Studies on the Comparative Anatomy of Sponges.

III.—On the Anatomy of Grantia labyrinthica, Carter, and the so-called Family Teichonidæ.

By

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With Plates I—IV.

Introduction.

During the past few years Mr. J. Bracebridge Wilson has, by perseveringly dredging in the neighbourhood of Port Phil!ip, accumulated a collection of sponges which already numbers something like 2000 specimens, and is probably the most complete collection ever brought together from the shores of any one country. The entire collection has been generously placed in my hands for investigation, and Professor McCoy has likewise kindly placed at my disposal the collection contained in the National Museum at Melbourne. The task of dealing with so large a mass of material is, I need hardly say, one of great magnitude, and the systematic investigation must necessarily extend over several years. The difficulty of the work, so far as identification of species is concerned, has been greatly lessened by the courtesy of Mr. H. J. Carter, who has generously sent me his own copy of his work on the Port Phillip Calcispongiæ (1), containing a large number of unpublished sketches; and of Dr. Günther, to whom I am deeply indebted for a large series of duplicate pieces of named sponges from the British Museum collection, most kindly sent to me since I left England.

It is hoped that the final account of the collection will be embodied in one of a series of reports on the marine zoology of Port Phillip, which it is intended to publish under the auspices of the Port Phillip Exploration Committee of the Royal Society of Victoria. Meanwhile, even during the preliminary arrangement of the collection, forms are constantly being met with which deserve special anatomical investigation. One such I have already described in the present series of studies (2); and I hope, as time permits, to be able to deal similarly with a number of others.

The more one studies the group, the more is one convinced of the necessity of thorough and minute anatomical investigation as a basis for classification. Especially in the present transitional state of our knowledge of the sponges anatomical investigation must precede systematic work; and the greater the number of types selected for such investigation, the greater will be the value of the scheme of classification ultimately arrived at. Polymorphism and homoplasy occur so generally and to such an extraordinary degree amongst the Porifera, that true genetic relationships can be determined only by most careful examination of the internal anatomy, and especially of the skeleton and canal system, although even these systems are by no means exempt from the general rule.

The sponge which forms the principal subject of the present contribution is a large and singularly beautiful calcisponge, originally described (3) by Mr. Carter under the name Teichonella labyrinthica. As Mr. Carter subsequently discovered, the sponge is very far removed from the genus Teichonella, and must be placed amongst the Sycons, where for the present, at any rate, it may be classed in the genus Grantia.[1]

The material at my disposal for investigating this sponge consisted principally of a number of fine adult specimens col-

[1] Vide Vosmaer's diagnosis of this (20).

lected by Mr. Wilson, and preserved in ordinary methylated spirit. This was supplemented by some fragments taken from a fresh specimen by myself when out dredging with Mr. Wilson, and preserved in absolute alcohol, and by three young examples of great interest. Sections were cut in different directions by hand, by the freezing microtome, and by the paraffin method. For studying the skeleton, hand-cut sections of unstained material and preparations of the spicules boiled out with caustic potash are most serviceable. For minute anatomical and histological work, thinner sections of material stained with borax carmine, and cut by the ordinary paraffin method, were found to yield good results.

The Anatomy of Grantia labyrinthica.

(*a*) Historical.

The sponge under consideration was, as I have stated above, originally described by Mr. Carter in the 'Annals and Magazine of Natural History' in 1878 (**3**), apparently from a dry and imperfect specimen in the British Museum collection. The brief description is confined almost entirely to the skeleton and the external characters, but the author observes that "in spiculation and in the structure of the lamina it is closely allied to Grantia compressa, Fleming." He refers the sponge, however, as already noted, to his genus Teichonella.

In 1886 Mr. Carter was able (**1**) to supplement his original description from the examination of specimens dredged and sent to England by Mr. Bracebridge Wilson. He observes that "the sponge is goblet-shaped in general form, and not simply 'vallate,' like T. prolifera; also that a quadriradiate forms part of its spiculation; hence these additional facts render it necessary that it should be relegated to the vicinity of Grantia compressa, where its generic name might be changed from 'Teichonella' to 'Grantia.'"

Previously to this date, however, Mr. Carter had published in the 'Annals and Magazine of Natural History' a remarkable paper (4) on the "Mode of Circulation in the Spongida," in which he advocates the theory that "the particles that are taken in with the water through the pores of the dermis fall *directly* into the subdermal cavities, and pass thence into the large excretory canals, from which they are afterwards *deflected* to their destination through smaller branches, whose apertures may be seen in the walls of the former." He adds, "This perhaps is best seen in *Teichonella labyrinthica*, wherein the chambers, which are arranged in juxtaposition perpendicularly to the lamina of which the sponge is composed, thus pass directly through it from one side to the other, having therefore on one side the pores or pore-dermis, and on the other the vent; in short, exactly like those of *Grantia compressa*, only there is no cloaca. We must, however, regard this chamber as at once ampullaceous sac and excretory canal; for the pore-dermis being at one end or side of the lamina and the vent at the other, the circulation passes into the former and out at the latter, through the chamber, where the nutritive particles are instantly taken up by the spongozoa lining its cavity. Hence the holes in the walls of the chamber, which are very numerous, may serve for the purpose of intercommunication, where the walls of the neighbouring chambers are in direct contact with each other, or for the purpose of allowing the ova developed in the intercameral tissue to pass into the chamber and thus be expelled. Therefore these holes would seem to have more functions than those ascribed to them in the wall of the ampullaceous sac of the so-called 'siliceous sponges,' ex. gr. *Spongelia avara*." For a further elucidation of Mr. Carter's views on the canal system of sponges in general, the student is referred to his paper (5) "On the Position of the Ampullaceous Sac and the Function of the Water Canal System in the Spongida;" at present I wish to consider only the particular case of *Grantia labyrinthica*. Mr. Carter's account of the arrangement of the canal system in this sponge is supplemented by a figure (Pl. IV, fig. 7), wherein the flagellated chamber (= ampullaceous sac or radial tube) is represented as being perfectly straight and cylindrical, with a pore-sieve opening into it at one end and a vent at the other.

Such, then, was the state of our knowledge of Grantia labyrinthica, one of the most remarkable of all the calcareous sponges, when I commenced my investigations. How far my own observations agree or disagree with Mr. Carter's descriptions will appear subsequently.

(*b*) External Characters.

Grantia labyrinthica is very large for a calcareous sponge, well-grown specimens being about three inches in height and a little more in breadth, so that it is probably the largest of all the Sycons. Hence it is peculiarly well adapted for anatomical investigation.

A better idea of the external appearance will perhaps be gathered from an examination of fig. 4 than from any description which I can give. It will be seen that the adult sponge consists essentially of a thin-walled cup or basin, with a widely open mouth showing no signs of constriction, and thus differing markedly from the oscula of all other known Sycons. The wall of the cup, however, which, as I shall show later on, is in the young sponge simple and not folded, in the adult becomes greatly convoluted and folded upon itself, without, however, ever losing its character of a single continuous lamella. Thus, while in most Sycon sponges the circumferential growth of the tube or cup after a time diminishes as the sponge grows older, giving rise to a more or less constricted osculum, in Grantia labyrinthica precisely the reverse takes place, and the circumferential growth so far outstrips the vertical growth that the sponge wall becomes thrown into numerous deep folds, while the osculum becomes enormously wide and bounded by a deeply sinuous margin. The cup thus formed is attached by the middle of its lower surface to a stout cylindrical stalk, which is also a subsequent development not present in the very young sponge. At its lower end the stalk is fixed to the rock or other body upon which the free swimming embryo may have chanced to come to rest.

This peculiar external form is to some extent paralleled by certain species of the genus Phyllospongia amongst the horny sponges, as will be evident on referring to Lendenfeld's figures (6). By far the most remarkable parallelism, however, is exhibited by a Renieriæ species, not yet determined, which so closely resembles a young Grantia labyrinthica in external appearance that I at first placed it along with other specimens of that sponge to be figured, and only found out my mistake on microscopical examination. This interesting example of homoplasy serves well to show the necessity of microscopical examination before even the approximate position of any particular sponge can be safely determined.

Both surfaces of the cup are smooth, and the inner surface is at once seen to be perforated by innumerable minute and closely placed apertures, the exhalant openings of the flagellated chambers. These give to the surface a minutely punctate appearance, which is absent immediately below the free margin, where the sponge wall becomes very thin and translucent. On the outer surface of the cup the pore-sieves form less obvious markings.

(*c*) The skeleton.

The Spicules.—The calcareous spicules composing the skeleton of the sponge are of three main types—triradiate, quadriradiate, and uniaxial (oxeote). Each of these types occurs in the sponge under more than one modification, according to its position.

Triradiate Spicules.

These form the main mass of the skeleton. The different modifications which they present in different parts of the sponge depend chiefly upon the relative length of the rays; and, to some extent, upon the proportions of the angles between them. Thus we find a more or less gradual series between approximately equiradiate and equiangular spicules on the one hand, in which all three rays are of about the same length, and the angles between them nearly equal (fig.

16), and extremely inequiradiate and inequiangular spicules, of the form termed by Haeckel (7) "sagittal," on the other. In the sagittal spicules two rays are about equal in length, while the third has either grown out into a very long and slender shaft, which may attain to three or four times the length of either of the others (figs. 13, 14), or (much more rarely) remained short while the other two have grown long (fig. 18). The angle between the two paired arms, or the oral angle, as Haeckel terms it, is greater than either of the other two angles, which are equal.

Figs. 13 to 19 represent seven triradiate spicules, and illustrate the variation in the proportions of the rays and angles. The commonest form is the sagittal, with one ray (the shaft) much longer than the other two. It is important to notice that, as a general rule at any rate, the three rays of the triradiate do not all lie in exactly the same plane, so that if the spicule were laid down upon an even surface it would rest upon the ends of the three rays, with the centre elevated. This fact is not shown in the figures, which are merely outlines drawn with the camera. In the sagittal spicules the shaft is usually perfectly straight, but often of the beautiful spear-like form shown in figs. 13 and 14. The two paired rays, on the other hand, are often slightly curved.

The triradiates vary considerably in size. The following measurements are taken from a well-grown spicule, of the form shown in fig. 13, and all the other spicules (from figs. 7 to 20 inclusive) are drawn to the same scale.

