Studies on the Comparative Anatomy of Sponges.

V. Observations on the Structure and Classification of the Calcarea Heterocœla.

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With Plates 10—14.

I. Preface.

The object of the present paper is to give a general account of the anatomy, histology, and classification of the Calcarea Heterocœla, from the point of view of one who has for some time past been engaged in an independent study of the group. The exceptionally fine collection of Calcarea Heterocœla which I am fortunate enough to have at my disposal must be my justification for making this attempt.

Concerning the anatomy and histology of the group, I have perhaps not much to say that is new, but I hope that by bringing together our information on the subject in a collected form I may be of some use to students of spongology. Serious errors have from time to time crept into our information as to the anatomy of the Heterocœla, and I can only hope that I have not reproduced any of them in this paper. As, however, by far the greater part of my information has been derived from personal observation, I feel tolerably safe in this respect.

With regard to classification, I have been obliged to depart

widely from the lines laid down by previous writers. The necessity for doing so was forced upon me when preparing my "Synopsis of the Australian Calcarea Heterocœla" (4). In that paper I proposed a classification of the group based upon a personal examination of forty-seven species, and a careful consideration of the published accounts of species which I had not seen. In the Synopsis, however, I had not space to justify the classification proposed, merely giving it as a skeleton upon which to arrange my descriptions of species. The task of justification I reserved for the present occasion, and I have endeavoured to fulfil it rather by a critical re-examination of the anatomy of the group than by a detailed criticism of the systems of other spongologists. A great deal depends upon whether one regards the canal system or the skeleton as affording the most reliable guide to the systematist, for the characters of the two certainly appear to contradict one another. Here, as in similar cases, I believe that a compromise is the only satisfactory way out of the difficulty, as neither set of characters is solely reliable. The skeleton evidently follows the canal system up to a certain stage of organisation, and then begins to vary independently. Up to this stage I believe the canal system to be most important; after it I think the skeleton has prior claims, while the canal system becomes of secondary value. According to this idea, which will be found elaborated later on, I regard the Leuconoid type of canal system as of polyphyletic origin, as also the "Sylleibid" type, and I abandon the old families Syconidæ (Sycones) and Leuconidæ (Leucones) of Haeckel, as well as the more recent Sylleibidæ of von Lendenfeld. I have previously shown (9) that the very generally accepted family Teichonidæ must be abandoned, and I am glad to see that von Lendenfeld follows my lead in this (10), although he declines to acknowledge any indebtedness to my writings.

As I have naturally adopted my own classification as a basis for the arrangement of the subject-matter of this paper, it may be convenient to the reader if I give an outline thereof at once, reserving further discussion as well as the

necessary diagnoses till later on. The following, then, is the classification proposed:

Families.	Genera.
1. Leucascidæ	1. Leucascus.
2. Sycettidæ	2. Sycetta.
	3. Sycon.
	4. Sycantha.
3. Grantidæ	5. Grantia.
	Sub-genus Grantiopsis.
	6. Ute.
	Sub-genus Synute.
	7. Utella.
	8. Anamixilla.
	9. Sycyssa.
	10. Leucandra.
	11. Lelapia.
	12. Leucyssa.
4. Heteropidæ	13. Grantessa.
	14. Heteropia.
	15. Vosmaeropsis.
5. Amphoriscidæ	16. Heteropegma.
	17. Amphoriscus.
	18. Syculmis.
	19. Leucilla.

Before concluding these introductory remarks it is my pleasant duty to express my sincere thanks to various friends, without whose assistance this paper could not have been prepared. To Mr. J. Bracebridge Wilson, M.A., I owe, as usual, the greater portion of my material, and I am also indebted to Professor W. Baldwin Spencer, Mr. T. Whitelegge, and the authorities of the Adelaide Museum for a number of very valuable Australian sponges; while numerous fragments of type specimens from the British Museum, most generously forwarded to me by Dr. Günther, have been of the greatest service. Lastly, I must again thank Professor G. B. Howes for most kindly undertaking the correction of the proof in my absence from England.

The numbers in parentheses, in the text, refer to the list of literature at the end. The technical descriptions of a large

number of the species referred to, or references to places where they are to be found, are given in my "Synopsis of the Australian Calcarea Heterocœla" (4).

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II. The Canal System of the Calcarea Heterocœla.

The simplest type of canal system in the group is found in the genus Sycetta. This is, unfortunately, a genus which I have never had the opportunity of personally examining, and I am indebted for my information concerning it to Haeckel's great work on the Calcarea (5).

A Sycetta individual consists, in the first place, of a central tube, which bears at its summit a single osculum leading from the cavity of the tube (gastral cavity) to the exterior. This central tube gives off all around and throughout its length numerous short, hollow, conical diverticula (the radial flagellated chambers). Each radial chamber communicates by a single exhalant opening at its proximal end with the central gastral cavity, and each has its wall perforated by numerous much smaller apertures (the prosopyles), through which the water passes from the exterior into the cavity of the chamber. It is important to notice that the radial chambers, of which there may be a large number, all stand perfectly free from one another and do not touch at any point, so that the water is free to circulate between them without obstruction of any kind, and to penetrate right in to the outer surface of the wall of the central gastral cavity. Hence there is no true inhalant canal system, further than the small prosopyles by which the water gains access to the interior of each chamber. The wall of the central gastral cavity is very thin, so that the chambers open almost directly into the latter, the wide "exhalant canals" which conduct the water through the wall being comparatively short and inconspicuous.

The collared cells are, of course, confined to the interior of the radial chambers, while the central gastral cavity and the

outer surfaces of the radial chambers and of the central tube are doubtless caused by a layer of pavement epithelium, as in other Heterocœla.

Such, then, is the simplest type of canal system met with amongst the Heterocœla; and, as it appears to me, all the higher types met with in the group may be derived from some such simple radiate one by modification in one or more of the following ways:

(1) By the outer surfaces of adjacent radial chambers coming in contact with one another and fusing together. This fusion at first takes place irregularly and partially, and then more completely and throughout the length of the chambers, so as to divide the water-containing space which surrounds the chambers into a series of more or less well-defined inhalant canals, sometimes called "intercanals" (compare figs. 2—5).

