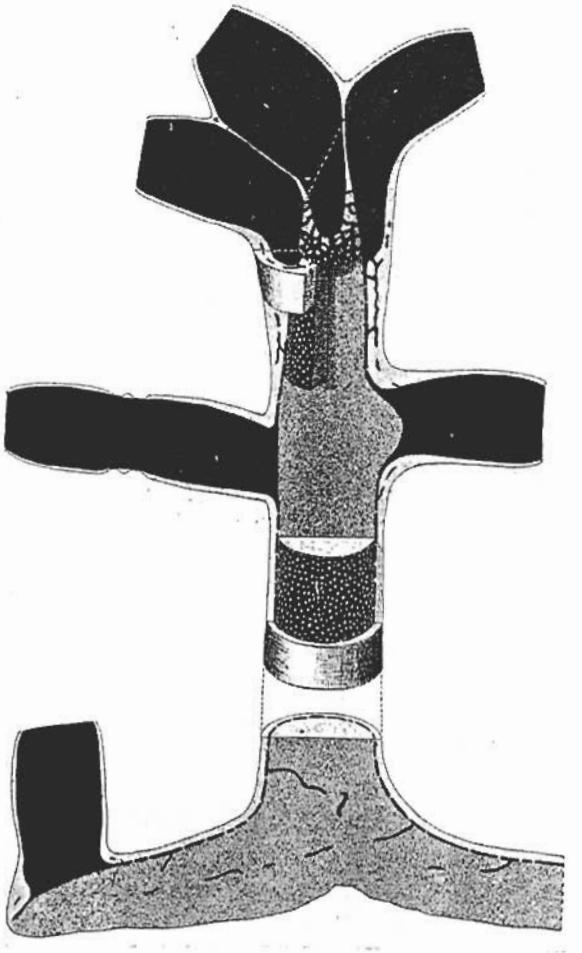

Fig. 13. *Anthothela grandiflora*. Diagram. × 5.

The lowest part of the drawing represents a section through the membranous extension. A few canals occur in the medulla. On the left side a zooid, in every respect identical with the zooids of the stem. Of all the

zooids only the anthosteles have been drawn; of the left lateral zooid the anthocodia has also been drawn. At the transitional part between anthostele and anthocodia the coenenchyma shows two narrowed parts. The coelenteric cavities do not extend far into the stem, for the cortex is very thin. All along their bases they are connected with the boundary space.

§ 4. The mesogloea.

In the medullary mass of *Anthothela grandiflora* Molander (1918 a, p. 8) found cell-strings and cell-vessels. In his opinion these strings and vessels are not only directly connected with each other, but also with the short coelenterons and further more indirectly with the solenia of the axis and the cortex. My research showed that Molander was right as far as concerns the existence of cell-strings as well as of cell-vessels in *Anthothela*. But they are nowhere connected with a cavity or a canal that is covered with endoderm. And it is not clear, what in the present case Molander means by indirect connections.

The cell-strings occur in the cortex in a small number and pass into the ectoderm. They are more numerous in the medulla, in which they form a meshwork (fig. 14). Close along the boundary space and on each side of it, the cell-strings widen into vessels. These vessels are filled with mesogloeal cells and are connected with the ordinary cell-strings. I did not see any communication with the boundary space; it is true that they are lying close to it, but everywhere there is a thin partition-wall of mesogloea between them. Moreover these vessels appeared to have the same remarkable extension round the stem as the boundary space, to which they run parallel. They are strongly flattened (mostly 0.015 mm in height, max. 0.030 mm), but in longitudinal and in tangential direction they are so much united, that in fact they form one space, since the partitions have been reduced. So we can hardly speak of "vessels". Also in the thin (0.06 mm) partition-walls between two neighbouring zooids and in the anthosteles we find cell-strings and cell-vessels.

Besides these spaces, filled with mesogloeal cells and running parallel to the boundary space, there are still other vessels in the coenenchyma of *Anthothela grandiflora*. These vessels are most clearly to be seen in the outer layer of the medulla, close against the above mentioned cell-vessels, but they differ from the latter by the lack of any trace of mesogloeal cells. Nor could I discover any flat epithelial cell against the wall. And finally they do not form one space, but they can easily be recognized as separate vessels forming a meshwork. This meshwork, too, runs parallel to the boundary space and on this account it could be so well observed in tangential

sections. The width of these vessels is greater than that of the cell-vessels and the boundary space. They are mostly 0.15—0.25 mm in width! These vessels without cells are often difficult to distinguish from the cavities, left by the spicules, for they are often as wide as these cavities. But of

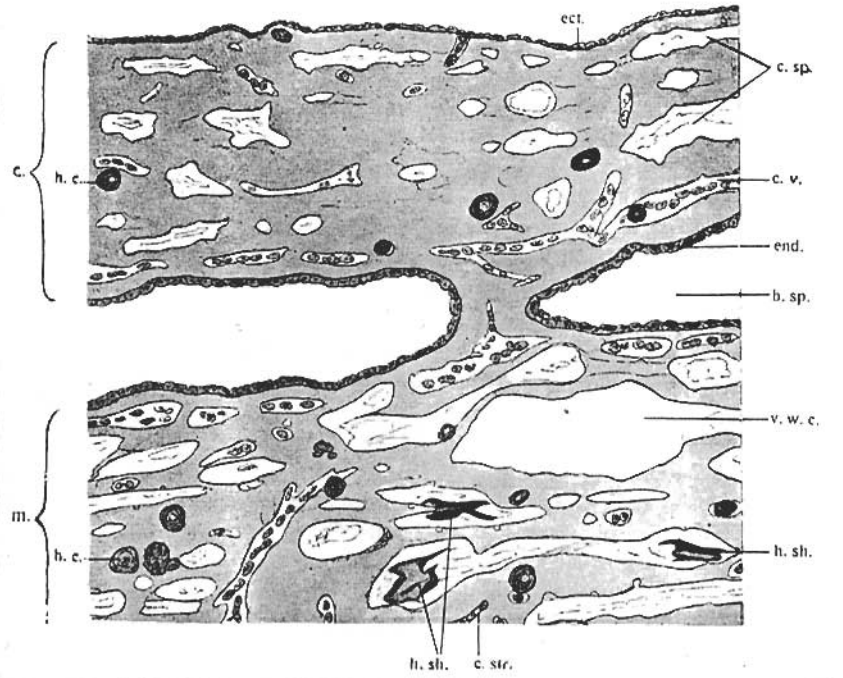

Fig. 14. *Anthothela grandiflora*. Longitudinal section through the stem. b. sp., boundary space; c., cortex; c. sp., cavities of spicules; c. str., cell-strings; c. v., cell-vessels; ect., ectoderm; end., endoderm; h. c., horny cells; m., medulla; v. w. c., vessels without cells. × 240.

course, in the vessels the organic matter, often left in the spicular cavities, is lacking.

Occasionally I saw that a cell-string passed into these vessels without cells; the cells, however, had remained in the string, in spite of the fact that there was a direct connection between the lumina. I did not find such vessels without cells in other genera.

The great number of connective tissue-like threads in the mesogloea of

cortex and medulla is striking. In the cortex they are often united into bundles and they are running in a direction that is now more longitudinal and now more radial or tangential. Of course these differences are connected with the direction of the section: in a transverse section the radial and tangential threads will be more conspicuous, in a radial section besides the radial threads also the longitudinal ones, etc. In the medulla, too, the bundles run into various directions.

In the medulla of the lower part of the stem there is often a cavity caused by the disappearance of the mesogloea. This brings on, that the spicules are lying quite detached, and in making a transverse section they drop out of it. It is clear that such cavities have nothing to do with any canal system.

§ 5. The spicules.

Some investigators have qualified the boundary between medulla and cortex as being not distinct; its place as indicated by Stiasny is not in accordance with reality (vide § 2). Therefore it is perhaps not superfluous to describe the spicules once more and to draw them again, although there are already many drawings of them (Broch, 1912; Verrill, 1922; Thomson, 1927; Stiasny, 1937). Broch insufficiently differentiates between the spicules of cortex and medulla, nor do Stiasny's representations illustrate the differences in the right way.

In the cortex rod-shaped, or usually spindle-shaped spicules occur, varying in length from 0.08—0.70 mm (fig. 15, a, b, c). Characteristic for all the cortical spicules are the numerous high processes in the shape of coarse verrucae or of flattened cones (volcano-shaped) with a wart on the top (very clear in b). Type a is one of the smallest specimens; b is an intermediate form, often met with; c represents one of the large cortical spicules; it resembles somewhat the club-shaped type, which is also found in the cortex (vide Stiasny, 1937, textfig. F1, b). Finally there are "Drillinge" and "Vierlinge" as aberrant forms (cf. Kölliker, 1865, pl. XVIII fig. 2; pl. XIX figs. 28 and 33).

In the medulla the irregularly curved spindles are prevailing (fig. 15, d, e). They are provided with lower cone-shaped processes, which are much more sparingly distributed on the surface of the spicule; here and there these are all but or entirely missing (Stiasny, 1937, textfig. F 1, p and q). The breadth of the medullary spicules corresponds to that of the large cortical spicules (viz., 0.030—0.045 mm, without the tubercles) or they are a little thicker (0.050 mm). The length is up to 0.74 mm. Here and there spicules occur in the medulla, which, by their higher and more densely

placed processes, remind one of the cortical spicules. Such spicules occur everywhere in the medulla, but sporadically. They are certainly not confined to a central part of the medulla and Kükenthal (1919, p. 44) consequently

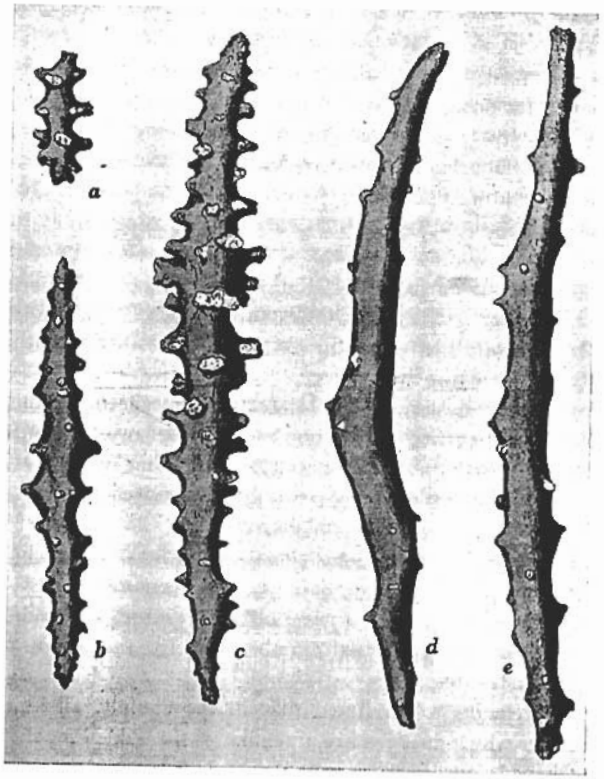

Fig. 15. *Anthothela grandiflora.* Stem. a, b and c, spicules from the cortex; d and e, spicules from the medulla. × 200.

is right, when he says, that a "Markstrang" is lacking in *Anthothela grandiflora.*

Now, how are the several types of spicules distributed in cortex and medulla? In the cortex the small and large spicules are found scattered, so that a regular increase of size towards the inside is out of the question. In the surface layer of the cortex the spicules are crowded close together, mostly in a longitudinal direction; the larger ones are more numerous,

of the smaller ones there are only few. Farther inward the cortex the spicules are scattered about in all directions.

§ 6. The horny substance.

About the presence of a horny substance in *Anthothela grandiflora* we are again informed in the most divergent way. Broch (1916, p. 15) was the first to give a correct description and a plain drawing of the division of the horny matter. His observations are in conformity with mine: the horny substance on the whole envelopes the medulla-spicules as sheaths; in many places the neighbouring spicules are connected by it. Here and there this formation of horn is so intense, that almost the whole spicule is surrounded by it; in this way longitudinal "strings" of horny substance may be formed, but such strings are nothing but large horny sheaths joined together. In the basal parts of the colony the formation of horny sheaths is stronger, but yet in the young parts of the colony and in the tips of the branches many sheaths occur, in contradiction with Molander's remark (1918a, p. 8) in this respect.

Besides the above named sheaths, many horncells occur in the medulla all scattered about (cf. fig. 14). They are round or oval and measure mostly from 0.014 to 0.018 mm, rarely 0.030 mm. They consist of concentric hornlayers. In the centre there is a light coloured nucleus. Fine black coloured granules are often found here. Origin?

Many horncells lie in the mesogloeal cell-strings, others lie isolated or in little groups together. Especially in the membranous extension, particularly in the lower layers, their number is large. Horncells also occur in the cortex, but only in a small number. For the rest any horn-formation in the cortex is lacking.

Finally it remains to be stated that in the medulla all kinds of horny masses occur, which usually are irregularly shaped. Now they are phantastically shaped cavities surrounded by a horny wall, now they look like lumps or lamellae of horn, etc.

Kükenthal's opinion about the division of the horny substance is quite unlike mine. According to him (1919, p. 681) there is a cylinder of "Schwammgewebe" round the medulla-canals, in which no horn occurs. In the spaces between the "Schwammgewebe" the horn is abundantly present, so that a network of "Hornfasern" is formed. These "Hornfasern" apparently consist of sheaths of spicules, which are often connected with one another.

I have looked for Kükenthal's "Schwammgewebe", but I have not found it anywhere. It is true that in some places there are more horny sheaths

than in others, but parts without horny substance I have not seen anywhere in the medulla. Neither around the few medullary canals, occurring in the basal parts of the colony. Close alongside such canals I have still found the horny sheaths.

The drawing of the medulla of *Anthothela grandiflora*, given by Kükenthal (1919, fig. 315) reminds one more of the medulla of *Paragorgia*! Only the number of medulla-canals is much larger in the latter. For *Anthothela* this drawing is certainly not characteristic! Stiasny did not stain his free-hand sections. No wonder therefore that his idea about the occurrence of horn is quite incorrect (1937, p. 21 sq.).

VI. SEMPERINA BRUNNEA NUTTING

After the first short description by Nutting (1911) a more detailed essay by Kükenthal (1919) followed. No news about this species in Thomson & Dean (1931). Stiasny (1937) described the habitus of various specimens of the "Siboga"-Expedition and he added some remarks concerning spicules, canal system, horny substance, etc.

§ 1. The material.

The "Siboga"-material from Station 273 (cf. Nutting and Stiasny) was examined. Transverse and longitudinal microtome-sections were made of branches and of a top-most piece and a series of longitudinal sections of a bifurcation. Further free-hand longitudinal sections of top-pieces were made and longitudinal and transverse free-hand sections of large branches as well as of the basal stem. This proved to be sufficient for the examination of spicules and especially of the canal system.

The stem I investigated was 15 × 18 mm in thickness, it was rather twisted (cf. Stiasny, 1937, p. 32, specimen 2b and 3). This appeared outwardly from the course of furrows which ran from the right-hand bottom to the left-hand top at an angle of 60 degrees. But also inwardly the torsion appeared from the course of the canals (§ 4). The medulla-chord (§ 5) ran straight on, quite in accordance with what we can expect from torsion. Other stems, however, were not twisted; it follows that torsion is by no means a general phenomenon in *Semperina brunnea*.

§ 2. Medulla and cortex.

In *Semperina brunnea*, too, we can easily distinguish these two layers, viz., by the following differences:

1. The coelenteric cavities lie entirely in the cortex; the broad, round or oval base adjoins the medulla.

2. The needle-shaped spicules, characteristic for the medulla, are lacking in the cortex.

3. Horny substance only occurs in the medulla.

Both layers are separated from each other by means of a crown of boundary canals.

In *Semperina brunnea* the zooids, as we know, are only found on the front and the lateral sides of the stem and the branches, but not on the back. Round about the zooids the cortex is thicker, but on the back it remains thin. In the big stem, as well as in the thinner branches, even in the tips of the branches, the cortex of the back is everywhere equally thick, viz., about 0.2 mm. So the medulla only varies in thickness in stem and branches.

According to fig. 20 of Kükenthal the tips of the branches show a deep, upwards widening groove on the back. In my material such grooves also occur, but they are much smaller than those drawn by Kükenthal. There are, however, also numerous top-pieces, which are round and smooth and without grooves.

In connection with this, something must be said about the relation between medulla and cortex in the tips of the branches. The reason is that in the tips without grooves, I found the cortex lying all over the tip, and separated from the medulla by a meshwork of canals (to be discussed in § 4). The cortex, as far as it is a continuation of the back of the branch, is normal in thickness (0.2 mm). In the tips with a groove, the state of affairs proved to be different. In the groove the cortex is lacking, for there is no meshwork of boundary canals that could separate the cortex from the medulla. Moreover, just under the ectoderm in the groove, beside numerous oval and spindle-shaped cortical spicules (see § 6) also tiny needle-shaped medullary spicules are met with. In *Solenocaulon*-species, too, the cortex is missing on the inside of grooves and channels.

§ 3. The zooids.

Every zooid has a verruca (anthostele), into which the anthocodia can retract. The verrucae are more or less isolated. The wall of the verruca is formed by a continuation of the cortex and is about 0.1 mm thick. Between the verrucae the cortex is thicker than on the back. The partition-walls between the coelenterons may be thin or thick, depending on the mutual distance of the zooids. In these walls there are cortical solenia, which mutually connect the coelenterons (§ 4).

On the top the verruca shows eight furrows radiating from the opening. The latter pore is an oblong fissure, running mostly parallel to the longitudinal axis of the branch. The dorsal aspect of the zooids is mostly turned downwards, i.e., abaxial. Some zooids, however, have an oblique median plane; rarely the dorsal side is adaxial. The muscle-banners have been drawn correctly by Kükenthal (1919, fig. 308). The specimen examined by me was a female one. The eggs were stalked; the diameter was up to 0.38 mm.

§ 4. The canal system.

According to the situation we may distinguish: a. the meshwork of boundary canals, b. the cortical solenia, c. the medullary solenia. All these endodermal canals are connected with one another.

a. The boundary canals (cf. figs. 16 and 17). In a transverse section of the coenenchyma they are mostly oval, 0.05—0.25 mm in breadth (on an average 0.15—0.20 mm) and 0.05—0.15 mm in height. Some canals run straight on in a longitudinal direction for a distance of a few mm. But a great many other canals can hardly be traced longitudinally, for they have a twisting course and anastomose frequently. So they form a close network, in which a definite lengthwise direction is often entirely lost. Consequently, in *Semperina brunnea* we can hardly speak of "longitudinal canals", in contrast, e.g., with *Iciligorgia orientalis*. In the stem the canals are wider and ascend in an oblique manner when the stem is twisted.

b. The cortical solenia (vide figs. 17 and 18). These only occur in the thicker cortex round and between the zooids and so they are lacking in the thin cortex on the back of stem and branches. They form an intricate fine network and in numerous places they are connected with coelenterons. If the partition-wall between two zooids is thin, the cortical solenia can directly connect the body-cavities. The cortical solenia may be extremely narrow, to 0.03 mm in diameter; the widest are about 0.15 mm in diameter.

c. The medulla-canals (fig. 16). In the stem they are met with in a great number (in one transverse section as many as 35). In the thick branches they are fewer in number (about 6 in a branch of 8 mm diameter). In the thin branches finally they are totally lacking. Medullary canals are rather varying in width: from 0.15—0.55 mm.

In the twisted stem the medullary canals run from the right bottom to the left top, in torsionless stems they penetrate the medulla in a longitudinal direction. Sometimes they are to be traced in this direction for a long

distance, but often they are strongly twisted or frequently bifurcated, and connected with each other by transverse canals. The latter always run in a radial direction, either to neighbouring canals or to the boundary canals.

In the large branches the medulla-canals likewise run almost longitudinally, while the transverse canals keep the radial direction and pass into the meshwork of boundary canals. We also see the medulla-canals themselves gradually pass into the boundary canals apicalwards or basalwards; they become ever more situated in the peripheral layer of the medulla and ramify into the meshwork of the boundary canals. And this is the reason why the medullary canals disappear more and more in the thinning branches.

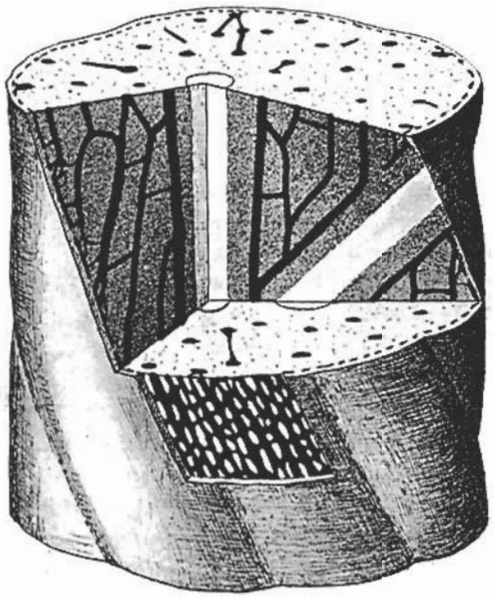

Fig. 16. *Semperina brunnea*. Diagram of stem. × 5.

How do the medullary solenia behave, when a branch bifurcates? Then we see that the canals which are lying in the left and right part of the plane of bifurcation straightway penetrate the side-branches. But the canals lying more inside ramify once or more than once dichotomously after which the canals bend into the branches.

The diagrams. Fig. 16 represents a piece of a twisted stem of about 15 mm in diameter. Outwardly the torsion appears from the obliquely upwards running furrows.

In the lower half of the drawing only a part of the thin cortex has been removed, so that the meshwork of boundary canals becomes visible. They run obliquely upwards to the left-hand side, in accordance with the torsion. The medullary canals also run obliquely, at least the more peripheral ones. To show this, a part of the upper half of the stem-piece was cut away, bordered by planes standing also obliquely. So it is in these radial planes that we can follow the course of the medullary canals. In the left-hand radial plane we see that the medullary canals generally have the tendency of running in an oblique direction from the outside to the inside, and pass into canals, which are found in the vicinity of the medulla-chord. The last-mentioned canals run in a more longitudinal direction, thus accompanying the medulla-chord (§ 5). All the medulla-canals are mutually connected by transverse canals, which run almost only in a radial direction and consequently their course may be observed in the radial planes (compare also the upper-side of the drawing).

In the right-hand radial plane a medulla-chord passing into a side-branch, which formerly was present has been drawn in blank. Medulla-chords, curving laterally like that, are not rare in the stem. We see, how, under the influence of this chord, the canals coming from above, move sidewards and run on in the direction of the chord.

The two lateral planes intersect in the centre of the stem in the medulla-chord, which has been drawn blank as well.

I have not drawn the zooids, which occur scantily on the stem. The relation between the coelenterons and the canal system appears sufficiently from figs. 17 and 18.

Fig. 17 represents the canal system of a branch of about 4 mm in width. On the left the front of the branch with the zooids, on the right the back, where zooids are lacking. So we get a lateral view of the branch. In the lower part of the drawing the slit-shaped apertures, surrounded by eight radial furrows, denote the zooids. In the middle piece the cortex has been removed. The meshwork of boundary canals has been represented exactly as it has been found in one of the free-hand sections and consequently it has not been diagrammatized. We see how the longitudinal direction is often lost, and how the coelenteric cavities are connected with each other by means of these canals. In the upper part of the figure a longitudinal section of the branch is represented. The lighter part is the medulla-chord again, lying somewhat excentrically, but not having a constant place in reality.

On the left four zooids have been drawn in the cortex. The third from the top is just superficially cut off. Of the solenia a reconstruction has been made in one plane. We see in what ways the coelenteric cavities may be connected with each other by the cortical solenia as well as by the boundary solenia. The latter, too, are drawn here wholly continuously. On the right

the zooids are lacking and the cortical solenia too. In accordance with reality, the boundary canals have been drawn with interruptions.

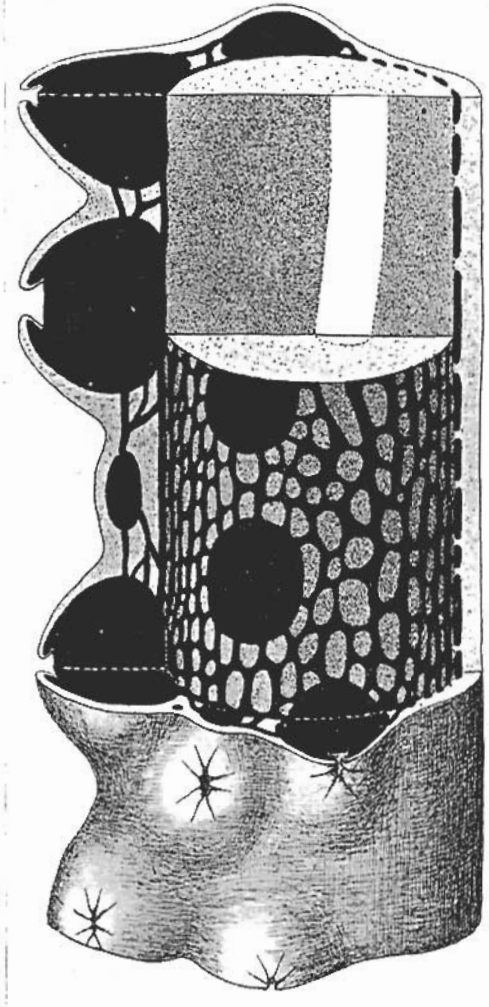

Fig. 17. *Semperina brunnea*. Diagram of a branch, 4 mm in width. × 15.

Fig. 18 shows the reconstruction in one plane of canals, etc., of the tip of a branch. In § 2 I have pointed to the difference between tips with and without groove, and I stated that in the first the meshwork of boundary canals is lacking on the inner side of the groove, so that the medulla goes on as far as the groove. In fig. 18 such a tip has been drawn, that is to say a frontal section of it, paying attention to the front and back of the branch. So, the zooids I represented are lateral zooids; the groove on the tip lies in the median plane of the branch.

I did not mark a medulla-chord here, because I could not find it in my sections. Apparently the differentiation of the medulla in chord and outer layer appears further down.

The medulla on both sides is bordered by the boundary canals, which are sometimes rather thick in the tip. In the cortex between the coelenterons there is a close net

of solenia, which have a very variable lumen: from very tiny capillaries to spacious solenia.

§ 5. Mesogloea and medulla-chord.

a. The medulla-chord. In the medulla of stem and branches there is a central or excentrical medulla-chord, in transverse sections appearing as a lighter spot against the medulla round it; the latter transmits less light. This medulla-chord consists of homogeneous mesogloea. Here the spicules are much less dense than in the surrounding medulla and scattered pell-mell. All of them are needle-shaped just like the other spicules of the medulla, but still they differ from the latter in some respects (cf. § 6).

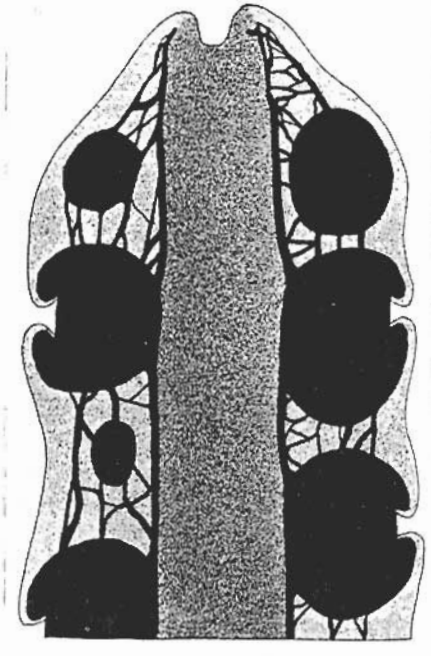

Fig. 18. *Semperina brunnea*. Diagram of the extremity of a branch. × 15.

Shape and thickness of the medulla-chord are rather subject to alteration: in transverse section it is round or oval, in some cases oblong-kidney-shaped. In the stem the thickness is about 1 mm; in branches it is sometimes thicker (in one of the branches the chord measured 3.5 × 1.5 mm); in the smaller branches the diameter is about 0.5 mm. At a bifurcation the medulla-chord also divides in two.

Besides the above-mentioned spicules there are spacious mesogloeal vessels in the chord, mostly 0.03 mm, sometimes 0.05 mm in width. They form a longitudinally stretched meshwork; there are relatively few cells in it. In the thinner branches the spicules of the chord are surrounded by a small number of thin horny sheaths. But in the chord of the stem a good deal of horny substance occurs (§ 7).

Immediately round the medulla-chord there is a thin borderlayer, consisting of needle- and spindle-shaped spicules lying close together. Espec-

ially in free-hand sections this dark, thin borderlayer stands clearly out against the rest of the medulla, and forms thus a rather sharp limitation of the chord.