Length of the shaft 0·38 mm.
Length of the paired rays 0·12 mm.

Quadriradiate Spicules.

These are probably to be regarded only as further modifications of the fundamental triradiate type, for although they are quadriradiate they are still only triaxial. Their shape is usually that represented in fig. 20. It will be seen that the third ray of a normal triradiate spicule has become much shortened, while an additional fourth ray has appeared as a direct continuation of the third ray in the angle between the two paired rays. The cessation of growth of the third ray in its usual direction is perhaps to be accounted for by the outgrowth of the new fourth ray in the exactly opposite direction. The additional fourth ray is usually slightly hastate in form, the surface of the spear-head being at the same time slightly roughened. Occasionally, as shown in fig. 21, this peculiarity in form is very much more strongly marked. The size of the quadriradiates may be estimated from fig. 20.

Uniaxial Spicules.

The shape of these spicules is a modification of the oxeote type, in which one end is markedly broader than the other, and often decidedly hastate (figs. 10, 11). Fig. 11 represents a spicule of the more usual size and form; figs. 7, 8, 9 represent giant modifications of the same from the margin of the osculum, and fig. 12 represents the large-sized form found in the stem. All the figures are drawn to the same scale as the triradiates.

The Arrangement of the Skeleton.—In dealing with this part of my subject I propose to follow the plan laid down by Haeckel in his 'Monograph of the Calcareous Sponges,' which seems to be in all respects the most satisfactory.

In the Sycons Haeckel distinguishes the following skeletal systems, which, for the sake of convenience, I arrange in an order slightly different from his :

1. The dermal skeleton, protecting the outer or dermal surface of the tube or cup, of which the Sycon individual consists.

2. The gastral skeleton, protecting the inner or gastral surface.

3. The skeleton of the peristome, protecting the margin of the osculum.

4. The tubar skeleton, lying between the dermal and gastral systems, and affording support to the flagellated chambers.

5. The skeleton of the base or stalk (where one is present).

It will be evident from the following account that Grantia labyrinthica conforms very closely in the arrangement of the skeleton to the normal Sycon plan.

The Dermal Skeleton.

This forms a distinct cortex of somewhat varying thickness over the outer surface of the sponge (figs. 22, 25). The main mass of this cortex consists of large sagittal triradiates, arranged so that the long unpaired ray points towards the base of the sponge. Even within the limits of the dermal cortex the triradiates exhibit considerable individual variation in shape and size. In the inner portion of the cortex numbers of the singularly beautiful sagittal triradiates represented in figs. 13 and 14 occur.

The outermost portion of the dermal skeleton consists of great numbers of small oxeote spicules of the form represented in figs. 10 and 11, placed at right angles to the surface, with their narrow ends embedded amongst the large triradiates, and their broad ends projecting freely (fig. 22). In the pore-areas the dermal skeleton is practically reduced to this outer layer of small oxea, many of which appear to be quite flat in the thin dermal membrane.

The Gastral Skeleton.

The gastral skeleton (figs. 22, 25) forms a protective cortex over the inner surface of the cup, exactly as the dermal skeleton does over the outer. The gastral and dermal cortex do not differ very greatly in thickness, although in this respect there seems to be a good deal of variation. In the specimen before me as I write the gastral cortex is decidedly thinner than the dermal. Like the latter it is made up principally of triradiate spicules interwoven to form a feltwork; as before, the spicules are usually sagittal, with the long arm pointing towards the base of the sponge. The beautiful sagittal triradiates represented in figs. 13 and 14 occur also in the gastral cortex; and here, too, we meet with the quadriradiate spicules. The latter surround the short exhalant canals of the flagellated chambers, being arranged as shown in figs. 21 and 24, with the additional fourth ray projecting towards or into the lumen of the canal. Occasionally an unusually small exhalant canal is met with, cut transversely, in tangential sections of the cup-wall, a little below the level of the ordinary exhalant canals. Such small canals (fig. 21) are surrounded by quadriradiate spicules of the slightly different form already described.

On the extreme outside of the gastral cortex (i. e. the extreme inside of the cup-wall) there occur abundant oxeote spicules like those of the dermal skeleton, and arranged, in close-set tufts, perpendicularly to the surface with their broad ends outwards (fig. 22). Mr. Carter (3) states that the linear (oxeote) spicules on the "vent-side" of the cup-wall are twice the length of those on the "pore-side." This does not hold good as a general rule, for in the specimen before me the reverse is the case (fig. 22).

The Skeleton of the Peristome.

This consists of a fringe of the giant oxeote spicules already described (figs. 7—9), arranged with their broad ends projecting freely around the margin of the osculum, and their narrow ends embedded amongst a mass of approximately equiradiate triradiates, into which the dermal and gastral skeletons merge. The oscular fringe (fig. 25, *o. sp.*) thus formed is so very slightly developed in proportion to the size of the whole sponge that it is scarcely noticeable with the naked eye.

The Tubar Skeleton.

According to the manner in which the spicules are arranged around the flagellated chambers (radial tubes) Haeckel (7) distinguishes two types of tubar skeleton, (1) articulate (gegliedertes) and (2) inarticulate (ungegliedertes). The articulate tubar skeleton is always composed of triradiates, and is distinguished by the fact that along the length of the chamber there are always two or more transverse zones or "joints" of triradiates, one behind the other. The triradiates are usually sagittal, and the shaft is directed towards the dermal surface. The longer the flagellated chamber the greater is the number of joints in its skeleton.

Haeckel adds that in most Sycons with an articulate tubar skeleton the separate joints of the latter become specially differentiated. Thus the first or innermost joint is longer than the following; the outermost, on the other hand, is the shortest. The triradiates of the first joint, again, are most markedly sagittal, while their basal ray is unusually elongated, and their paired lateral rays are placed with convex, curved margin beneath the gastral surface. The triradiates of the following joints are usually less markedly sagittal, their basal ray less hypertrophied, and their oral angle generally smaller. Finally, at the distal end of the tube, towards the dermal surface, the sagittal triradiates generally pass over into the regular or subregular, and often into the irregular form.

The tubar skeleton in Grantia labyrinthica (fig. 22) is articulate, and agrees very exactly with the general description of such a skeleton given by Haeckel. The first joint is much longer than any of the others, and the sagittal triradiates composing it (=subgastral triradiates of Haeckel) are modified precisely as he describes, their short, curved, lateral arms lying beneath, or, indeed, forming a portion of, the gastral skeleton. The number of joints depends upon the length of the flagellated chamber, and this again varies with its position in the sponge, the older and longer chambers being situate nearer the base, and the younger and shorter ones nearer the margin of the cup.

It is hoped that fig. 22, which is drawn on the same plan as that adopted by Haeckel, will make all these points clear without further description.

It remains to be added that the two shorter arms of each triradiate curve slightly towards one another, so as partly to embrace the chamber which they help to support. This is seen in figs. 28 and 29, where, owing to the direction of the section at right angles to the long axes of the flagellated chambers, the shafts of the triradiates are cut off, while the paired lateral arms are seen partially surrounding the chambers.

The Skeleton of the Stalk.

This consists essentially of a confused mass of closely interwoven sagittal triradiates with very long and slender arms. One of these spicules is represented in fig. 19; often they are more or less irregular in form. On the extreme outside there is a layer of oxeote spicules disposed at right angles to the surface. Most of these spicules are small, and very like those found over the surfaces of the cup, but a large number are modified into giant forms (fig. 12), differing somewhat in shape from those which form the oscular fringe. These giant spicules give to the surface of the stalk a more or less hispid character. They are remarkable from the fact that they project to an unusual extent, so that commonly less than a quarter of the length of the spicule is embedded in the tissues of the sponge. The outer ends of the spicules are consequently generally worn or broken.

(*d*) The canal system.

Grantia labyrinthica appears to agree more closely with respect to the arrangement of the canal system with Haeckel's Sycortis lævigata (7) than with any other described form. The canal system of all the Sycons is, of course, fundamentally the same, but numerous, by no means insignificant, variations occur, especially with regard to the inhalant pores and canals.

The canal system of calcareous sponges may be described in precisely the same terms as that of the siliceous and horny sponges, and since it is advisable to preserve uniformity of nomenclature wherever possible, I shall follow Poléjaeff's example (8) in making use of such general terms as "flagellated chamber" and "inhalant canal" in preference to such special terms as "radial tube" and "intercanal" used by Haeckel for the Calcarea. The term "gastral cavity" I propose to retain in the present paper, because, although the gastral cavity corresponds functionally to the oscular tube of siliceous and horny sponges, it is very improbable that the two structures are homologous.

The Inhalant Pores.

According to Haeckel (7), in certain of the Sycons a portion of the inflowing water obtains direct access to the tubular flagellated chambers by means of "dermal ostien" situate at the distal extremity of the latter. This never takes place in Grantia labyrinthica, although Carter maintains, as I have already mentioned, that the pore-sieves are placed over, and lead into the distal ends of the chambers. As a matter of fact, the pore-sieves, or pore-areas, lie between the ends of the flagellated chambers, and over the ends of the inhalant canals. The blind ends of the flagellated chambers, on the other hand, are covered over by the well-developed dermal cortex.

Each group of pores—for which we may conveniently use the term pore-area as in other sponges—is usually more or less oval in outline, and contains a dozen or more small round pores (fig. 30). The longer diameter of the pore-areas averages about 0·33 mm. in length, and the diameter of the pores themselves about 0·033 mm. The pore-areas and pores are best studied in tangential sections of the dermal surface, a method the importance of which cannot be too strongly insisted upon. In the pore-areas the cortex is reduced to a mere thin membrane, corresponding to the dermal membrane of other sponges (e. g. Monaxonider), containing large numbers of small oxeote spicules, and perforated by the pores. If the section be very thin—only of about the thickness of the dermal membrane—it is not easy to determine the boundaries of the pore-areas, which lie very close together. If, however, the section be fairly thick, then a portion of the mesodermal trabeculæ separating the subdermal cavities will be included, and the appearance shown in fig. 30 will be presented, where each pore-area is seen overlying the end of an inhalant canal. Fig. 31 shows a single pore more highly magnified.

The Inhalant Canals.