(2) By the closing in of the inhalant canals at their distal ends by the outgrowth of a thin, pore-bearing, dermal membrane from the walls of the radial chambers at or near their distal extremities. In this way true "dermal pores" are formed, through which the water gains access to the inhalant canals (compare figs. 3, 6—8).

(3) By the increase in thickness of the dermal membrane and the development in it of a special skeleton, so as to form a thick cortex, which not only stretches between but also covers over the ends of the radial chambers. The formation of such a thick cortex necessitates the development of a more or less highly specialised "cortical inhalant canal system," which places the dermal pores in communication with the deeper parts of the inhalant canal system (compare figs. 9—12, 23).

(4) By the branching of the radial chambers, and consequently of the inhalant canals which lie between them (compare figs. 7, 9, 10, 18, 20).

(5) By increase in thickness of the wall of the central tube (gastral cortex), and consequently also in the length of the exhalant canals (compare figs. 4, 9, 10).

(6) By retreat of the collared cells towards the distal

extremities of the chambers, their place being taken by pavement epithelium. This results in elongation and branching of the exhalant canals, and in corresponding shortening of the chambers, which may be thus converted from the elongated radial chambers of the Syconoid type to the short, rounded, and irregularly arranged chambers of the Leuconoid type. Branching of the primitively straight chambers is of course also necessary in order to effect this change (compare figs. 10, 19, 21, 17, 16).

(7) By evagination or folding of the wall of the central gastral cavity, which also results in elongation of the exhalant canals, and possibly also in branching of the same (compare fig. 7). As pointed out by Sollas (6), it is often extremely difficult, if not impossible, to decide which of the two sets of causes indicated in this and the preceding paragraph respectively have operated in the production of a particular type of canal system, though in some cases the arrangement of the skeleton (fig. 7) may furnish a clue to the problem. Though I do not doubt that in some cases a certain amount of folding of the wall of the gastral cavity has taken place, I do not believe that this cause has operated to any great extent, in the production of the Leuconoid from the Syconoid type of canal system.

(8) By the fusion of different Syconoid or Leuconoid individuals[1] of a branching colony to form a compact whole, in which the individuality of the different members is more or less completely obliterated (compare fig. 15).

Other minor causes have also doubtless aided in the production of various modifications in the canal system; such are the enormous dilatation of the gastral cavity and osculum in Grantia labyrinthica (9), and the strong development of the mesoderm in the walls of the flagellated chambers which takes place in some forms. The causes (or sets of causes)

[1] By the terms Syconoid and Leuconoid individuals I mean simply individuals or "persons" consisting each of a single, central osculum-bearing tube enclosing the gastral cavity, and surrounded by flagellated chambers and canals arranged according to the "Sycon" or "Leucon" type, as the case may be.

given above are, I believe, the principal ones to which we must look for an explanation of the peculiarities in the canal system about to be described in different genera of Heterocœla.

The various genera (with the possible exception of Leucascus) might, as regards the canal system, be arranged in a gradually ascending series, commencing with Sycetta and ending with those genera, such as Leucandra, in which the Leuconoid type reaches its maximum development. Such a series would not, however, as I believe, represent a natural arrangement of the group, for there is, as I hope to show later on, strong reason for concluding that the most highly modified Leuconoid type of canal system has been independently arrived at in several distinct genera. At present, however, we need not concern ourselves with this question, but pass on to consider to what extent the various causes indicated in the above scheme have operated in modifying the canal system in each separate genus. I propose to deal with the genera in the order in which they occur in my system of classification. In this manner, having first of all disposed of Leucascus, we shall be able to start with Sycetta, and trace the gradual evolution of the canal system from its simplest Syconoid form in that genus, to its most complex Leuconoid one as exhibited in Leucandra. We shall then, in each of the two remaining families (Heteropidæ and Amphoriscidæ) which are distinguished by skeletal peculiarities, be able to start fresh with a Syconoid type of canal system, and work up again to the Leuconoid.

Leucascus (fig. 1).

In this genus the sponge is more or less massive or lobate, and it is not possible to distinguish a single central gastral cavity. There may be several oscula, which perhaps indicates that the whole sponge is then to be regarded as a colony composed of several fused individuals. The arrangement of the canal system in L. simplex, as seen in a vertical section through the osculum, is shown in fig. 1. The flagellated chambers are very long, and copiously branched. Their blind distal extremities lie beneath the dermal surface, towards

which they are directed more or less at right angles, so that the chambers certainly exhibit a more or less radial arrangement. At their proximal ends the chambers open into wide and long exhalant canals, which converge towards the osculum. The distal ends of the chambers are covered over by a thin membrane, strengthened by spicules and perforated by numerous inhalant dermal pores. These pores lead into a series of quite irregular spaces lying between the branching chambers. These spaces represent the inhalant canals, and convey the water to the prosopyles in the thin walls of the chambers. In all specimens which I have seen of L. simplex and in one of L. clavatus (4) the mesoderm is feebly developed, so that the dermal membrane, the walls of the chambers, and the walls of the exhalant canals are all very thin, and the entire sponge has consequently a soft and delicate texture. In one of the specimens which I have referred to, L. clavatus, the mesoderm is very strongly developed; the sponge thereby acquires a dense and solid texture, and the canal system is correspondingly reduced in dimensions. This strong development of the mesoderm is perhaps to be associated with the fact that the specimen contains very numerous embryos; for the normal condition of the genus appears to be one with all the canals and chambers thin-walled.

This genus, as already indicated, does not appear to come into what may be called the typical series of Heterocœla; and its relationships and systematic position will be discussed later on. Though I do not suppose that it has ever passed through a Sycetta stage in its history, it is easy to see how its canal system may have been derived from a radiate ancestral type, by modification along the lines suggested above.

Sycetta.