Kükenthal (1919, fig. 25) as well as Stiasny (1937, textfig. I) have drawn a round or oval part in the medulla lying more or less excentrically and reminding one of the medulla-chord. Kükenthal does not give a further description of this part. On the other hand, he writes (1919, p. 54): "Der innerste Teil der Markschicht enthält in konzentrischer Anordnung eine teilweise auch mit rundlichen Scleriten erfüllte Schicht, die den Scleriten der Rinde gleichen". Perhaps Kükenthal means here the thin borderlayer, mentioned by me. But in this layer round "cortical" spicules do not occur. In the chord itself the round, oval or spindle-shaped spicules are totally missing too. And this is contradictory to Kükenthal's conceptions about the phylogeny of the Briareidae Gray in general and about the origin of the medulla-chord in particular. A medulla-chord as Kükenthal meant it, does not occur in *Semperina brunnea*. In all the rest of the medulla, however, a few round or oval spicules do occur here and there.

For the sake of completeness we may discuss here, what Stiasny (1937, p. 34) states: "In den Endzweigen ist ein centraler fast hornfreier Strang ausgebildet,...". But, as already has been said, the medulla-chord occurs also in the thick branches and even in the massive stem. Stiasny further writes that the central chord "von einer dünnen Hornscheide umgeben... ist". We have here, however, not one large horn-sheath, but a particular, thin borderlayer (see above), consisting of spicules with numerous horn-sheaths. Stiasny is right when he remarks that the medulla-chord is not pierced by endodermal canals.

b. Round the medullary canals lies a zone of homogeneous mesogloea, varying in width (0.03—0.30 mm; cf. Kükenthal, 1919, p. 682). The boundary canals are surrounded by a thinner zone (0.015—0.030 mm), but the homogeneous mesogloea is strongly developed between the boundary canals, connecting the zones in this way. These mesogloeal sheaths are marked by the absence of spicules and horny substance. This is why the sheaths are more or less transparent, although they contain numerous cell-strings, forming an irregular network. In the mesogloeal zone round the boundary canals, however, I occasionally noticed small spicules (cf. § 6), while round this zone especially on the cortex-side, there is a meshwork of cell-strings, which may widen to cell-vessels now and again.

c. The rest of the medulla. The spicules are densely packed here, so that there remains less mesogloea between them. The mesogloea contains cell-strings, running more or less longitudinally; more inwardly they may widen to cell-vessels.

d. In the cortex also there are cell-strings, running in every direction. They are frequently connected with the cell-strings and cell-vessels round the mesogloeal sheaths of the boundary canals on the one side and with the ectoderm on the other, as it has been drawn by Kükenthal in his fig. 26. This may be considered as a typical phenomenon in *Semperina brunnea* and it is very conspicuous in comparison to other Anthothelidae.

Kükenthal distinguished two layers in the cortex, an outer layer with spicules, cell-strings and narrow cell-vessels, and an inner layer consisting of homogeneous mesogloea, almost without cells or cell-strings. It is clear that this homogeneous mesogloea-layer, which, according to Kükenthal also occurs on the inside of the crown of canals, is identical with the mesogloeal sheaths which I described.

§ 6. The spicules.

Kükenthal's description and his drawings of the spicules are sufficient to characterize *Semperina brunnea*. Kükenthal pointed out the gradual transition of the round and oval outermost cortical spicules into more slender "Gürtelstaben" farther inside the cortex, which in their turn change into thin, needle-shaped medullary spicules. I can wholly confirm this observation. Particularly in the medulla we find a great number of remarkable intermediate forms (fig. 20, d and e).

In some details, especially as regards the spicules of the medulla-chord, Kükenthal's statements need some emendation.

1. The cortex spicules. a. Surface layer. Kükenthal distinguishes between the outermost spicules of the branches and those of the stem and says that those of the stem are somewhat smaller than those of the branches. I think the difference between these extremely small. In the branches too, there are very small globular spicules with a diameter of 0.095 mm and oval ones of 0.11 mm in length, but also larger ones, of an average length of 0.18 mm (as stated by Kükenthal) and the latter occur also in a large number in the cortex of the stem! It is questionable, whether the difference mentioned by Kükenthal really exists.

b. Subjacent cortical layer. The spicules are slenderer, but on an average the length remains equal to that of the outer layer, viz., about 0.18 mm. The greatest length I found was 0.24 mm. In the stem these spicules are somewhat shorter, viz., 0.16 mm; not much indeed! The longest in the stem was 0.19 mm. The breadth (without warts) is 0.027 mm, while the outermost spicules are 0.045 mm in breadth. The warts are smaller and more sparsely distributed; sometimes they are even reduced to blunt spines (intermediate forms to medullary spicules!).

c. The anthosteles. The spicules of the anthosteles and those of the cortex are alike. However, round the slit-shaped oral pore there are spicules of another shape (fig. 19): they are more or less spindle-shaped or of a rather irregular appearance, sometimes slightly curved and provided with tiny processes. Their length varies from 0.12—0.17 mm. They are arranged round the aperture like an aureole, and form there one layer.

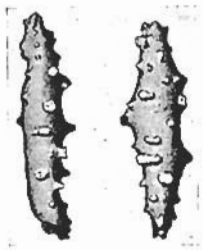

Fig. 19. *Semperina brunnea*. Spicules of the top of a verruca. × 200.

2. In the mesogloeal sheaths of the boundary canals there exist here and there very small, perfectly smooth and needle- to spindle-shaped spicules (fig. 20a). Their length varies from about 0.045—0.095 mm, but there are intermediate forms to the equally smooth spicules to be found in the next layer.

3. This layer, the most peripheral layer of the medulla, contains spicules, that are straight or faintly curved needles with bluntly pointed ends and perfectly smooth, with the exception of a few rudimentary spines in the middle of the rod, so that this middle-part seems to be somewhat thicker (fig. 20b). These smooth needles are now few in number, now more numerous. I found them for instance accumulated in great numbers in some tips of branches. They are, however, always to be found on the medulla-side of the mesogloeal sheaths of the boundary-canals and also round the mesogloeal sheaths of the medullary-canals. The length varies from about 0.09—0.50 mm and the breadth from 0.009—0.012 mm.

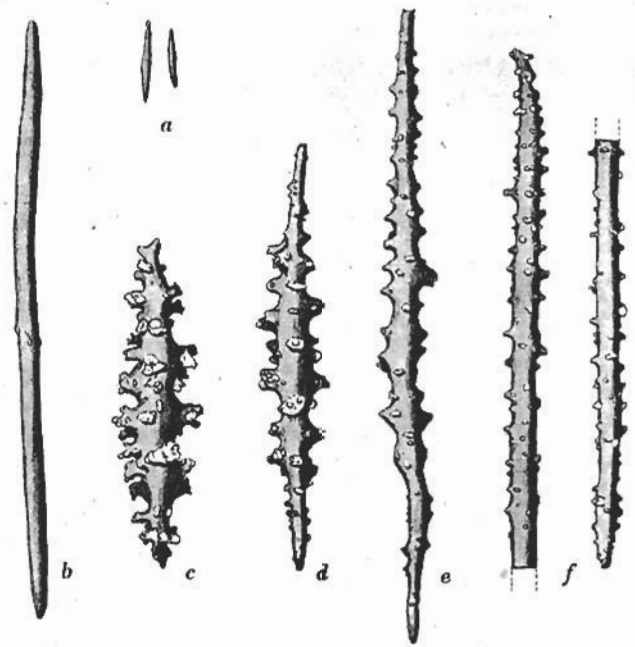

Fig. 20. *Semperina brunnea*. Spicules from the medulla. × 200.

4. Now follows the thick medulla layer between the peripheral layer mentioned sub 3 and the medulla-chord. Here are two main types of spicules, with their intermediate forms. We may distinguish:

a. The sometimes oval, but mostly spindle-shaped spicules, rather scantily provided with high warts (fig. 20c). The oval ones, numerous especially in the stem, are about 0.16 mm in length; the spindle-shaped ones as a rule vary in length from 0.22—0.30 mm. As to the shape, they somewhat resemble the spicules of the subjacent cortex-layer, but they are considerably larger than these, which are on an average 0.18 mm in length. The spindle-shaped medullary spicules vary a great deal in breadth: most of them are 0.025—0.030 mm (without the warts), but there are some of 0.040 mm in breadth. Usually these are at the same time the shorter spicules. Generally speaking there is a gradual change from short and thick spicules to long and thin ones.

b. Spindle-shaped spicules with thin, almost smooth ends (fig. 20d). This type clearly demonstrates the change from the above mentioned type to the needle-shaped medullary spicules. The ends are already similar to those of the needles, the middle piece still recalls the real spindle-shaped type. But this transition is also indicated by their length and breath, for they are of an average length of 0.27—0.33 mm and on an average 0.017—0.023 mm broad. The warts also are lower and often appear as blunt spines.

c. A next phase has been represented in fig. 20e. This rod is 0.47 mm in length and 0.018 mm in breadth. The tubercles are mostly low, blunt spines.

d. Finally, the real needles follow (fig. 20f), with sparsely distributed tiny spines. As to the length Kükenthal's and Stiasny's opinions differ. Kükenthal mentions that they are up to 0.6 mm in length. Stiasny thinks Kükenthal's measurements a little too high and takes 0.4—0.5 mm as a maximal length. I found, however, that the maximal length given by Kükenthal was too small! In a branch of normal width I noticed as the average length of the needles 0.40—0.64 mm, a few were 0.70 mm. In a branch of 8 mm in width there were still longer ones to be found, and not rarely either. Several of them measured 0.77 mm and I have even found one

of 0.88 mm. (In the medulla-chord there are still longer ones, see below.)

Now what about the distribution of these various types in the medulla? The needles occur everywhere compactly and pell-mell, although there is sometimes a tendency to a longitudinal direction. The spindle-shaped ones are scattered everywhere among the needles. But in some places they are found more compactly, so, for instance, in the outer medulla near the cortex. This was to be expected for they are intermediate forms between cortical spicules and medullary spicules. But also elsewhere in the medulla they will suddenly occur in a larger number. For instance round the medulla-chord in the borderlayer.

5. The borderlayer round the medulla-chord. In § 5 some data are given concerning the spicules of this layer, so I may refer to this paragraph.

6. The medulla-chord. Distribution and density of spicules have also been discussed in § 5. I wish to repeat once more that in the medulla-chord only needles are met with. But these needles are differing somewhat from those of the rest of the medulla. In the medulla-chord of a branch of 8 mm in width, needles of 0.70 mm and 0.80 mm are not rare; some of them measure even 1.05 mm! The ordinary medulla needles are on an average 0.019 m in breadth, whereas those in the medulla-chord measure about 0.012 mm in breadth; consequently, the former are longer and also a little thinner then the latter. The warts, too, sometimes are different. In the stem the warts of the spicules of the medulla-chord are higher than those of the spicules of the rest of the medulla and they are not cone-shaped, but more cylinder-shaped and flat-topped. In the branches, however, the spines are more conical and often even lower than those of the ordinary medulla spicules. So there is evidently not always the same difference in this respect.

In § 2 I mentioned already that occasionally the boundary canals are lacking in the proximal extremities of some branches, so that the medulla goes on as far as under the ectoderm. Needle-shaped medulla spicules lie beside typical cortex spicules. Downwards the number of needles increases, but there are relatively many round, oval, or spindle-shaped cortex spicules to be found. Their number gradually decreases, however. In the peripheral medulla-layer in the proximal ends of the branches there are found, sometimes in a large number, the smooth types of fig. 20a and b. The small ones are about 0.04 mm in length, the large ones 0.30 mm.

§ 7. The horny substance.

The horny substance exclusively occurs in the medulla, namely as spicules-sheaths. In particular it occurs at the extremities of the needles, connecting neighbouring spicules with each other. The horny sheaths envelop all the medullary spicules, also those in the medulla-chord (cf. § 5). But as the few spicules are rather sparsely scattered in the medulla-chord, the presence of horny substance is less conspicuous. Hence Kükenthal could write (1919, p. 55): "Im centralen Teile der Markschicht nimmt diese Hornsubstanz erheblich ab, wenn sie auch nicht ganz verschwindet". (Incidentally I may remark that the word "medulla-chord" is avoided by Kükenthal also in this case.)

The state of things found by Kükenthal in the stem, was quite different from that in the branches. Kükenthal writes (1919, p. 682): "Um jedes dieser Längsgefässe (viz., of the medulla) und ihre gallertartige Umhüllung bildet die Hornsubstanz ein Rohr, ähnlich wie bei *Anthothela*". As in *Anthothela*, in *Scmperina brunnea* I could not find anything of this tube of horny matter. The occurrence of horny substance in the stem is exactly like that in the branches. Only in the medulla-chord of the stem, the horn-formation is much stronger than in the branches: there are horny sheaths to be found of almost 0.04 mm in thickness, whereas the corresponding spicule is about 0.01 mm in breadth.

VII. THE GENUS SOLENOCAULON GRAY

Before giving my results of an examination of some species of the genus *Solenocaulon*, it is necessary to discuss some technical terms used in the literature concerning this genus, in order to state the meaning of these terms in the following pages. For some authors made use of a nomenclature to describe morphological or anatomical details, which did not fail to cause confusion.

In a *Solenocaulon* three parts may be distinguished. First the solid cylindrical part, at the base more or less flattened or broadened to a spoon-shape. Then follows a tubular or gutter-shaped part, which may be unbranched in some specimens and in many others dichotomously branched. Finally narrow, more or less flat branchlets.

By most of the authors the first-mentioned part is called stalk ("Stiel") which name I adopt. The tubular part is called trunk or stem ("Hauptstamm"); in the following pages I will call this part stem. If, however, the colony branches close above the stalk or higher, then I will use the word branches, but there is no essential difference between stem and branches. The narrow, flattened or grooved branchlets are called terminal branches or twigs ("Zweige, Endzweige"). Henceforth I will call them twigs.

The nomenclature mentioned above was not consistently adopted by all authors. So we see, e.g., that Thomson & Simpson (1909) in dealing with different specimens of *Solenocaulon tortuosum* J. E. Gray mistook the word stalk for trunk (e.g., in specimen A: "The basal portion or trunk(!)..." and: "The main stem or stalk(!) is tubular...". But in other places, e.g., in the diagram on p. 160 we read sub axis: "Lower part (stalk); upper part (stem)"!

Far greater, however, is the confusion existing with regard to the word axis. Many authors use the word in the sense of medulla. Studer (1879), for instance, distinguishes "Achse und Rinde" (= axis and cortex). Others, however, use the word axis in two different meanings, so that it is not always clear, what is meant. In Wright & Studer (1889, p. XXX) we read: "The axis consists of a cortical substance in which the polyps are placed, and a medullary substance"; and on p. XXXI we read that the Briareidae are "Scleraxonia in which the coenenchyma consists of a polyp-bearing cortex and a medullary substance of closely packed spicules". From these quotations it appears that axis is synonymous with coenenchyma. But in other places the authors mean "medulla" again, when using the word axis!

Especially in *Solenocaulon* the word axis is used in more than one meaning. This started already in Genth's description of *Solenogorgia tubulosa* (= *Solenocaulon tubulosum*). According to Genth (1867, p. 432) the stalk consists of "Rinde" and "Axe". From the further description it appears that here by "Axe" the medulla is meant. But on p. 434 he says: "Das Innere des ganzen Stockes von Ernährungscanälen durchzogen, mit Ausnahme einer in den Aesten vorkommenden nicht scharf begrenzten kleinen Axe. Spicula mit Ausnahme dieser Axe nicht verschmolzen". And on p. 438: "Die Kalkkörper des centralen Theiles verschmelzen hier zu einer soliden Axe, welche an der hinteren Seite, an der Knickungsstelle des Rohres liegt". In these two quotations exclusively the aggregate of medullary spicules is meant by the word axis!

Probably influenced by Genth's statements, Germanos (1897) also used the word axis in a double sense, viz., sensu medulla and sensu aggregate. This caused confusion as appears, e.g., from what Janower (1904, p. 526) writes: "...hier (that is in the stem and branches of *Solenocaulon sterroclonium* Germ.) hat sich dieser Process (viz., the fusion) auf die ganze Achse ausgedehnt, so dass lose Spicula nur in der Achse des Stiels vorkommen". In this quotation the word axis is used in the sense of medulla, whereas Germanos meant the aggregate only! On account of this constant confusion it is almost impossible to understand p. 526 in Janower's paper.

There are other authors who made mistakes in this respect. Hickson, for instance, writes (1903, p. 496, sub C): "axis divided into two main branches". A similar instance occurs on the same page sub H, here Hickson apparently means the stalk! But on p. 497 (20th line from the top) "axis" is used in the sense of medulla. It is not always clear, not even after reading pp. 498 and 499, what Hickson means by the word axis.

In my descriptions of the *Solenocaulon*-species I shall avoid the word axis and only use the words cortex, medulla, and aggregate (= "solid axis", "porous rod" of Hickson, 1903, and Harrison, 1919; "pseudo-axis" of Thomson & Simpson, 1909).

On the interior side of the stem of *Solenocaulon tortuosum* Harrison (1909) noticed spicules of a different type. She called this layer "inner bark". In the present paper I will pay attention to this remarkable layer.

It seems to be very difficult to distinguish the species of *Solenocaulon*, recorded in literature. In my opinion this is caused by the shortness and inadequacy of the descriptions, while at the same time the drawings, e.g., of important spicules are bad or totally lacking. Sometimes the dimensions of the spicules are not even mentioned! Hickson (1903, p. 497) pointed to the accordance in length of medullary spicules in six species of *Solenocaulon*. Indeed there seems to be a great uniformity in shape and size among the medullary spicules. But in the spicules of the cortex and the anthosteles it is different! As far as I could ascertain, there are typical differences in shape and size among these spicules in the species examined by me.

Finally I found that "the variation in size and shape of the spicules of the various parts of one specimen" (Hickson, 1903, p. 497) was of great importance. This variation is so great that it is not sufficient to describe or to draw a few spicules only of one definite part of the colony. It is also absolutely insufficient to describe or to draw spicules without mentioning, whether they occur in the stalk, the stem, the twigs, the anthosteles or the anthocodiae. I found that it is even necessary to distinguish between the upper part and lower part of the stalk and between the back and the front and lateral sides of the stem.

VIII. SOLENOCAULON JEDANENSE NUTTING [1])

This species was mentioned for the first time by Nutting in 1911. It is really amazing that a new species could be described so inadequately and

1) Stiasny (1937, p. 38, foot-note) remarks that it had been better, if Nutting had called this species *Solenocaulon jedanense* instead of *S. jedanensis*. Stiasny is quite right here and consequently I changed the name of the species. For the same grammatical reason I changed *Solenocaulon ramosa* Hickson into *S. ramosum*.

defectively as Nutting did. A satisfactory description of the spicules with an account of their dimensions, etc., is lacking and the drawings of the spicules are absolutely insufficient. As a main character Nutting mentions the spiculation of the calyx-walls, while the peculiar Y-shaped spicules of the anthocodiae are lacking. The first-mentioned character will be discussed in § 4, but now already it may be said that the Y-shaped forms also occur in *Solenocaulon jedanense*. However, other characteristic features may be discovered; in the summary of the genus *Solenocaulon* I will discuss this matter more fully.

After Nutting, *Solenocaulon jedanense* is mentioned by Kükenthal (1919) as a species dubia. Stiasny (1937) also examined this coral.

§ 1. The material.

I could make use of the "Siboga"-material (Stations 164 and 273) that Nutting and Stiasny had at their disposal. Meanwhile I found that the material, collected at Station 274 (close to the Jedan-islands, near Station 273) also belongs to *Solenocaulon jedanense* and not to *S. sterroclonium* as it is stated by Nutting and Stiasny.

I examined more closely the anatomy of the specimens from Station 273 (especially the specimen recorded by Stiasny, 1937, p. 45, sub 2b) and from Station 274. The material from the latter station consisted of a few fragments only. Among these there was the upper part of a stalk (3.7 mm thick) with the transitional part between stalk and stem, further wide tubular parts of either stem or branch and some twigs. The latter are dark-red on the upper side and white on the under side. It is not quite impossible, that the fragments of the branches have belonged to two different specimens of *Solenocaulon jedanense*, for some fragments are light-brown tinted and have dark-brown anthosteles, whereas other fragments are very light-pink in colour and have red anthosteles. At the transition of the stalk into the stem, a small groove arises on the front-side of the stalk, which very soon becomes deeper. Consequently, in a transverse section the stem is more or less horse-shoe shaped. Along the edges of the groove zooids are met with; there are also some on the stalk, close under the starting-point of the groove. For the rest they are lacking on the stalk.

The richer and completer material of Station 273 gives a better insight in the structure of *Solenocaulon jedanense*. The stalk is mostly 7—9 mm thick. In some specimens the groove appearing at the transition of the stalk into the stem is more or less covered by an outgrowth of the edge of the groove, sometimes in the shape of a thin valve. In some specimens

the tubular stem is rather straight and unbranched, in others, how it is branched a few times. In this case, the thick branches are winding fairly regularly in one plane; on the convex side of every bend there is a lateral opening, that may grow out to a short tube. The edges of the openings or tubes pass into the twigs. So the lateral twigs regularly alternate in position. This structure seems to be quite characteristic for *Solenocaulon jedanense*. The zooids are distributed along the edges of the openings and of the twigs, and moreover they occur on the front of the stem in two longitudinal rows. The stem of some specimens also shows openings on the front; then the zooids are placed so irregularly that hardly anything remains to be seen of two rows.

Longitudinal and transverse microtome sections were made of different parts of the stalk, of the transitional part between stalk and stem, of the branches and the twigs. Making free-hand sections was often hindered by the presence of an aggregate of medullary spicules. Especially this difficulty was met with in the twigs, because here the medullary layer almost entirely consists of the aggregate. But also in the back of the branches and in the upper part of the stalk the aggregate caused the difficulties mentioned above.

§ 2. Cortex and medulla.

In the stalk of the *Solenocaulon*-species most investigators distinguished two layers, viz., cortex and medulla. But about the structure of stem and twigs opinions do not agree, as I have said already in the preceding chapter. Let us first see what differences may be found between the cortex and the medulla in the stalk of *Solenocaulon jedanense*, and further try to find out if these layers also occur in the stem and the twigs. In the stalk the cortex is 0.4—0.5 mm thick and consists of a few strata of spicules. The cortex is separated from the medulla by a complex of boundary canals. Differences between cortex and medulla are:

1. In either of the two layers there are characteristic spicules (the globular spicules are characteristic for the cortex, the needle-shaped for the medulla).
2. Horny substance only occurs in the medulla.
3. Solenia are lacking in the cortex, except in the neighbourhood of the zooids.
4. The coelenteric cavities are embedded in the cortex and consequently do not penetrate into the medulla.

The two layers of the stalk pass into the stem. The cortex only occurs on the outside of the tubular stem and is lacking on the inside. It is true that the cortex still continues for a short distance on the bottom of the groove, which appears at the transition of the stalk into the stem, but soon the cortex disappears entirely. So, the inner layer of the stem is always the medulla [1]), the outer layer the cortex. Both layers are always separated by boundary canals.

On the back of the stem, in its basal portion, the medulla is rather thick, but in higher regions it gradually becomes thinner; on the front and lateral sides the medulla is always very thin (about 0.3—0.7 mm). The cortical layer also is thin and varies from 0.1—0.2 mm in thickness. With this varying thickness the division of spicules into one or two strata is linked: the cortex being only 0.1 mm thick, the different types of spicules are irregularly scattered in one stratum. In other places, e.g., on the back or round the zooids, the cortex is 0.2 mm thick; then the spicules are found in two strata, the outer consisting of round or oval, the inner of longer, spindle-shaped spicules.

In the twigs also, both layers—cortex and medulla—occur, again separated by boundary canals. The cortex here is 0.15—0.25 mm thick and contains two strata of typical cortical spicules. In the medulla the spicules are fused into an aggregate, except the undermost layer of spicules. In transverse sections the twigs are round or flattened, depending on the shape, shown by the aggregate in transverse section.

§ 3. The canal system and the zooids.

Besides the boundary canals, which occur everywhere, we find also solenia in the medulla of the stalk and of the basal part of the stem. Cortical solenia are lacking, except between the coelenterons.

a. The stalk. The boundary canals are found here in a circle on the boundary of cortex and medulla. Contrary to Stiasny's opinion, I saw nowhere that this circle was lacking. Textfig. M, v of Stiasny has been drawn from a transverse section through the stalk of a specimen that was damaged in the front region, just at the height of this section; hence the medulla had become visible at the surface. It is clear that in this way the boundary canals may have disappeared too.

The canals are mostly oval in transverse section. The larger ones are flattened on the cortical side, but on the medullary side they are excavated as a deep gutter. One canal is always much larger than the others. In the

1) The "inner bark" has no relation to the cortex; cf. § 4.

transitional part between stalk and stem this canal is always found on the left side, but in lower regions the course of this canal appears to show individual differences. In the specimen from Station 274 it is curved along the front of the stalk towards the right-hand side. In another specimen (Station 273, cotype) it remains on the left side, but it gradually removes basalwards from the cortex and passes into the medulla as a wide medullary solenium. The lumen of this large canal in the last-mentioned specimen measures 1.1 mm (in tangential direction) × 1.6 mm (in radial direction); in the first-mentioned specimen 0.85 × 0.70 mm respectively. The other boundary canals strongly vary in width; most of them are 0.3—0.5 × 0.15—0.40 mm. But narrower (0.15 mm in diameter) and wider canals (0.65 × 0.55 mm) occur too.

The boundary solenia run either straight or obliquely upwards. They are separated from each other by thin walls (0.13—0.40 mm thick), which are frequently perforated by mostly minute transverse canals. A coalescence into one boundary space is out of the question (cf. fig. 21).

The presence or absence of medullary solenia seems to be connected with the thickness of the stalk. I found, for instance, only one medullary solenium in the relatively thin stalk of the specimen from Station 274, but in the thick stalk of the specimen from Station 273 they occur in a larger number, which is not constant (cf. fig. 21). The lumen of the round or oval medullary canals varies strongly; the smallest that I observed, was 0.13 mm in diameter, the largest was 0.50 × 0.88 mm. Most of the canals, however, are about 0.3—0.4 mm in width. Usually they occur in the peripheral parts of the medulla and run straight or obliquely upwards; they are often somewhat curved and may also be branched. The most peripheral ones are connected with the boundary canals by means of anastomoses, or they pass into such a boundary canal themselves.

b. Stem and branches. At the transition of the stalk into the stem, some changes appear in the canal system. As has been said already, a groove is formed on the front of the stalk. This groove soon deepens upwardly and is limited on both sides by more or less upright edges. Now we see that on the bottom of the groove the cortex of the stalk continues for some distance, whereas on the interior side of the rims the cortical layer has disappeared, so that the medulla immediately reaches the surface. The thin cortical layer, occurring on the bottom of the groove, upwards becomes narrower and thinner and finally disappears wholly, and with it the boundary canals on the inside of the tubular stem disappear too.

On the outside of the stem the cortex is everywhere present and consequently the system of boundary solenia too. With the naked eye we see

that the stem is very feebly grooved on the back. Large boundary canals, hidden under the thin cortex, correspond with these grooves. It follows that outwardly we can see the course of the canals by the course of the grooves: they run with feeble windings in a longitudinal direction, forming a long-stretched meshwork. These large boundary canals are 0.3—1.0 mm in breadth and 0.2—0.7 mm in height and, like the large boundary canals in the stalk, flat on the cortical side and gutter-shaped on the medullary side. Among these large canals there are some narrower ones (0.1—0.3 × 0.05—0.13 mm). They are connected with each other and with the larger canals by numerous anastomoses. Along the lateral sides and the front there are on the boundary of medulla and cortex exclusively the above mentioned narrower canals. Outwardly nothing is visible of these.

In the lower part of the stem where the medulla is still fairly thick, there are still some medullary solenia. But higher in the stem they are lacking.

c. Twigs. Here we find also some longitudinal boundary canals. They are about 0.25 mm in breadth and 0.11 mm in height and so they are much the same in type as the narrower canals in the stem. They are again separated from each other by thin walls (mostly about 0.07 mm thick), but these walls, too, are frequently perforated by fine transverse canals. They run fairly straight through the twig, sometimes they pass into a coelenteron. In the rather thin walls between the coelenterons boundary solenia occur too. They are very narrow and connect the coelenterons directly or indirectly (cf. fig. 22). Along the edges of the twigs a remarkable canal runs straight on from the base to the tip; here it passes into a terminal coelenteron. The lateral coelenterons are connected with this lateral canal by numerous anastomoses.