These commence as widely expanded cavities immediately underlying the pore-areas. These cavities correspond in position to the subdermal cavities of other sponges, but they merge so gradually into the deeper parts of the inhalant canals, with which they are directly continuous, that it is impossible to distinguish the boundaries between the two. The inhalant canals (intercanals of Haeckel) are by no means regular; they may anastomose and they may branch. The anastomosis takes place—most frequently, at any rate—just below the surface, so that the pores of two contiguous areas may lead almost directly into one and the same inhalant canal. The branching takes place chiefly at the far end of the canals, towards the gastral surface.

At first very wide, the inhalant canals, as they penetrate below the dermal cortex and between the flagellated chambers, rapidly diminish in diameter, and finally come to an end just below the gastral cortex where the flagellated chambers are just commencing (figs. 25, 26, *in. c.*). In figs. 28 and 29, which represent sections taken at right angles to the long axes of the flagellated chambers, the inhalant canals are seen cut transversely between the chambers. In fig. 28, which represents a section taken not very far from the middle of the sponge-wall, the inhalant canals are still wide; but in fig. 29, which represents a section from near the gastral surface, the inhalant canals have become very much reduced in size.

The Prosopyles.

The term "prosopyle" is used by Sollas (9) to designate the openings of the inhalant canals into the flagellated chambers, and to distinguish them from the inhalant pores on the surface of the sponge. As it is a decided advantage to employ two separate terms for these two very distinct structures, I shall adopt Sollas's nomenclature.

The prosopyles in Grantia labyrinthica are numerous small circular apertures, each about 0·018 mm. in diameter, which place the inhalant canals in direct communication with the flagellated chambers. On looking down upon the wall of a chamber the prosopyles are seen fairly regularly scattered over it (figs. 23, 25). In this way they are most readily recognised, but in order to see the actual communication between the flagellated chambers and the inhalant canals it is necessary to examine very thin sections. We then see that the amount of mesodermal tissue intervening between the inhalant canals and the chambers which they supply is by no means great. On approaching a prosopyle (fig. 26, *pr.*) it thins away altogether, and the flattened epithelial lining of the inhalant canal meets the lining of collared cells of the chamber around the margin of the circular aperture. The prosopyles are scattered over the whole of the chamber, so that some are found quite close to the exhalant aperture (fig. 26); in such cases the water can only just enter the chamber and leave it again almost immediately.

Mr. Carter gives a very different account of the prosopyles in Grantia labyrinthica, which I have already quoted on a previous page. They do not, as he suggests, "serve for the purpose of intercommunication where the walls of the neighbouring chambers are in direct contact with each other, or for the purpose of allowing the ova developed in the intercameral tissue to pass into the chamber and thus be expelled." In the first place it appears, as I shall show presently, that the walls of neighbouring chambers never are in direct contact with each other, nor have I found their cavities ever in direct communication; and, secondly, I have been able to prove (**10**) that the embryos escape in a very different manner from that suggested.[1] In short, the prosopyles of Grantia labyrinthica agree in function and position with those of other Sycons as described and figured by Schulze (**11**), Poléjaeff (**8**), and others.

The Flagellated Chambers.

These have the usual Sycon character of more or less

[1] Cf. next page.

cylindrical tubes penetrating the sponge-wall at right angles to its two surfaces—not extending, however, completely from surface to surface, but terminating at either end just beneath the cortex (figs. 23, 25—27). In transverse section (figs. 28, 29) the chambers appear approximately circular, or at all events more or less rounded in outline, and not, as in many Sycons, polygonal from mutual pressure. The retention of the primitive cylindrical character is doubtless due to the fact that the chambers are not very closely packed, but separated by a fair amount of intervening mesoderm. At their peripheral ends the chambers terminate blindly beneath the dermal cortex, there being, as already stated, no dermal ostia to place them in direct communication with the exterior. At their peripheral ends also the chambers exhibit a marked inclination towards branching. I have endeavoured to represent the most striking instance of this which has come under my notice in fig. 23. This tendency towards branching of the chambers appears to be not very uncommon amongst the Sycons, and is mentioned by Schulze in the case of Sycandra raphanus (11). I hope to be able to discuss its possible significance at a later date.

In specimens, or in those parts of specimens which contain pretty far advanced embryos, the walls of the flagellated chambers are frequently seen to exhibit little shallow pits on their inner surface (fig. 23, *em. c.*). These little pits or pockets, instead of being lined by the usual collared cells, are lined by flattened pavement-cells. They are the remains of cavities in the mesoderm from which embryos have escaped by bursting through the wall of the chamber and tearing away part of it with them. The collared cells of the part torn away first become stretched out and flattened, as shown in fig. 38, by the pressure of the growing embryo beneath them; finally they appear to degenerate altogether, so as to form a structureless membrane, which is carried away bodily by the escaping embryo. For further particulars as to the mode of escape of the embryos the student is referred to my paper "On the Pseudogastrula Stage in the Development of Calcareous Sponges" already cited.

The stream of water leaves the flagellated chamber through the gastric ostium or exhalant aperture, a wide opening guarded by a delicate, membranous, sphincter diaphragm, as already described (4) by Carter (vide figs. 23—26).

In sections such as that represented in fig. 29 I have not infrequently met with peculiar structures having the appearance shown at *x* in the figure. These structures evidently represent some probably normal phase in the life-history of the flagellated chambers, and it appears to me not improbable that they may be chambers in process of dying.

That the Sycon chamber, as an individual, can die, is perhaps a somewhat novel idea; but if, as everyone will admit, an Ascon individual dies, there is no difficulty in supposing that a single chamber of a Sycon, which in many respects corresponds to an entire Ascon, should also die. Indeed, it is evident from the ontogeny of Grantia labyrinthica (vide infra) that as the stalk develops the first formed chambers must perish (fig. 27); and if so, why not individual chambers later on? Haeckel, in his work on the 'Challenger Deep-sea Keratosa' (12), suggests that the flagellated chamber is to be regarded as the individual, comparable to an individual person of a hydroid colony; and in accordance with this view we may certainly expect to find individual chambers perishing, while the sponge as a whole continues to exist healthily.

In the cases alluded to (fig. 29, *x*), the skeleton of what I believe to have been an originally normal and healthy chamber is still present in exactly its normal position and enclosing the normal space. This space, however, is no longer completely filled by the chamber, but the latter has shrunk away from the surrounding tubar skeleton into the centre, where it occupies little more than a third of its original diameter. The remains of the collared cells are distinctly visible, closely, if not exactly, resembling the collared cells which line the surrounding chambers, only less regularly arranged and in more than one layer. In the process of shrinking the mesoderm around the chamber has been pulled out into delicate strands forming a kind of network, but mostly radially disposed, and thus serving to suspend the dying or dead chamber as shown in the figure.

Fig. 28 (x) shows what is perhaps a later stage in events. The chamber occupies a still smaller space, and the surrounding mesoderm has become solid and homogeneous again. The arrangement of the spicules and of the surrounding chambers still indicates the space originally occupied by the dying chamber.

If the individual chambers die it is probable that they are replaced by new chambers; and, indeed, I shall give reasons later on, in describing the exhalant canals, for supposing that new chambers are actually interpolated between the old ones. Thus the older parts of the sponge may be kept alive and vigorous by the gradual replacement of the old flagellated chambers, as they reach their limits of existence and die off, by new ones. I have unfortunately found no evidence to show how the new chambers originate, but since the older flagellated chambers frequently branch it is not unlikely that they may also bud, or the new chambers may be developed from amœboid cells as in the embryo of Stelospongos (2). The problem is on much the same footing as the question, how are new chambers constantly added around the margin of the growing sponge-cup? and, so far as I am aware, no one knows. All I can say is that they commence life very small, and gradually increase in size as they grow older (figs. 25, 27); they make their first appearance in about the middle of the thickness of the sponge-wall, and apparently do not originate as outgrowths of the gastral cavity.

Another explanation of the unusual condition of the flagellated chambers described above is suggested by some observations of Sollas, in his report on the "Challenger" Tetractinellida (13), to the effect that the walls of the flagellated chambers in this group sometimes appear contracted, under which condition "fine filaments may be frequently observed produced from the base of the choanocytes and extending radially from the chambers into the surrounding matrix." "The whole appearance is suggestive of a contraction of the choanocytal wall under the influence of some strong stimulus, possibly of the alcohol into which the sponge was plunged on removal from the dredge."

Doubtless the unusual appearances of the chambers observed by Sollas and myself are in both cases due to contraction; and had I seen only such cases as that represented in fig. 29, *x*, I should have been strongly inclined to regard the contraction either as a merely temporary condition or as a post-mortem condition, produced, as suggested by Sollas, by the action of the alcohol. The appearances presented in fig. 28, however, in which the gelatinous matrix around the chamber has regained its normal condition, while the chamber is more contracted than ever, seem to me to demand a different explanation, which I have endeavoured to give above.

The Exhalant Canals.

Since the flagellated chambers do not extend to the actual gastral surface, but are separated therefrom by the entire thickness of the gastral cortex (fig. 26), the existence of special exhalant canals becomes necessary in order to place the chambers in communication with the gastral cavity. These exhalant canals are short, wide, cylindrical tubes, sharply marked off by the sphincter diaphragms already described from the chambers at the one end, and opening directly, without any narrowing or diaphragm, into the gastral cavity at the other (fig. 26).

I have already had occasion to mention that sometimes an unusually small exhalant canal is met with, cut transversely, in tangential sections of the cup wall a little below the level of the ordinary exhalant canals. Such small canals are surrounded by quadriradiate spicules of a slightly unusual form (fig. 21). I am at a loss to explain the existence of these smaller canals, with their slightly peculiar spicules, unless they be simply the exhalant canals of young interpolated flagellated chambers, surrounded by young spicules. This view is supported by the fact that the spicules in question are somewhat smaller than the more ordinary quadriradiates.

The Gastral Cavity and Osculum.

As already pointed out in my description of the external form of the sponge, the gastral cavity and osculum are greatly modified by the peculiar mode of growth of the sponge. The gastral cavity, instead of being narrow and tubular, has become wide and basin-like, and at the same time, owing to the convolutions of its wall, extremely irregular. The osculum has thus become wider than any other part of the gastral cavity—a condition the opposite of that which obtains in other Sycon sponges.

Sometimes traces of the gastral cavity may be found in the stalk even of adult sponges, causing the latter to be more or less hollow. This indicates that the gastral cavity originally extended all through the sponge—a fact which is proved, as I shall show later on, by the ontogeny.