The simple form of canal system met with in this genus has already been described. If we exclude from the genus Haeckel's S. strobulus, S. cupula, and S. stauridia, which are all corticate species, and include, as von Lendenfeld (10) has rightly done, Sycetta (Sycaltis—H.) conifera, we are

left with three species, all of which exhibit the same type of canal system, in which the radial chambers are short, straight, and unbranched, and project quite separately and independently from the wall of the central gastral cavity.

According to Haeckel (5) there is in Sycetta primitiva, and also in certain more highly organised species of Syconoid Heterocœla, a single larger aperture at the distal end of each radial chamber, which he terms a "dermal ostium." Poléjaeff, however, has (8) thrown considerable doubt on the existence of "dermal ostia" in any case, and I cannot help agreeing with him in attributing the supposed presence of these structures to an error of observation on the part of their describer.

Sycon (figs. 2—7).

In this genus we meet with a considerable amount of variation in the canal system. The simplest form is found in such species as the European S. ciliatum (Bauerbank's Grantia ciliata) and S. raphanus, and in the Australian S. Carteri and S. minutum (4). For a detailed account of S. raphanus I may refer the student to Schulze's well-known and admirable memoir (7).

These species mark but a slight step upwards from the Sycetta type. In Sycon Carteri, for example (fig. 2), the radial chambers are rather short, and more or less thimble-shaped; they touch one another in some places, and there fuse together by their outer surfaces. Their distal ends, however, project freely, and thus form well-marked "distal cones" on the surface of the sponge. By the fusion of adjacent chambers at the points of contact, the originally continuous water-containing space which surrounds all the chambers becomes broken up into more or less definite inhalant canals ("inter-canals"), whose exact form depends, of course, upon the shape of the chambers and the extent to which they fuse together, and is of no great importance. In the simplest cases, such as Sycon Carteri (fig. 2) these canals appear, in sections taken along the length of the chambers, as straight narrow gaps

between adjacent chambers. In the case of Sycon raphanus, Schulze (7) has shown that the different inhalant canals often inter-communicate through gaps left by the incomplete fusion of adjacent chambers, and this condition probably occurs to a greater or less extent in a great many cases.

Probably in most species of the genus Sycon, and certainly in the four with which we are now more immediately concerned, the distal ends of the inhalant canals ("inter-canals") are in no way closed in; in other words, the spaces between the distal cones of the radial chambers remain widely open. Thus the water still has direct access to the prosopyles, without having to pass through the pores of a dermal membrane. In Sycon ensiferum (4), a species closely related to S. raphanus, the basal rays of many of the most distally situated tuber triradiates are very strongly bent outwards from the walls of the chambers, so as to curve over and protect the entrances to the inhalant canals.

In the common Australian S. gelatinosum (figs. 3—6) we meet with a slight but very interesting advance in organisation. The radial chambers, though of considerable length, are still straight, and usually unbranched, subcylindrical tubes. The mesoderm of the chamber walls is strongly developed, and the inhalant canals between the chambers are very well defined and squarish in transverse section (fig. 8). The gastral cortex is rather thick, and consequently the exhalant canals take the form of distinct, though short and wide, tubes, sharply marked off from their respective chambers by well-developed chamber diaphragms, which appear to be almost universally present in calcareous sponges (fig. 4). A tangential section of the dermal surface (fig. 6) shows that the distal ends of the chambers, each crowned with its tuft of oxeote spicules, do not touch one another, but are separated by rather narrow gaps or spaces, across which stretches a delicate pore-bearing membrane (seen in section in fig. 3). This membrane is doubtless formed as an outgrowth of the ectoderm and mesoderm of the walls of the chambers. In Sycon gelatinosum it contains no spicules. The fusion

of adjacent chambers does not commence until a short distance within this pore-bearing membrane, so that the dermal pores lead at first into a continuous subdermal space, from which the true "inter-canals" penetrate between the chambers.

In another Australian species, to which I have given the name Sycon boomerang (4), we meet with yet further complication. The principal features in the anatomy of this species are shown in figs. 7 and 8. The radial chambers are very long, thin-walled, and very much branched, especially towards their distal ends.[1] The irregularity in the branching causes the tufts of oxea at the distal ends of the chambers to form an irregular series of prominences on the surface of the sponge (fig. 8). Owing to the branching of the chambers the inhalant canal system also becomes very irregular. The wall of the gastral cavity is rather thick, and the length of the exhalant canals appears to be further increased by an irregular and not very extensive folding of the same (fig. 7). As in S. gelatinosum, a thin pore-bearing membrane extends between the ends of the radial chambers, but in S. boomerang a few spicules are found in this membrane (fig. 8).

In Sycon giganteum (4), a very large species from the Gulf of St. Vincent, which closely resembles S. gelatinosum in structure, the radial chambers are narrow and greatly elongated; they branch repeatedly, and the branches run parallel with one another to the dermal surface. They communicate with the gastral cavity through rather long exhalant canals, which commence at some distance beneath the gastral cortex. These canals appear to have been formed by modification of the proximal portions of the radial chambers, from which they are separated as usual by diaphragms. They may unite together before opening on the gastral surface. The inhalant canals are irregular and very narrow, opening on the dermal surface through narrow, irregular chinks between the tufts of oxeote spicules which cram the distal ends of the chambers. I have not been able to detect any pore-bearing

[1] It appears from Schulze's researches that branching of the chambers may take place even in such a simple form as S. raphanus (7).

dermal membrane stretched across the openings, which are so narrow that such a structure could hardly be required.

In Sycon Ramsayi, a species common in Port Jackson and described by von Lendenfeld (11), the exhalant canals, though confined within the limits of the thick gastral cortex, are extraordinarily well-defined cylindrical tubes, and it is interesting to notice that although the long radial chambers are themselves unbranched, and there is no indication of the exhalant canals having been formed by modification of their proximal ends, yet these canals may unite together before opening on to the gastral surface, and thus present a branching structure. In other respects Sycon Ramsayi agrees in canal system with the simpler species of the genus.

Sycantha.