Fig. 21 illustrates the canal system of a stalk of *Solenocaulon jedanense*, viewed from the front. At the bottom of the drawing the cortex is still present, but in the part next to it the cortex has been removed. Now the network of boundary canals has become visible. In the upper part a piece of the medulla has been cut away. The tangential section shows the course of some medullary solenia and their connections with the boundary solenia. On the upper side we see part of a transverse section, showing the circle of boundary canals and some medullary canals. On the left the largest boundary canal is visible. The medulla is light dotted; some way to the right a sickle-shaped part was drawn, which is meant to represent a transverse section through the aggregate.

Fig. 22 is a diagram of the canal system in a twig of *Solenocaulon jedanense*. The zooids are placed along the lateral edges of the twig, some of the zooids are provided with anthocodiae. In the middle,

at a, a piece of the medullary layer has been cut away to show the shape and the relative thickness of this layer. For the rest only the cortex has been removed. In the centre there are some longitudinal boundary canals, running straight to the top of the twig. A single canal passes into a coelenteric cavity, the bottom of which is represented by large, black, more or less oval shaped spots. The cavities are connected with each other by narrow boundary canals. On the right-hand side the lateral boundary canal, connected with the coelenterons also by small boundary canals, is visible. At b and c two transverse sections through the cortex have been drawn, at b exactly in accordance with the median plane of a zooid, at c the cortex has been sectioned between two coelenterons; one cortical solenium is visible here.

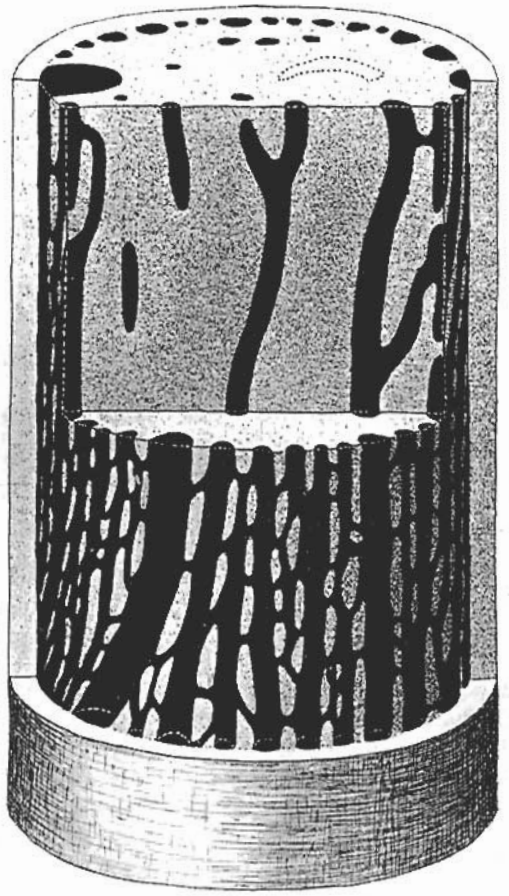

Fig. 21. *Solenocaulon jedanense*. Diagram of the canal system of the stalk. × 8.

At the end of this § I must record something about the zooids. The ventral side of all zooids is turned to the under-(medullary-)side of the twig and consequently the dorsal aspect to the upper side. If we imagine a twig in an upright position, the ventral aspects of the zooids

are neither abaxial nor adaxial: the median planes are standing athwart.

Finally I may remark that I noticed stalked eggs in the zooids of *Solenocaulon jedanense*.

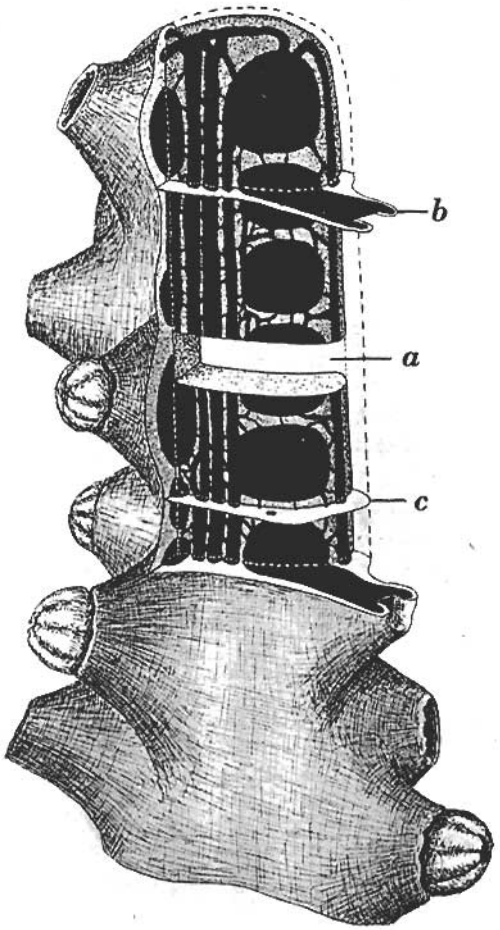

Fig. 22. *Solenocaulon jedanense*. Diagram of the canal system in a twig. × 12.

§ 4. The spicules.

Nutting's description of the spicules of *Solenocaulon jedanense* is absolutely inadequate. He denies the presence of Y-shaped forms in the anthocodiae. Stiasny (1937, p. 46) is the first to give satisfactory drawings of the spicules, but the dimensions given by him are worthless, nearly all of them; the spicules as a rule are 1.5—2 × longer than Stiasny states. Furthermore Stiasny does not distinguish between the spicules of the anthosteles and those of the anthocodiae: the types r and s (textfig. M) originate from the anthosteles, the types o, p and q from the anthocodiae. As appears from the text and drawings Stiasny did find the Y-shaped spicules.

I had at my disposal the "Siboga"-material, which has been examined by Nutting and Stiasny, and so I had the opportunity to examine the specimens as far as regards this point, more closely. From each specimen two anthocodiae were carefully removed and the spicules were disconnected with "Milton". It appeared that in the retracted tentacles the well-known flat Y-shaped spicules did occur in longitudinal rows, exactly as this is known of other *Solenocaulon*-species (cf., e.g., Germanos, 1896, pl. XI fig. 16, T). In the pinnulae there are still smaller, often curved spicules. In fig. 23 a few spicules from tentacles and pinnulae have been drawn in their mutual position. And so Stiasny is right in recording the Y-shaped forms.

At the bases of the tentacles the long thin spindle-shaped spicules form a crown and points, in about the same way as in *Solenocaulon sterroclonium*, according to the above-mentioned drawing by Germanos. The totally retracted anthocodiae of *Solenocaulon jedanense* are protected by this crown and points.

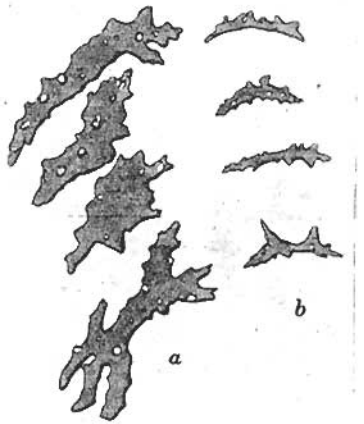

Fig. 23. *Solenocaulon jedanense*. Spicules of the tentacles (a) and of the pinnulae (b) in their mutual position. × 200.

To characterize *Solenocaulon jedanense*—and also the other *Solenocaulon* species—it is not sufficient to know the shape and size of the spicules of one part of the colony, but one should know, as much as possible, the distribution of the various types of spicules in the different parts of the colony: stalk, stem, twig, anthosteles, anthocodiae. For in each of the parts mentioned, even in different portions of these parts—basal or apical portion, front or back—the spiculation may be different. Moreover it is not sufficient to state that the spicules become slenderer and smaller distally.

Here follows a detailed description of the spicules (all the measures of thickness include warts or thorns, unless otherwise stated).

1. The spicules of the cortex.

a. In the basal portion of the stalk the spicules are largest and thickest. Stiasny (1937, p. 47) states: "Unter den Spicula fallen hier als characteristisch die grossen, farblosen, dicht, niedrig und rauh bewarzten Walzen und Kugeln auf". These large and thick globes and ovals, however, are not peculiar to *Solenocaulon jedanense*, for I noticed them in *S. grayi*

too. But in the latter they are somewhat smaller, whereas the large globes are lacking here.

At the surface of the basal portion of the stalk the spicules are exclusively globular and oval. The globes are mostly 0.24—0.30 mm in diameter (minimum 0.15 mm, maximum 0.37 mm). The oval ones are up to 0.56 mm in length and on an average 0.30 mm in diameter (up to 0.35 mm) (fig. 24a

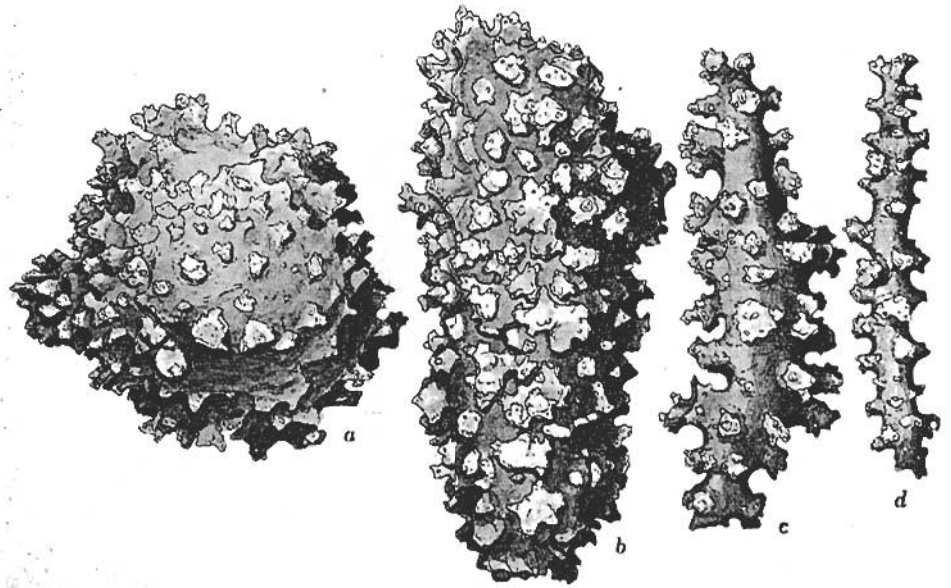

Fig. 24. *Solenocaulon jedanense*. Cortical spicules of the basal portion of the stalk. × 200.

and b). The second layer contains thinner (0.15—0.20 mm) cylinders and clubs, mostly 0.30—0.50 mm in length (fig. 24c). In the subjacent cortical layers there are finally rods and spindles, which are still thinner (0.04—0.065 mm without warts, 0.08—0.13 mm warts included). The length varies from 0.25—0.50 mm (fig. 2d). Close to the boundary canals we still find smaller spindles, about 0.15 mm in length.

There is also some difference in the distribution of the warts. The globular and cylindrical spicules of the outer layers are usually more thickly set with warts than the spindles in the more subjacent layers. It stands to reason that numerous transitions are found between the various types.

b. In the middle region of the stalk there are still large globes (0.16—0.22 mm in diameter) and ovals (up to 0.4 mm in length and 0.21 mm in breadth), but the great majority consists of small, oval spicules (0.10—0.13 mm in length, fig. 25). Under this surface layer a second one follows, exclusively consisting of larger globes (up to 0.32 mm in diameter), and ovals having the same dimensions as those from the outer cortical layer. Farther inward the same spindles and rods follow, which were mentioned above for the more subjacent cortical layers in the basal portion of the stalk.

c. In the upper portion of the stalk the outer cortical layer appears to consist entirely of the above mentioned small, globular or oval spicules (0.09—0.13 mm in length); they are again closely set with warts. In the subjacent layers we find again spindles and rods, but they are smaller now, viz., 0.15—0.32 mm in length (mostly 0.25—0.30 mm) and 0.065—0.095 mm in breadth (without processes 0.024—0.042 mm). The processes of the thinner spindles and rods are now more thorn-shaped and only 0.008—0.011 mm in height; those of the thicker ones are wart-shaped and 0.014—0.028 mm in height.

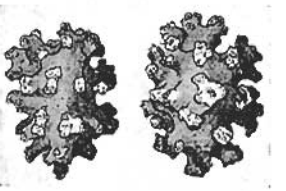

Fig. 25. *Solenocaulon jedanense*. Outermost cortical spicules of the upper part of the stalk. × 200.

So we find a gradual and important change in size of the stalk-spicules: in the outer cortical layers the big globular or cylindrical spicules disappear in a distal direction to make place for small and oval ones. The more subjacent spindles are below longer as well as thicker than the more distal ones.

d. In the stem and branches the spiculation of the cortex is not everywhere alike either. But instead of a contrast between the basal and the distal portion of the stem, there is a difference between the back and the front and lateral sides.

On the back—where also the large boundary canals and the aggregate of medullary spicules are found—the cortex is 0.2 mm thick. The spicules occur there in two strata. The outer consists again of globes and ovals: those of 0.09—0.13 mm in length form the majority, but there are also many larger globes (0.15—0.32 mm in diameter) among them. The second stratum contains spindles and rods; these spicules sometimes lie half-way among the spicules of the outer stratum. The rods especially occur close to the medulla and so they form more or less transitional forms between the cortical and the thin needle-shaped medullary spicules. The length of the rods and spindles is mostly 0.15—0.30 mm; so there is no difference

between these spicules and those of the upper portion of the stalk.

On the lateral and front sides the cortex here and there is also 0.2 mm thick, especially in the vicinity of the zooids; in this case the spiculation is like that on the back. But usually the cortex is thinner (0.1 mm) and now the spicules practically form one stratum, in which the spicules of all sizes lie scattered. Large globes, however, are lacking; a few still have a diameter of 0.16 mm. The ordinary small globes and ovals of 0.08—0.13 mm, thickly set with warts, form the majority (fig. 26a and b); very rarely an oval of 0.19 mm in length still occurs. Among these globular and oval spicules there are numerous spindles, clubs and rods (fig. 26c, d and e), but they are strikingly larger and thicker than those on the back of the stem: spindles and clubs are mostly 0.30—0.50 mm (up to 0.64 mm) in length and 0.08—0.13 mm thick. The rods measure 0.30—0.45 mm (up to 0.48 mm) in length and 0.032 mm in breadth (without processes), they are rather scantily provided with low blunt thorns. Usually the spindles and rods are curved.

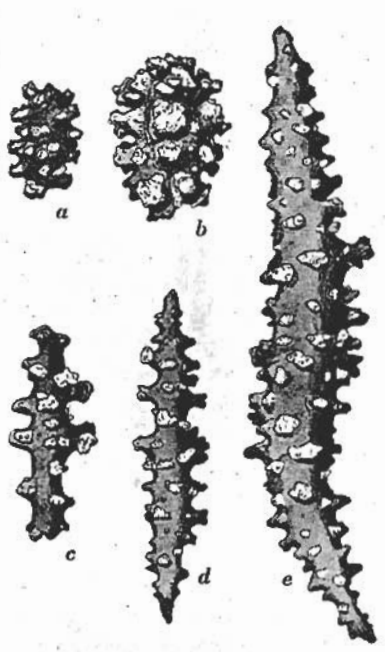

Fig. 26. *Solenocaulon jedanense*. Cortical spicules of the frontal and lateral surfaces of the stem. × 200.

So we see that on the front and lateral sides the globes are smaller —the large ones are lacking—, but especially that the spindles and rods are larger than those on the back.

e. In the twigs the cortical spicules lie in two strata again. In the outer stratum we find globular and oval spicules (0.08—0.15 mm in length, up to 0.2 mm) and mostly 0.1 mm thick, and wholly covered with warts. In the inner stratum there are spindles and rods again, mostly 0.25—0.40 mm in length: they may, however, reach a length of 0.53 mm. The rods are thinner than the spindles (about 0.03 and 0.09 respectively, warts included). The spindles are densely covered with high warts, the rods have only low thorns as in the stem.

f. The anthosteles. As a character of *Solenocaulon jedanense*, Nutting mentions the presence of "heavy, coarse tuberculate clubs and spindles" in the inner wall of the "calyces", whereas oval and round, closely warted spicules are found in the outer layer. I cannot but affirm this observation of Nutting's. The last mentioned spicules are nearly always oval; the length varies from 0.10—0.21 mm (average length about 0.15 mm); the thickness varies from 0.07—0.14 mm. In one of the specimens numerous globes and ovals are found, having no projections, but instead of these low, smooth knobs; as intermediate forms some spicules are met with, being warted on one half and all but smooth on the other.

Towards the top, and also in the second layer of the verruca, the clubs and spindles follow, which were mentioned by Nutting. Most of these are 0.30—0.55 mm in length (up to 0.60 mm) and 0.05—0.11 mm thick. But smaller spindles, 0.15—0.30 mm long, also occur: the thicker the spindles, the higher the warts, the height varies from 0.007—0.014 mm. Round the aperture of the verruca the spindles are arranged parallel to each other and to the longitudinal axis of the anthostele; they rise only a little above the edge, so that the edge is only slightly undulate.

g. In the beginning of this § mention has already been made of the spicules of the anthocodiae. The crown and points are composed by spindle-shaped spicules, mostly 0.30—0.50 mm in length (up to 0.54 mm) and 0.050—0.065 mm thick; they are mostly curved to one side, others being more irregularly curved, or having 1—3 branchlets, or being somewhat branched at the ends. The spicules of the tentacles and pinnulae (fig. 23) were discussed already. Finally in the stomodaeum minute (about 0.06 mm long) spindle-shaped spicules are met with, provided with low spines; some have irregular shapes, e.g., "Vierling"-shape (fig. 27).

Fig. 27. *Solenocaulon jedanense*. Spicules from the stomodaeum. × 200.

2. The medullary spicules.

a. Part of the medulla spicules have fused into a hard calcareous mass, called the aggregate. In stalk, stem and twigs the aggregate is met with. In some specimens it occurs in the upper portion of the stalk, in others it begins already in the middle of the stalk. In transverse section it has different forms, e.g., a sickle-like shape, the convex side being turned to the back, or the shape of a three-rayed star (one ray pointing backwards, the two others being turned to the left and to the right and slightly bent forward).

At the transition of the stalk into the stem the backward turned ray

disappears, so that here the aggregate becomes sickle-shaped too. This shape remains unchanged all through the stem; the aggregate then lies on the back of the stem and branches, exactly as described by Genth for *Solenogorgia tubulosa* (*Solenocaulon tubulosum*) "an der Knickungsstelle des Rohres" (Genth, 1867, p. 438). Here the medulla is thicker than on the front and lateral sides, and in a transverse section we see the aggregate contrast with the rest of the medulla by its whiter colour. But in *Solenocaulon jedanense* the aggregate locally appears also on the lateral sides of the stem, entirely independent from the aggregate on the back. This occurrence is linked up with the situation of the twigs. For the medullary layer of the twigs consists practically entirely of fused spicules. That is the reason, why the twigs are not flexible, but hard and difficult to break. In order to fix these twigs firmly to the stem, the aggregate of the twig passes into the medullary layer round the lateral openings and farther into the lateral sides of the stem. In this way the twigs are firmly implanted. In the twigs the aggregate has a triangular or sickle-like shape.

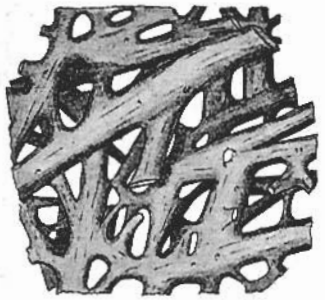

Fig. 28. *Solenocaulon jedanense*. Aggregate from a twig. × 200.

By cutting thin fragments from the aggregate by means of a razor, we see that the spicules have lost all individuality; numerous oval and triangular openings are left between the fused rods, which are very scantily provided with tiny tubercles (fig. 28). On the surface of the aggregate the mutual fusion has not yet reached that stage; so the forms of the spicules are better recognizable: they are needle-shaped, with rather thinly distributed low, blunt tubercles. Shape, thickness, etc., of these already partly fused spicules are like those of the ordinary free medullary spicules. So we see that there is a more or less gradual transition between the free and the fused spicules, and consequently the aggregate is part of the medulla.

Meanwhile the fusion of medullary spicules is not restricted to those places where a solid aggregate has been formed. For also among the free spicules we repeatedly find some fused needles (fig. 29).

b. The free spicules have not all the same shape. In the middle of the stalk three types may be distinguished. First the fusiform type, mostly 0.15—0.30 mm (max. 0.48 mm) in length and 0.011—0.017 mm thick (spines excluded). Many of these are perfectly smooth, except just in the middle,

where there are some low, volcano-shaped spines. Other needles also have some blunt projections elsewhere. Further we find rod-like spicules, at the blunt ends and also elsewhere provided with some low thorns. The length of the rods is equal to those of the needles. The third type (fig. 30) is likewise rod-shaped but it is shorter (about 0.16 mm long) and 0.03 mm thick (without warts). The projections are higher and wart-like and are more closely packed than in the two first-mentioned types; and so this type shows much likeness to some cortical spicules. Between the three types all kinds of transitions occur.

Fig. 29. *Solenocaulon jedanense*. Fused medullary spicules from a branch. × 200.

In a transverse section of the stalk we see with transmitted light lighter spots here and there; then the spicules are not packed so closely as in other places. All the medulla spicules lie pell-mell, also the short rods of the cortical-like type. In some parts of the medulla the latter are more numerous than elsewhere, but I could not find an accumulation in the centre, so that a medulla-chord, sensu Kükenthal, is lacking.

Regarding the medulla spicules of the stem one cannot detect any difference between the back and the front and lateral sides. The same types as in the stalk are met with, but in the stem the needles and rods on an average are much longer and also a little thicker than in the stalk. The average length, however, is difficult to ascertain, because it varies from 0.15—0.90 mm! But most of the spicules are about 0.30—0.65 mm in length and 0.017—0.022 mm in diameter (without projections). The spicules are irregularly distributed, but on the medullary side of the boundary canals they lie chiefly longitudinally.

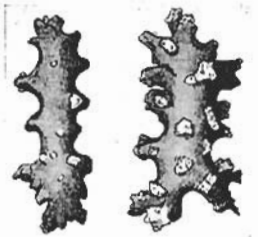

Fig. 30. *Solenocaulon jedanense*. Medullary spicules of the third type. × 200.

c. On the interior side of the tubular stem I looked for an "inner bark". In fact, the spicules occurring there differ somewhat from

the ordinary medulla spicules. They are shorter (0.16—0.24 mm), but of about equal thickness (0.017 mm), while there is no difference in the distribution of the thorns either. Among these rods, however, others are met with which are not only much shorter (0.075—0.160 mm), but besides they are conspicuous by two facts: firstly, they often show a longitudinal brown line in the centre, from which laterally little brown lines issue into the spines and, secondly, the spines are higher (0.014 mm instead of 0.008 mm) and more cylindrical with rounded top. Consequently the "inner bark" is devoid of typical cortical spicules and so a medulla-chord, sensu Kükenthal, is lacking in the stem too.

On the undermost side of the twigs the smooth types are most numerous.

Nutting (1911, p. 9) and Stiasny (1937, p. 45, sub 3) recorded a specimen of *Solenocaulon jedanense* collected on Station 164. This perfectly white specimen in appearance, etc., is very much like one of the specimens from Station 273, which was likewise white and unbranched and in which the anthosteles were hardly visible on the outside. There is, however, a difference in the spicules. In the above mentioned circumstantial description of the spicules of a specimen from Station 273, the small ovals from the stem are mentioned, having a length of 0.09—0.13 mm. In the specimen from Station 164 these small spicules are only 0.05—0.06 mm in length (this is the same on all sides of the stem). In the twigs these ovals are still smaller, viz., 0.03—0.06 mm long. The processes are deformed into flat plates, often standing in transverse rows, so that they show much likeness in shape and size to the spicules of *Solenocaulon tortuosum*, drawn by Stiasny (1937, textfig. Q, a).

Now I had no material of *Solenocaulon tortuosum* at my disposal. I could, however, make use of some preparations, made by Stiasny from a specimen from the Frankfurt Museum (Stiasny, 1937, p. 54, sub 3). As appears from these preparations the small cortical spicules from the stem of *Solenocaulon tortuosum* are 0.03—0.05 mm in length, so that also as far as regards the length, there is no essential difference between these small spicules of *S. tortuosum* and of *S. jedanense* (Station 164!). So we see that in this respect the two species more or less pass into one another.

According to Nutting, however, the structure of the anthosteles is an important character of *Solenocaulon jedanense*. In comparing the anthosteles of the type-specimens of *S. jedanense* with those of *S. tortuosum* we see that in both cases the wall consists of two layers; in the outer layer there are small ovals, whereas the inner layer consists of larger spindles. But in both species there is a great difference as to these spindles. The

"heavy, coarse tuberculate clubs and spindles" (Nutting) of *S. jedanense* are much larger and thicker (0.05—0.11 mm) than those of *S. tortuosum* (in the above-mentioned specimen 0.015—0.025 mm thick).

Finally I observed two more differences in the preparations: the cortex of the stem in *S. tortuosum* is thinner (0.06—0.08 mm) and in the medulla of the stem there are a few solenia. As I have no sufficient material of *S. tortuosum*, I cannot further compare *S. jedanense* and *S. tortuosum*. For the time being *S. jedanense* should be regarded as a distinct species anyway.

The specimens collected on Station 273 still show among them the most similarity in appearance, colour, cortical spicules, fused medulla-spicules, etc. The specimen from Station 164 is perhaps an intermediate form between *S. jedanense* and *S. tortuosum*. But, once more, complete material for comparison is lacking, and the literature does not give any useful data!

§ 5. The mesogloea.

In the medulla of the stalk, especially in its peripheral layers, cell-vessels occur. They form a wide-meshed network. The lumen of the meshes usually measures up to 0.035 mm in diameter, seldom up to 0.050 mm. In these rather spacious vessels the cells are found in one or two rows. The boundary canals are surrounded by a zone of homogeneous mesogloea, which is devoid of spicules; usually a network of vessels occurs in it, situated parallel to the endoderm of the solenia and at a little distance from it. In the cortex the vessels are fewer in number, sometimes they seem to open at the surface, but I am not quite certain of this.

In the stem, in both layers of the coenenchyma, the vessels occur too. Often they are connected with the ectoderm, which lines the central channel. From the endoderm of the solenia they are always separated by a very thin mesogloeal layer.

In the twigs the mass of medullary mesogloea is reduced, in connection with the presence of the aggregate: it forms very fine, ramified plates. Cell-strings are rare in it. Round the boundary canals the mesogloea is more strongly developed and contains cell-vessels, running parallel again with the endodermal epithelium. In the cortex there is a meshwork of wide vessels, sometimes they seem to open at the surface, while the mesogloeal cells pass into the ectodermal ones.

§ 6. The horny substance.

As regards the horny substance very little need be said. In the stalk it is abundantly present in the medulla, especially in its peripheral layers.

It forms very numerous sheaths round the spicules, connecting the latter with each other. The cortex is devoid of horny substance. In the stem—except in its basal portion—and in the twigs, the horny substance is totally lacking.

IX. SOLENOCAULON GRAYI STUDER

This species has been dealt with by Studer (1878), Hickson (1903), Janower (1904), Thomson & Simpson (1909), Nutting (1911), Kükenthal (1919) and Stiasny (1937). Thomson & Simpson did not examine a specimen of *Solenocaulon grayi* themselves.

§ 1. The material.

I examined the specimen from the "Siboga"-Expedition, Station 51, that has been described by Nutting and Stiasny. Longitudinal and transverse sections were made of the stalk (slightly over 1 cm in thickness); moreover microtome-sections in different directions of the hollow tubular stem and of the twigs. The spicules were examined again.

§ 2. Medulla and cortex.

Numerous are the resemblances between *Solenocaulon grayi* and *S. jedanense*. By way of example we may mention here that the differences between medulla and cortex in both species are the same. Both layers are always separated by boundary canals; in the twigs of *S. grayi* the cortical solenia are more strongly developed.

In *S. grayi*, as in *S. jedanense*, at the transition of the stalk into the stem there rises a shallow open groove, the edges of which are somewhat projecting. At first the pink-coloured cortex passes into the groove, but soon the cortex withdraws from the edges and remains on the bottom of the groove for some distance. But as the groove broadens, the width of the cortical strip decreases upwardly. Consequently the cortical layer only occurs in the lower part of the groove, for about a distance of 3 cm. Further upwards, the interior side of the groove and of the tubular stem is wholly formed by the medulla. There are no zooids on the stalk, nor on the edges of the groove. In the stalk the cortex usually is 0.5 mm thick; at the transition into the stem the cortex becomes slightly thinner (to 0.4 mm); at the bottom of the groove the cortex is still thinner, viz., 0.06—0.20 mm.