(*e*) The histology of the soft tissues.

The terms ectosome and choanosome, proposed by Sollas (**15**) and adopted by myself (**2**) in describing siliceous and horny sponges, are not convenient for at any rate the great majority of the Calcarea, and it is better to classify the tissues simply under the heads ectoderm, mesoderm, and endoderm. I must follow the example of Schulze (**14**) in considering that the ectoderm of the larval sponge (in the case of the Sycons, at any rate) furnishes not only the epithelium of the dermal surface, but also the epithelial lining of the inhalant canal system; while the endoderm lines the remainder of the canal system from the prosopyles to the margin of the osculum, and the mesoderm furnishes all the remainder of the sponge body.

The Ectoderm.

The ectoderm resembles exactly what Schulze has described (**11**) in Sycandra raphanus, consisting of a single layer of flat, polygonal epithelial cells lining the dermal surface of the sponge and the inhalant canal system. These cells are most readily distinguished around the inhalant canals, where they are less obscured by spicules and other mesodermal structures than on the dermal surface. The nucleus is surrounded by the very characteristic granules described by Schulze in Sycandra. In my preparations I have only after some trouble succeeded in making out the boundary lines between the individual cells, and Schulze himself observes that it is remarkable that the boundaries of these cells—sometimes so distinct—are not always clearly visible. Nevertheless I have been able to determine the shape of the cells pretty accurately, and found them to agree precisely with Schulze's drawings.

The Endoderm.

This consists, as in other Heterocæla, of two parts: (1) a layer of flattened epithelial cells lining the gastral cavity and the short exhalant canals of the chambers; (2) a layer of collared cells lining the flagellated chambers themselves. The epithelial portion of the endoderm exhibits no features of special interest and needs no further description, so we may pass on at once to the collared cells.

Dr. R. von Lendenfeld has recently (16) called in question the accuracy of my description of the collared cells, with their connecting membrane, in Stelospongos (2), observing, "Es ist jedoch seine schematische Darstellung dieser Membran (Taf. xxxii, fig. 9) keineswegs Vertrauen-einflössend, sondern eher ein Beweis der theoretischen Unwahrscheinlichkeit der Existenz derselben." Notwithstanding this criticism, I still maintain the correctness of my original description and figures, and have already published a note (17) in the 'Zoologischer Anzeiger' in reply to Dr. von Lendenfeld's observations. The latter are apparently based partly on imperfect observation, and partly on the convenient, albeit somewhat unphilosophical, assumption that all sponges must be exactly alike in this respect. Dr. von Lendenfeld finds that in certain sponges examined by him "der Raum zwischen den Kragenzellen von einer durchsichtigen, der gewöhnlichen Grundsubstanz der Zwischenschicht der Spongien sehr ähnlichen Substanz ausgefällt sei;" and the only conclusion at which he is able to arrive with regard to the question of Sollas's membrane is that it does not exist, and that Professor Sollas and I have only misinterpreted what it has been reserved for him to correctly describe. But in spite even of a preconceived "theoretische Unwahrscheinlichkeit" I adhere to my original opinion. For my own part, I am unable to see where the theoretical improbability comes in. Quite recently Mr. Carter has, in a private letter, afforded me valuable corroborative evidence of the existence of Sollas's membrane. He says, "I have seen in the brim of the collar of the Calcisponge spongozoon plastic amalgamation like that produced by two semi-fluid bits of gum—under which circumstances, if all became amalgamated, then you would have Sollas's membrane. Might it not so happen that at one time they may be so amalgamated and at another not, and thus produce the difference?" That Sollas's membrane originated in the almost accidental manner here indicated there can be no doubt, but I am inclined to think that in many sponges it has become a more or less fixed and constant character—a view supported by the fact that, as I shall show later on, it is still recognisable when both collars and flagella are withdrawn. It is exceedingly likely from the nature of the case that it may have originated independently in several groups, so that in each group forms with and forms without it may exist. If so it is only another instance of that homoplasy so characteristic of the Porifera.

I am not aware that there is anything particularly new in Dr. von Lendenfeld's observation that "die Kragenzellen stehen nicht frei auf der Oberfläche der Zwischenschicht, sondern sie sind in dieselbe Eingesenkt" (16). Indeed, in my paper on Stelospongos (2) I have said, "I have not been able to trace any definite outline to the body of the cell which is embedded in the highly granular ground-substance." It is amusing to see Dr. von Lendenfeld so vigorously opposing one of my observations which does not happen to fit in with his idea of the fitness of things, and at the same time taking another from my very next page and putting it forward as though it were original.

Sollas's membrane, however, and the intercellular substance which exists between the bases (and, so far as I have seen, between the bases only) of the collared cells have nothing whatever to do with one another. The former is endodermal in origin, and is separated by a wide empty space from the probably mesodermal ground-substance between the collared cells. In the case of Stelospongos, if the mesodermal ground-substance really filled up the whole of the intervals between the collared cells it would be at once recognisable by its highly granular appearance; but it does not, as a glance at my figures will show; it stops at the bottom of the neck.

I must now describe the condition of things in Grantia labyrinthica. All the collars and flagella of the collared cells are retracted in my preparations. This is not to be regarded as a purely artificial and post-mortem condition, but probably rather as a periodically recurring phase in the life-history of the cells. Carter has shown long since (**18**) that the individual collared cells may become amœboid, and probably in the living sponge they often spontaneously retract their collars and flagella and enjoy a period of rest.

In this retracted condition the collared cells (figs. 32, 33) of Grantia labyrinthica are somewhat pyramidal bodies, polygonal in transverse section, and with the narrow end pointing towards the lumen of the chamber. They measure about 0·0048 mm. in height and about the same in breadth at the base. The nucleus is situate in the apex of the pyramid (fig. 33). This position of the nucleus appears at first sight a little curious, but it is interesting to observe that it agrees with the position of the nucleus in the long prismatic cells of the embryo (fig. 38) from which the collared cells of the adult are admittedly derived. Thus the collared cells in a state of rest revert more or less to their embryonic condition, the chief distinction being that they are now very much shorter.

Even at their bases the collared cells appear to be separated from one another by distinct intervals (fig. 32), but these may possibly be due to shrinkage. The apices of the cells are still further apart, and in longitudinal sections (fig. 33) are seen to be connected by a fine, sharp line running from one to the other. This line is Sollas's membrane seen in section, no longer supported on the tops of the collars, which have been retracted, drawing the membrane after them close down into the apices of the cells. So Sollas's membrane remains visible even when the collars of the cells are retracted, which indicates that it is probably a more or less permanent structure, and no mere temporary fusion of the margins of adjacent collars.

Owing to the great transparency of the gelatinous mesodermal ground-substance—which is a very characteristic feature of calcareous sponges—it is not possible to determine, as in the case of Stelospongos, exactly how far it extends between the collared cells. Probably there is considerable individual variation in this respect, and it is a matter of little importance to ascertain exactly how far each cell happens to be sunk in the matrix. I cannot believe, however, that the actual collars are ever embedded.

I understand that Mr. Bidder has already pointed out that Sollas's membrane occurs in a calcareous sponge, Leuconia aspera, but I have neither been able to see his paper nor to find out where it was published.

The Mesoderm.

The constituents of the mesoderm may be divided into two main classes, the cells and the cell-products. We will consider the cell-products first; they consist of the intercellular ground-substance and the spicules, and as the spicules have been already fully described we have only to deal with the ground-substance. The ground-substance[1] consists of the usual transparent jelly, exhibiting no differentiation excepting a slight concentration around the spicules, forming the so-called spicule sheaths. These are very distinct, and are always seen to be continuous with the surrounding ground-substance when the spicules themselves have been dissolved out by the

[1] Maltha of Haeckel (12).

action of weak hydrochloric acid. This view regarding the nature of the spicule sheaths has been already expressed by Haeckel and Schulze (**11**), and is doubtless the correct one.

The mesodermal cells, which lie embedded in the ground-substance, may be classified as follows :

(1) Amœboid.
(2) Stellate.
(3) Glandular :
  (*a*) Spicule-secreting.
  (*b*) Slime- or cuticle-secreting.
(4) Endothelial.
(5) Muscular.
(6) Nervous.
(7) Reproductive.

Amœboid Cells.—Concerning the amœboid cells proper I have no information to add to that which we already possess. They are distinguished from the stellate cells by their more rounded and massive form, and their more abundant and more granular protoplasm. Certain of them, as is well known, develop into ova, and these I shall describe later on.

Stellate Cells.—These, which may be regarded as the connective-tissue cells of the sponge body, have also the usual form, characterised by the long, slender, and often branched processes given off from an inconspicuous central mass of protoplasm surrounding the nucleus (fig. 26, *st. c.*). It is very probable that, as in the case of Stelospongos (**2**) and other sponges, adjacent stellate cells may be united by their slender processes, but I have not succeeded in clearly demonstrating the connection here.

Glandular Cells.—These are of two kinds—spicule-secreting, and slime- or cuticle-secreting cells. We will consider the spicule-secreting cells, or calcoblasts, as they have been termed by Poléjaeff (**8**), first.