We owe our information concerning this sponge entirely to von Lendenfeld, who has recently described it from the Gulf of Trieste, and from his work (10) the following details as to the canal system are taken.

Sycantha tenella (the only species) is a large, tubular sponge, with a single terminal osculum. The gastral cortex is thin, and forms a cylindrical tube. From the outer surface of the gastral cortex project tufts, which are partially united together by membranes, and attain a length of 2—4 mm. Each tuft runs out into a number of flexible points. These points are the free distal ends of the flagellated chambers of which the tufts are composed. Ten to twenty chambers, united at their bases, form a tuft, each of which is thus a group of flagellated chambers. The chambers themselves are long and narrow. At the base they are irregularly prismatic, generally quadrangular in cross-section. The free, always unbranched, terminal portion is circular in cross-section, and runs out into a conical point. In their basal portions the chambers touch one another, and here there are no inhalant canals (inter-canals) between them, so that collared cells are found on both sides of all membranes which occur in the interior of the basal portions of the tufts. In these membranes,

which separate the different chambers from one another, roundish openings occur, which place the cavities of all the chambers of a group in direct communication with one another. One or several of the chambers of each group are placed in connection with the central gastral cavity through openings in the gastral cortex.[1] Small circular inhalant pores (prosopyles) occur in large numbers in the free distal portions of the chamber walls. Sycantha tenella is said to be distinguished from all other Sycons by the fact that the chambers do not all communicate directly with the central gastral cavity, and also by that of their non-communication with one another in groups, the stream of water passing partly from chamber to chamber before it reaches the gastral cavity.

I am inclined to think that the apparent intercommunication of the chambers may be due to an error of observation. It is by no means the first time that such a condition has been described. Poléjaeff observes (8) that "there is no doubt that what Haeckel declares to be 'dermal ostia' and 'dermal pores' in the individuals of his 'Syconusa type' were merely the pores of the intercanals; and what he calls 'conjunctive pores,' these latter uniting, according to him, the cavities of the radial tubes, were nothing but the common pores on the side walls of the radial tubes connecting these latter with the intercanals. To anyone who will notice Professor Haeckel's remark that these 'conjunctive pores' are best to be observed in sections of dry Sycones, the error into which he fell will be easily comprehended." It is a noteworthy fact in this connection that von Lendenfeld himself observes that his specimens of Sycantha tenella had been preserved for some time in not very strong spirit, so that he was unable to make any observations on the finer histological characters. He also refers to the extraordinary delicacy of the mesoderm in all parts.

I may also remind the reader that Carter (12) bases an

[1] Later on in the work referred to (p. 192) we are told that "jede Kammergruppe ist durch eine einzige grössere Oeffnung in der Gastralmembran mit dem centralen Oscularrohr in Verbindung."

entire genus (Hypograntia) on the supposed presence of such "large holes of inter-communication between the chambers."

On the whole it appears to me that Sycantha tenella probably presents a slight modification of the simpler Sycon type of canal system, having the radial chambers united in groups.

Grantia (figs. 9, 10).

The canal system of this genus may be regarded as derived from the Sycon type by the conversion of the thin, pore-bearing, dermal membrane which we first met with in Sycon gelatinosum (figs. 3 and 6) and then, with the addition of a few spicules, in S. boomerang (figs. 7 and 8), into a more or less strongly developed spicule-bearing cortex, which not only extends between the ends of the radial chambers, but also covers them over, so that we no longer find in this genus distal cones projecting from the dermal surface.

A thoroughly typical example of the genus is afforded by the Australian Grantia extusarticulata (4), the anatomy of which is represented in fig. 9. The radial chambers are almost straight, cylindrical, and only slightly branched; between them lies the irregular and more or less lacunar inhalant canal system. The dermal or inhalant pores are irregularly scattered through the dermal cortex, which is well developed and about 0·07 mm. thick. The gastral cortex is of about the same thickness, and is perforated by the short, wide exhalant canals; one coming from each chamber, and separated from it by a constricting diaphragm.

Grantia Vosmaeri (4), another Australian species, whose anatomy is represented in fig. 10, illustrates in an extremely interesting manner the gradual shortening of the radial chambers and the corresponding elongation of the exhalant canals, accompanied by a strong development of the mesoderm which surrounds the latter. Here, again, the junction between exhalant canals and flagellated chambers is clearly marked by well-developed diaphragms. The dermal cortex is very thick, and the dermal pores communicate with the deeper parts of

the inhalant canal system through distinct, though not very regular, cortical canals.

I have already, in an earlier paper (9), given a detailed account of the anatomy of the somewhat aberrant and very remarkable Grantia labyrinthica. In its essential features the canal system agrees with that of G. extusarticulata, and there are only two points to which I need refer again in this connection. The first concerns the inhalant pores, which, in this species, tend to be collected together in groups or pore areas, where the cortex forms only a thin dermal membrane, and overlies wide lacunar spaces perhaps comparable to the subdermal cavities of some higher sponges, though not at all sharply separated from the deeper parts of the inhalant canal system. The second concerns the central gastral cavity and osculum, which, though in most calcareous sponges so uniform in structure as to require no special notice, are here enormously enlarged, so that the entire sponge takes the form of a funnel whose thin wall is thrown into deep folds, and the margin of the osculum is no longer evenly curved, but extremely sinuous. Since my memoir on the species was written Mr. Bracebridge Wilson has dredged some very large specimens, one of which measures no less than five inches across the top, so that the actual circumference of the osculum is something enormous.

Grantia labyrinthica also illustrates very clearly the branching of the radial chambers, which is of very general occurrence in Syconoid sponges higher than the Sycetta type.

Grantiopsis (fig. 11).

The only species of this sub-genus, Grantiopsis cylindrica (4), though evidently derived from the ordinary Grantia type by no very great amount of modification, is in many ways a very remarkable sponge. The entire sponge forms long cylindrical tubes, which may branch and which are provided with single terminal oscula. The largest tube which I have seen is unbranched and slightly crooked, 57 mm. long, and with a nearly uniform diameter of 5 mm. The wall of the

tube surrounding the central gastral cavity is about 1 mm. thick, and is divided into two sharply defined concentric layers of about equal thickness. The outer of these layers forms a firm cortex, with a very strongly developed skeleton. The inner layer is soft and spongy, consisting almost entirely of the thin-walled radial chambers.