The stem of *Solenocaulon grayi* is an almost entirely closed tube with short lateral tubes, which are continuous with the twigs. Along the edges of these tubes and twigs the zooids are met with. On the front side of the stem the zooids do occur too, not so distinctly in two separated rows as in *Solenocaulon jedanense*, but in one irregularly shaped border. The coenenchyma of the stem consists of a medullary layer, immediately surrounding the central channel, and a cortical layer. On the back of the stem both layers are thickest: the cortical one is about 0.17 mm thick; the medullary one decreases in thickness in an apical direction. On the lateral sides both layers are thinner (0.07 mm and 0.50 mm respectively).

The twigs also consist of a cortical and a medullary layer, which are the continuations of the same layers of the stem. The cortex is 0.1 mm thick and contains the spicules in 2 or 3 strata. More towards the end the zooids are so closely packed, that there hardly remains a cortical layer between them. The medulla is always guttered on the bottom-side. In transverse sections we see that the medulla is thickest in the middle and gradually becomes thinner towards the lateral edges; it resembles a triangle with a concave base. At the proximal end of the twigs the medulla is thickest, width and thickness are regularly diminishing distally.

Janower's fig. 3 represents a transverse section through the extreme tip of a twig. Here the cortex is bent over the medulla; and in making transverse sections through this extremity of the twig, the medulla is not yet to be seen. A few sections lower the medulla would be visible already, separated from the cortex by boundary canals; see the top of my diagram, fig. 32b. So the triangular shape in Janower's figure has nothing to do with the triangular shape of the medulla lower down in the twig.

§ 3. The canal system and the zooids; diagrams.

Boundary and medullary canals also occur in *Solenocaulon grayi*; cortical solenia are present in the twigs only.

a. The stalk. The boundary canals run chiefly in a longitudinal direction; they ramify and anastomose again and again, forming an irregular long-stretched meshwork. Farther upwards in the transitional part between stalk and stem, the course is more regular, straight or oblique (fig. 31 at the top). In numerous places the boundary canals are connected with the medullary canals, or they are straightway continuous with the latter (fig. 31 to the right). In transverse sections their shape is oval: the width in tangential direction being 0.5—0.8 mm, the height in radial direction 0.2—0.5 mm.

As has been pointed out, the cortex passes into the frontal groove for some way. This cortical layer is separated from the medulla by boundary canals. The partition-walls between these canals, however, have been reduced to numerous little columellae, so that the canals have coalesced

into one space, a boundary space! This space is rather low (0.15 mm) and is only to be found in the groove (fig. 31, right-hand bottom corner).

The medullary canals are very numerous in the stalk; they are irregularly round or oval in shape, and more spacious than the boundary canals, viz., about 1 mm in diameter; on the left of the front there is a more spacious solenium again, with a diameter of 2.5 mm. They show an irregular course in a longitudinal direction; they repeatedly branch out and are frequently connected with boundary solenia. Finally it should be stated that in my material all the canals were entirely filled with a grey detritus, containing grains of sand, siliceous needles of sponges, and globigerinae.

In his textfig. L, q. Stiasny already represented a transverse section through the stalk at the height of the groove; so it is not a cross-section through an "Ast in mittlerer Höhe", as Stiasny says.

In fig. 31 the canal system of the upper part of the stalk has been drawn. On the front the groove, in the lower part of which a thin cortical layer occurs, upwards ending in a boundary line (a) of parabolic shape. A fragment of this cortical layer has been removed (right-hand bottom corner), so that the boundary space becomes visible. On the upper side of the diagram we may distinguish the crown of boundary canals and in the dotted medulla the medullary solenia. The part where fused spicules occur, is bounded by a dotted line; so the aggregate (cf. § 4) is to be found close to the frontal groove. The course of the boundary canals is shown in the thin cortical layer that is placed at the top of the drawing. In the section-plane to the right, the course of the medullary solenia and their connection with the boundary canals is visible.

b. The stem. The boundary canals mostly are strongly flattened here, especially on the cortical side. They have not all the same size; those on the back are largest: 0.30—0.35 mm in breadth and 0.08—0.11 mm in height. All the other canals are smaller and more flattened, the dimensions are 0.07—0.17 × 0.015—0.040 mm. No endodermal canals occur in the medulla any more, and so Stiasny's textfig. L, r is incorrect.

c. The twigs. The canals of the stem are continuous with those of the twigs; here also they lie in the boundary of medulla and cortex. In the medulla itself there are no solenia. The canals are oval and generally flattened against the cortex. The width varies from 0.15—0.30 mm, the height from 0.05—0.30 mm. They run again in a longitudinal direction and pass into the coelenterons, but first they ramify irregularly in the thickening cortical layer (fig. 32b at the bottom). So we have to do with cortical solenia here.

The zooids are closely packed together, so that between the coelenterons only thin partition-walls remain. In the thicker parts of these walls there are also narrow endodermal canals. They form a meshwork, running

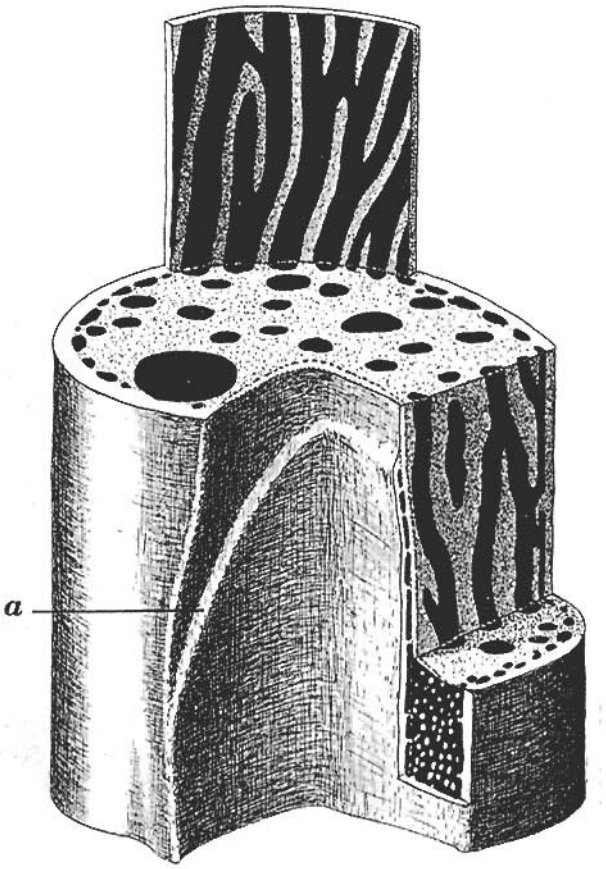

Fig. 31. *Solenocaulon grayi*. Diagram of the canal system in the transitional part between the stalk and the stem. × 6.

parallel with the endodermal epithelium on both sides of the walls. By means of this meshwork the coelenteric cavities are indirectly connected with each other. But there are also larger openings (0.05—0.13 mm) in the partition-walls, so that the coelenterons are connected directly too.

Finally, in *Solenocaulon grayi* too there is a longitudinal canal along each lateral side of the twig; this canal in its topmost part is connected with the coelenterons found there. The zooids along the edges of the twig

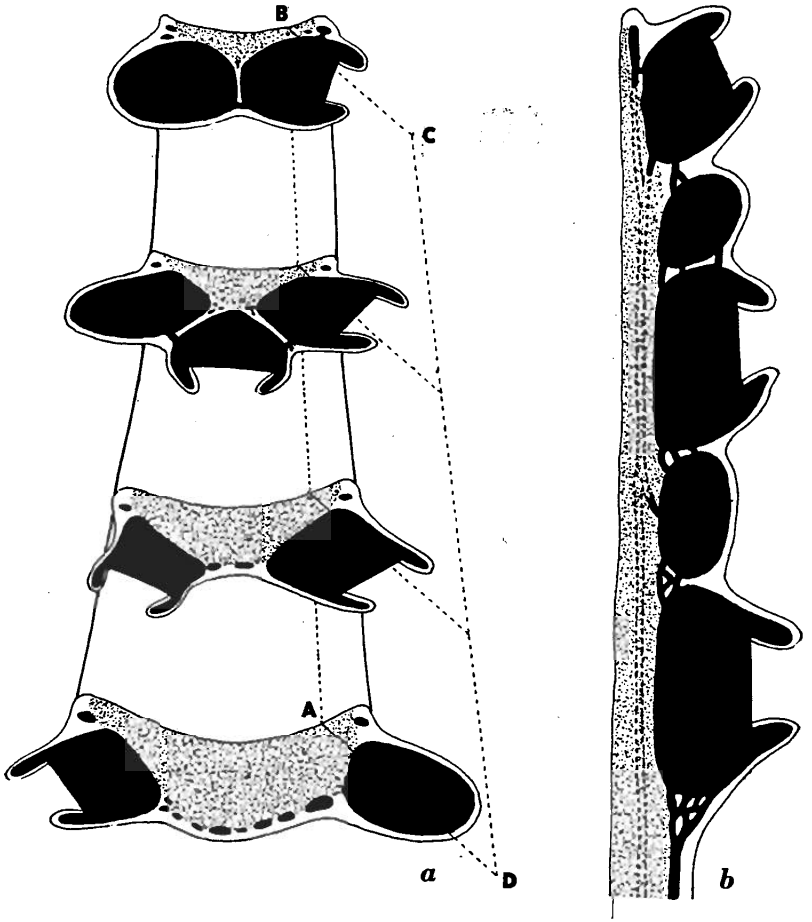

Fig. 32. *Solenocaulon grayi.* Diagram of the canal system of a twig. × 14.

are connected with these canals by means of short solenia, just as in *Solenocaulon jedanense.* So in any transverse section of a twig we see a solenium in the basal corners of the triangular medulla (fig. 32 a).

It was not easy to render the complex structure of the canal system of

a twig in one diagram in a sufficiently distinct way. Therefore in fig. 32 a I represented four transverse sections. The topmost is made through the twig close under the extremity, the undermost section traverses the twig at a few cm's distance from the top. In the topmost section the medulla (dotted) is still imperfectly developed and triangular in shape with concave base; downwards the medulla increases in width and thickness. In the top the zooids are still closely packed and separated by thin walls with cortical solenia. Lower down the zooids are more and more separated; between them there is a stratum of boundary canals. On both sides of each section the lateral canals are visible likewise in the boundary of medulla and cortex.

Fig. 32 b is a diagrammatical reconstruction of a longitudinal section, according to plane ABCD of fig. 32 a. Here the medulla is also darkly dotted and the cortex lightly tinted. A dotted canal runs in the medulla; it represents one of the lateral canals, which does not lie in the drawing-plane. Both the lateral canals are connected with each other in the tip of the twig; so the canal is sectioned in the tip, and therefore this part has been drawn in black. The coelenteric cavities are connected with each other and also with the lateral canals by numerous solenia.

Finally a few remarks. Firstly, the spherical female gonads, measuring up to 0.40 mm, are all stalked. And, secondly, the median plane of the zooids may have different situations: the ventral side of the zooids may be either abaxial or adaxial or it may be turned in any other direction. And this again is a difference from *Solenocaulon jedanense.*

§ 4. The spicules.

As a character of *Solenocaulon grayi* it has repeatedly been stated, that the cortex among other spicules contains small fir-cone-like ("tannzapfenförmige") spicules (Janower, 1904; Thomson & Simpson, 1909; Kükenthal, 1919), but the authors have omitted to give drawings of these important spicules!

In examining the spicules of the specimen at my disposal, I found that the variability in the various parts of the colony is fairly extensive again. In the next part I will therefore give a description with drawings of spicules from all parts of the colony.

1. The cortical spicules.

a. The stalk. In *Solenocaulon grayi,* too, there is an important difference between the cortical spicules of the lower and the upper part of the stalk, while from the outside to the inside a certain arrangement according to size and shape may be observed.

The basal portion of the stalk has been compressed from the left to the

right, and in this way has become more or less spoon-shaped. The right-hand side is all but flat, the left-side is convex. Now I found that there is even a difference between the spicules of the right and of the left side of the spoon; although this is of not much consequence.

First of all the convex side. Large, more or less oval or club-shaped spicules are found at the surface; the ovals (fig. 33 a) are 0.25—0.40 mm in length; the clubs are longer, up to 0.57 mm; the breadth varies from 0.15—0.27 mm, warts included. These spicules are densely covered with high, coarse warts, which again are thickly set with minute thorny points.

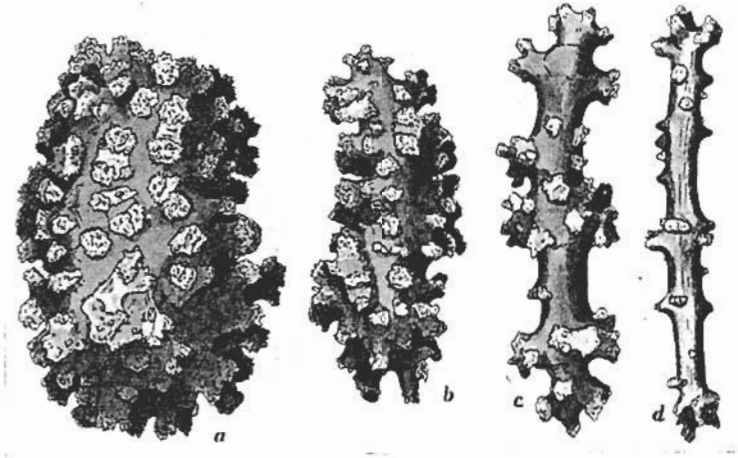

Fig. 33. *Solenocaulon grayi.* Cortical spicules from the basal portion of the stalk. × 200.

In this respect they differ from those of *Solenocaulon jedanense*, for the rest these large spicules remind one strongly of the corresponding spicules of *Solenocaulon jedanense*. Inwardly the spicules gradually become thinner (fig. 33 b, c and d). Most of these are rods with high-stalked warts. The length always varies from 0.17—0.32 mm (up to 0.45 mm), the thickness (without warts) diminishes inwardly from 0.060—0.025 mm. The outer rods (fig. 33 b) are still closely packed with warts, measuring 0.028 mm in height. The processes of the inner rods (fig. 33 d) are lower (0.011 mm) and are more sparsely distributed; they have the shape of blunt spines now, or they have been transformed into a kind of transversely placed little plates. These inner spicules thereby form transitional types to the medullary spicules.

As regards the flat right-hand side of the spoon, in the surface layer the spicules are slightly smaller (0.16—0.30 mm) and thinner (0.15 mm or less, warts included), so that they are more like type fig. 33 b. The thinner rods of fig. 33 c and d are scarcer probably because the cortex is thinner here.

In the upper part of the stalk the cortical spicules are of a quite different kind. Instead of the large, often irregularly formed spicules of the outer cortical layer we find here small oval bodies, 0.08—0.11 mm in length and covered with a compact mass of irregular processes (fig. 34 a). Beside these and also farther inside we find the type of fig. 34 b (0.11—0.13 mm in length). The surface of the spicule itself now is visible; the processes, often standing in transverse rows, have blunt or slightly broadened and wart-like ends. In the inmost cortical layer, still longer forms are met with (fig. 34 c), 0.16—0.18 mm in length and spindle-shaped. Finally we find here the type of fig. 34 d, 0.22—0.32 mm in length (one specimen even reached a length of 0.48 mm), these are more rod-shaped and in this way form a transition to the long, thin medullary spicules. The processes, which in the types c and d (fig. 34) are deformed into transverse plates, are not seldom higher than the thickness of the spicule. Therefore the spicules have a conspicuously spiny appearance.

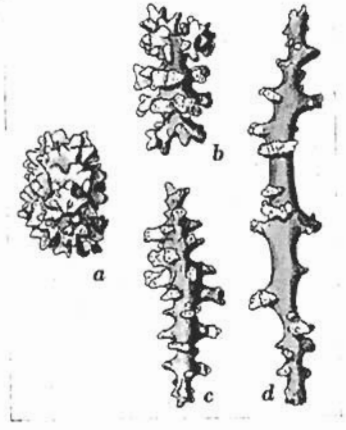

Fig. 34. *Solenocaulon grayi.* Cortical spicules from the upper part of the stalk. × 200.

b. The stem. On the back, where the cortex is thickest (about 0.17 mm) the spicules occur in a few strata. The outer spicules are 0.065—0.100 mm in length (fig. 35 a and b); they are short little rods with projections, 0.017 mm in height and having the shape of transversely arranged plates. Probably this type was represented by Studer (1878, pl. V fig. 40, d). Inwardly the rods successively become longer, up to about 0.25 mm (fig. 35 c), but the processes become lower (0.007 mm) and more cone-shaped: transition to medullary spicules. The thickness of the spicules always remains about 0.014 mm, without warts.

On the lateral sides of the stem the cortex is thinner (0.07 mm); the spicules now are arranged approximately in one stratum. All of them are

little rods of about the type as in fig. 35 a and b, and fig. 34 c; the length varies from 0.08—0.20 mm. So there is, practically, no difference between these spicules and those on the back of the stem—only on the lateral sides all the types lie promiscuously, in one stratum, whereas on the back they are arranged according to size.

c. The twigs. The cortex is thicker again and contains some strata of spicules. As in the stalk and in the stem the spicules increase in size from the outside to the inside. The outer spicules are 0.08—0.16 mm in length and show a great likeness to the cortical ones in the stem (fig. 35 b). Farther inside longer rods and spindles follow, about 0.3 mm in length, up to 0.5 mm, with more distant high spines. The thickness is much like that of the cortical spicules of the stem. In the twigs they are arranged chiefly in a longitudinal direction.

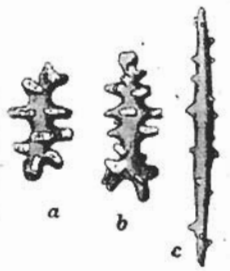

Fig. 35. *Solenocaulon grayi*. Cortical spicules from the back of a branch. × 200.

In the partition-walls between the zooids there are spicules of a different type, viz., needles or long-stretched spindles, straight or slightly curved, sometimes a little S-shaped, and closely beset with spines. They are 0.2—0.4 mm in length and 0.03 mm thick.

d. The anthosteles. The cortical spicules described above are also found at the bases of the verrucae. But towards the top the spicules become larger: 0.5—0.65 mm in length and 0.03—0.045 mm in breadth. They are rather closely covered with high, blunt, cone-shaped thorns. Round the aperture at the top of the verruca the spicules lie parallel to each other and to the longitudinal axis of the anthostele, but they do not rise above the edge of the verruca, so that the edge remains almost straight.

In comparing this spiculation with that of the anthosteles of *Solenocaulon jedanense*, we see that in the latter all the spicules are coarser and larger. In *S. jedanense* the outer spicules are thick oval or globular bodies; in *S. grayi* they are tiny rods. In *S. jedanense* the more subjacent clubs and spindles also are much thicker and have coarser warts than in *S. grayi*.

e. The anthocodiae. The spicules composing crown and points are rod-shaped, densely provided with very low blunt thorns. The spicules of the crown are longest: 0.25—0.50 mm, up to 0.60 mm in length and 0.022—0.035 mm broad; mostly they are curved to one side. Between the Y-shaped forms on the aboral side of the tentacles and the small spicules of the pinnulae of *S. grayi* and of *S. jedanense* no important differences are detectable.

2. The medullary spicules.

In the medulla of the stalk there are only needle-shaped spicules (fig. 36 a). They are all but straight; the middle part is sometimes almost smooth, towards the extremities the number of processes increases. These processes often are transversely placed little plates with finely serrated edges (fig. 36 b). I cannot discover that the needles are flattened (Janower, 1904, p. 507). The average length is 0.55—0.80 mm, but longer ones also occur, up to 1.07 mm. The thickness is always about 0.014 mm. They lie pell-mell and closely packed, but here and there, especially in the neighbourhood of the medullary canals, they are less crowded. In a transverse section the places, where they are closely packed, are outlined as dark bands (cf. textfig. L, q of Stiasny, 1937).

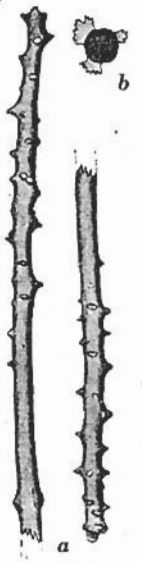

Fig. 36. *Solenocaulon grayi*. a, medullary spicule from the stalk; b, transverse section through a medullary spicule. × 200.

In the medulla of the stem we must distinguish between fused and free spicules. The free spicules (fig. 37 a) are needle-shaped, straight or slightly curved and equally covered with spines or little transverse plates, which are mostly somewhat larger towards the extremities. The length of the needles generally is 0.5—0.7 mm (Studer, 1878, p. 671, says 0.37 mm and 0.40 mm; Janower, 1904, p. 507 and 532, records 0.3—0.7 mm).

In *Solenocaulon grayi* too, fusion of medullary spicules occurs. The aggregate lies in the same places as in *S. jedanense* and in *S. sterroclonium*, viz., on the back of the tube. In *S. grayi* the inner medulla-layer with a thickness of about 1 mm consists of the aggregate. The fusion does not seem to have reached the same degree as in *S. jedanense*, so that the separate spicules are easier to distinguish (fig. 37 b). So it may be

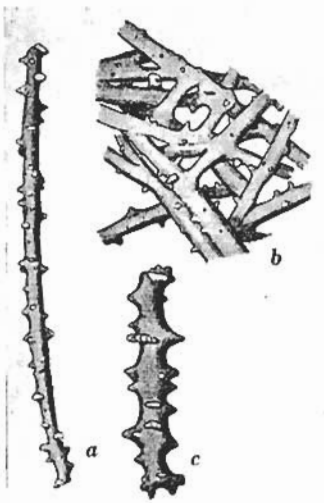

Fig. 37. *Solenocaulon grayi*. a, medullary spicule from the stem; b, fused medullary spicules; c, spicule from the "inner bark" of the stem. × 200.

explained, perhaps, that former investigators did not notice the fusion. In the transitional part between stalk and stem the aggregate is already present. It is to be found on the bottom of the groove, which here arises on the front-side. The lower part of the groove is covered with the cortex for a distance of about 3 cm, but also in this part the aggregate is found, on the inside of the boundary canals. I did not examine how far the aggregate is continued downwards in the stalk, in order not to spoil the material.

On the inside of the tubular stem we find, close under the ectoderm, spicules of a somewhat different type: they are short (0.14—0.19 mm) and thick (0.020—0.024 mm) little rods with broad ends and provided with flat processes (fig. 37 c). These spicules together form the "inner bark".

In the medulla of the twigs there are again straight or slightly curved rods, of an average length of 0.2—0.4 mm (up to 0.75 mm) and mostly 0.012 mm thick; here and there the rods are somewhat fused. Consequently in this respect there is a great difference between *Solenocaulon jedanense* and *S. grayi*.

§ 5. The mesogloea.

The mesogloea is well-developed between the spicules of cortex and medulla. Nowhere did I discover separate cells or cell-strings. On the other hand I found numerous spacious mesogloeal vessels in medulla and cortex. In the medulla the vessels show a strongly winding course, the lumen varies from 0.015—0.045 mm. In the cortex and the verrucae they are narrower. It is remarkable that the vessels in the cortex open at the surface through openings in the ectoderm (fig. 38). A similar state was described by Genth (1867) for *Solenogorgia tubulosa* (*Solenocaulon tubulosum*). In *S. jedanense* I noticed the same, but in this species it was not so distinct. In the case of *S. grayi* the ectoderm turns inwards in these openings, from which it follows that the mesogloeal cells in the vessels are of ectodermal origin. This appears also from the fact that in the mesogloeal as well as in the ectodermal cells the same peculiar bodies occur, viz., sickle-shaped little rods, resembling curved sausages. Perhaps they are parasitical organisms (vide fig. 38, par.).

In the vessels the mesogloeal cells are flattened against the wall. To speak of a connected and distinct epithelium is out of the question, in contradistinction to the solenia. In the last-mentioned canals the epithelium is high and the nuclei are very small and globular. Nowhere did I find any communication between solenia and mesogloeal vessels, although they run sometimes close beside one another.

In *Solenocaulon grayi* only a layer of homogeneous mesogloea occurs on the medullary side of the boundary canals.

§ 6. The horny substance.

Janower (1904, p. 509 sq.) remarks that he could not find anything like horny substance in *Solenocaulon grayi*. Conform to Janower's statement,

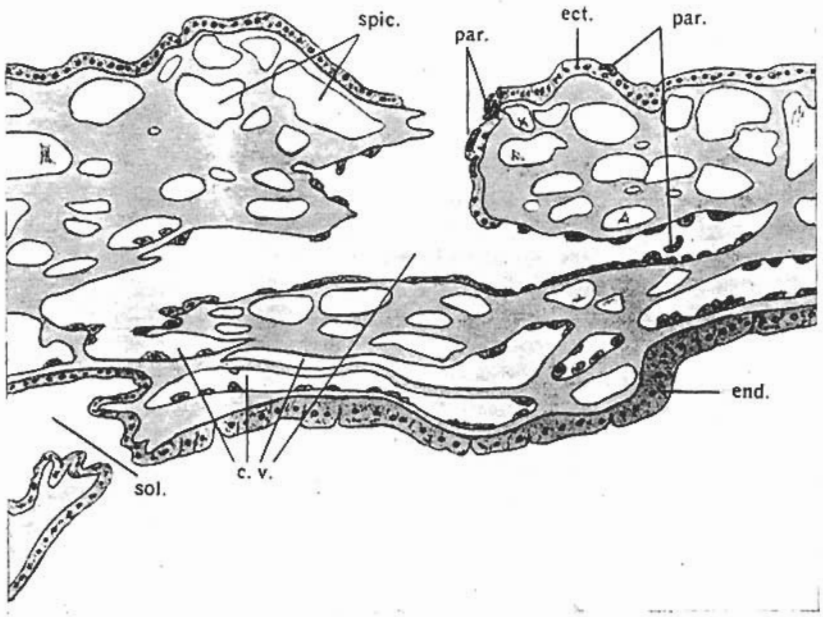

Fig. 38. *Solenocaulon grayi*. Transverse section through the anthostele. c. v., cell-vessels; ect., ectoderm; end., endoderm; par., parasitic sporozoon (?); sol., solenium; spic., cavities left by spicules. × 360.

Thomson & Simpson (1909, p. 160) also deny the presence of horn; they did not examine this species themselves. Nutting does not write anything about it. Stiasny (1937, p. 43) mentions "deutlich ausgebildeten bräunlich/gelblichen Hornsträngen" in the stalk ("Ast"!) of *S. grayi*; and a little further he says: "Die Gefässwände sind mit gelblich/bräunlicher Hornsubstanz wie austapeziert". Stiasny examined only sections, cut by hand and unstained. In relatively thick sections like these the epithelium of the canals together with the subjacent mesogloea seems to cover the walls as a yellowish layer. But not all that is yellow/brown is horny substance. And

most certainly not in these canals. So Stiasny's observation is totally incorrect. Only Kükenthal (1919, p. 901) noticed horny matter in the medulla "als dichtes Netzwerk", viz., in Studer's type-specimen.

From my microtome-sections it appears that the horny substance occurs again in the ordinary way: it forms only rather thin sheaths round the medullary spicules of stalk, stem and twigs. The yellow/brown "horny chords" mentioned by Stiasny, have nothing to do with horny substance; they are the result of the closer accumulation of spicules.

X. SOLENOCAULON RAMOSUM HICKSON AND SOLENOCAULON STERROCLONIUM GERMANOS

1. *Solenocaulon ramosum* (vide foot-note p. 61).

Prof. Hickson was kind enough to send me a few fragments of the stem of his type specimen, consisting of parts of the "belts" with some twigs; the back of the stem was not distinguishable.

I cannot give an eleborate description of the characters of this species, but some facts have to be mentioned to facilitate a comparison with other *Solenocaulon*-species.

The cortex of the stem is thin (0.07—0.08 mm). The spicules form one stratum; in some places the cortex seems to be somewhat thicker and the spicules lie in two strata: the outer ones are small again, the inner ones are larger. All the cortical spicules are more or less spindle-shaped. In size they vary from 0.11—0.32 mm, but larger ones also occur, up to 0.60 mm in length (not drawn by Stiasny). Spindles of this length do not occur in any other species examined by me. The thickness of the spicules, without processes, usually is about 0.018 mm, the larger spindles are up to 0.025 mm in breadth. The spicules are rather closely covered with high processes, which at the base are volcano-shaped, but at the top they are flattened into little transverse plates, exactly as in *Solenocaulon grayi*, *S. sterroclonium* and *S. tortuosum*. These plates, however, are thicker and larger than in *S. grayi*. They differ in height: those of the smaller ones are 0.017—0.022 mm in height, those of the larger ones 0.008—0.011 mm. In the latter case they also stand wider apart. These spicules strongly resemble the stem spicules of *Solenocaulon grayi*. The differences, especially in the thickness and height of the processes, are perhaps of minor importance. Like those of *S. grayi* they make a very spiny impression. They also strongly resemble the corresponding spicules of *S. sterroclonium*, but in this species the spicules are smaller.