It is generally admitted that both calcareous and siliceous spicules originate within special mother-cells, but probably in both cases they subsequently receive additional layers of the calcareous or siliceous material from other cells. Poléjaeff (**8**) figures a "conjectural calcoblast" attached to the outside of a spicule of Leuconia multiformis. This cell has the form of an ordinary stellate mesodermal cell, and such, so far as structure is concerned, I believe the calcoblast to be. In the horny sponges the corresponding spongoblasts, although somewhat specialized in form, are clearly only slight modifications of stellate cells, as I have elsewhere shown (2). In the calcareous sponges the calcoblasts have acquired the function of secreting carbonate of lime without undergoing any corresponding modification in form. It should, however, be borne in mind that there are probably two kinds of calcoblasts, primary and secondary. The primary calcoblasts are the mother-cells in which the spicules originate, and the secondary calcoblasts are the cells which secrete additional layers of calcareous matter around the spicule after it has been formed. In the same way I have no doubt that there are primary and secondary silicoblasts.[1]

The slime- or cuticle-secreting cells have, so far as I am aware, not hitherto been observed in calcareous sponges, although well known in the Keratosa through the researches of von Lendenfeld. In Grantia labyrinthica the gland-cells in question occur in a single layer just beneath the epithelium of the surface of the sponge. They are very distinct and plentiful on the gastral surface (fig. 26, *gl. c.*), but less so on the dermal. Each gland-cell consists of an irregular, granular, nucleated body, which closely resembles an ordinary amœboid cell, but which may be seen under favorable conditions to be connected with the overlying epithelium by one or more processes. Fig. 26 shows the layer of gland-cells beneath the gastral epithelium, and fig. 34 is a more highly magnified drawing of an individual gland-cell and its surroundings, as it appeared under a Zeiss F objective and ocular 4. At the particular spot figured an irregularity in the surface caused the epithelium to be cut somewhat tangentially, while the gland-cell itself was cut vertically; the connection between the two is, however, very well shown. Four processes are shown in this

[1] For an illustration of a primary silicoblast the student is referred to the 'Report on the "Challenger" Monaxonida,' pl. xxi, fig. 13.

instance connecting the gland-cell with the epithelium, but it is very unusual to see so many. Just on the right of the gland-cell the epithelium is raised up by a projecting spicule which does not itself appear in the section. On the dermal surface of the sponge the gland-cells are more like ordinary amœboid cells immediately underlying the epidermis.

The essential agreement of these cells with those described by von Lendenfeld in, for example, Dendrilla cavernosa (19) is obvious, both as regards structure and arrangement. According to this author the cells secrete a cuticle which is not to be distinguished from the spongin of the horny fibres. I agree that they probably secrete a cuticle, but, as Vosmaer points out (20), no grounds are given for supposing that this is identical with the spongin, and the fact that similar gland-cells occur in the Calcisponges argues against the assumption. Very possibly the cuticle, after a time, more or less entirely replaces the original epithelium, and not only, as suggested by von Lendenfeld,[1] so much of it as may have been accidentally damaged. Hence, perhaps, arises the difficulty of making out the structure of the surface epithelium.

Endothelial Cells.—The embryos, which I have described elsewhere (10), lie each in a separate cavity in the mesoderm around the flagellated chambers. These embryo-containing cavities (fig. 38, *em. c.*) are lined each by a single layer of pavement-cells, which are not to be distinguished in my sections from the pavement-cells already described. These cells I regard with Schulze (11) as being of mesodermal origin, and hence endothelial.

In my memoir on Stelospongos flabelliformis (2) I regarded the embryo-containing cavities in that sponge as probably, though by no means certainly, specialized parts of the exhalant canal system. As the result of further study, however, I must relinquish this view, and regard the cavities as special excavations in the mesoderm, and the remarkable giant pavement-cells which line them as of mesodermal origin.

[1] For an abstract of von Lendenfeld's observations on the subject vide 20.

Muscular Cells.—Certain spindle-shaped cells lying in the membranous diaphragms of the exhalant apertures of the flagellated chambers are probably muscular in function. The cells in question are shown in fig. 24, which renders further description unnecessary.

Nerve-cells.—The only cells which I have found in Grantia labyrinthica to which a nervous function can possibly be assigned are certain structures which occur around the margins of the inhalant pores, as shown in fig. 31. These cells are elongated radially in relation to the circular pores which they surround. The nucleus is distinct and is placed at the distal end of the cell, and the main mass of protoplasm stretches from the nucleus to the edge of the pore, where it ends in an expansion along the free margin. There may also be indications of smaller processes given off near the base of the cell. It is probable that the thickening of the main protoplasmic process of each cell as it touches the margin of the pore may simply indicate a retracted, sensitive, hair-like process such as Stewart (21) and Lendenfeld (22) describe; but it seems also just possible that each nerve-cell naturally ends in a sensitive plate or expansion at the free margin of the pore. If we adopt the former of these two views the sensitive cells will be seen to agree pretty closely in structure with those described and figured by Stewart in Grantia compressa; but I have met with no evidence of the grouping of the cells into "synocils," as described and figured by von Lendenfeld. Von Lendenfeld, however, has also described single sensitive cells ("Sinnes-Ganglienzelle") around the inhalant pores of his Chalinissa communis, var. flabellum (23), which in structure and arrangement almost exactly agree with those found by me in Grantia labyrinthica except that he figures the end of the main protoplasmic process projecting for a short distance beyond the margin of the pore. This slight difference may, as will be gathered from what I have already said, be due to differences in state of contraction in the two cases. It is interesting to note that the sense-cells of Grantia labyrinthica agree more closely with those of so different a sponge as

Chalinissa communis than they do with those of the closely related Grantia compressa. We must associate with this fact the fact that the arrangement of the pores in Grantia labyrinthica also agrees much more closely with that which usually obtains in the Chalininæ than with that found in Grantia compressa, thus affording another instance of homoplasy.

The cells which Sollas (13) describes and figures as possible sense-cells ("æsthocytes") in the Tetractinellida appear to be of a more problematical character.

Reproductive Cells.—The only reproductive cells which I have met with are the ova. These, as in other sponges, are obviously derived from amœboid cells, and in the earliest stages of their development it is impossible to distinguish between the two. Later, however, the ova become more rounded off, and the nucleus becomes large and distinct.

It is now generally admitted that the ova of sponges are fertilised by spermatozoa probably of other sponges, which gain admission to the sponge with the inflowing current of water. No one, however, so far as I can discover, has attempted to find out whereabouts in the sponge the union of ovum and spermatozoon takes place. Having followed the spermatozoon into the canal system they leave it there to take care of itself, forgetting that, unless some special arrangement exists to prevent such a catastrophe, it will speedily be washed out again through the osculum without ever having had a chance of fulfilling its errand. The general assumption would seem to be that the spermatozoon loses its way through the walls of the canals, and wanders about in the gelatinous mesoderm until it happens to come across an ovum. It seems highly improbable that this should be the case, for it would be a strange thing if the spermatozoa bored their way through the epithelium, as they would have to do in order to get into the gelatinous ground-substance, without any obvious inducement to do so. Mr. Carter seems to have come nearer to the truth than anyone, but without realising the true significance of what he saw. He says (24) that the ovum in Grantia compressa "may be seen to be hanging, pear-shaped, upon the surface of the excretory canals, where it remains for a certain time locomotive, until, after further development, it becomes permanently fixed, and the locomotive envelope seems to pass into a capsule." It is obvious that by "excretory canals" Mr. Carter means the inhalant canals, and he is probably wrong in considering that the locomotive envelope of the ovum passes into a capsule; but the main fact, that the ovum at a certain stage of its existence hangs freely from the surface of a portion of the canal system, is clearly brought out.

In Grantia labyrinthica I have distinctly observed the ova hanging from the epithelial lining of the inhalant canals by means of short peduncles, and projecting freely into the lumen of the canal, where they must be washed by the incoming stream of water. Fig. 35 represents an amœboid ovum approaching the surface of an inhalant canal; and figs. 36 and 37 represent it, after having passed through the epithelium, hanging freely by its short peduncle, awaiting fertilisation. In fig. 37 the nucleus of the ovum appears very near the surface, in a position suggestive of the formation of a polar body. Probably the ova pass through the epithelium of the inhalant canals in the same way that the white blood-corpuscles pierce the walls of the capillaries in higher animals.

After fertilisation the ovum probably migrates back into the gelatinous ground-substance, and takes up its position near the wall of a flagellated chamber, there to undergo the earlier stages of its development. This seems more probable, from what we know (10) of the position of the embryos, than the supposition that it remains and develops in the spot where it is fertilised.

It is probably a general rule in sponges that the ova are fertilised while hanging from the walls of the canal system, and that they migrate first of all through the canal-wall to be fertilised, and then back again into the gelatinous ground-substance to undergo development; hence the necessity for the amœboid movements so characteristic of sponge ova. Thus we see that the sponge ovum plays an unusually active part in the process of fertilisation, as it were meeting the spermatozoon halfway. The migrations of the ova in sponges remind one forcibly of Weissmann's descriptions of the migrations of the ova in various hydroids (25).

The Post-embryonic Development of Grantia labyrinthica.

The embryology of Grantia labyrinthica, so far as the material at my disposal has allowed me to work it out, forms the subject of a special memoir (**10**), so that it is unnecessary for me to deal with the question in this place. The post-embryonic development, however, has not as yet been dealt with, and although there is but little to be said about it, yet that little is of interest as clearly indicating the manner in which the very peculiar external form has been evolved.

Fig. 1 shows the youngest stage found, in which it will be seen that, as regards both size and shape, the sponge differs but little from an ordinary Grantia. The wall of the tube is even and not convoluted, although already the osculum is the widest part of the gastral cavity. Fig. 27 represents somewhat diagrammatically a longitudinal section of this specimen, and is important chiefly because it shows how the stalk arises by the filling up of the lower portion of the gastral cavity with a copious growth of mesodermal tissue in which numerous spicules are developed. As I have already pointed out, remnants of the gastral cavity may sometimes be recognised in the stem even of adult specimens. Figs. 2 and 3 represent two stages intermediate between that just described and the full-grown sponge (fig. 4). The specimen drawn in fig. 3 is very much compressed, so as to be bilaterally symmetrical. This may either be accidental, or it may indicate the commencement of folding in the wall of the cup. All figures are drawn of the natural size, and they render further description needless.

I may conveniently here describe the only case of budding with which I have met in the species. On the outer surface of the wall of the cup in a well-grown specimen, and not far below the margin, a small individual had budded off from the parent sponge. This is represented, twice the natural size, in fig. 5. The gastral cavity of the young sponge is still connected with that of the mother by a very evident aperture, and it is interesting to notice that in this case the osculum is distinctly constricted, so that the bud has the typical Sycon form.

The So-called Family Teichonidæ.

The very artificial group of sponges now generally known under the name Teichonidæ has been unfortunate from first to last. It was not even christened properly, for the title of Mr. Carter's original paper (3) is printed "On Teichonia, a New Family of Calcareous Sponges, with Descriptions of Two Species;" while subsequently, on the same page, the name Teichonellidæ is given to the new family, which is concisely diagnosed as "vallate." Then the genus Teichonella is diagnosed as follows: "Vallate or foliate, without cloaca. Vents numerous, confined to the margin or general on one side of the lamina only; naked."