Fig. 11 represents a portion of a transverse section of the sponge. It will be seen from this that the radial chambers are arranged side by side with great regularity. Each is a straight, wide, unbranched (or very slightly branched), thin-walled tube, extending completely through the chamber layer. In cross-section the chambers vary from nearly square to nearly circular. Each opens directly and separately into the gastral cavity, the gastral cortex being so thin that no special exhalant canals are required. Each is provided at its proximal end with a membranous diaphragm, which, in spirit specimens, almost closes the exhalant opening. There is, of necessity, a well-developed cortical inhalant canal system. The inhalant pores, scattered over the dermal surface, lead into sharply defined cortical canals, which unite into larger trunks, which conduct the water to the ordinary "intercanals" between the radial chambers. Hence it appears that, as regards the canal system, the points to be specially noticed in Grantiopsis are the strong development of the cortical canal system and the great elongation of the gastral cavity.

Ute (figs. 12—14).

The canal system of a typical Ute agrees essentially with that of a typical Grantia. In Ute syconoides (4) the canal system is unusually regular, and the radial chambers have a remarkably definite and constant form. The anatomy of this species, which in general form closely resembles the European U. glabra, is represented in figs. 12—14. The radial chambers are straight, and circular in transverse section for the greater part of their length (fig. 13). Towards their distal extremities, however, they widen out in a direction at right angles to the long axis of the gastral cavity of the

sponge, and at the same time become hour-glass shaped in transverse section (fig. 14), while each has a slight depression at its extreme end (fig. 12). The extraordinary regularity with which these chambers are arranged, and the very definite relation which they bear to the lines of huge oxeote spicules in the dermal cortex, will be sufficiently evident from the figures referred to. The inhalant pores are thickly scattered over the dermal surface between the parallel lines of oxeote spicules. They lead into spaces which are at first somewhat lacunar, but soon give place to sharply defined "inter-canals" as they pass in between the radial chambers (vide figs.). The gastral cortex is very thin, and the exhalant canals are consequently very short.

The canal system of Ute argentea, another Australian species, has been figured by Polejaeff (8). It appears to differ from that of U. syconoides principally in the relatively greater thickness of the dermal cortex, and consequent shortness of the radial chambers, and in the less regular arrangement of the inhalant canal system.

In a colonial species from Port Jackson, which I have named Ute spiculosa (4), we find the canal system much more irregular, in accordance with an unusually strong development of the mesoderm and its contained skeleton. The gastral cavity is narrow and cylindrical, occupying about one third of the total diameter of the sponge. The flagellated chambers are long and narrow, and more or less radially arranged. They do not extend nearly through the entire thickness of the sponge wall, and they communicate with the gastral cavity through long, sometimes branched exhalant canals. The inhalant canal system consists of scattered pores on the dermal surface, leading into elongated canals which lead down between the chambers, but the typical radial arrangement of the canal system is greatly obscured by the strong development of the mesoderm, and the dense, irregular skeleton. There is a very thick dense cortex on both dermal and gastral surfaces.

In Ute Spenceri (4), from the same locality, we find another species with a very strongly developed mesoderm and

skeleton. This sponge is solitary, and is remarkable for its globular or subspherical shape, with correspondingly situated gastral cavity and narrow osculum. The dermal cortex is very strongly developed, occupying more than one third of the entire thickness of the sponge wall. The inhalant pores, scattered over the surface of the sponge, lead into wide, irregular subdermal cavities lying in the cortex, from which inhalant canals lead down between the radial chambers. The chambers themselves are arranged parallel to one another with considerable regularity. They are long and narrow, and at their distal ends they branch in a curiously irregular manner, the branches sometimes penetrating for some little distance into the dermal cortex. The proximal ends of the chambers are all situate at about the same level, which is some little distance from the gastral cavity, and even from the gastral cortex, which latter is very much thinner than the dermal cortex. Hence we find a number of rather short, cylindrical, radially arranged exhalant canals, which look exactly like continuations of the radial chambers without the collared cells, and which may unite together in groups before opening on the gastral surface. The points of junction of these exhalant canals with the radial chambers are marked as usual by diaphragms. The "intercanals" between the chambers are narrow and irregular.

Ute spiculosa and U. Spenceri occupy a position in the genus Ute very similar to that occupied by Grantia Vosmaeri (fig. 10) in the genus Grantia. In both cases the typical radial arrangement of the canal system is more or less disturbed in accordance with the strong development of the mesoderm and skeleton.

Synute (fig. 15).

In this interesting sub-genus we meet with a very unusual, if not unparalleled condition, in the complete fusion of a large number of Syconoid individuals to form a compact, solid sponge invested in a common cortex. The anatomy of Synute pulchella, as seen in horizontal section, is represented in fig. 15. As I have already pointed out (13), the canal system,

apart from the fusion of the individuals, closely resembles that of Ute argentea, as figured by Polejaeff (8). A horizontal section of the colony shows a number of circular spaces scattered at intervals, generally, but not always, in a single row. These are the gastral cavities of the Syconoid individuals cut across. Each cavity is surrounded by its own radial chambers, arranged in a perfectly normal manner, except for the fact that on the adjacent sides of any two neighbouring gastral cavities the chambers are much shortened, and sometimes appear bent outwards as though to avoid one another. The inhalant pores are scattered over the dermal surface, and lead into irregular canals, which pierce the thick cortex to reach the radial chambers. At their lower ends the gastral cavities of the fused Syconoid individuals all communicate with one another, indicating that this peculiar form of colony has arisen from fusion of adjoining individuals of a branching colony. The radial chambers are approximately octagonal in transverse section, while the much smaller "intercanals" between them are square. The exhalant openings of the chambers are protected by very well-developed diaphragms, and each gastral cavity has also a single large, well-developed diaphragm situate just within the osculum.