The medulla is not invariable in thickness: along the edges of the "belts"

it is thicker—about 1.40 mm—than elsewhere, where it is only 0.35 mm thick. The medullary needles show nothing particular. They are up to 0.48 mm in length and 0.011 mm broad, and scarcely provided with tiny tubercles. However, there occur also peculiar types. These are shorter (0.20 mm) than most of the ordinary needles, rather equally thick, more rod-shaped and closely set with small tubercles or spines. Fusion of medullary spicules probably does not occur in the belts. An inner bark of particular spicules was not detectable.

On the boundary of cortex and medulla, boundary canals are found again. They are here and there visible on the outside already; they dimly appear through the thin cortical layer. But for the rest the boundary canals are so flat that they are difficult to find in free-hand sections. It strongly makes the impression that the canals were coalesced into a boundary space! Consequently the cortex is easily removed from the medulla. Columellae are distinctly visible. In this boundary space there are many zooxanthellae. In the medulla no solenia occur.

The twigs have different forms in transverse sections. Some are wide and flat, others are almost round, and only flattened on the medullary side. The spicules of the cortex form one stratum and are similar to those of the stem. Besides the ordinary free medullary needles, numerous fused needles occur. The fusion may go so far as to form a solid, hard aggregate much resembling that of *Solenocaulon jedanense* (fig. 28). The aggregate lies in the flat twigs as a thin plate, all over the width of the twig; in the rounder twigs it lies in the centre. Only the undermost medullary layer always consists of free spicules.

I could not discover horny substance in the medulla of the stem. But that does not mean that it is also lacking in the medulla of the stalk!

The anthosteles are very thin-walled and contain large spindles, lying side by side in one stratum only (difference from *S. jedanense* and *S. grayi*!). At the base the spicules are still small (0.16 mm), but for the rest they are all 0.40—0.56 mm in length and 0.028—0.043 mm broad. All of them lie about parallel to the longitudinal axis of the anthostele and are covered with blunt thorns (0.008—0.014 mm in height).

The spicules of the anthocodiae show nothing particular. The crown and points are formed by mostly curved spindles, 0.24—0.40 mm in length, covered with very low processes. The Y-shaped spicules of the tentacles strongly vary in shape and are mostly 0.19—0.24 mm in length.

2. *Solenocaulon sterroclonium.*

I had at my disposal the excellent material of this species collected by

the "Siboga"-Expedition. I specially examined the specimen from Station 154 (see Nutting, 1911, p. 5 and Stiasny, 1937, p. 52): I cannot possibly add a detailed description of this species to the previous ones. But I want to draw the attention to some facts we must know, when discussing the genus *Solenocaulon* in the next chapter.

First of all the spicules. In the surface layer of the basal portion of the stalk I noticed again globular but mainly oval bodies, which often had an irregular shape. Most of them are 0.13—0.24 mm in length; a few large globes have a diameter of 0.29 mm. Spindles or thick rods occur in the more subjacent cortical layers, 0.16—0.24 mm in length, up to 0.32 mm and 0.08—0.11 mm broad, warts included. In an apical direction the globular and oval bodies become smaller (0.065—0.150 mm), whereas the more subjacent spindles become larger (0.19—0.32 mm in length, up to 0.42 mm).

The medullary spicules of the stalk are needle-shaped, up to 0.5 mm in length and 0.020—0.026 mm in breadth, without processes. Among these needles many short rods are met with, 0.15—0.25 mm in length, and rather closely covered with high warts; the breadth of the rods measures about 0.032 mm, without warts, and 0.070 mm, warts included.

In the stem there is a difference again between the spicules on the back and on the lateral sides. On the back the spicules form several strata in the cortex, which is here of the same pale-red colour as the cortex of the stalk. In the surface layer exclusively small ovals occur, 0.05—0.08 mm in length and 0.03 mm broad, without processes; 0.050—0.056 mm broad, processes included. The processes are spine-shaped, split in two at the top, so as to resemble transversely placed plates. In the more subjacent cortical layer the spicules again are spindle-shaped, 0.16—0.32 mm in length, up to 0.45 mm.

On the front and lateral sides of the stem the cortex is almost white. The spicules lie scattered in one stratum again. The small spicules, however, are rod-shaped now ("Gürtelstabe"); they are of about the same length (0.05—0.10 mm) as the oval bodies on the back, but they are about half as thin, viz., 0.012—0.017 mm, without processes. The processes are alike in both. Further we find spindles in all sizes from 0.11 mm up to 0.45 mm—so no difference with the back—but most of them are 0.11—0.16 mm in length.

In the twigs we find rod-shaped cortical spicules as on the front side of the stem. The medullary spicules are fused, forming an aggregate: the thin twigs therefore are extending to the left and to the right as hard spines.

The anthosteles have thin walls, the spicules form one layer, as in *Solenocaulon ramosum*. At the base there are still small spindles, 0.08 mm in length, among which there are others, being already about 0.32 mm long. Towards the top of the verruca the spindles become very large and thick, 0.50—0.65 mm in length and 0.05—0.06 mm broad. They are rather closely set with low (0.005—0.008 mm) thorns, which are sometimes slightly split. They are arranged in a longitudinal direction again and form 8 groups, which rise above the edge of the verruca as sharp points. This seems to be a character of *Solenocaulon sterroclonium* (cf. Germanos, 1896, pl. IX fig. 2, zooid in left top corner).

In the anthocodiae we see that the crown and points consist of spindles, which are 0.30—0.55 mm in length, mostly 0.48 mm, and 0.028—0.048 mm broad. Furthermore there are the well-known Y-shaped spicules of the tentacles.

The horny substance is to be found in the medulla of the stalk; it forms only sheaths round the spicules.

The stalk of the specimen from Station 154 is 5—6 mm thick. In addition to the boundary canals, two medullary canals still occur in a cross-section. It is possible that more medullary canals occur in the thicker stalks. They are mentioned already by Germanos.

On closer investigation it appeared that textfig. P, u of Stiasny (1937) really represents a transverse section of the 5 mm thick stalk of the specimen from Station 154. But his textfig. P, t does not show a transverse section through a "Seitenästchen" (twig), but through the 3.5 mm thick stalk of the specimen of Station 279! And the textfig. P, s is meant to represent a transverse section through the basal, spatula-shaped portion of the stalk of the specimen from Station 279, about 7 times enlarged, but Stiasny did not draw a sufficient number of canals.

XI. SOME RESULTS CONCERNING THE GENUS SOLENOCAULON GRAY

Hickson (1903, p. 494) upholds the opinion that the presence of fused spicules in *Solenocaulon* has not been proved. It appears, however, that the fusion is a rather general phenomenon in this genus! We find the aggregate in *S. tubulosum* (Genth) (according to Genth, Janower, and Kükenthal), in *S. sterroclonium* (according to Germanos, Thomson & Simpson, Kükenthal and the present author), in *S. tortuosum* (according to Harrison; Thomson & Simpson, however, deny the presence of fusions), in *S. simplex* Brundin (according to Kükenthal), not, however, in *S. chi-*

nense Kükth. (according to Kükenthal). Finally, as appears from my investigation, fused spicules occur also in *S. grayi*, *S. jedanense* and *S. ramosum*.

The aggregate appears most clearly in the transitional portion between stalk and stem and further upwards on the back of the stem. In transverse sections the shape is always that of a sickle, which makes the hollow, tubular stem much stronger.

As regards the variability of the spicules I found that in *S. jedanense*, *S. grayi* and *S. sterroclonium* the exterior cortical spicules in the base of the stalk are much larger than those in the upper part of the stalk. These basal spicules are always more or less globular, oval or irregularly club-shaped. Therefore the spicules in the species mentioned always strongly resemble each other, although there are also differences. The warts in *S. grayi*, for instance, are much coarser than in *S. jedanense*, because of the numerous tubercles and spines, while the irregularly shaped globes and ovals of *S. sterroclonium* remain much smaller than those of the two other species.

On the other hand, the more subjacent cortical spicules do not show a tendency to become smaller in an apical direction. This holds good for *S. jedanense*, but in *S. grayi* the rods on an average are of equal length. In *S. sterroclonium* they even show an increase in length in an apical direction.

In the stem there is often a difference between the spicules on the back and those on the lateral and front sides. This difference is most considerable in *S. jedanense*, especially with regard to the large rod- and spindle-shaped spicules. In *S. grayi*, on the other hand, no difference of any importance is detectable. In *S. sterroclonium* the small spicules of the back are twice as thick as the equally long rods on the other sides of the stem; the larger spindles show no differences on the various sides of the stem. In *S. ramosum* there are very large spindles, up to 0.6 mm.

In the twigs of *S. jedanense* the ovals are somewhat larger again than in the stem, while the more subjacent spindles show no differences with those occurring on the lateral sides of the stem. In *S. grayi*, however, these more subjacent rods are twice as long as those in the stem. In *S. ramosum* and *S. sterroclonium* there is no important difference between the cortical spicules of the twigs and those of the stem.

So we come to the conclusion that there are all kinds of differences in the variability of the spicules. Apparently a hard and fast rule cannot be found, which is a reason to maintain the different species.

In the anthosteles of all the species examined we find the same phenomenon, viz., that the spicules rapidly increase in size from the base towards the top of the verruca. However, there are differences. In *S. jedanense* the wall of the anthostele is thick and consists of several strata of spicules; the exterior ones are small and oval, the interior ones large and spindle- to club-shaped. In *S. grayi* the anthostele also consists of several strata of spicules, at least at the base, but in the two other species the anthostele is thin and consists of one stratum. The spindles in the verrucae of *S. jedanense* differ distinctly from the similar spindles of the other species by their striking thickness: they are up to 0.11 mm in thickness, whereas in *S. sterroclonium* they are up to 0.06 mm and in the two other species up to 0.045 mm in thickness. As to the length there are no important differences between the spindles in the different species: they always reach a length of about 0.55 mm.

In *S. jedanense*, *S. grayi* and *S. ramosum* the edges of the verrucae are straight or slightly sinuous, but in *S. sterroclonium* the large spicules are united into eight groups, rising above the edge as long, sharp points.

In *S. jedanense* the spicules which form the crown and points are thicker (0.050—0.065 mm) than in the other species: in *S. sterroclonium* up to 0.048 mm, in *S. grayi* up to 0.035 mm. The length is approximately the same; in *S. ramosum* it is perhaps a little shorter.

There are no important differences between the needle-shaped medulla spicules in the species examined. In *S. jedanense* and *S. sterroclonium* there are besides these needles shorter and thicker rods, which remind one of cortical spicules. In *S. ramosum* there is moreover a particular type of spicules in the medulla: these are shorter than the others and closely covered with tubercles. But in *S. grayi* I have found only needles.

On the inside of the stem of *S. tortuosum* Harrison noticed spicules of a different type; she called this layer "inner bark". In *S. jedanense* and *S. grayi* I could observe such an inner bark consisting of medulla spicules of a different type: shorter and sometimes (in *S. grayi*) thicker. In *S. ramosum* an inner bark does not occur, so that its presence is not a general character of *Solenocaulon*.

Concerning the canal system there are also some differences to be mentioned. On comparing the figures 21 and 31 with each other, we see that in *S. grayi* between the boundary canals fewer anastomoses occur than in *S. jedanense*, where the partition-walls are perforated by numerous transversal openings. The coalescence of the canals increases in *S. ramosum*, forming a boundary space. Medullary canals occur in *S. grayi*, *S. jedanense* and *S. sterroclonium*.

In the stalk one of the canals is always larger than all the others. Kükenthal (1919, p. 64) observed that this canal always occurred on the front. I found that Kükenthal was right as regards the middle and the lower part of the stalk. In *S. grayi,* for instance, I observed that the large canal runs downwards in a slightly winding manner as a boundary canal along the front of the stalk, to end in numerous branches on the convex side of the spoon-shaped base. Upwards, however, the canal is strongly curved to the left, so that its position is almost on the back, but finally it passes into the stem on the left side of the groove (fig. 31). In the upper part of the stalk of *S. jedanense* and of *S. sterroclonium* the large canal does not lie on the front, but on the left side too. In the comparatively thin stalk of the specimen of *S. jedanense* from Station 274 the course of the large canal could be traced by a simple staining-experiment: haematoxylin was sucked through the stalk. The cortex remained colourless, and through the cortex the course of the large canal could be distinctly followed. I found that the canal runs from the left above along the front to the right below.

From what is said above, it appears, that the position of the canal on the front is hardly constant.

In the four species examined sheaths of homogeneous mesogloea are found, especially on the medullary side of the boundary canals. The thickness of these sheaths shows only small differences.

It has been stated that the horny substance occurs in *S. tortuosum* (Janower, 1904; Thomson & Simpson, 1909) and in *S. tubulosum* (Genth, 1867; Janower, 1904). I have been able to ascertain the presence of horny substance in *S. grayi,* in *S. jedanense* and in *S. sterroclonium*; in all cases it forms fine sheaths round the medulla spicules. In the stem of *S. ramosum* no horny substance was found; it is likely to occur in the stalk.

Finally I may draw attention to Chapter VIII, § 4; here I compared *S. jedanense* with *S. tortuosum.*

XII. DIODOGORGIA CERATOSA KÜKENTHAL

This coral was first examined by Kükenthal (1919). To his description of the spicules and of the interior structure something may be added here and there. His drawings of the spicules are excellent and render their characters very well. After Kükenthal, the coral is mentioned by Deichmann (1936) and by Stiasny (1937).

§ 1. The material.

I had at my disposal some fragments of the material examined by Stiasny and collected by J. Versluys at Tortugas (cf. Stiasny, 1937, p. 68). From a tip-fragment of about 5 mm in length I made a series of longitudinal microtome-sections; besides, transverse and longitudinal sections of a branch, some cm under the tip. Of other parts of the branch I made free-hand sections.

§ 2. Medulla and cortex.

Both Kükenthal and Stiasny distinguish two layers in the coenenchyma, a cortical and a medullary layer. Kükenthal does not state where the boundary between these two is. According to him the horny substance is found in the medulla only and his fig. 52 shows, that in this case the boundary coincides with the inner crown of longitudinal canals. Stiasny states this more plainly: the interior crown of longitudinal canals lies close round the medulla. I wholly share the opinion of Kükenthal and Stiasny. The longitudinal boundary canals of the interior circle form a rather distinct partition between medulla and cortex. The differences between medulla and cortex are now about similar to those in the other genera; they are as follows:

1. The zooids are embedded in the cortex, the coelenterons reach as far as the medulla.

2. In the middle of the cortex a crown of solenia occurs, in the medulla of the branches they are lacking (§ 3).

3. There is a distinct difference between cortical and medullary spicules, though there are also typical cortical spicules in the medulla.

4. Horny substance is only found in the medulla.

5. Only in the cortex cell-vessels are met with.

In his textfig. W, Stiasny represented the medulla too thin, for the thickness of the medulla is about two thirds of the diameter of the branch. The cortex has not the same thickness in all places and varies from about 0.3—0.6 mm. That is why the medulla is sometimes situated a little excentrically (cf. Kükenthal, 1919, fig. 52). But in other sections the cortex is round about of the same thickness and the medulla then has a concentrical position (fig. 39). In the top of a branch the medulla ends between the terminal zooids. Here also the medulla contains horny substance and therefore it is always recognizable as such in the sections.

§ 3. The coelenterons and the canal system; diagrams.

a. The coelenterons. The zooids of *Diodogorgia ceratosa* are equally distributed over the branches. But at the terminals the zooids are more closely packed, so that these tips of the branches are a little swollen and club-shaped. The terminal coelenterons are flattened against each other from the sides; consequently they have become long and narrow and

gradually become narrower towards the medulla (fig. 40, b), in contradistinction to the lateral zooids lower down, which partly surround the medulla with a broad base (fig. 39). Moreover, the terminal coelenterons continue for some distance in a basal direction, but they terminate blindly

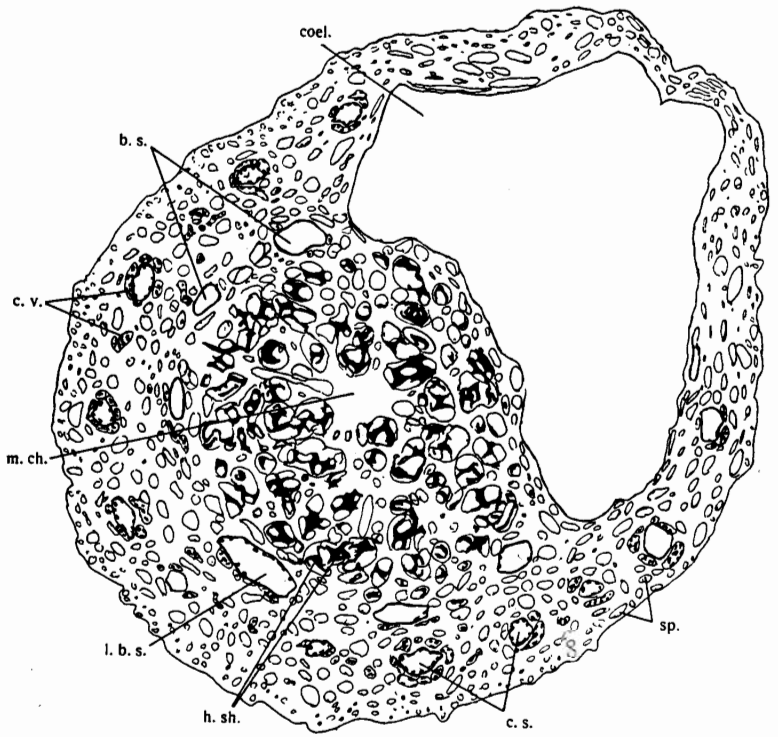

Fig. 39. *Diodogorgia ceratosa*. Transverse section through a branch. b. s., boundary solenia; c. s., cortical solenia; c. v., cell-vessels; coel., coelenteron; h. sh., horny sheaths; l. b. s., large boundary solenium; m. ch., medulla-chord; sp., cavities left by spicules. × 66.

and are more or less rounded. Some boundary canals pass into the coelenteron here. The walls between the terminal coelenterons are thin and do not contain solenia, but neighbouring coelenterons are connected directly by some openings in the walls. Where the walls become thicker, e.g., towards the periphery, there are solenia indeed, which are continuations of the cortical ones (see below).

Only the most terminal zooids show the shape described. Close under

the tip the mutual distance between the zooids is larger already, so that they do not flatten each other any longer. Moreover the zooids are placed rectangularly on the branches, and the coelenterons are no longer continued in a basal direction. In a transverse section of a lateral zooid its gastral cavity has a round or oval shape (fig. 41, k). The broad base tends to enclose the medulla to the right and the left.

The anthosteles have thick walls (continuations of the cortex) and are transformed into relatively high verrucae. The anthocodiae are wholly retracted into the anthosteles. The verrucae are smooth all-round, only round the aperture there are eight radial grooves.

The ventral aspect of most of the zooids is turned adaxially, in a few cases the ventral aspect is abaxial.

b. The canal system. Both Kükenthal and Stiasny noticed two crowns of longitudinal canals in the coenenchyma. Kükenthal (1919, p. 99) says that the outer crown is formed by narrow, the inner by wide tubes. According to Stiasny the opposite is true: there is an exterior circle of wide, round canals and an interior one of small, oval canals. Now it is possible that in the basal portions of the colony the outer canals are narrower than the inner ones, as drawn by Kükenthal (1919, fig. 51); I did not examine a stem. However, in the free-hand transverse sections of branches I saw that the outer canals are rounder and wider than the inner, which are flatter and more oval. So I can confirm Stiasny's statement. I suppose that Kükenthal's fig. 52 was made after a decalcified microtome-section, for in my own microtome-sections the canals of the outer crown are more shrunk than the inner canals, so that it cannot possibly be decided, which canals were widest before decalcification. Here the free-hand sections gave the answer. An argument can be no more derived from Kükenthal's fig. 52 than from my fig. 39.

The lumen of the canals (outer and inner crown) varies from about 0.05—0.15 mm in height, their breadth is about 0.07—0.20 mm. One of the canals of the inner crown is often much wider than all other canals, viz., 0.15 × 0.8 mm, so that it is visible to the naked eye (fig. 39, l. b. s.).

Now what about the course of the canals, their mutual connection and that with the coelenteric cavities? First the boundary canals. Kükenthal states that these are frequently connected with each other and that they pass into the base of the coelenteric cavities with wide openings. This statement corresponds with my observations, but instead of "frequently", I prefer the word "occasionally". For the boundary solenia proceed in a longitudinal direction, ramifying little or not at all, so that we can hardly

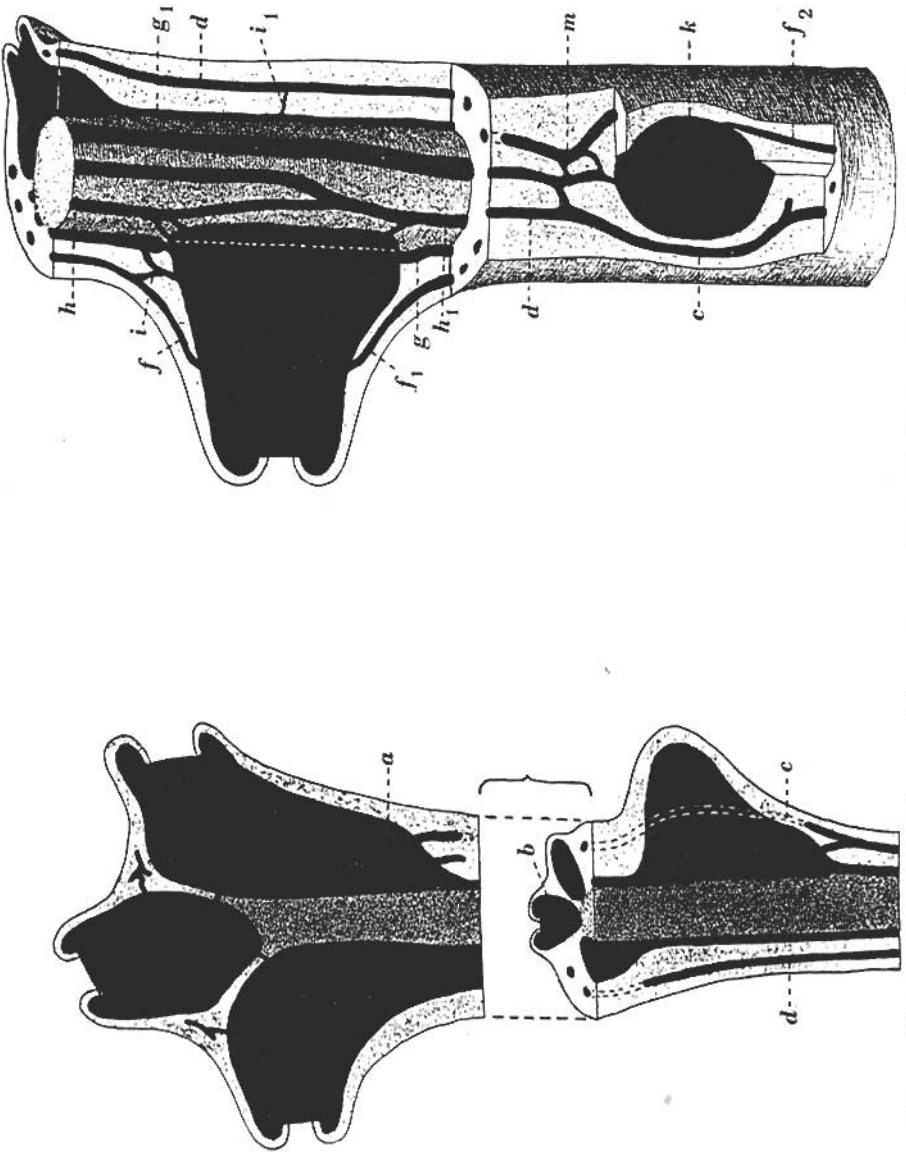

Fig. 40. *Diodogorgia ceratosa*. Diagram of the canal system in the tip of a branch. Explanation in the text. × 12.
Fig. 41. *Diodogorgia ceratosa*. Diagram of the canal system of a branch. Explanation in the text. × 12.

speak of a meshwork. In the vicinity of the coelenterons only they are more largely connected with each other.

According to their position with respect to a coelenteron we may distinguish two kinds of canals: median and lateral canals. The median boundary canals lie in or close to the median plane of a zooid and consequently they meet on their way from bottom to tip (or the reverse) the coelentic cavity. Such median canals pass into the cavity without ramification (fig. 41, g, g_1). The more lateral boundary canals just run along the coelenteron, but we observe that they send out side-branches to the cavity once or twice (fig. 41, h, h_1).

The canals of the outer crown, the cortical solenia, also for the greater part run in a longitudinal direction (d in fig. 40 and 41). Anastomoses are pretty much restricted to the environs of the zooids; here they form a feebly developed meshwork, especially on that side of the zooid, which is turned to the tip of the branch (fig. 41, m). The anthostele of a zooid is nothing but the continuation of the cortex and therefore it is no wonder that the cortical solenia are continued into the anthostele. Here, too, we must distinguish between lateral and median cortical solenia. The median solenia, above as well as below the zooid, pass into the anthostele, but then open into the coelenteric cavity about half-way the height of the anthostele (fig. 41, f, f_1, f_2). The lateral solenia in the anthostele have a slightly curved course, it is true, but afterwards they run past the coelenteron, without passing into it (c in fig. 40 and 41). However, they may be connected with the coelenteron by a few side-canals.

Between the boundary and the cortical solenia there occur very narrow anastomoses (fig. 41, i, i_1), but these are relatively rare.

Finally, regarding the canal system as a whole, we see that the boundary canals and the cortical canals run in a longitudinal direction and each of them only form an imperfectly developed meshwork. There is little mutual connection between both systems. The coelenteric cavities are on all sides connected with both systems. The canals cannot be considered in any way as parts of coelenteric cavities; all of them are solenia.

A short explanation of the diagrams (fig. 40 and 41) may follow. In both figures the medulla is darkly dotted. The medulla-chord has not been drawn. Fig. 40 represents a longitudinal section of the tip of a branch. In order to show the narrow shape of the terminal coelenterons, the fragment was also tranversely sectioned; so both fragments belong together. The left and the right terminal coelenterons (a) downwards pass into boundary canals. The lateral gastral cavity on the right is cut off rather

superficially; the cortical solenium c runs past the cavity, but gives off a side-canal to the cavity; d, too, is a cortical solenium.

In the upper part of fig. 41 only the front-half of the cortex has been removed, so that the course of the boundary canals becomes visible. In the lower part only a thin layer of the cortex round a zooid (k) has been cut away. The cortical solenia with their anastomoses now are visible. In the right-hand bottom corner, the cortex was cut away less deeply to show the opening of a median cortical solenium into the coelenteric cavity; this is still better visible in the left zooid (f and f_1).

§ 4. The mesogloea.

Kükenthal mentions only the abundant occurrence of cell-strings in the tips of branches of *Diodogorgia ceratosa*. A closer investigation reveals the following:

In the mesogloea many cell-vessels occur, but solely in the cortex. In a transverse section of a branch I observed that the cortical solenia are surrounded by a crown of these vessels. This is a very striking feature. The cell-vessels lie close beside the solenium and are only separated from it by a thin membrane. I nowhere observed a connection between the lumina of the vessels and the solenium. In a longitudinal section I found that the vessels run more or less parallel to the solenium. Round the boundary canals only a few vessels are met with, especially on the cortical side of the canals; so a crown of vessels is lacking. And this is a remarkable and conspicuous difference between the solenia of both crowns. In § 3 I mentioned the little canals connecting the cortical and the boundary solenia. These little canals are also surrounded by cell-vessels. Moreover, here and there in the cortex cell-vessels occur, which do not surround the solenia.

In the medulla cell-vessels are lacking. In the centre I noticed a medulla-chord, consisting of homogeneous mesogloea, without spicules. Only a few spicules penetrate from the surrounding medulla into the medulla-chord. And these spicules have no horny sheaths, at least as far as those which penetrate the medulla-chord are concerned. In this chord isolated cells and little groups of cells are met with, but cell-strings and cell-vessels are lacking. In fig. 39 the medulla-chord is distinctly visible. It is not sharply bounded and irregular in shape, the mesogloea being continuous with that of the rest of the medulla.