Teichonella prolifera is described as the first species of the genus, and in the same paper Grantia labyrinthica is described as a second species. Subsequently, as I have already said, Mr. Carter withdrew Grantia labyrinthica from the genus Teichonella, and recognised its true position amongst the Sycons.

Now we see upon what slight foundations spongologists build their edifices. Poléjaeff (8) adopts the new family, altering the name, however, to Teichonidæ. He states that the main character of the family consists in the differentiation of the outer surface into two planes, one bearing oscula, the other pores exclusively; and he enters into a curious speculation as to whether a Teichonid is "a colony with dislocated oscula and pores," whatever that may be. But what authority had Poléjaeff for stating that the outer surface was differentiated into two planes, one bearing oscula and the other pores? Mr. Carter never said so. His diagnosis of the family is "vallate," while even his generic diagnosis says nothing about the pores. In the description of the type species (Teichonella prolifera), however, we find the words "pores invisible to the naked eye, scattered over the surface thickly, and generally vents slightly marginated, . . . arranged more or less in a single line along the margin only." I have myself most carefully examined Teichonella prolifera by means of stained sections cut by the paraffin method, and I find that it is nothing but an ordinary Leucon, with pores on both surfaces of the low, thick walls of which the sponge consists, and oscula along the raised margin (fig. 6). The surface is certainly not differentiated into anything like a pore-bearing and an osculum-bearing plane.

The fact appears to be that Poléjaeff wanted a place for his new genus Eilhardia, and so he seized upon the Teichonellidæ and altered both the name and the characters of the family to suit his own ideas, apparently without having so much as ever seen a specimen of Teichonella. Of course, both Teichonella and Eilhardia duly appear in an elaborate genealogical tree.

Eilhardia, if Poléjaeff's figures be correct, is a Leucon. True, the pores appear to be on one surface and the oscula on the other, but can anyone possessed of the slightest knowledge of the subject regard this as a family character? I think certainly not, and in support of my opinion venture to call attention to the following extract from Ridley and Dendy's report on the "Challenger" Monaxonida (26):—"Before leaving the question of the pores we must consider briefly the condition of flabellate sponges in this respect. It is an almost invariable rule that in flabellate sponges the pores are to be found on one surface and the oscula on the other. Thus in Phakellia ventilabrum, var. connexiva (pl. xxxv, figs. 3, 3*a*; pl. xlix, fig. 3), and Phakellia flabellata, nobis (pl. xxxiv, figs. 2, 3, 3*a*), this arrangement is very well illustrated; and the same condition occurs in Myxilla frondosa, nobis (pl. xxvi, figs. 1, 1*a*), and Gellius flabelliformis, nobis (pl. xxvi, figs. 5, 5*a*). Again, in that very remarkable sponge, Esperiopsis Challengeri (pl. xviii), the pores occur only on the concave surfaces of the lamellæ (pl. xviii, fig. 4), while the oscula are all on the convex surfaces.

"By far the most remarkable instance of this kind is, however, afforded by a boring Suberite which we have described under the name Cliona dissimilis (p. 227, pl. xxv, fig. 5, &c.). Here the sponge has bored its way into a flattened coral which it completely surrounds; hence it has itself acquired a flattened, lamellar form, and we find the pores collected in areas (woodcut, fig. 11, *pa.*) on one side of the sponge, and the oscula (woodcut, fig. 11, *o.*) on the other.

"There is no other known example, so far as we are aware, of a lamellar Suberitid sponge; and even the species in question is lamellar only because it has bored into a lamellar coral, and yet the pores and oscula are arranged just as they would be in a free-living frondose sponge, such as Phakellia. There must be some strong reason why as soon as a sponge, for any cause, acquires a lamellar form, the oscula become confined to one surface and the pores to the other, and to account for the occurrence of this condition in genera so widely separated as Gellius, Myxilla, Phakellia, and Cliona. What this reason may be we cannot at present say."

I am still no better able to give an explanation of this curious phenomenon than I was when the above passage was written; but the facts appear to me to be conclusive evidence against the value of the peculiar arrangement of the pores and oscula as a family character.

But even if it were allowed that the arrangement of the pores and oscula were a character of family importance we could not put Eilhardia and Teichonella in the same family, for, as I have shown, they differ widely from one another in this respect. Then, according to Poléjaeff's diagnosis, not Eilhardia, but Teichonella, would have to come out of the family Teichonidæ. As a matter of fact the family ought to be abandoned altogether, and the three species which have been at various times placed in it distributed as follows:

Teichonella prolifera	Leuconidæ.
Eilhardia Schulzei	Leuconidæ.
Grantia labyrinthica	Syconidæ.

It would not have been necessary to deal with this question so carefully had not Poléjaeff's emended family Teichonidæ met with such general and unquestioning acceptance. Thus Vosmaer adopts it in his most important work (20), and Lendenfeld (6) gives it a place in his system and in the inevitable genealogical tree. Haeckel also accepts the family in his latest work on sponges (12).

In conclusion I wish again to record my great indebtedness to Professor Howes for his kindness in correcting the proofs of this paper in my absence from England.

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DESCRIPTION OF PLATES I—IV,

Illustrating Mr. Arthur Dendy's paper "Studies on the Comparative Anatomy of Sponges. III.—"On the Anatomy of Grantia labyrinthica, Carter, and the So-called Family Teichonidæ."

PLATE I.

Figs. 1, 2, 3.—Three early stages in the post-embryonic development of Grantia labyrinthica. Nat. size.

Fig. 4.—Adult specimen of Grantia labyrinthica, growing upon a mass of foreign matter. Nat. size.

Fig. 5.—Portion of an adult specimen of Grantia labyrinthica, with a bud attached to the outer surface. × 2.

Fig. 6.—Specimen of Teichonella prolifera, showing the oscula distributed along the raised margin. Nat. size.

PLATE II.

Skeleton of Grantia Labyrinthica.

Figs. 7, 8, 9.—Large linear spicules (oxea) from the margin of the osculum. Zeiss, D, ocular 2, camera.

Figs. 10, 11.—Oxea from the surface of the cup. Zeiss, D, ocular 2, camera.

Fig. 12.—Large oxeote spicule from the surface of the stem. Zeiss, D, ocular 2, camera.

Figs. 13, 14, 15, 16, 17, 18.—Different forms of triradiate spicules from the wall of the cup. Zeiss, D, ocular 2, camera.

Fig. 19.—Sagittal triradiate spicule from the stem. Zeiss, D, ocular 2, camera..

Fig. 20.—Quadriradiate spicule from the gastral cortex. Zeiss, D, ocular 2, camera.

Fig. 21.—Arrangement of quadriradiate spicules around the exhalant canal of a young flagellated chamber.

Fig. 22.—Arrangement of the skeleton as seen in vertical longitudinal section of a chamber from gastral to dermal surface.

PLATE III.

Anatomy of Grantia Labyrinthica.

Fig. 23.—A single flagellated chamber and its exhalant canal, in part laid open by longitudinal section. *ex. c.* Exhalant canal. *di.* Diaphragm. *pr.*

Prosopyle. *fl. c.* Cavity of flagellated chamber. *em.* Embryo. *em. c.* Embryo-containing cavity (the embryo has already escaped in this case). The collared cells are coloured red, and the embryos brown. Zeiss, D, ocular 2.

Fig. 24.—Exhalant opening of a flagellated chamber, with its membranous diaphragm (*di.*). *mus.* Muscle-cells. The spicules are coloured blue, and the collared cells (which lie somewhat below the level of the diaphragm) red. Zeiss, F, ocular 2.

Fig. 25.—Part of a section vertical to the margin and to the two surfaces of the wall of the cup. *em.* Embryo. *o. sp.* Spicules of the oscular fringe. *p.* Inhalant pore. *p. a.* Pore-area. *in. c.* Inhalant canal. *g. s.* Gastral skeleton. *d. s.* Dermal skeleton. *t. s.* Tubar skeleton. Other lettering and colouring as before. Zeiss, A, ocular 3.

Fig. 26.—Gastral portion of a thin section similar to the last, but more highly magnified. *gl. c.* Gland-cells lying beneath the gastral epithelium. *st. c.* Stellate cell. Other lettering and colouring as before. Zeiss, F, ocular 2.

Fig. 27.—Vertical section through the young specimen represented in Fig. 1. *gas. c.* Gastral cavity. *mes.* Growth of mesodermal tissue filled with spicules, to form the stalk. Flagellated chambers red, spicules blue.

PLATE IV.

Anatomy of Grantia Labyrinthica.

Fig. 28.—Portion of a section taken parallel to the surface of the sponge-wall, and somewhat nearer to the dermal than to the gastral surface. It will be noticed that the inhalant canals are still of large size. *s. sp.* Sections of the shafts of the triradiate spicules of the tubar skeleton. *x.* Peculiarly modified flagellated chamber. Other lettering and colouring as before. Zeiss, D, ocular 2.

Fig. 29.—Portion of a section similar to the last, but taken near the gastral surface, showing the diminution in diameter of the inhalant canals, &c. Lettering and colouring as before. Zeiss, D, ocular 2.

Fig. 30.—Portion of the dermal surface sliced off, showing the pores arranged in pore-areas. Some of the spicules are omitted. Lettering and colouring as before. Zeiss, A, ocular 2.

Fig. 31.—A single pore more highly magnified, showing the nerve-cells (*n. c.*) around its margin. Zeiss, F, ocular 2.

Fig. 32.—A group of collared cells (with retracted collars and flagella), seen from above or below. *n.* Nucleus. Zeiss, F, ocular 3.

Fig. 33.—A row of four collared cells (with retracted collars and flagella), seen from the side. *n.* Nucleus. *s. m.* Sollas's membrane shrunk down upon the apices of the cells. Zeiss, F, ocular 3.