Probably Synute pulchella is the only known example of a calcisponge with a Syconoid canal system, which has become at all strikingly modified in accordance with the principle set forth in section 8 of the scheme given above.

Utella.

This genus, founded entirely on skeletal characters for the reception of Haeckel's Sycandra hystrix, and perhaps also Schmidt's Ute utriculus (5), presents no features of special interest in its canal system, which appears to conform to the ordinary corticate Syconoid type, like that of Grantia.

Anamixilla.

This genus is also founded entirely on skeletal characters, and the only known species, A. torresi, Polejaeff (8), appears

to possess the typical corticate Syconoid canal system, well shown in Poléjaeff's figure of the anatomy of the sponge.

Sycyssa.

Here, again, the same remarks apply as in the case of the last two genera. The anatomy of Sycyssa Huxleyi is illustrated by Haeckel in his great monograph (5).

Leucandra (figs. 16, 17, 25).

In this genus we meet for the first time with the well-known Leuconoid type of canal system, the essential features of which are shown in fig. 16, representing a portion of a transverse section through the wall of Leucandra phillipensis (4). It will be seen from this figure that the flagellated chambers are small and more or less rounded, and scattered quite irregularly but abundantly through the thickness of the sponge wall. Each communicates by several small prosopyles with the irregular inhalant canal system, and by a single larger opening with the exhalant canal system. The gelatinous ground substance of the mesoderm is sparingly developed, except in the region of the dermal and gastral cortex, and the inhalant and exhalant canals are very wide and irregular. Numerous small inhalant pores, scattered over the dermal surface, lead first into small canals in the dermal cortex; these unite into much larger ones, which lead inward, and break up in the thickness of the sponge wall. The very wide exhalant canals open into a perfectly well-defined gastral cavity from which the water passes out through a single terminal osculum.

Such a sponge as Leucandra phillipensis forms a thoroughly typical Leuconoid individual, and we find the type of canal system above described repeated in a large number of species with singularly little variation; the flagellated chambers being irregularly scattered, ovoid or subspherical in shape (fig. 25), and about 0·1 mm. in diameter.

In a few species of Leucandra, however, we find the flagellated chambers much larger, more or less elongated in form,

and arranged radially around the exhalant canals, features which characterise von Lendenfeld's family Sylleibidæ (10).

The only instance of this Syllectoid condition which I have myself observed in the genus Leucandra is in the case of L. australiensis (4), the anatomy of which is represented in fig. 17. This is a rather large, solitary species, of the typical sac-shaped form. The flagellated chambers are irregularly sac-shaped, and average about 0·3 by 0·1 mm. in size, though very variable. Their radial arrangement around the exhalant canals is not nearly so well marked as in some other species to be mentioned directly; but it is obvious that the chambers of any sponge must be arranged more or less radially around these canals if, as in Leucandra, a large number open directly into them.

In Leucandra aspera, according to Vosmaer (14), we find much the same condition, except that the radial arrangement of the somewhat elongated, sac-shaped chambers around the exhalant canals is more regular, a condition which is very closely paralleled by Leucilla uter (vide infra and fig. 21).

Von Lendenfeld's Polejna telum and Vosmaeria corticata (10), both of which belong to the genus Leucandra as here understood, likewise afford, according to this author's figures, good illustrations of the more regular Sylleibid type of canal system, with the flagellated chambers somewhat elongated, and arranged radially around the exhalant canals.

This Sylleibid condition, first described by Polejaeff (8), appears to be intermediate between the typical Syconoid and the typical Leuconoid conditions, but approaches more nearly to the latter than to the former. Indeed, it would be extremely difficult to say where the Sylleibid condition ends and the Leuconoid begins, for even in such a typically Leuconoid form as L. phillipensis (fig. 16) some of the chambers, especially towards the outside of the sponge, may be markedly elongated, and thus approach the Syconoid type; and the same variation in the form of the chambers is found to an even greater extent in some species belonging to other genera, as will be seen later on. This fact, and the fact that the Sylleibid type of canal

system is met with in species with very distinct types of skeletal arrangement (as will be seen subsequently), cause me to believe that it is of no value for systematic purposes, although it is of great interest, as probably representing a late stage in the evolution of the Leuconoid from the Syconoid type of canal system by branching of the radial chambers and restriction of the collared cells to the branches. (It is also conceivable that the Sylleibid type may have originated from the Syconoid by folding of the wall of the gastral cavity, but there is very little evidence in favour of this view; while, in some species of Sycon and Grantia, we have a certain amount of evidence, in the arrangement of the skeleton, for believing in the direct conversion of flagellated chambers into exhalant canals. That both processes may have taken place together I do not for a moment deny.)

In some species of Leucandra we find, as in the case of Synute pulchella, a very strong tendency towards the formation of massive, irregular colonies, by the more or less complete fusion of a number of Leuconoid individuals. Hence we find species which, instead of having a single well-defined central gastral cavity, with a single terminal osculum and a correspondingly definite sac-shaped external form, as in Leucandra phillipensis, exhibit an irregular massive form with a larger or smaller number of oscula scattered over the surface, each osculum being the outlet of a wide exhalant canal, which probably corresponds to the gastral cavity of a single Leuconoid individual. Synute pulchella is of great interest as showing us how such forms have probably arisen. As far as my experience goes, all such massive colonial species have in other respects a typical Leuconoid canal system with small rounded chambers, as in the Australian L. gladiator (4).

Lelapia.

The canal system of this remarkable genus is unfortunately unknown, but from the fact that Mr. Carter (12), who has personally studied it, places it amongst the "Leucones," it seems probable that it conforms to the Leuconoid type.

Leucyssa.

This genus also appears, from the very scanty information which we possess with regard to the canal system (5), to conform to the ordinary Leuconoid type.

Grantessa (fig. 18).