§ 5. The spicules.

In § 2 I mentioned the striking difference between the spicules of the cortex and the medulla, facilitating the indication of the boundary between

the layers. On the cortical side of the boundary canals the spicules drawn in Kükenthal's fig. 48 are met with, which are closely set with warts; the shape is oval-oblong, the colour wine-red. On the medullary side we find the types of Kükenthal's fig. 49; they are more rod-shaped and the colour is pink to colourless; the warts are much more distant and often provided with long stalks. Here and there, however, typical cortical spicules with their characteristic shape and colour may be seen in the medulla. These spicules do not form a medulla-chord, sensu Kinoshita and Kükenthal, because they occur everywhere in the medulla and are not restricted to a central chord.

Branchlets of *Diodogorgia ceratosa* can be easily cut in a longitudinal direction with a razor, because almost all the spicules lie in the same direction. In making transverse sections especially the cortex is apt to crumble off.

Kükenthal gave excellent drawings of the spicules; his correct description needs only a little completion. Firstly, in the outer cortical layer among the small oval spicules of Kükenthal's fig. 47 there are numerous smaller spicules, in shape like those of his fig. 46: they have 3—5 rays, at the extremities of which there are large warts; the length is 0.05—0.065 mm only. Farther inside the cortex the spicules gradually increase in size, up to averagely 0.32 mm, the maximal length being 0.37 mm. The colour of all the cortical spicules is wine-red; occasionally there are parts of the cortex with yellow spicules.

The verrucae show exactly the same spiculation as the cortex. Kükenthal (1919, p. 98) says, that yellow spicules occur in the "Polypenkelche" (verrucae), spicules of the same small shape as those occurring in the anthocodiae, but also larger ones, up to 0.09 mm. Furthermore, there are, according to Kükenthal, here and there still red spicules in the verrucae. So the verrucae were yellow in the specimen, examined by Kükenthal; consequently Kükenthal mentions as a character of the genus *Diodogorgia*: "Farbe... der Kelche gelb".

In the material examined by Stiasny and myself, the conical verrucae are of exactly the same red colour as the cortex of the branches and they also contain exactly the same red spicules as the cortex; only the extreme tops of the verrucae, close round the aperture, are yellow in colour on account of the yellow spicules, present there. So there is a difference between the specimen described by Kükenthal and the material that Stiasny and myself had at our disposal. Now, the conclusion drawn by Stiasny is wrong; he writes (1937, p. 68): "Die Kelchspicula scheinen gelb zu sein, trotz der roten Farbe des Calyces". No, the spicules in our specimen are red, except the most distal ones. In my opinion, this

difference is of no systematic value. Kükenthal does not indicate where the yellow colour of the anthosteles changes into the red colour of the cortex: in my specimen at the tips of the verrucae. In all other respects the conformity with Kükenthal's description is so great that in my opinion a specific separation is not justified.

The medullary spicules are up to 0.48 mm in length; they strongly vary in breadth (0.025—0.070 mm).

§ 6. The horny substance.

There is not much to be said about the horny substance. In *Diodogorgia ceratosa* too, it exclusively occurs in the medulla, viz., as sheaths round the spicules. Already immediately on the medullary side of the boundary canals the spicules show such horny sheaths, which are still thin there. Farther inside, the sheaths become thicker, so much so, that the closely packed spicules are united by it. In the medulla-chord the horny substance is lacking again (fig. 39).

XIII. ICILIGORGIA ORIENTALIS RIDLEY

There is rather an extensive literature on this coral. After Ridley (1884) it was more or less fully described by Studer (1887), Wright & Studer (1889), Nutting (1911), Broch (1916), Kükenthal (1908, 1916b, 1919), Thomson & Dean (1931), Dean (1932), Macfadyan (1936), Stiasny (1937) and Hickson (1938).

§ 1. The material.

I have examined the material of the "Siboga" Expedition, Station 315. It consists of a thick branch (diameter 6.6 × 3.4 mm) with several side-branches and many top-pieces. Moreover, a main stem from Station 273 was thoroughly examined.

The last-mentioned stem first deserves a closer examination (fig. 42). It is 80 mm in height and divides at the top into two thick branches. In the middle of the stem there is an oval opening of 4 × 11 mm. Like all the branches the stem, too, is flattened; breadth and thickness vary. At the height of the oval opening mentioned above, the stem measures 23 mm in breadth. The thickness below the opening amounts to 8 mm and above it to 6 mm. The sides are devoid of zooids, but along the rounded edges they do occur. The oval opening divides the stem into two portions. The lower part, about 35 mm in length, downwards passes into a more or less cone-shaped, hollow foot, whereas in the centre of this piece there is a

channel, which upwards ends in the oval opening and basalwards widens into the hollow foot. The channel (3.5 mm in diameter) was entirely filled with grey detritus, containing, besides all sorts of slimy particles, different species of globigerinae, fragments of radiolarians and many smooth siliceous needles of sponges. In the upper part of the channel a small mussel was found. The wall of the channel is brown, but a distinct horny basal membrane is not distinguishable. Numerous sponge spicules penetrate either wholly or partly through this brown layer into the medulla of the coral.

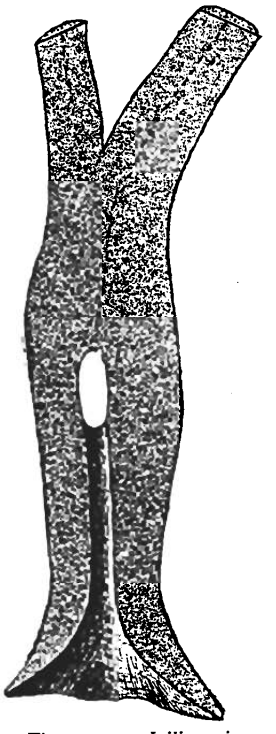

Fig. 42. *Iciligorgia orientalis.* Longitudinal section through a stem. Dotted line, medulla-chord. Natural size.

Probably the colony has developed on a siliceous sponge with tube-shaped elevations. I could see this much more distinctly in another specimen of *Iciligorgia orientalis*, also from Station 273: on the inside of a likewise hollow stem there was still a completely undamaged sponge-layer. Here, too, numerous siliceous needles had penetrated into the medulla of the coral, so that siliceous needles of the sponge were lying among the calcareous spicules.

Other investigators (Broch, Dean, Hickson) also noticed a central channel in the lowest part of the stem. Macfadyan (1936, p. 68) states: "the base (of the lower portion of a colony) has grown over a hollow tube (probably of some worm?)". Hickson (1938, p. 591) mentions a similar fact.

In the stem represented in fig. 42 the portion above the oval opening is massive and contains, like the branches, in the centre a medulla-chord (§ 5). This chord begins just at the top side of the oval opening, therefore diametrically opposite the extremity of the central channel in the lowest portion of the stem.

§ 2. Medulla and cortex.

These two layers were distinguished already by Ridley (1884, p. 351). He wrote about a "central spicular axis", separated from the cortical layer "by a single annular series of four to six circular or oval longitudinal canals..." Later on, investigators as, e.g., Wright & Studer, Nutting,

Broch and Hickson distinguished also two layers in the coenenchyma, viz., a well-bounded "axis" (medulla), separated from the outer layer ("coenenchym" or cortex) by a crown of longitudinal canals. I wholly concur in this opinion.

The following differences between medulla and cortex may be mentioned:

1. The coelenteric cavities are embedded in the cortex.

2. Besides those, which occur in the medulla as well as in the cortex, characteristic spicules also occur in each layer (cf. § 6).

3. Horny substance only exists in the medulla (§ 7).

4. There is a difference between the mesogloeal cell-vessels of the medulla and those of the cortex (§ 5).

On the boundary of the two layers there lies a crown of canals (mentioned already by Ridley), i.e., the boundary-canals. In the terminals of the branches the medulla ends close below the ectoderm; so the cortical layer is very thin here and separated from the medulla by a net of narrow solenia (fig. 43). For the rest the cortex of the stem and that of the branches is much the same in thickness, viz., 0.25—0.50 mm, in the stem up to 0.70 mm. Consequently only the medulla increases basalwards in thickness.

Hickson (1938, p. 592) says that the cortex of most of the branches is about 0.25 mm in thickness and that the greatest diameter of the axis is 1.2—1.25 mm. And he draws the conclusion that Kükenthal is not right in mentioning a thin cortex as a character of *"Machaerigorgia" orientalis*. I want to make the remark that in the stem and the thick branches the proportions are such that with Kükenthal we may speak of a thin cortex.

The cortex passes into the anthosteles. Between the zooids the cortex has thickened so much, that isolated anthosteles are no longer distinguishable. But this will be further discussed in the next §.

§ 3. The zooids.

It is well-known that the zooids of *Iciligorgia orientalis* may occur isolated, especially on the thick stems and branches. In this case they have the appearance of low hillocks. Mostly, however, they are arranged in series. In the thinner branches two or three of these series are found longitudinally. If there are two series, the branches are flattened, showing an oval shape on a transverse section, while the zooids are arranged along the straight thin edges or borders, formed by coalescence of the verrucae of one series. Outwardly nothing is visible of the zooids themselves; only the remarkable groove resulting from the fusion of the "slit-like apertures" of the verrucae points to the presence of zooids. It is, however, somewhat exaggerated to speak of "knife-like edges" as, e.g., Ridley, Kükenthal and Stiasny do; "sharp edges" is more than sufficient. Thick stems and branches have quite rounded borders, the nearer to the tip the flatter the twigs and the sharper the edges. If the zooids are arranged in three or four rows on the branchlets, the latter of course assume a rounder form.

The basal portion of the stem is devoid of zooids. Higher up, we find the zooids not only in the borders, but also on the two flat sides of the thick branches, isolated or in rows, the latter running mostly longitudinally, but sometimes, mainly in ramifications, across the branch.

A flattened front and a convex back, as Kükenthal observed in *Iciligorgia ballini* Kükth., do not exist in *I. orientalis*; the zooids occur here on both sides.

In a transverse section the coelenteric cavities appear to be more or less triangular. The base is broad and lies against the medulla (textfig. H, p and q, of Stiasny (1937) therefore is somewhat misleading). Towards the oral aperture the cavity becomes narrower. The walls between the coelenterons may be very thin, in the tips of the branches they are thicker (cf. § 4 and the diagrams). The zooids stand perpendicularly on the branches. Only a very few terminal coelenterons run a little obliquely downwards (fig. 43).

All the zooids had retracted anthocodiae, except one. Although this fact is not important in itself, it gave the opportunity to get a better insight into the course of mesenteries, etc. The eight mesenteries run on to nearly the bottom of the body cavity. It appears further that all the zooids are orientated in the same way to each other and to the longitudinal axis of the branch. The median plane of the zooid always coincides with the longitudinal direction of the groove, which connects them on the outside. And now we see that the dorsal aspect is turned downward, i.e., abaxial.

The chambers formed by the mesenteries are not equally broad: the dorsal and the ventral ones are the smallest, the dorso- and ventro-lateral ones are about as broad again, the lateral ones are still broader. The muscle-banners are very much like those of *Semperina brunnea*, as drawn by Kükenthal (1919, fig. 308). In the mesenteries the genital organs originate, male in the specimen examined by me. The sperm-sacs are irregularly shaped, with more or less flattened sides. They are fairly large (up to 0.45 mm) and when the zooid has a retracted anthocodia they entirely fill the remaining space of the coelenteric cavity. Then they fit like bricks and consequently flatten each other. When the zooid has expanded, the gonads are lying more scattered, but the flattened sides remain in the preserved material. A few times I found spermaria provided with stalks.

§ 4. The canal system.

Concerning the endodermal canal system we have to distinguish between the boundary canals, the cortical canals and the medullary canals.

a. The boundary canals. As already has been said in § 3, the coelenteric cavities reach as far as the medulla. The boundary solenia are lacking between the bottom of the coelenteron and the medullary layer. But for the rest they occur everywhere in the wide spaces between the longitudinal series of zooids and also between the zooids of the same series, connecting the coelenterons with each other. The boundary canals may be divided into two types, wide and narrow. Although it is sometimes difficult to decide whether a canal belongs to the wide or to the narrow type, as a rule both types are very well distinguishable. In transverse sections the wide ones are mostly oval, sometimes round on the medullary side and flattened on the cortical side. In the stem the height of the canals amounts to 0.2—0.3 mm and the width to 0.3—0.4 mm. The oval narrow canals are mostly 0.08—0.15 mm in height and 0.16—0.30 mm in width. In the branches both types of canals become narrower, but they are always distinguishable as wide and narrow canals.

In the stem and the branches the wide canals are still regularly distributed round the medulla, but in the thin branches the wide canals are always found on either side of a series of zooids (see diagram, fig. 44).

b. Cortical solenia. Observing the thin cortex, we see in the middle of this layer a second system of endodermal canals. They are rounder and also somewhat narrower (viz., 0.04—0.05 mm) than the above-named narrow boundary canals. This system of cortical solenia forms a close and irregular meshwork, running rather parallel to the ectoderm (fig. 44 a). Inwardly this meshwork is connected with the boundary canals by numerous anastomoses. Outwardly, too, a great number of small canals arise from the meshwork. These canals have the same lumen as those of the meshwork and run, and this is very remarkable, in a radial direction to the periphery of the cortex, where they terminate blindly. Sometimes they are slightly bent here, or forked for a little distance, sometimes the end is somewhat broadened. But in any case they end blindly, closely under the ectoderm (fig. 43 on the right). This peculiar phenomenon (which as far as I know, does not occur in other Anthothelidae) accounts for the fact that in a series of microtome sections, tangentially through the cortex, we find numerous round endodermal canals between the spicules. A slightly more inward section distinctly shows the above-mentioned tangential meshwork of cortical solenia.

In the walls between the zooids we also find numerous solenia, now connecting the coelenteric cavities with each other directly. Some of them form connective canals at the base of the coelenterons, which lie closely round the medulla; they may be regarded as short boundary canals. There are further solenia at any height in the partition-walls. Sometimes they run parallel to the wall of the coelenteron. Close under the ectoderm a network is formed, identical with that of the cortical solenia described above.

In the endoderm of the boundary canals a few zooxanthellae occur; these are more numerous in the cortical solenia; in the above-mentioned radial blindly ending solenia, they are so numerous that the canals fairly often are quite filled with them.

c. The medullary canals. These occur only in the stem and in the very thick branches. In a branch of 6.6 × 3.4 mm they occurred no more, but in one of 10 × 6.6 mm they were to be found. They always occur in the peripheral portion of the medulla and sometimes form a crown inside the boundary canals. They are rather round with a diameter of about 0.3 mm. Generally they run fairly straight through the medulla in a longitudinal direction, do not ramify much and are seldom connected with each other by transverse canals (fig. 45). The system of these canals hardly can be regarded as a network. As they are found close to the boundary canals, they may be connected with them by anastomoses and they may also pass into the boundary canals.

Opinions differ strongly concerning the presence or absence of medullary canals in *Iciligorgia orientalis*. Ridley (1884) did not find them ("central axis imperforate"), nor did Wright & Studer (1889). Nutting (1911) records them for the first time in the "Siboga"-material. Broch (1916) has found them too (secondary canals). Thomson & Dean (1931) investigated "a very fine "Challenger"-specimen of *Iciligorgia orientalis* Ridley, in which no medullary canals even in a stem with diameters of 1.2 cm by 8 mm" occurred. But Dean (1932) again has found "two or three very small canals in the medulla of the main stem". Stiasny (1937), like Nutting and the present author, examined the "Siboga"-material. Stiasny noticed medullary canals and represented them in his textfig. H, o. But Hickson (1938) again denies the presence of medullary canals.

These divergent results in my opinion are caused by the great variability in the number of medullary canals. In the stem represented in fig. 42, I found the following numbers of canals at different levels: 1 to 2 cm below the oval opening (i.e., in the medulla round the channel) 12 or 13 canals; in the portions left and right of the oval opening 1 and 10

respectively; a few mm above the opening 19; 1 cm below the bifurcation 3: in the left side-branch at the base 0, at the top 0; in the right side-branch (being a little thicker) at the base 0, but at the top 4. This right side-branch at the bottom was 15 mm in breadth and 6.5 mm in thickness and had, notwithstanding this fair thickness, no medullary canals there. But 3 cm higher there were 4 of them again! So it follows that only in the stem and in the thickest branches the medulla-canals may be found. And moreover, that transverse sections have to be made at different heights in order to be certain about the occurrence of medullary canals.

It seems questionable whether the different investigators really investigated a stem. Are they quite certain to have examined a stem and not only a thick branch? Did a basal extension occur or a central channel, and was the medulla round the cavity still sufficient in thickness?

Nutting, Stiasny and myself have studied several genuine stems in the "Siboga"-material. Further it is almost certain that Broch and Dean also examined a true stem, for both authors mention round channels. Broch's opinion is that these are the result of the activity of a parasitic organism, whereas Dean does not give her opinion about their origin, but confines herself (1932, p. 8) to a short description of "a large central canal closely packed with a mass of agglutinated debris, sand grains etc.", a description that agrees very well with the central channel I have found. Dean (l.c.) noticed "two or three very small canals... in the medulla of the main stem". In the stem examined by me in different levels the number is strongly varying, but generally we may say: the more basal, the larger the number of canals. It is remarkable that Dean did not find medullary canals "at the base of the two main branches, where one has a maximum diameter of 12 mm", for I came to the same result.

Hickson (1938, p. 591) had specimens in which the base of attachment was lacking. He then describes a stem, a remarkable one "as it is a hollow tube 8 mm in diameter folded round the fibrous tube of some Polychaete worm". This stem is very similar to a small stem in the "Siboga"-material. It was 5 mm in diameter, and had formed itself round the tubular branch of a siliceous sponge. This branch was 3 mm in diameter, so that the coenenchyma of the coral was only about 1 mm in thickness. I did not find medullary canals in this coenenchyma; in my opinion it is too thin for it. So we can understand that Hickson did not find medullary canals either! One must needs have very thick stems, with a well-developed medulla-layer, to find medullary canals.

Finally one more remark: when looking for medullary canals, one should be careful not to mistake the often numerous mesogloeal chords for canals; these chords will be discussed in § 5.

The diagrams.

Fig. 43 represents a longitudinal section through the tip of a twig. In the lower part of the medulla (darkly dotted) the lightly dotted medulla-chord is visible. The coelenteric cavities are embedded in the cortex. The two topmost were drawn after a median section, the others were drawn after a section more or less beside the median plane. On the right-hand side the canal system of the cortex has been reconstructed to an idealized section. Besides the boundary canals we see here the cortical solenia, connecting the coelenterons with each other, and more outwardly the narrower cortical solenia with the radial blind canals running to the surface. On the left side we see a longitudinal section through the cortex as it occurs in reality, but a little simplified and diagrammatized.

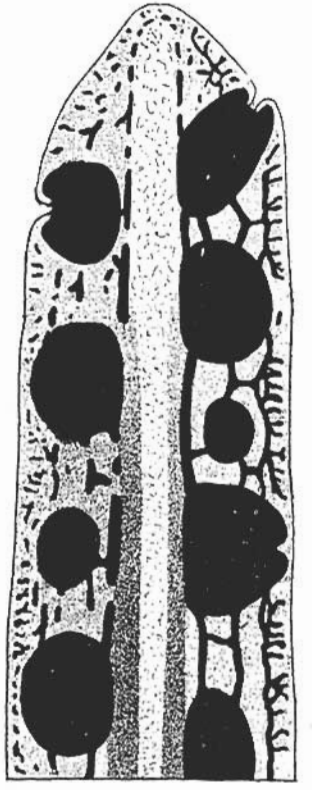

Fig. 43. *Iciligorgia orientalis*. Diagram of the canal system in the tip of a branchlet. × 20.

Fig. 44 a shows the reconstruction of a thicker part of a branch at a greater distance from the top. Some parts have been removed from the branch. In the lowermost part the surface layer of the cortex has been cut away. In this tangential section the radial cortical solenia are visible in transverse section as small round dots. Somewhat higher another layer of the cortex was removed, with the result that the meshwork of cortical solenia, running more or less parallel to the surface, becomes visible. Further upward follows a larger portion of the branch, in which the cortex was removed as far as the medulla. The latter is encircled by the boundary canals, running parallel to each other and being connected by numerous transverse canals. Wide and narrow canals occur here. In the upper part, moreover, a sector of the medulla was cut away and now in the centre we see the medulla-chord.

The cortex on the right-hand side has been sectioned in a longitudinal

direction along the median plane of the zooids (the lowest zooid but one just beside the median plane). In the right-hand top corner a zooid with expanded anthocodia. On the left side the peripheral parts of the coelenteric cavities are just visible. On both sides idealized sections of the cortical solenia.

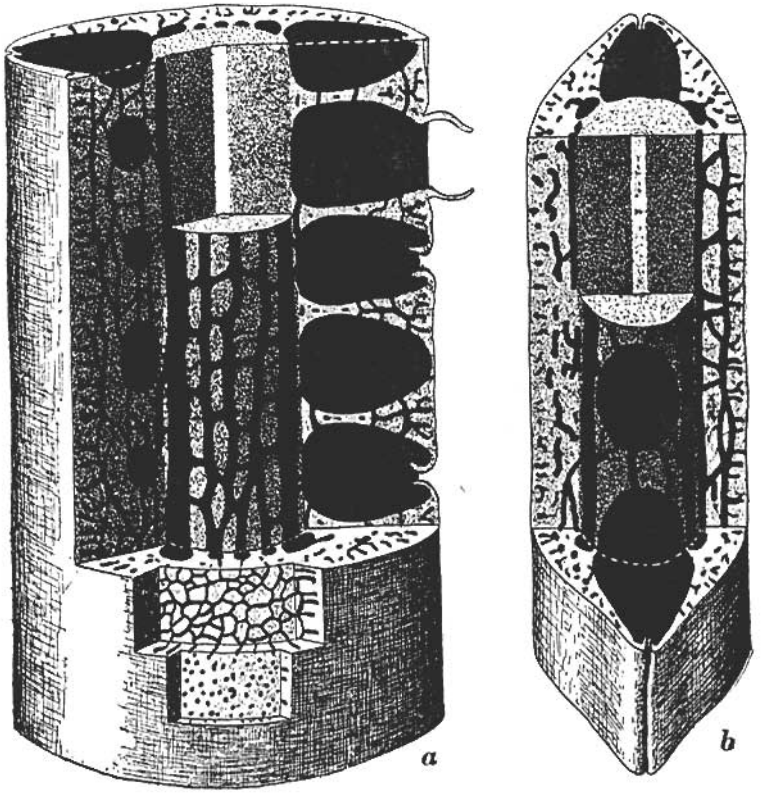

Fig. 44. *Iciligorgia orientalis*. Diagrams of the canal system of a branch. × 20.

In fig. 44b the flattened branch of fig. 44a has been represented again, but now turned 90°, so that the zooids now are situated along the front and the back. On the upper surface we see a transverse section through a coelenteron; furthermore cortical solenia and round the dotted medulla the boundary canals (the same on the upper side of fig. 44a). The upper portion of the branch has been sectioned longitudinally through the centre of the medulla. Here the medulla-chord (light) is again distinguishable

from the outer layer of the medulla (dark). In the thin cortex at the left and the right there are of course no coelenteric cavities, but cortical solenia do occur there. On the left side a longitudinal section more or less true to nature has been drawn, on the right side a reconstruction, an "idealized" section. In the next part of the branch only the cortex has

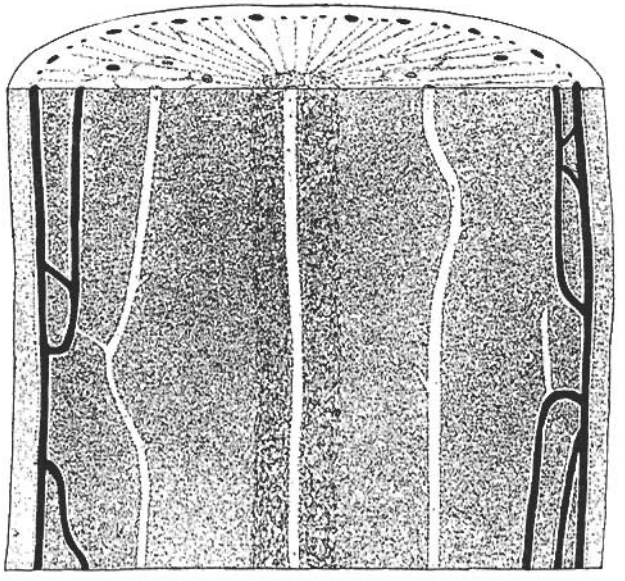

Fig. 45. *Iciligorgia orientalis*. Diagram of the canal system of a stem. × 5.

been removed. The broad bases of two coelenterons have been drawn and moreover some boundary canals.

Fig. 45 represents part of a stem also flattened and sectioned longitudinally along the long axis of the ellipse. In the centre the medulla-chord (white), surrounded by the tube-like zone of the short, thick medullary spicules of fig. 48 e and f (vide § 6) . In the medulla on both sides of the medulla-chord one mesogloeal chord (§ 5, c) has been drawn on either side, which, like the medulla-chord, has been left white. Here and there they have blindly terminating ramifications. On the left we see how such a mesogloeal chord is connected with the mesogloeal sheath of a medullary canal. On the right another short blindly ending mesogloeal chord, likewise merging into the sheath of a medullary canal. Some more medullary canals have been drawn, as well as the way in which they may anastomose with the boundary

canals. The latter are those lying as far to the right and to the left as possible. As appears from the upper surface they form a circle round the medulla. In the cortex outside of this circle all solenia, coelenterons, etc., have been left out. The sheaths surrounding each medullary and boundary canal, have been drawn in the longitudinal section only, not on the upper surface. Two more medullary canals and three more mesogloeal chords are represented in the upper surface. Furthermore we see there round the medulla-chord the above-mentioned tube-like zone of short, thick spicules and radiating from it the plates, containing the same spicules. In the spaces between these plates the rod-shaped spicules occur and at the same time also the boundary canals and contingently present medullary canals and mesogloeal chords.

§ 5. The mesogloea.

Broch (1916, p. 21) says that none of the investigators before him has found cell-strings in the mesogloea of *Iciligorgia orientalis*. And Broch himself could not examine the mesogloea, because he had only a dried specimen of this species at his disposal. On account of the fact that nobody mentioned the cell-strings Broch classifies this coral in his subfamily Spongioderminae.

After Broch the mesogloea of cortex and medulla has not been investigated by anyone either. I found, however, that there is still much to be told about the mesogloea. A detailed description may follow here.

a. The medulla-chord. In microtome as well as in free-hand sections we see in the centre of the medulla [1]) a chord of homogeneous mesogloea, in which there occur relatively few spicules of a special type (fig. 49), with little horny substance. In the transverse sections made with a razor this chord is transparent and consequently easily recognizable.

Besides the spicules mentioned above the mesogloeal cell-strings and cell-vessels are striking peculiarities in the chord. They show a distinct tendency to run in a longitudinal direction, and are connected with each other by transverse or oblique cell-strings or -vessels and so they form a long-stretched meshwork. The vessels are small (0.02, rarely 0.03 mm) and filled with mesogloeal cells.

The medulla-chord is of about the same width in the stem and in the branches, viz., 0.25—0.40 mm. In the thinner tips of the branches the diameter is about 0.13 mm only. The chord could be distinguished to

1) If the basal part of the stem has developed round a sponge or some other organism (tubular worm), the central part of the medulla is lacking and so is of course the medulla-chord.

within two mm from the end of the branches. It appears that the medulla-chord of a side-branch basally not always ends in the same manner. In § 1 I mentioned a large branch (6.6 × 3.4 mm) with several side-branches. In longitudinal microtome sections, made of a part of this branch, the relation between the medulla-chord of the main branch and that of the side-branches could be traced (fig. 46). It appeared that the medulla-chord of the main branch had forked once. One chord then ran straight on through the main branch, the other bent sidewards into one of the side-branches. The medulla-chord of the other branch, however, ended basally with a broad, flattened base, at some distance of the chord of the main branch; so there was no connection whatever between these two medulla-chords. Kinoshita (1913) observed a similar condition in *Paragorgia*; but in this coral both medulla-chords are separated from each other by a cortical layer and this is not the case in *Iciligorgia orientalis*. Chester (1913, p. 743) observed the same in *Pseudoplexaura crassa* W. & St. He stated "a break between the marrow of the branch and that of the stem".