Fig. 34.—A single gland-cell (*gl. c.*) connected by four processes with the

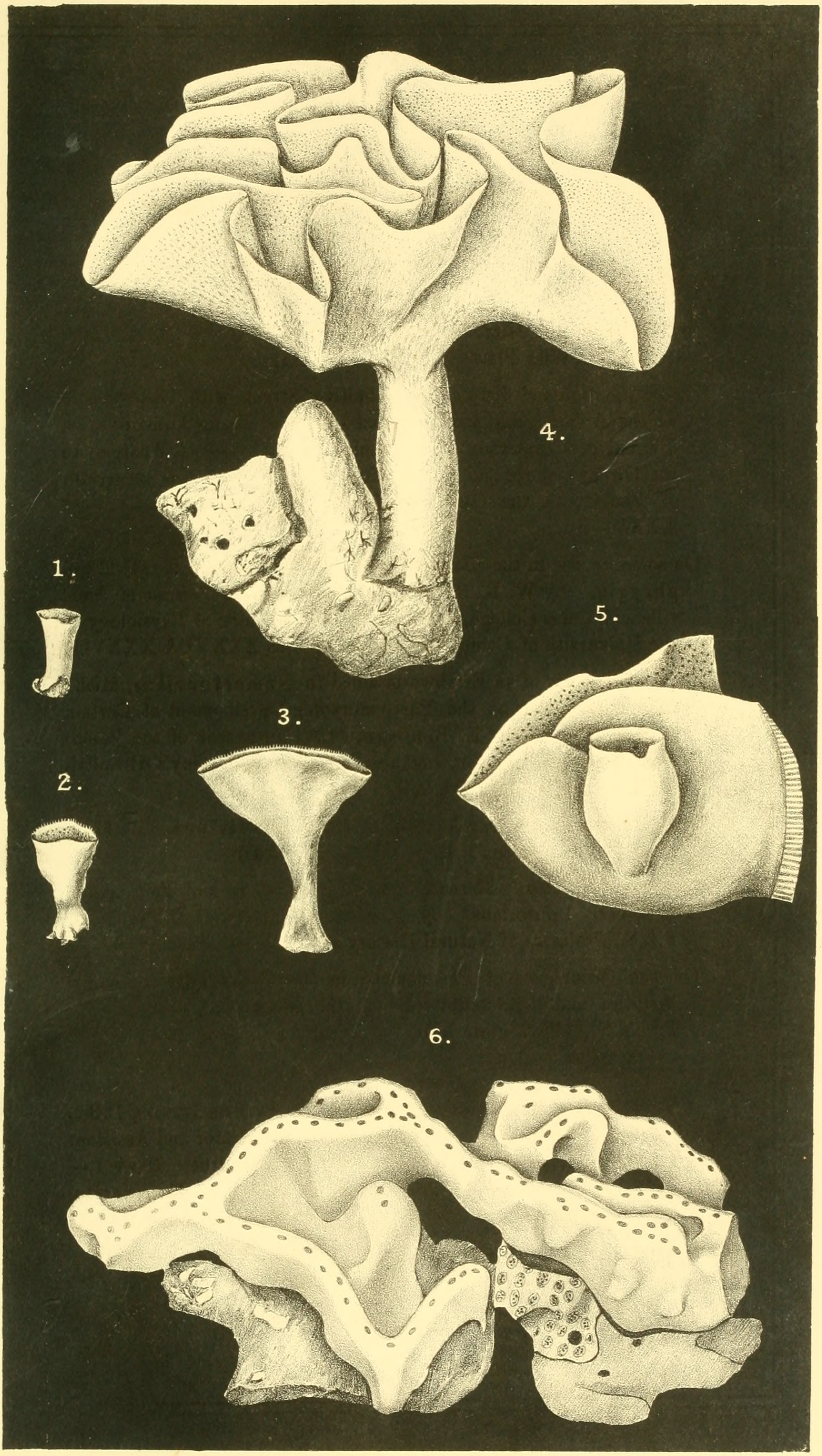
overlying epithelium (*ep.*), which latter is cut almost tangentially owing to the unevenness of the surface. *p. ep.* Projection of the surface epithelium around a protruding spicule, which latter is not itself seen in the section. Spicules blue. Zeiss, F, ocular 4.

FIG. 35.—An amœboid ovum (*ov.*) lying in the gelatinous ground-substance of the mesoderm, near the epithelium (*ep.*) of an inhalant canal. Zeiss, F, ocular 3.

FIG. 36.—An ovum (*ov.*) hanging by a stalk from the epithelium (*ep.*) of an inhalant canal. Zeiss, F, ocular 3.

FIG. 37.—Another example of an ovum (*ov.*) hanging by a stalk from the epithelium (*ep.*) of an inhalant canal. Zeiss, F, ocular 3.

FIG. 38.—An embryo (approaching the pseudogastrula stage) lying within the embryo-containing capsule in the mesoderm, between two flagellated chambers of the mother sponge. *col.* Collared cells of mother sponge. *sp.* Spicule of mother sponge. *end.* Prismatic cells (future endoderm) of the embryo. *mes.* Incipient mesoderm of the embryo. *gr.* Layer of large granular cells of the embryo. Other lettering as before.



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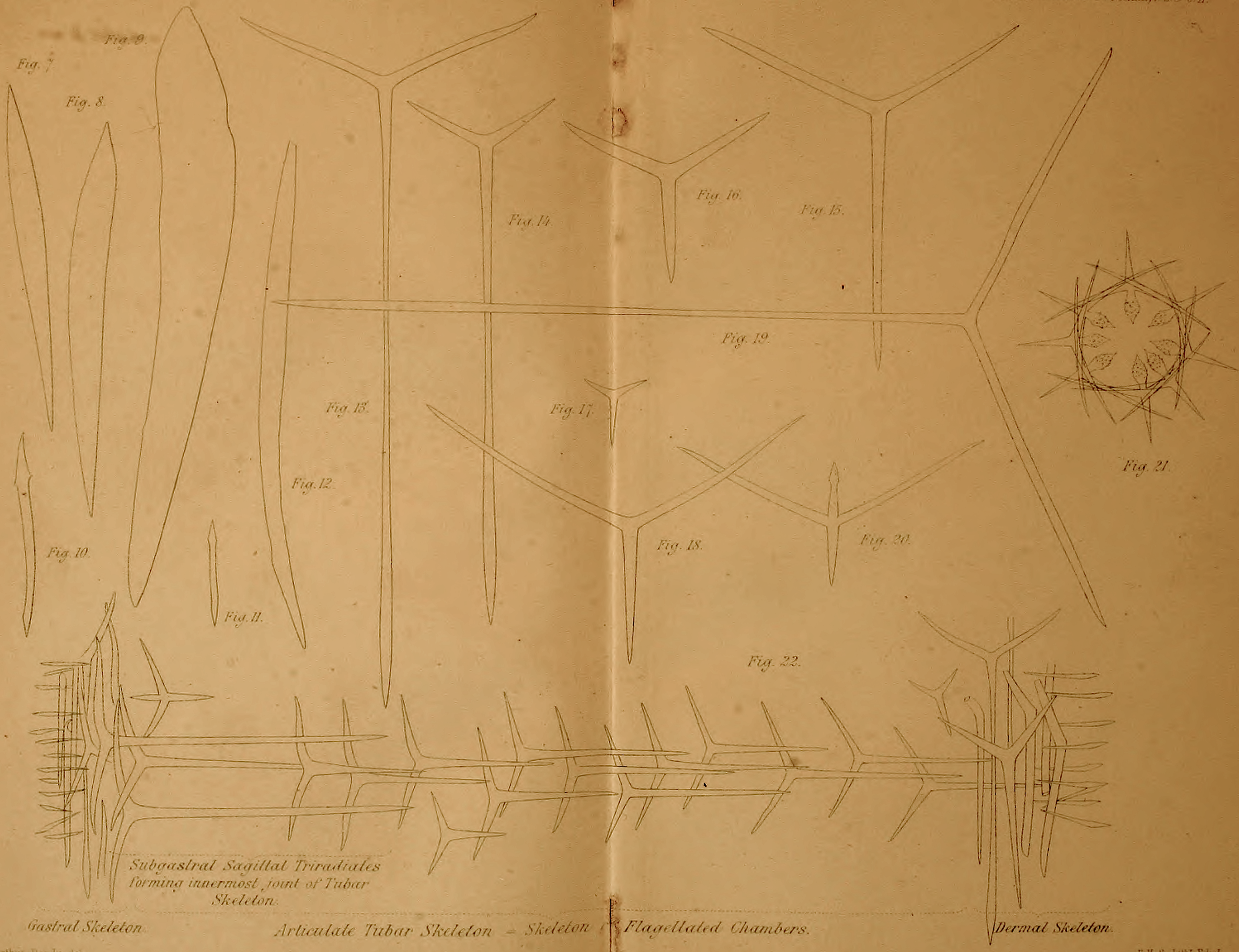

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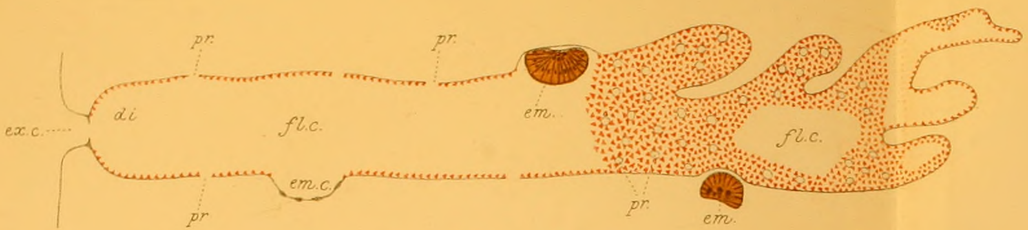

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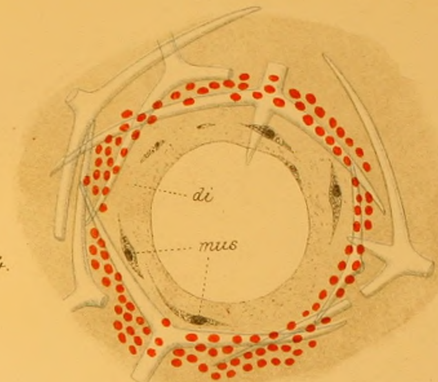
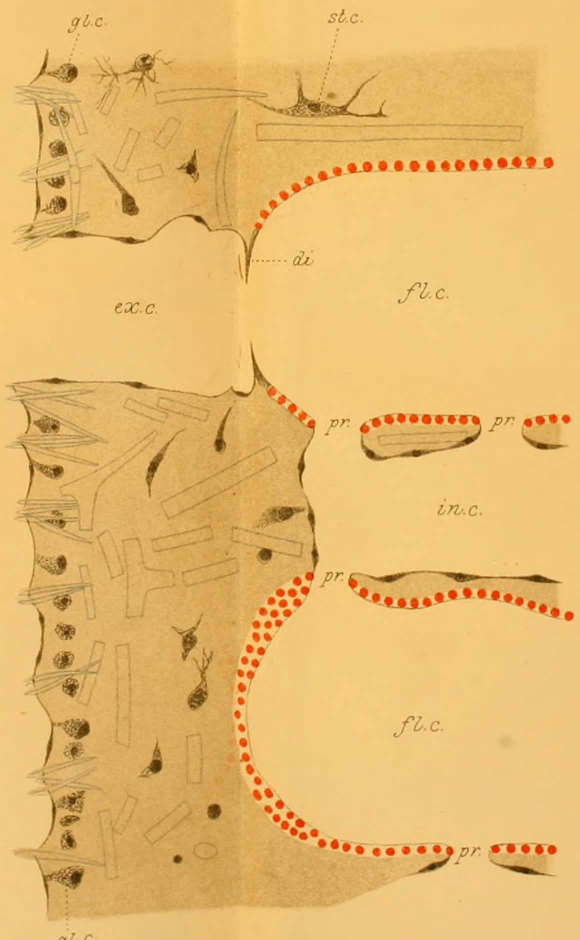


Fig. 24.