In this genus we find ourselves returning to a canal system which is emphatically Syconoid, and agrees closely with that which we have already described in the genus Grantia. This will be rendered obvious by a comparison of fig. 18, representing a portion of a transverse section of Grantessa intusarticulata with fig 9, representing a similar section of Grantia extusarticulata. In Grantessa sacca, one of the most beautiful of our Australian sponges, the chambers are very long and copiously branched (4). All the known species are solitary Syconoid individuals or branching colonies, never completely fused into solid, massive forms. In Grantessa erinaceus we meet with a very striking peculiarity, in the presence of ingrowths of mesoderm from the gastral cortex, covered by a single layer of flattened epithelium, into the gastral cavity. These ingrowths form a series of irregular "endogastric septa" without any spicules. They are present in both the specimens in my possession, and, as Mr. Carter also mentions them (12), they would seem to be constant in the species. In G. erinaceus also, the flagellated chambers are very irregular and much branched, and they communicate with the gastral cavity by unusually long exhalant canals, which unite together in groups.

The anatomy of Grantessa (Amphoriscus) poculum has been figured by Poléjaeff (8) and re-investigated by myself. The canal system of this species agrees closely with that of G. intusarticulata (fig. 18).

Heteropia.

The only species which I propose to retain in this genus is Carter's Aphroceras ramosa (15), which appears to have a typical radiate Syconoid canal system, complicated only by the development of a strong dermal cortex resembling that of the genus Ute.

Vosmaeropsis (fig. 19).

In this genus we find (4) at present only three species—V. macera, V. depressa, and V. Wilsoni,—all of which are interesting with regard to their canal system. The canal system is never truly radial and Syconoid, but the shape and size of the flagellated chambers, and in V. macera (fig. 19) the arrangement also, clearly indicate a condition intermediate between the typical Syconoid and the typical Leuconoid plan; in other words, a Sylleibid condition. In V. macera, the anatomy of which is represented in fig. 19, the chambers are thimble-shaped, and mostly widely separated from the central gastral cavity; they communicate with this by wide exhalant canals, into each of which a number of chambers discharge their contents. Each chamber has, as usual, whether it be large or small, a number of small inhalant prosopyles, and a single much larger exhalant aperture, guarded by a well-developed diaphragm (fig. 31). Those chambers which lie next to the dermal surface still exhibit a more or less radial arrangement in relation to the central gastral cavity.

Vosmaeropsis depressa is, unfortunately, known only from a single specimen, so that it is impossible to tell how far the peculiarities of its canal system are constant. There is no single wide gastral cavity, but several large branching exhalant canals converge to a single small osculum situate near the middle of the upper surface of the cushion-shaped sponge. The inhalant canal system is quite irregular, commencing in wide lacunar spaces beneath the thin pore-bearing dermal cortex. The flagellated chambers are irregularly but thickly scattered through the thickness of the sponge, with no trace of radial arrangement around a central gastral cavity. They are, however, more or less sac-shaped or thimble-shaped, measuring about 0·2 by 0·09 mm. This sponge, from the fact that it possesses but a single osculum, probably corresponds to a single individual, but it is interesting to note how the central gastral cavity has become indistinguishably merged into the branching system of wide exhalant canals.

Vosmaeropsis Wilsoni is a large species found abundantly

in the neighbourhood of Port Phillip. The sponge is colonial, and consists of short, thick, subcylindrical or truncatedly conical individuals, united together basally in larger or smaller agglomerations. Each individual has a single well-defined wide gastral cavity, with a single terminal osculum, protected by a remarkably distinct membranous diaphragm situated a short distance within its margin. The wall of the sponge surrounding the gastral cavity is thick, and there is a dense thick cortex on both gastral and dermal surfaces. Between the dermal and the gastral cortex lie the flagellated chambers, thickly but irregularly scattered. These chambers vary to a remarkable extent both in shape and size, from approximately spherical ones of about 0·072 mm. in diameter, to elongatedly sac-shaped ones of as much as 0·37 by 0·13 mm. It is right to state that these measurements were taken from different specimens, but the species is so well characterised that it would be difficult to make a mistake in identification, and we also find considerable variation in the chambers, even in the same section. Most remarkable, however, is the inhalant cortical canal system, a portion of which, from an osmic acid preparation, is represented in fig. 23. The inhalant pores, thickly scattered over the surface of the sponge, lead each into a separate narrow canal lined by a flattened epithelium. These canals unite together into larger and larger canals as they penetrate the dermal cortex, and also form frequent anastomoses by cross-branches. This canal system conducts the water to the chamber-bearing layer of the sponge wall and distributes it to the chambers; from these it is collected again by the exhalant canals, which, uniting into tolerably large trunks, penetrate the gastral cortex and open into the central gastral cavity. I have never seen the inhalant cortical canal system so well illustrated as in this sponge, doubtless because I took the precaution to treat a piece of a living specimen with osmic acid. It finds a close parallel in the corresponding cortical canal system of the Syconoid Grantiopsis cylindrica, and may probably be taken as representing the typical condition for Heterocœla having a very strongly developed dermal cortex.

Heteropegma (fig. 20).

In this genus we again go back to a Syconoid arrangement of the canal system, though not a very typical one. In H. nodus-gordii, the anatomy of which has been admirably illustrated by Poléjaeff (8), and of which I also venture to give a drawing (fig. 20) based upon personal examination, the sponge forms irregular agglomerations of small Syconoid individuals, each with a single osculum and a central gastral cavity. The flagellated chambers have extremely thin and delicate walls, and branch in an extraordinarily copious and irregular manner (fig. 20). The gastral cortex is also extremely thin, but the dermal cortex is very strongly developed, and penetrated by irregular canals which lead from the inhalant pores on the surface of the sponge into the quite irregular lacunar system of spaces ("inter-canals") between the chambers.

In Heteropegma latitubulata, which is found off the south coast of the continent of Australia (H. nodus-gordii being found off the north), we meet with an identical canal system and external form (4). The peculiarities of the canal system in these, the only known species of the genus, are brought about by the copious and irregular branching of the chambers and the extremely slight development of the mesoderm everywhere except in the dermal cortex.

Amphoriscus.