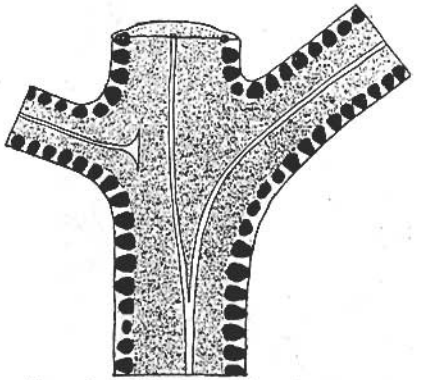

Fig. 46. *Iciligorgia orientalis*. Longitudinal section through a branch with two side-branches. In the centre of the medulla (dotted) the medulla-chord (white). Along the margins the zooids (black). × 3.

Probably Thomson & Dean also saw the medulla-chord described above. For they write (1931, p. 190): "The centre of the stem, both at the base and towards the tips, shows a differentiation which looks as if it were due to a relative preponderance of organic matter". And on p. 191: "There is an ill-defined organic differentiation, but there is no central canal in the middle of the medullary portion". Stiasny also (1937, p. 28 and 123) affirms this observation. And probably Hickson, too, referred to the medulla-chord, when he wrote (1938, p. 593): "At the base of some of the large branches there is a central canal, which is not lined by endoderm, has an irregular ragged wall, and has all the appearance of being due to contraction". Why contraction?

b. The mesogloeal sheaths round the medullary canals and boundary

canals. All these canals are surrounded by a layer of homogeneous organic matter, in which spicules and horny substance are lacking. Only in the zones or sheaths round the boundary canals there are a few small spicules (fig. 48 a). The thickness of this zone varies strongly, viz., from about 0.015 mm to 0.080 mm. Once I observed a sheath which was almost as wide as the canal contained in it, but then there were vacuoles in the sheath. Round the sheaths there is first a meshwork of cell-strings, then the spicules follow.

In the sheaths as well as in the mesogloea of the rest of the medulla the well-known connective tissue-like threads occur.

c. Mesogloeal chords without canals. When we make a transverse section through a stem or a thick branch, we see in the medulla not only the medulla-chord already described and the medullary canals, but there are also many round, light spots in the section, which at first might be easily mistaken for medullary canals with the inherent sheaths of homogeneous matter. But with a low power already we see that no canals occur in it. So these light spots consist only of homogeneous mesogloea; they are the transverse sections of chords running in a capricious way in a longitudinal direction (fig. 45). Their diameter is usually like those of the medullary canals, viz., 0.25—0.35 mm. They may be distinguished from the medulla-chord by the lack of the characteristic spicules. It is true that numerous spicules from the surrounding medulla sometimes penetrate inside, but they are ordinary rod-shaped medulla spicules of type fig. 48 b and c, which are almost smooth. So we must discern between mesogloeal chords and the single medulla-chord in the centre.

In the mesogloeal chords there are always numerous cell-strings and -vessels forming a meshwork. It is remarkable that a rather thick cell-string is often found in the axis of a mesogloeal chord, which is traceable for a long distance. The mesogloeal chords are devoid of horny substance.

And what about the course of these chords in the medulla? There are various possibilities. Tracing them in longitudinal sections we sometimes see them end abruptly and disappear among the spicules. Others are connected with or pass into the mesogloeal zones round the medullary or boundary solenia. Others again run nearly straight through the medulla longitudinally and sometimes give off blindly-ending side-twigs. Or they do not run straight, but wind in all sorts of irregular turns. In fig. 45 a few possibilities have been drawn.

d. The rest of the medulla. In the rest of the medulla the spicules lie more or less closely packed (see § 6). In the mesogloea numerous cell-strings and -vessels are met with, forming an irregular meshwork. Many strings, however, run in a longitudinal direction.

e. The cortex. In the cortex, too, there are cell-strings, but the cell-vessels are much more numerous. They are wider than those in the medulla: most of them are about 0.03 mm in width, a few are 0.04 mm and some even up to 0.055 mm. They are nearly always lying close against the cortical solenia and are only separated from them by an extremely thin mesogloeal membrane. In the outer cortical layer they are lacking.

The cells in the cortical vessels can be stained profoundly, especially the nuclei become almost black with haematoxylin, in contradistinction to cells and nuclei of the medullary cell-vessels, where the nuclei are hardly to be stained. In my preparations the cells in the medullary vessels are also larger than those in the cortical ones. Cell-vessels and -strings of cortex and medulla, however, have to be considered as the same mesogloeal formation, for we see them pass into each other. I cannot tell what the differences mentioned must be ascribed to.

In the cortex the cell-vessels may be easily distinguished from the solenia, because they are narrower, but especially because zooxanthellae are lacking, which is properly speaking a matter of course; but in the preparations it is an obvious and convenient distinguishing mark.

As was said at the beginning of this §, in Broch's opinion *Iciligorgia orientalis* belongs to the Spongioderminae, because, according to him, cell-strings are lacking. But, as I have noticed, cell-strings as well as cell-vessels do occur. Consequently Broch's opinion is incorrect, and *Iciligorgia orientalis* should be placed in the subfamily Anthothelinae Broch. Another question is whether Broch's division into two subfamilies can be maintained. This question will be discussed in chapter XIV.

§ 6. The spicules.

Stiasny (1937, p. 30) remarks that his measurements of the spicules are considerably smaller than those given by Broch. Stiasny undoubtedly means the measurements mentioned by Broch in the text, and if so he is right. But the measurements of the spicules figured by Broch differ greatly from the lengths recorded in Broch's text! When measuring Broch's figures again, it appears that these lengths agree fairly well with those recorded by Stiasny. For according to Broch's text the medullary spicules are mostly 0.8 mm and up to 1 mm in length, but according to his figures they are only 0.23 mm. This certainly is more than 0.15 mm, which is the greatest measurement mentioned by Stiasny, but in this way the difference becomes considerably smaller. The lengths of the cortical and the calyx spicules are still better in accordance with each other. The cortical ones are

according to Broch's text 1 mm (!), but according to his figures 0.3 mm in length, whereas Stiasny mentions 0.297 and 0.315 mm. The calyx spicules are in Broch 0.85 mm (text) and 0.18—0.23 mm (figures) long respectively; Stiasny records as their length 0.258 mm. We come to the conclusion, that Broch's statements in the text must be erroneous.

In his diagnosis of "*Machaerigorgia*" *orientalis* Kükenthal (1919, p. 50) mentions the same wrong measurements of Broch, viz., 0.85 mm for the spicules, which form a "small crown" and 1 mm for the cortical spicules!

I examined the spicules once more. The variation in shape is great, as Stiasny already stated. A closer investigation of the different types and their distribution in the coenenchyma did not appear to be superfluous. I have figured the spicules again, but as much as possible I took normal types of an average size, neglecting aberrant forms.

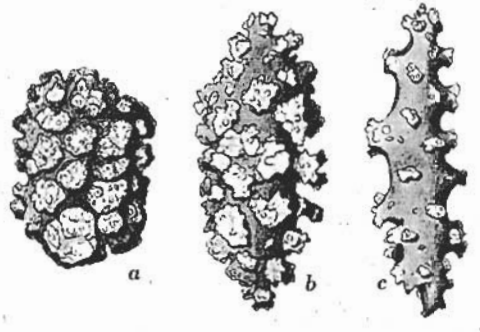

Fig. 47. *Iciligorgia orientalis*. Cortical spicules. a, from the surface layer; b, transitional form; c, from the inner layer. × 200.

1. Cortical spicules. In the cortex Hickson distinguishes three types (1938, p. 593): "(a) long slender spindles with numerous large tubercles usually irregularly arranged, but in some cases showing some girdles. Large spicules of this type are 0.45 mm in length by 0.05 mm in breadth; (b) intermediate spindles about 0.3 × 0.06 mm; and (c) short stumpy forms 0.15 × 0.1 in size". "Between these three types there is a complete series of intermediate forms".

Before I received this paper of Hickson's, I had already examined the spicules of *Iciligorgia orientalis* and I had distinguished two main types, viz.,

a. Mostly small, thick, more or less cylindrical or oval forms (fig. 47a), with blunt extremities and closely covered with large, coarse warts. Most of them are 0.15—0.25 mm in length and 0.08—0.11 mm in breadth (warts included).

b. Spindles with smaller warts, lying rather far apart (fig. 47 c). As to the size of these spicules I was struck by a difference between the spicules found in the ordinary thin cortex and those present in the anthosteles. For the latter are on an average larger than the former: in the anthosteles I noticed several specimens of 0.37 mm in length, and even one of 0.40 mm, whereas the longest in the cortex was 0.32 mm.

The largest cortical spicules recorded by Hickson measured up to 0.45 mm, but Hickson himself has found that the dimensions of his type (a) vary strongly; so I think I had not much luck with my material, for I did not notice such large spicules. Meanwhile neither Broch (figures) nor Stiasny seem to have found them.

The most conspicuous difference between my main types a and c consequently consists in the shape of the spicules, in the more or less close distribution of the warts and their size. Between these two extreme forms there are all kinds of intermediate forms. Of numerous spindles, e.g., the warts are more closely packed and they are also larger than those of fig. 47 c; fig. 47 b represents such an intermediate form. The distribution of the two main types is quite conform to Hickson's description: smaller spicules in the peripheral parts; long spindles close to the medulla.

In the cortex of the stem the spindles of fig. 47 c are lacking; only the oval type a is found. Moreover, spicules exist having the same length as those of type a (viz., about 0.16 mm), but these are thinner and more rod-shaped and are more scantily provided with warts.

Aurivillius (1931, p. 12) found within *I. boninensis* Auriv. "spicules of verruca arranged en chevron". In *I. orientalis* nothing like such an arrangement is to be found: the small spicules of type a are lying round the slit-like aperture side by side in all directions.

2. Spicules of the mesogloeal sheaths round the boundary canals (cf. § 5). These spicules are small rods (0.07 × 0.015 mm) with low spines (fig. 48 a). They also lie in the mesogloeal layer on the medullary side of the coelenterons and here and there also in the side-walls of these cavities. Usually they are found in the middle of these homogeneous layers, more or less parallel to the canal or to the wall of the coelenteron.

3. Medullary spicules (with the exception of the medulla-chord). In the medulla I found spicules, which, although strongly different in shape, could be regarded as belonging to two main types, or to intermediate forms between them. These two extreme forms are represented by b and c and by f in fig. 48. The types b and c are straight or feebly curved rods scantily covered with low conical thorns. The average length is abouth 0.32 mm, maximum length 0.42 mm; breadth mostly 0.015 mm. Length and breadth and also the shape of the processes are quite in keeping with those of the "long slender spicules", noticed by Hickson (1938, p. 593) in the outer layer of the medulla. (But the distribution in the stem is different from what Hickson states, which will appear later on). Type fig. 48 f shows a striking likeness

to type fig. 47 a. I could not detect characteristic differences between these two.

The main types mentioned above are connected by numerous intermediate forms. We see, e.g., many spicules, which are somewhat thicker and shorter than b, while the processes have a flat top and thus begin to show a likeness to warts (fig. 48 d). When the spicules become still shorter and thicker and the warts become larger and coarser, we get nearer to the type of fig. 48 e. Most of the spicules of this type are rods, just as the less numerous intermediate forms between d and e. This is an important point of difference with the more spindle-shaped cortical spicules of

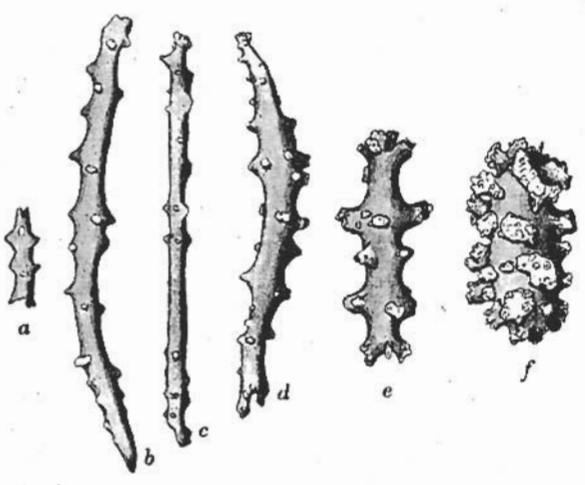

Fig. 48. *Iciligorgia orientalis*. Medullary spicules. × 200.

fig. 47 c; the last-mentioned thick spindles are totally lacking in the medulla.

And what about the distribution of these types of spicules in the medulla? Let us first examine the distribution in the stem. In a freehand section across the stem we see, with the aid of a handlens, round the medulla-chord a zone of almost 1 mm in thickness, slightly but conspicuously whiter in colour than the rest of the medulla. But from this white zone lines or bands are radiating, which are likewise whiter than the medulla lying between them. These lines sometimes branch out and mostly become indistinct towards the periphery (fig. 45, topside). This difference in tint is caused by a difference in the spicules. For we see that the zone whiter to the eye exclusively consists of the short, thick spicules of fig. 48 e and f. They are packed very closely and nearly all placed longitudinally; the white tint is caused by the numerous transversely broken spicules. The white lines radiating outwards appear to consist of the same spicules, which can especially be observed in a tangential section through the stem. For the lines, visible in a transverse section, are in reality radial plates or sheets, exclusively consisting of the short, thick spicules mentioned. In the spaces between these plates, on the contrary, we find exclusively the rod-shaped spicules of fig. 48 c and d. These spicules, however, are lying pell-mell and not so closely packed; hence the greyer tint.

With transmitted light we see the radial plates standing out as dark bands (because of the many intransparent spicules), whereas the spaces between them transmit more light (thin spicules, less closely packed).

Finally the situation of the medullary canals and of the boundary canals with respect to the above-named plates is worth being paid attention to. For we see that the canals in question are always lying in the spaces between these plates; and because the spaces are filled with the thin rods, the canals and their mesogloeal sheaths are always surrounded by these rods, the boundary canals only on their medullary side.

In the very thick branches the distribution of the spicules is still the same as in the stem, but in the somewhat thinner branches (e.g., a branch of 6 × 3.5 mm) the medulla round the medulla-chord is almost exclusively occupied by the zone of short, thick spicules. The plates radiating from it, then are very short and now the spaces with rod-shaped spicules are restricted to narrow strips along the medullary side of the boundary canals. Therefore Hickson (1938, p. 593) writes, that the "surface (of the axis) shows a felt-work of long slender spicules...". From this observation Hickson concludes: "This sheath of long very slender spicules covering the axis seems to be quite characteristic of the genus *Iciligorgia*". But we have to drop the word "sheath" now, at least as far as the stem is concerned, because the distribution of the rods is different, as was described above.

Besides, in *I. ballini* Kükth. and *I. boninensis* Auriv., too, there is no sheath of needles, as appears from the descriptions of Kükenthal (1916 b) and Aurivillius (1931); in both species the rods or needles seem to occur throughout the medulla.

In the extreme tip of a branch the distribution is as follows: the medulla, 0.5 mm in thickness, contains the small spicules of fig. 48 a on the outside. Further inward numerous little rods occur of slightly larger size (0.10—0.19 mm), but as thick as the former: they are intermediate between the types a and b of fig. 48. Among these rods there are several spicules of type e; they are as long as the rods, but thicker and they have scattered, high warts,

which are often divided at the top. The farther from the tip, the more numerous the spicules of type e become; perhaps the above-mentioned rods are juvenile stages of these spicules. At a distance of a few cm from the tip the medulla—of about 1 mm in thickness—consists nearly exclusively of spicules of type e; only round the medulla-chord the rods still occur.

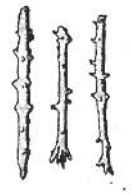

Fig. 49. *Iciligorgia orientalis*. Spicules from the medulla-chord. × 200.

4. The spicules of the medulla-chord. These are of a divergent type, viz., very thin needles or rods, covered with rather high conical or cylindrical processes, their ends often branched in a tree-like manner (fig. 49). The length varies from about 0.10—0.16 mm, the thickness is only 0.005 mm. They are lying pell-mell. No "cortical" spicules occur!

5. Spicules of the anthocodiae. I have little to add to Hickson's description and drawing (text-fig. 1). Only the shape of the spicules, drawn by Hickson, and composing the basal parts of the "points", is not in agreement with what I found in my preparations. Therefore I give once more a drawing of a typical spicule from the basal part and another from the tip of a tentacle (fig. 50). Measurements 0.30 × 0.03 mm (up to 0.4 mm in length) and 0.11 × 0.025 mm respectively.

§ 7. The horny substance.

There are only few data in literature about the presence of this substance in *Iciligorgia orientalis*. Stiasny (1937, p. 30) shortly speaks of "much horny substance". He does not indicate where this substance occurs. Kükenthal does not mention this substance at all. And Broch in his diagnosis of the genus "*Alertigorgia*" Kükth. only mentions a "wenig verhornte Achse".

Meanwhile the examination of the presence and the distribution of the horny matter does not yield important results: only in the medulla horn occurs, in the shape of thin sheaths round the spicules. Also round the needles of the medulla-chord horn occurs as thin sheaths; for the rest this chord does not contain horny substance. So Stiasny's statement about "much horny substance" is not correct.

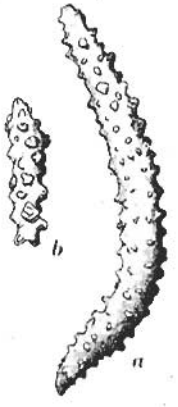

Fig. 50. *Iciligorgia orientalis*. a, spicule from the crown, b, spicule from the top of a tentacle. × 200.

§ 8. *Iciligorgia* or *Alertigorgia*?

Opinions still differ as to the question to what genus the species *orientalis* has to be referred: *Iciligorgia* or *Alertigorgia*.

Duchassaing (1870) introduced the name *Iciligorgia* for the new species *I. schrammi*. Important is, what the author says in his description of the genus: "la partie médullaire... est creusée de canaux circulatoires semblables à ceux que nous avons signalés, dans un ouvrage précédent, pour les Briarea". In this former paper Duchassaing & Michelotti (1864, pl. 1 fig. 4) give a figure of a transverse section of *Briarcum asbestinum*, which leaves nothing to be desired in distinctness: numerous medullary canals have been drawn here. And I do not see any reason to assume that Duchassaing (1870) was mistaken in describing the medullary canals in *I. schrammi*, as Deichmann (1936, p. 83) thinks.

Ridley (1884) has described the species *I. orientalis* for the first time and he referred it to *Iciligorgia* Duch., the diagnosis of which he thus emended: "axis... not penetrated by, but surrounded by, longitudinal canals"!

And that is the source of much misunderstanding! Wright & Studer (1889, p. XXXIV) already deemed it uncertain, whether *Iciligorgia* Ridley was identical with *Iciligorgia* Duch. Kükenthal (1908, 1916 b, and 1919) and Stiasny (1937) are of opinion that *I. orientalis* wrongly was added to the genus *Iciligorgia* Duch. Kükenthal (1908) therefore erected the new genus *Alertigorgia*, a name replaced by him in 1916 by *Machaerigorgia*. But Stiasny (1937, p. 26) rightly pointed out that the reasons for this last-mentioned change of name are insufficient and consequently he retains the name *Alertigorgia orientalis*.

On what grounds Kükenthal maintains that the species *orientalis* must not be regarded as belonging to the genus *Iciligorgia* Duch.? In his paper of 1908 he does not mention any reason. In 1916 b he neither mentions concrete, well-defined points of difference, but one can find differences in the diagnoses given by Kükenthal. Only in 1919 does Kükenthal record the following four points, in which *orientalis* differs from *Iciligorgia* Duch.: 1. *orientalis* has medullary canals in the stem; 2. In *orientalis* the "Polypenkelche" (verrucae) are lacking; 3. The cortical spicules of *orientalis* are formed differently; 4. The geographical distribution.

These differences have been more closely examined by Hickson (1938, p. 594 and 595) and he comes to the conclusion that they are insufficient to justify the establishment of the genus *Alertigorgia*.

As regards the points 2, 3 and 4 I agree with Hickson's criticism. But as to point 1: the presence or absence of medullary canals, my opinion differs from Hickson's: the presence of these canals in *I. orientalis* is an undeniable fact. And this indeed is a difference from *I. ballini* Kükth. and *I. boninensis* Auriv.

But it is no difference from *Iciligorgia* Duch.! And here, in my opinion, lies the criterion in giving an answer to the question: does the species

orientalis belong to *Iciligorgia* Duch. For Duchassaing explicitly recorded the presence of medullary canals, as may appear from the above-mentioned quotation.Taking into account this quotation one would have to conclude that Kükenthal wrongly regarded the species *ballini* as belonging to the genus *Iciligorgia* Duch., for the medullary canals are lacking in *I. ballini*!

Deichmann examined dry material of *I. schrammi*. It is remarkable again that she did not find medullary canals! And Duchassaing did find them! The supposition that Duchassaing would have been mistaken in his description is hardly assumable in my opinion. And so in *I. schrammi* there is the same difference of opinion about the medullary canals as in *I. orientalis*!

Now I have pointed out in § 4 that the medullary canals only occur in the stem and the very thick branches of *I. orientalis*, that the number of these canals in the same stem strongly varies at different heights and that there are stems, in which the medullary canals are totally lacking. In anatomical respect they consequently play a subordinate part, and therefore they are of little practical value as taxonomical character. So I am of opinion that we cannot regard the species *schrammi* and *orientalis* as belonging to different genera, only on the ground of the presence or absence of medullary canals. The genera *Alertigorgia* and *Machaerigorgia* consequently must be abandoned.

Kükenthal (1916b, p. 483) places the species *ballini* into the genus *Iciligorgia* Duch., mentioning the following arguments: a thin cortex; the axis filled with long needle-shaped spicules; the lateral arrangement of the polyps; and the presence of "Polypenkelche" (verrucae). But for the same reasons we can also regard the species *orientalis* as belonging to *Iciligorgia* Duch.! For, in *I. orientalis* also (see, e.g., the diagnosis of "*Machaerigorgia*" in Kükenthal, 1916b, p. 483) the cortex is thin, the axis contains long, thin, spined rods and the zooids are situated along the edges of the branches. Kükenthal denies the presence of "Kelche" (verrucae) in "*Machaerigorgia*" *orientalis*, but this is certainly incorrect: on the very thick branches we frequently see zooids on the flat front and back, which, quite isolated from one another, form separate verrucae of about 1 mm in height. And the zooids along the edges of the branches have verrucae too, although the latter have been fused together. In this respect I cannot find a fundamental difference between *I. orientalis* and the other species.

Stiasny is the only one who, after Kükenthal, defends the establishment of the genus *Alertigorgia*. Let us check the differences mentioned by him (1937, p. 26) in a few words.

1. In *A. orientalis* the edges are as sharp as a knife. But the stem and the thick branches have rounded edges; thinner branches have no sharp edges either, when the zooids stand in three rows along the branch.

2. For *Alertigorgia* holds: "Kelche vorwiegend in tiefen seitlichen Rinnen sitzend". This opinion is incorrect and must be the result of a wrong conception of the "Kelche" and "Rinnen" in *Iciligorgia orientalis*. For the edges are nothing but the anthosteles ("Kelche") themselves, but coalesced. And the "Rinnen" (grooves) are but the apertures of the verrucae, connected with each other. The only difference from *I. ballini* and *I. boninensis* and probably also from *I. schrammi* is, that in these latter species the coalescence is omitted.

3. The presence of thin needles in both genera is one more reason to unite all the species in the genus *Iciligorgia* Duch.

4. I pointed out above that the presence or the absence of medullary canals in *Iciligorgia* has no real systematic significance.

5. The colour cannot be a character of a genus; differences in colour are frequently observed even within a distinct species (*Paragorgia arborea*, *Solenocaulon* species, etc.).

6. The argument about the geographical distribution has been sufficiently refuted by Hickson.

Like Hickson (1938, p. 595) I consequently come to the conclusion, that the arguments mentioned by Stiasny are not convincing and that the species *I. schrammi*, *I. ballini*, *I. boninensis* as well as *I. orientalis* have to be placed into the genus *Iciligorgia* Duch.

XIV. CONCLUSIONS

§ 1. Cortex and medulla.

In *Erythropodium caribaeorum* and *Briareum asbestinum* it is impossible to point out the boundary between cortex and medulla: the two layers very gradually pass into one another. In *Paragorgia arborea* the boundary is slightly more distinct, but it is not sharp either. In the three species mentioned the cortex is fairly thick (1.5 mm, 2—2.5 mm and 1 mm respectively). In all the other species examined by me there is a sharp separation between cortex and medulla caused by the presence of boundary canals. The cortex is mostly thin (0.1—0.7 mm); only in *Solenopodium excavatum* it is about 1.5 mm in thickness. Usually the cortex is equally thick in stem and branches.

The following differences between cortex and medulla hold good for all the species:

1. The coelenteric cavities are found in the cortex. In two species

(*Briareum asbestinum* and *Paragorgia arborea*) the terminal coelenteric cavities are continued in the so-called coelenteric canals.

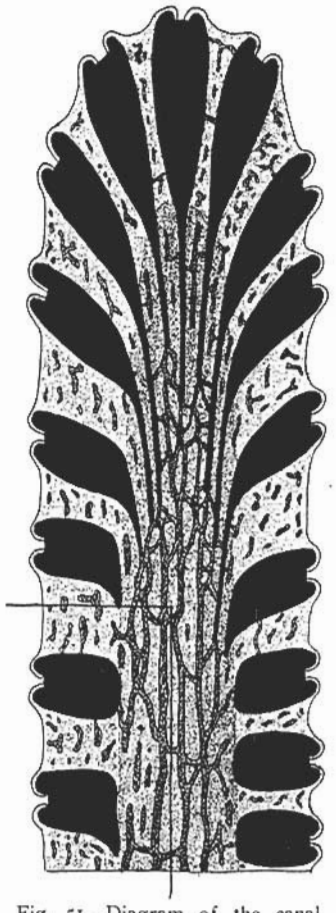

Fig. 51. Diagram of the canal system in the tip of a branch, as it occurs in the families Briareidae Auriv. and Paragorgiidae Auriv.

2. In most of the species we find in each of the two layers spicules, characteristic for that layer.

3. Only in the medullary layer, round the spicules, horny sheaths are met with.

The cortex proceeds into the basal part of the body-wall of the zooids, viz., the anthostele. In *Erythropodium caribaeorum* and *Briareum asbestinum* the whole anthostele may be retracted into the cortex.

§ 2. The canal system.

On account of the canal system, the family *Briareidae* Gray may be divided into two groups of genera. One of the groups comprises the genera *Erythropodium, Briareum,* and *Paragorgia,* the other all the other genera examined.

The first group is characterized by the lack of boundary canals. Cortical and medullary solenia gradually pass into each other, and accordingly a sharp separation between cortex and medulla is lacking (see § 1). The terminal zooids of *Briareum* and *Paragorgia* (of course in a membranous form like *Erythropodium* they are lacking) proceed in so-called coelenteric canals, which have to be considered as parts of the coelenterons, and not as solenia; therefore they are drawn entirely in black in fig. 51. In their turn the coelenteric canals pass into—are connected with—a meshwork of ordinary medullary solenia. So, in the tips of the branches we find numerous medullary canals, some of which have to be regarded as coelenteric canals.

In the genus *Erythropodium* there are no branches and consequently no terminal zooids. Still the genus *Erythropodium* typologically belongs to the same group as *Briareum* and *Paragorgia,* since in these genera the lateral zooids have no coelenteric canals either. At most we may find here and there an indication of such a canal. And the dorsal excavation of the coelenterons in *Erythropodium* may also be considered as such!

So we see that the canal system in *Briareum, Paragorgia,* and *Erythropodium* shows a definite typologic character, which I have tried to represent in fig. 51. The part below on the left, indicated by straight lines, more especially refers to *Erythropodium.*

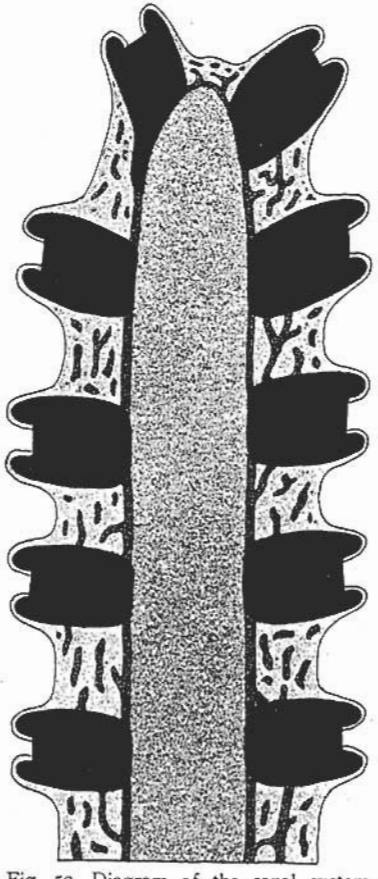

Fig. 52. Diagram of the canal system in the tip of a branch, as it occurs in the family Anthothelidae Broch.