Fig. 26.



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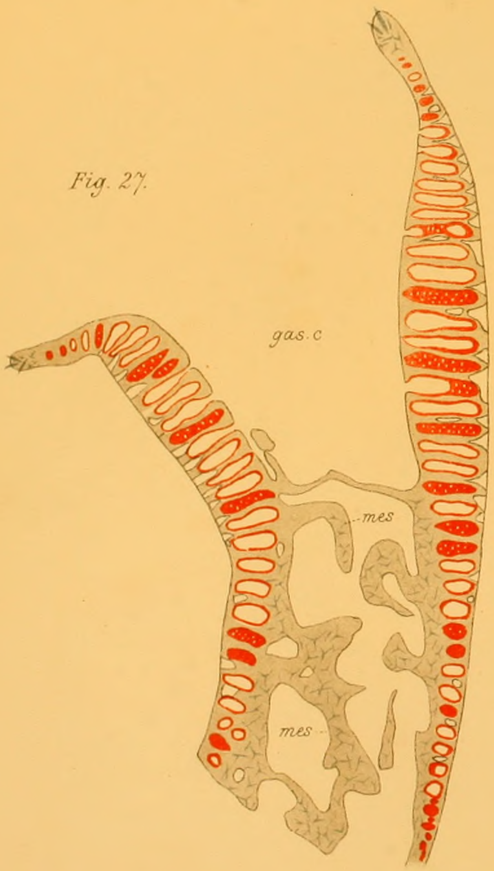

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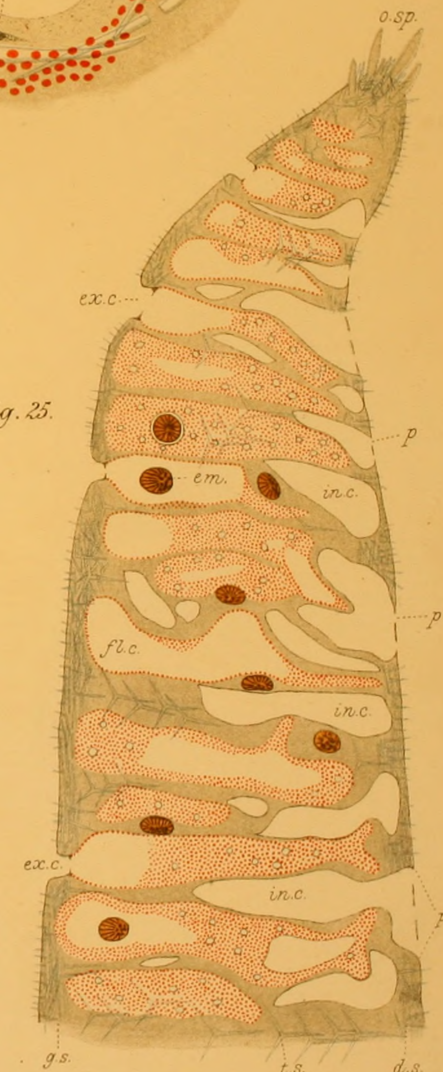

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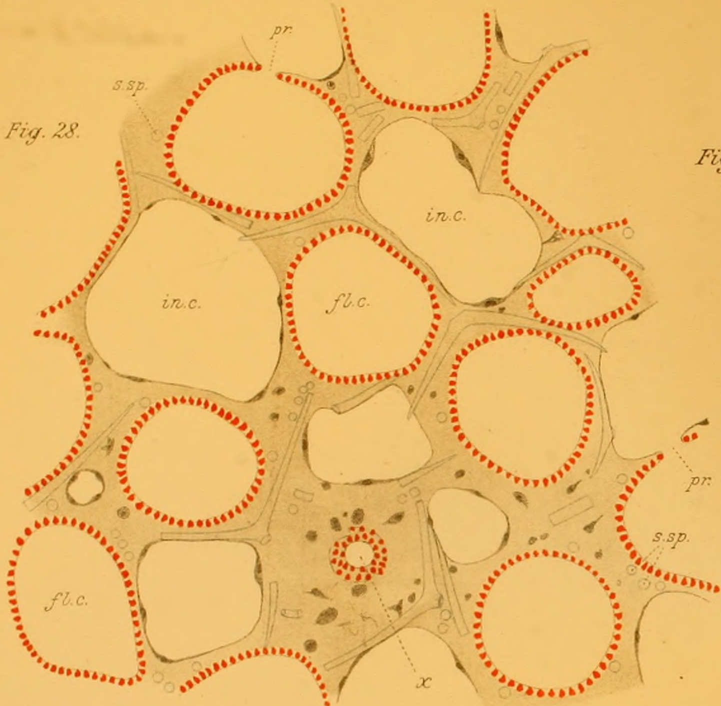
Fig. 28.



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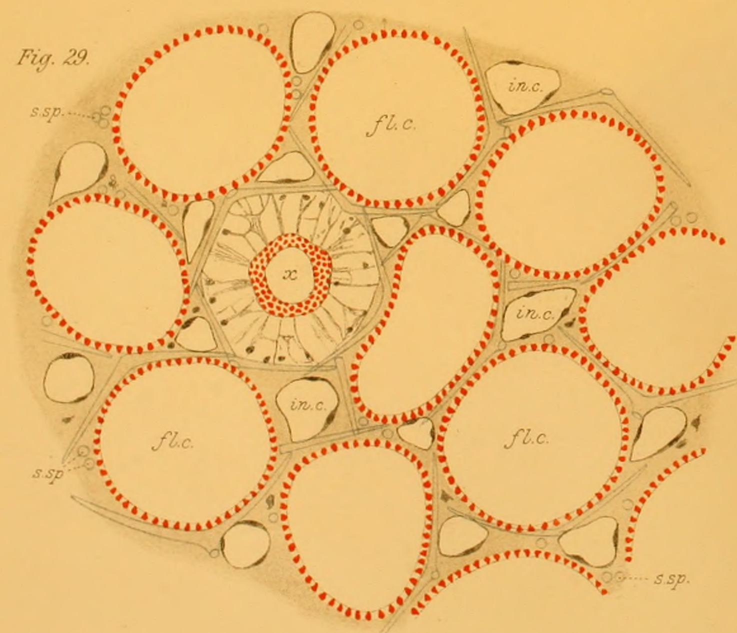

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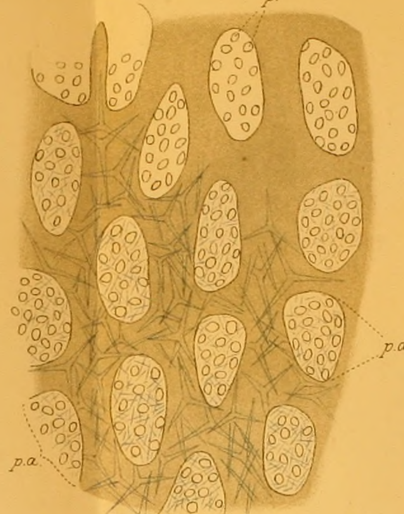

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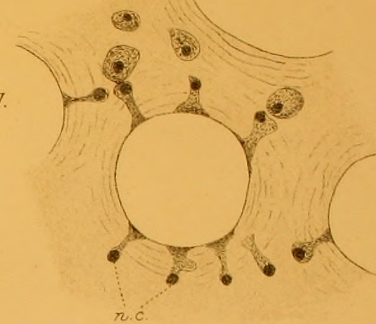

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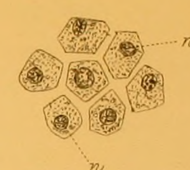
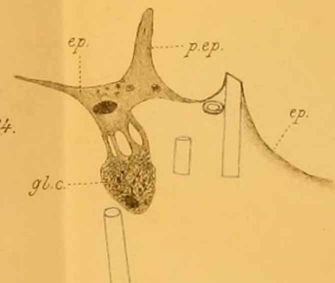


Fig. 33.

Fig. 34.



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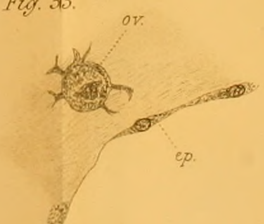

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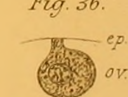
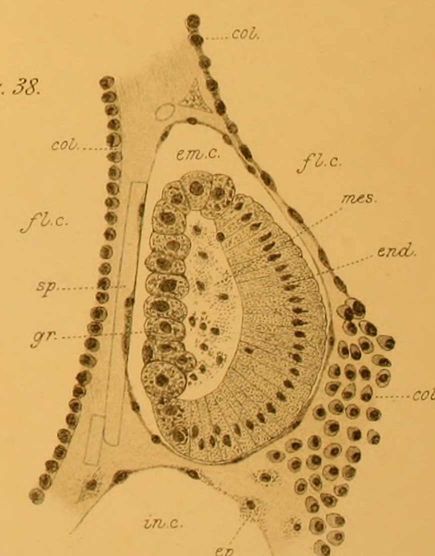


Fig. 37.

Fig. 38.



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