Quite a different type is shown by the canal system of all the other genera. For here the medullary solenia are lacking in the apical parts of the branches. The coelenterons are as it were cut off abruptly and do not proceed into coelenteric canals. The boundary between cortex and medulla is always sharply indicated by the so-called boundary canals; the coelenterons are at their bases connected on all sides with these canals and the latter therefore in no way may be considered as parts of coelenteric cavities. This is especially clear in those species, in which the boundary canals are coalesced into one boundary space (*Anthothela grandiflora, Solenocaulon grayi* (locally) and *S. ramosum* (also locally?)). In *Semperina brunnea* the boundary canals form a very close and irregular meshwork, so that we can hardly call them longitudinal canals. In other species (*Solenocaulon jedanense, Iciligorgia orientalis*) we can distinguish longitudinal canals, although they are connected by numerous

transverse canals. And finally there are species, in which there is only little connection between the boundary canals, and which consequently form a long-stretched meshwork (*Solenocaulon grayi, Diodogorgia ceratosa*).

So we find all kinds of gradual differences between separated longitudinal canals and the formation of one boundary space. A fundamental difference among these types does not exist.

Fig. 52 shows the diagram of all species mentioned above (it also holds good for *Titanideum* Verr. and *Paratitanideum* Kükth.). This diagram is also valid for the twigs of *Solenocaulon* and for the tubular branches of *Solenopodium excavatum*. But in these cases we must imagine the diagram as representing a longitudinal section, so that only the left or the right half of the drawing may constitute the diagram of these genera.

In the last-mentioned group of Briareidae Gray the medullary canals are lacking, as stated, in the tips of stem and branches. But that does not mean that they are also lacking in the more basal parts of the colony. On the contrary! I found that endodermal canals occur in the medulla of the basal parts of nearly all the species. And as a rule the medullary solenia increase in number together with the thickness of the stem or the branch. This appears from the following table:

Species	Thickness of stem or branch	Number of medullary canals
Anthothela grandiflora . . .	stem: 4 mm	a few
Semperina brunnea	stem: 15 mm	numerous (35)
	branch: 8 mm	a few (6)
Solenocaulon iedanense. . . .	stalk: 8 mm	about 7
	stalk: 3.7 mm	1
S. grayi.	stalk: 13 mm	numerous
S. sterroclonium	stalk: 5—6 mm	2
Iciligorgia orientalis	stem: 23 × 8 mm	numerous (very variable)
	branch: 12 × 5 mm	0—4
	branch: 6.6 × 3.4 mm	0

In this table *Solenopodium excavatum*, *Solenocaulon ramosum* and *Diodogorgia ceratosa* are not mentioned, because I only examined apical parts of these species, in which medullary canals do not occur.

So we see that the number of medullary canals is dependent upon the thickness of the stem or the branch. Young specimens, with a thin stem, have few or no medullary canals; older specimens, with thicker stems have numerous medullary canals. In my opinion, we may not classify the species, which in other respects are closely related, in different genera or sub-families on the strength of the presence or absence of medullary solenia in the basal parts of a colony (cf. chapter XIII, § 8). And thus we must understand the words of Aurivillius (1931, p. 11): "A feature that I do not consider to be of the importance attached to it by previous authors is whether the axis is perforated by nutritive channels or not" (cf. Stiasny, 1937, p. 6). The presence or absence of solenia in the basal portions of the medulla is of no taxonomical value.

Cortical solenia occur in every species examined.

§ 3. The spicules.

As regards the shape and the size of the spicules of Briareidae Gray I refer to the excellent summary given by Kükenthal (1919, p. 27). But I want to point out the fact that in nearly all the species there is a gradual transition in size and shape of the outer to the inner cortical spicules and in many cases even to medullary spicules. The outer ones as a rule are only 0.05—0.15 mm in length, the inner ones about 0.25—0.40 mm, while the medullary spicules may become very long, up to 1 mm and longer (*Solenocaulon grayi*). As far as concerns *Briareum asbestinum* this gradual increase in length appears from the graph in fig. 3. Only in the outer cortical layer of *Anthothela grandiflora* spicules occur which are nearly as long as the medulla spicules (0.70 mm).

Also in a vertical direction, from the base to the tips of the colony, there is in some species a gradual change in size and shape of the spicules, especially of the cortical ones. In discussing the *Solenocaulon*-species (chapter XI) I fully dealt with this matter. The cortical spicules in the basal parts of *Solenocaulon* are even of a quite different type than the spicules in higher parts.

In a few other species I have also found some differences. In *Iciligorgia orientalis* the cortical spicules in the basal parts of the stem are smaller than those in the apical parts of the branches. In *Semperina brunnea*, however, I noticed hardly any difference again. Kükenthal (1919, p. 54) says that the outer spicules of the stem are slightly smaller than those of the branches, but I cannot ascertain this difference, nor does it appear from Kükenthal's figs. 22 and 23.

In this connection an observation of Durivault (1937 a) may be referred to. In *Alcyonium palmatum* Pall. she noticed also spicules of different forms in various basal and apical parts of the colony.

In *Briareum* and *Paragorgia* Kinoshita (1913) found spicules in the

centre of the medulla which strongly recalled the cortical spicules. He called this layer "Centralstrang". Kükenthal (1919) found a similar layer also in other Scleraxonia and he called it "Markstrang" (medulla-chord). Kükenthal further points out (1919, p. 689) that in many Briareidae the central part of the medulla is occupied by a somewhat horny or non-horny column of mesogloeal substance, in which spicules occur of the same shape as those in the outer cortical layer (this was not actually asserted by Kinoshita, but the difference is of little consequence).

Now the medulla-chord (or, what comes to the same thing, the similarity between the outer cortical spicules and the inner medullary ones) is mentioned by Kükenthal (1919) in the following species (examined by Kükenthal): *Erythropodium marquesarum, Solenopodium stechei, Briareum asbestinum, Semperina brunnea, Solenocaulon tortuosum* (p. 683), *Paragorgia arborea, Suberia clavaria,* and *Spongioderma verrucosa,* and also in *Titanideum suberosum* (1916, p. 478). But no medulla-chord is mentioned in the following species: *Spongioderma chuni, Diodogorgia ceratosa, D. cervicornis,* and *Iciligorgia ballini* (1916, p. 482), and in all the other *Solonocaulon*-species. In *Anthothela grandiflora* only, the presence of a medulla-chord is denied by Kükenthal.

In all the species I had at my disposal I looked for a medulla-chord, sensu Kükenthal. As a result I found that in some species a particular layer occurs in the central part of the medulla and that this layer is characterized by the spicules being more scattered. Hence in the slides the mesogloea appears more homogeneous and more transparent. Isolated mesogloeal cells, cell-strings and cell-vessels are met with. The spicules lying in it are not surrounded by horny sheaths, except in *Semperina brunnea.* Such a medulla-chord I have found in:

a. *Semperina brunnea* — thickness of chord 0.5—3.5 mm; contains very long and thin needles, which are perfectly different from the round and oval cortical spicules.
b. *Diodogorgia ceratosa* — thickness of chord in branchlet 0.1 mm; ordinary medullary spicules, few in number.
c. *Iciligorgia orientalis* — thickness 0.13—0.40 mm; spicules of a special type: fig. 49; no cortical spicules!

In *Briareum asbestinum* there are spicules in the centre, which are, as far as concerns their average and maximum lengths, smaller than the other medullary spicules (vide fig. 3), but a distinct medulla-chord is lacking. In *Solenopodium excavatum, Paragorgia arborea, Anthothela grandiflora* and in the *Solenocaulon*-species I did not find anything resembling a medulla-chord. In the medulla of *Iciligorgia orientalis* and *Solenocaulon jedanense* I did find spicules, much resembling the cortical ones, but they are scattered in the whole medulla so that an arrangement in the centre is out of the question. The spicules of the "inner bark" of *Solenocaulon,* too, have nothing to do with cortical spicules. Only in *Erythropodium caribaeorum* have I found spicules in the undermost layer of the coenenchyma, in colour and size resembling the cortical spicules. So in any of the species examined, except in the last-mentioned, I did not find a medulla-chord (sensu Kükenthal!) consisting of spicules, which unmistakably show the character of cortical spicules.

The fusion of medullary spicules into an aggregate is rather a general phenomenon in the various species of *Solenocaulon* (cf. chapter XI). But only part of the medullary spicules are fused, so that sometimes the aggregate is not very conspicuous. Probably this explains why some authors overlooked it. In anatomical respect the aggregate is not very important, nor is it in my opinion of much importance in taxonomical respect. Perhaps later it may appear that the aggregate occurs in all *Solenocaulon*-species, so also in *S. simplex* Kükth. If this might be the case it is a character of the whole genus *Solenocaulon.*

§ 4. The mesogloea.

The mesogloeal medulla-chord has been discussed in the previous §, together with the spicules.

Broch (1916) divided his family Anthothelidae into two subfamilies, viz., Anthothelinae ("Anthothelidae, deren Achse von Zellsträngen oder feinen Zellkanälen durchwebt sind", l. c., p. 14) and Spongioderminae ("Anthothelidae, deren Achse Zellstränge und Solenien entbehren", l. c., p. 19).

Kükenthal (1919, p. 655) examined nearly all the genera of the Briareidae Gray by means of microtome sections and he came to the conclusion, that only isolated cells and cell-strings occur in the mesogloea. I found, however, that also numerous cell-vessels are met with. The strings then have a lumen and have become vessels, as, e.g., Kükenthal (1919, p. 655) has described it in the family Melitodidae. In my opinion the strings and vessels are fundamentally alike and they reciprocally pass into one another—a sharp separation between strings and vessels is not to be made, and therefore the occurrence of cell-vessels is of no taxonomic value.

I found cell-strings and -vessels in *Erythropodium caribaeorum, Solenopodium excavatum, Briareum asbestinum, Paragorgia arborea, Anthothela grandiflora* (just like Molander, 1918, who thought, however, that the mesogloeal cells were of endodermal origin), *Iciligorgia orientalis,* and

Semperina brunnea. In *Solenocaulon grayi*, and probably also in *S. jedanense*, the spacious vessels open at the surface (vide fig. 38). In the branches of *Diodogorgia ceratosa* only cell-vessels are found, exclusively in the cortex.

As the only representative of the Spongioderminae, Broch mentions the genus *Alertigorgia*, so the species *A. orientalis*. But I did find cell-strings and cell-vessels in this species. I do not know other Briareidae Gray, in which cell-strings and vessels are lacking. Consequently the subdivision of the Anthothelidae into Anthothelinae and Spongioderminae has to be abandoned.

Kükenthal (1919, p. 658) points out that the solenia may be enveloped by a zone of homogeneous mesogloea. I have found this zone in various species. In *Semperina brunnea* and especially in *Iciligorgia orientalis* these zones occur round the medullary and boundary canals. But in other species (*Erythropodium caribaeorum, Solenopodium excavatum, Briareum asbestinum, Anthothela grandiflora* and *Diodogorgia ceratosa*) nothing like a homogeneous mesogloeal zone is to be found. In the *Solenocaulon*-species the development of these zones is different, but always the zones occur only round the boundary canals; on the medullary sides the zones are invariably thicker than on the cortical side. In the mesogloeal zones we usually find cell-strings and cell-vessels.

A very peculiar state of things is found in *Paragorgia arborea*. Here the zone of homogeneous mesogloea has developed into a thick layer of "circumsolenial medulla", in which spicules and horny substance are lacking. It contains, however, numerous spacious mesogloeal vessels, forming a close meshwork (figs. 5, 8 and 9) and running through the zone in a radial direction. See further chapter III.

Generally speaking I refrained from more detailed cytological investigations. I always used the term "mesogloeal cells", making no difference between interstitial cells, nutritive cells, etc. I did not pay much attention to the origin of these cells.

As regards the ectodermal origin of the scleroblasts the authors generally agree, but the origin of the other mesogloeal cells is still uncertain. Kükenthal (1919, p. 654) holds that all the cells and cell-strings in the mesogloea of Gorgonaria are derived from the ectoderm. Without giving a definite conclusion I must say that my observations agree with Kükenthal's. But at the same time I must add that not all the material examined by me was sufficiently preserved and that occasionally the material had suffered by decalcification, etc., so that in these cases I could not make distinct observations.

Of some species, however, I obtained excellent microtome sections, and then I always noticed that the cell-strings, etc., were separated from the endodermal basement membrane by a thin mesogloeal layer. I did not see anywhere that the endodermal cells passed into the mesogloeal ones. I refer especially to chapter II, § 6, where I defended the ectodermal origin of the mesogloeal cells in *Briareum asbestinum*. In *Semperina brunnea* I saw very distinctly that the cell-strings are connected with the ectoderm in the same way as shown in Kükenthal's figure (1919, fig. 26). Finally I refer again to my fig. 38, concerning *Solenocaulon grayi*, where the vessels directly open on the surface and the mesogloeal cells pass into the ectodermal ones.

But, contrary to this, Bock (1938, p. 22) saw that in *Paragorgia arborea* the mesogloeal cells are connected with the endoderm, and the latter passing through the basement membrane into the mesogloea! Certainly we have not yet come to a final conclusion in this difficult matter. Presumably some kinds of mesogloeal cells originate from the ectoderm and others from the endoderm (cf. Chester, 1913, p. 754), while in the various species, genera, families and orders the relative quantity of each kind may be different. The cells, endodermal in origin, are perhaps the most numerous in the Alcyonaria (cf. Hickson, 1895, 1901; Woodland, 1906; Pratt, 1906; Bock, 1938).

§ 5. The horny substance.

In all the species examined the horny substance only occurs in the medulla. It always forms thin or thick sheaths round the spicules; neighbouring spicules are often connected with each other by the sheaths. In the medulla of some species (*Anthothela grandiflora, Erythropodium caribaeorum*) irregular lumps of horny substance are met with, in the last-mentioned species also in the cortex (cf. Broch, 1916, p. 15).

In discussing the various species I pointed out that Stiasny repeatedly gave incorrect statements about the presence and the distribution of horny substance. In unstained sections it is impossible to recognize the horny substance as such. Kükenthal frequently speaks of "ein Netz von Hornfasern", or of "ein Netzwerk bildenden Hornscheiden". I cannot find anything like such a network. And it is certainly not to the point to term the horny sheaths "Hornfasern"!

Now, where do the horny sheaths occur in largest numbers? Kükenthal (1919, p. 689) states that in most of the genera the horny substance occurs in a tubular shape, whereas the central part of the medulla is occupied by the medulla-chord, which contains little or no horny substance. This distribution

really seems to occur in some genera; it is also mentioned by Broch (1916) in *Titanideum mjöbergi* Broch. But this distribution does not hold good for all Briareidae Gray. In *Briareum asbestinum*, e.g., I found most of the horny substance in the very central part of the medulla. In *Semperina brunnea* it occurs everywhere in the medulla, also in the medulla-chord; in *Diodogorgia ceratosa* likewise everywhere in the medulla, except in the medulla-chord. In all *Solenocaulon*-species (also in *S. ramosum*?) it occurs in the stalk and basal part of the stem. In *Anthothela grandiflora* it is found everywhere in the medulla again (anything like "Schwammgewebe" was not found; cf. chapter V, § 6). In *Paragorgia arborea* it shows a peculiar distribution, for it occurs only in the intersolenial medulla (vide fig. 8 and chapter III, § 5 and 7).

As was stated in chapter I, the differences in respect to the presence of horny substance in *Erythropodium caribaeorum* on the one side and in *Parerythropodium coralloides* and *Alcyonium digitatum* on the other, are very slight. In *Erythropodium caribaeorum* I found that horny sheaths are only met with in a very thin layer on the underside of the coenenchyma. They are connected with the horny basal membrane. In the other species mentioned the horny sheaths are lacking; the horny membrane may even become obliterated. Now Kükenthal (1925, p. 692) states that a horny substance also occurs in the Alcyonaria "als Umscheidung der Skleriten". It follows that the presence of a horny substance cannot be a character of the Gorgonaria only. One might ask therefore how much horny substance has to be present to classify a species as a Gorgonarian. Hickson (1930) also strongly criticized the value of the horny substance as a taxonomic factor.

§ 6. The zooids.

In § 2 I already made a few remarks on the shape of the coelenterons and their connection with the canal system. Now I must add a few remarks about the positions of the zooids and about the gonads.

Kükenthal (1919, p. 660) remarks that in all Gorgonaria the polyps are orientated so as to have the ventral (sulcar) aspect turned abaxially. The same position of the zooids is also recorded by Pax (1936, p. 260). I found that in many species the real condition is different. So in *Semperina brunnea* I noticed that the ventral aspect of many zooids is adaxial, of some abaxial, while some others are placed transversally in respect to the longitudinal direction of the branch. In *Briareum asbestinum, Anthothela grandiflora* and *Solenocaulon grayi* the zooids are also placed in all sorts of positions; but in *Solenocaulon jedanense* the dorsal aspect of the zooids

placed on the twigs is turned to the upper (= cortical) side of the twig, and so the ventral aspect to the under (= medullary) side. In *Diodogorgia ceratosa* the ventral aspect of most of the zooids is adaxial, in *Iciligorgia orientalis* the same aspect of all the zooids is adaxial. In *Paragorgia arborea* only the ventral aspect of most autozooids and siphonozooids is abaxial. So all kinds of positions may occur!

According to Kükenthal (1919, p. 667) the ova of Gorgonaria have a stalk; only in *Briareum asbestinum* and in *Spongioderma verrucosa* an ovum-stalk does not seem to be formed. As a matter of fact I have found female gonads provided with stalks in *Paragorgia arborea, Anthothela grandiflora, Semperina brunnea, Solenocaulon jedanense* and *S. grayi*, whereas in *Briareum asbestinum* the ova are not provided with stalks indeed, but this may be owing to the fact that I probably had zooids with young ova only. Male gonads may also be provided with stalks, viz., in *Briareum asbestinum, Anthothela grandiflora*, and *Iciligorgia orientalis*. In *Briareum asbestinum* the spermaria still show the particularity that not a single central cavity is found in them, but that several cavities occur, filled with the tails of the spermatozooids (cf. fig. 4). In *Paragorgia arborea* gonads are found in the autozooids as well as in the siphonozooids. In the latter they are more numerous and they originate on the short ventral mesenteries (vide fig. 6).

XV. REMARKS ON TAXONOMY

At the end of chapter XIV, § 2, I mentioned that I did not set any taxonomical value on the presence or absence of solenia in the medulla of the basal parts of the colony.

Studer (1887) did not distinguish between medullary canals in the upper and the basal parts of the colony. He divided the Briareidae into two sub-families: Briareinae, with medullary canals, and Spongioderminae, without medullary canals. It stands to reason that I cannot accept this division. Not the canal system in the basal parts, but that in the apical parts of the colony should be the foundation for a systematic division. Therefore the sub-division suggested by Broch (1916), has to be regarded as a step in a good direction. Broch distinguished primary and secondary longitudinal canals. In *Briareum* and *Paragorgia*, according to Broch, the primary canals have to be regarded as direct continuations of the coelenteric cavities (Kinoshita, 1913!), consequently as parts of the coelenterons. Although this opinion is not quite correct, the important difference with the other Briareidae did not escape Broch's observation. For that reason

Broch wants to divide the family Briareidae Gray into two families, viz., the Briareidae s.str. (with primary longitudinal canals; *Briareum*, *Paragorgia*) and the Anthothelidae (without primary canals).

This classification is quite in accordance with the principle that underlies the classification of Aurivillius, who writes (1931, p. 8): "Among the other genera two groups are distinguishable, differing in axial structure, viz. those in which the tip of the axis is encircled by a ring of nutritive channels, which are not found inside the axis itself, and those with the tip of the axis perforated by numerous nutritive channels but not encircled by them, viz. the Briareidae s. str." I fully agree to this division of the old family Briareidae Gray on the strength of my own observations; the canal sysem of the two groups of genera is in accordance with my figs. 51 and 52.

The family Anthothelidae Broch can be maintained; it comprises the genera, the canal system of which is similar to fig. 52. But the family Briareidae Broch has to be sub-divided. For, in accordance with Aurivillius (1931) and Stiasny (1937), the dimorphism of the zooids renders a separation of the genus *Paragorgia* necessary. Both authors regard this genus (and so does Stiasny with *Sibogagorgia* as well) as belonging to a separate family, the Paragorgiidae Auriv. I accept the great difference between *Briareum* and *Paragorgia* in this respect. Therefore I want to divide the family Briareidae Broch into two families, corresponding to the families Briareidae Auriv. and Paragorgiidae Auriv. Both families are provided with a canal system fundamentally resembling fig. 51.

Now we have to answer the question, into which order(s) these families have to be classified. May all of them be included into the Gorgonaria (sub-order Scleraxonia)?

In comparing the canal system of the Briareidae Auriv., the Paragorgiidae Auriv. and the Anthothelidae Broch with that of the Alcyoniidae Verr. (not only with membranous forms, but also with normal colonies, e.g., of *Alcyonium digitatum* L. or of *A. palmatum* Pall., we see that the canal system of the two first families (fig. 51) shows more likeness to that of the Alcyoniidae than to that of the Anthothelidae. For in the Briareidae and the Paragorgiidae as well as in the Alcyoniidae the coelenteric cavities penetrate into the coenenchyma at different distances. They are either directly or indirectly connected by solenia, which occur everywhere, also in the interior of the tips of the branches. It is difficult or even impossible to point out the boundary between a cortical and a medullary layer.

On the other hand, I want to stick to the character of Gorgonaria (Gorgonacea): the coelenterons are short. This fully holds good for the Anthothelidae Broch.

And so I come to the conclusion that the line of separation between the Alcyonaria and the Scleraxonia should be drawn at another place than it has been done up till now. The Briareidae Auriv. and the Paragorgiidae Auriv. should be added to the order Alcyonaria (Alcyonacea) as new families. But the Anthothelidae Broch should be regarded as belonging to the suborder Scleraxonia, order Gorgonaria (Gorgonacea), as before. The diagnoses of these families are:

Family Briareidae Auriv. emend.: Alcyonaria (Alcyonacea) with a medullary layer penetrated throughout its length, even in the tips of the branches (if present), by numerous endodermal canals and not separated from the cortex by a circle of boundary canals. Zooids monomorphous, with feebly developed anthosteles. Terminal zooids with coelenteric canals. — *Briareum* Blainv., *Erythropodium* Köll.

Family Paragorgiidae Auriv. emend. differs from the Briareidae only in having dimorphous zooids — *Paragorgia* M. Edw., *Sibogagorgia* Stiasny.

Family Anthothelidae Broch: 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 is not perforated by solenia; in the basal medullary portion solenia may occur. Coelenterons 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 monomorphous. — *Anthothela* Verr., *Solenopodium* Kükth., *Semperina* Köll., *Iciligorgia* Duch. & Mich., *Solenocaulon* J. E. Gray, *Titanideum* Verr., *Paratitanideum* Kükth., *Suberia* Th. Stud., *Spongioderma* Köll., *Diodogorgia* Kükth.

As appears from this enumeration, I also refer *Solenopodium* to the Anthothelidae. For *S. excavatum* has no medullary solenia in the apical parts of the colony, while the medullary layer is sharply limited by boundary canals. The canal system resembles fig. 52. And what about *S. marquesarum* (Kükth.)? On the strength of the spicules Aurivillius and Stiasny refer this species to the genus *Solenopodium*, but the canal system shows a closer relation to *Erythropodium* (and consequently to *Briareum*; cf. Molander, 1929!), for there is no sharp boundary between medullary and cortical layer; there are solenia also in the undermost parts of the medulla. As regards *S. stechei* (Kükth.) and *S. contortum* (Kükth.) a closer examination is desirable. For the data recorded by Kükenthal, Stiasny, etc. are too incomplete to come to a decision. Aurivillius refers *S. stechei* to the Briareidae Auriv.; this would point to the fact, that Aurivillius noticed medullary canals in the tips of the colony. But he does not mention them in his description of the species. And in giving evidence for

the relationship with *Briareum* (1931, p. 8), he does not refer to the canal system, but to the spicules! So in this respect Aurivillius is not conform to his own principles.

Molander (1929) sets much systematic value on the canal system. On the very ground of this system he assumes that there is a sharp separation between the Alcyoniidae and the Briareidae Gray and in his opinion a transition from *Alcyonium* (*Parerythropodium*) *membranaceum* Kükth. into *Erythropodium* is impossible (pace Kükenthal). In fact, the canal system of *Erythropodium* shows more relationship with that of *Briareum* than with that of *Parerythropodium*: the short coelenteric cavities and the way in which the latter are connected by the solenia strongly reminds one of the conditions found in the lateral zooids of *Briareum*. Still more than the presence or absence of horny sheaths, the canal system gives evidence for placing *Erythropodium* in the family Briareidae Auriv.

Meanwhile there are also investigators, who attach less value to the canal system. I name Hickson (1928 and 1930) and Stiasny (1937). Hickson refers to Schimbke, who wrote (1914, p. 67) that the number of the canals varies at different heights in the colonies. But there is nothing particular in that! Transverse sections of any species of the Briareidae Gray at different heights will show that there are fewer canals in the apical sections than in the more basal ones! "Welches Niveau wäre... für die Beurteilung der Lage der Gefässe massgebend?" Stiasny (1937, p. 125) asks. My answer is: "One should not take one single level to ascertain the real situation of the canals and to get an insight in the whole canal system. One ought to combine transverse and longitudinal sections from all parts of the colony". I did so as well as I could and I tried to represent the results in plain diagrams.

Has the canal system indeed a doubtful taxonomic value? According to Hickson (1928, p. 332) it has: "These characters, however, cannot be used for distinguishing families, genera, or even species...". I do not agree with Hickson. The characteristic differences between the two diagrams of figs. 51 and 52 speak too clear a language. And Stiasny says (l.c., a little further on) that to the arrangement of the canals a certain value as a character cannot be denied.

Stiasny (1939) proposed a system of Octocorallia, in which he had removed the whole Scleraxonia from the Gorgonaria and included this group into the Alcyonaria, which order, as a whole, he now wants to name Scleraxonia. This is going too far. The separation between Alcyonaria (Alcyonacea) and Scleraxonia must be maintained.

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SAMENVATTING

In dit proefschrift worden de resultaten medegedeeld van het onderzoek van enige soorten van Octocorallia, behorende tot de familie der Briareidae Gray. De kennis van de anatomie van verschillende vertegenwoordigers dezer familie was nog zeer onvolledig, zelfs van vrij algemeen voorkomende soorten als *Paragorgia arborea* en *Anthothela grandiflora*.

Het materiaal, dat onderzocht werd, is grotendeels afkomstig van de „Siboga"-expeditie; bovendien ontving ik enige exemplaren van andere herkomst; in totaal werden 13 soorten, behorende tot 9 genera, min of meer uitvoerig beschreven.

Het hoofddoel van het onderzoek was het verkrijgen van een nauwkeuriger kennis van het kanalensysteem en van de samenhang van dit systeem met de gastrale holten. De resultaten werden zoveel mogelijk in diagrammen samengevat. Maar ook andere problemen, die in de literatuur vermeld worden, werden bestudeerd. Waar het nodig was, werden de spicula opnieuw onderzocht en afgebeeld. Voorts onderzocht ik de begrenzing van merg en schors en de verschilpunten tussen deze beide lagen, de mesogloea en de daarin voorkomende cellen, celstrengen en celvaten, het voorkomen en de ligging der hoornstof, enz.

De resultaten van het onderzoek kunnen als volgt worden samengevat:

1. Bij alle onderzochte soorten kunnen twee lagen in het coenenchym onderscheiden worden, n.l. een buitenste schorslaag en een daar binnen gelegen merglaag. Bij membraneuze vormen (*Erythropodium caribaeorum*) komen deze lagen overeen met de bovenste en benedenste laag van het coenenchym. Bij sommige species (*Erythropodium caribaeorum, Briareum asbestinum*) gaan deze beide lagen geleidelijk in elkaar over. Bij *Paragorgia arborea* is de grens iets duidelijker, maar toch nog onscherp. Bij de overige species bestaat een scherpe grens tussen de beide lagen, hetgeen toe te schrijven is aan de aanwezigheid van grenskanalen (zie beneden).

Gewoonlijk is er een belangrijk verschil tussen de spicula in de schors en in het merg, al worden ook in het merg soms spicula aangetroffen, die sterk herinneren aan die in de schors. De gastrale holten der zoïden liggen geheel in de schors (met uitzondering van de gastrale kanalen bij *Briareum*