In this genus the canal system is more typically Syconoid, such as we find in any of the Syconoid genera, like Grantia, with a dermal cortex. As I have never myself met with the genus, I may refer the reader to the account of Amphoriscus (Sycilla) cyathiscus and A. (Sycilla) cylindrus given by Haeckel (5).

Syculmis.

Here, again, the canal system appears to differ in no particular from the typical corticate Syconoid plan, like that of Grantia. I must again refer the reader to Haeckel's great work (5) for an account of the only known species (Syculmis synapta).

Leucilla (figs. 21, 22).

This genus includes species which never possess a truly radiate Syconoid type of canal system, but either a thoroughly typical Leuconoid arrangement with small, more or less rounded chambers, as in Leucilla australiensis (fig. 22), L. saccharata, and L. prolifera (4), or an arrangement like that of Leucilla uter (fig. 21), which indicates by the elongated form of the chambers and their radial arrangement around the exhalant canals a Sylleiboid condition, intermediate between the Syconoid and Leuconoid types.

The genus Leucilla, in short, occupies a position in the family Amphoriscidæ exactly analogous to that occupied by Leucandra amongst the Grantidæ, and we find in both genera the same variations in canal system. Thus the canal system of Leucilla uter[1] appears to be almost exactly paralleled by that of Leucandra aspera (14), while that of Leucilla australiensis and the other species with small, rounded, and irregularly arranged chambers, is paralleled by the similar arrangement found in numerous species of Leucandra, as will be evident on comparing figures 16 and 22.

Most remarkable is the canal system of Poléjaeff's Leucetta vera (8), which appears to belong to the genus Leucilla as now constituted. In this species, according to Poléjaeff (8), the chambers of the inner half of the sponge wall are rounded and irregularly scattered, while those of the outer half are elongated and radially arranged, and it thus affords a noteworthy commentary on the value of the canal system for purposes of classification.

A similar variation in the form of the chambers, only on a much smaller scale, is to be found in Leucilla australiensis (fig. 22).

Another interesting variation in the canal system is afforded by Leucilla cucumis (Haeckel's Leucandra cucumis, 5).

[1] For further information as to this species vide Poléjaeff (8). My drawing is made from my own preparations of a portion of the type specimen from the British Museum.

In this species we find a series of very distinct subdermal cavities supported by a special skeleton, for further information with regard to which the reader is referred to the sections of the present paper dealing with the skeleton and classification of the Heterocœla.

We find in some species of this genus also the same tendency to form colonies, by complete fusion of Leuconoid individuals, as we met with in Leucandra. An admirable example of this is afforded by Leucilla (Teichonella) prolifera, of which I gave an illustration in a previous memoir (9), showing the oscula arranged side by side in rows.

Summary.

Thus we find that the canal system varies considerably in what appear to be closely related genera of Heterocœla Calcarea; and that, if my view of the relationships of the genera be correct, the Leuconoid type has been independently evolved from the Syconoid type, along the lines indicated above, no less than three times. The Leuconoid type cannot, however, be produced until the corticate Syconoid type has been arrived at; and when this condition has been reached the conversion of the originally long and radially disposed chambers into short, rounded, and irregularly arranged ones seems such a simple matter that it may well have taken place again and again. The variation in shape and size of the chambers, even in the same species, may, as I have already shown, be very great. The branching of the radial chambers in Syconoid forms is of such common occurrence in the most diverse genera as to excite no surprise wherever we meet with it; and the shortening of the chambers and corresponding elongation of the exhalant canals, due simply to shifting of the limits of the lining of collared cells, has been repeatedly observed in various genera.

We may sum up our observations on the canal system of the Heterocœla by indicating again the various stages which appear to have been passed through in the gradual evolution of the most complex Leuconoid from the most simple Syconoid type.

Stage A (Sycetta stage).—The flagellated chambers are

perfectly straight, unbranched, and radially arranged. They do not touch one another at all, and there is no trace of a dermal cortex, hence there is no enclosed system of inhalant canals, but the water circulates freely between the chambers without any interruption. Sycetta appears to be the only genus in which this most simple condition is retained.

Stage B (Sycon stage).—This stage differs from the foregoing only in the more or less complete fusion of the walls of adjacent radial chambers wherever they come in contact. This results in the formation of more or less well-defined inhalant "inter-canals." The chambers may also branch. In this stage we find most species of the genus Sycon, and we may perhaps also include Sycantha. Those species of Sycon in which a thin pore-bearing membrane covers over the ends of the "inter-canals," as described above, are intermediate between stages B and C.

Stage C (Grantia stage).—The chambers are still elongated and radial, but their distal ends and the ends of the "inter-canals" between them are covered over by a dermal cortex, which contains true inhalant pores, and sometimes a complicated cortical inhalant canal system. In this stage we find Grantia, Grantiopsis, Ute, Synute, Utella, Anamixilla, Sycyssa, Grantessa, Heteropia, Heteropegma, Amphoriscus, and Syculmis.

Stage D (Sylleibid stage).—The chambers are no longer arranged radially around the central gastral cavity, but are still more or less elongated, and arranged radially around the usually radial exhalant canals. It was this condition, first described by Poléjaeff (8), which gave rise to von Lendenfeld's Sylleibidæ (10, 11). It is not, however, characteristic of any particular genus, much less of any particular family, but is found in a few isolated species, such as Leucilla uter, Leucandra aspera, and Vosmaeropsis macera.

Stage E (Leucandra stage).—The chambers are small, more or less spherical, and irregularly scattered through the sponge wall; and the inhalant and exhalant canal systems are correspondingly developed. We find this condition in most

species of Leucandra and Leucilla, and presumably also in Lelapia and Leucyssa.

No one of these five stages is very sharply marked off from the stage below it, and the five appear to me to indicate a process of evolution which has actually taken place. Von Lendenfeld (10) attributes to the Leuconoid type of canal system an independent origin from the Homocœle type, through his very problematical "Leucopsidæ," without passing through a radiate Syconoid stage at all, although he admits the derivation of the Sylleibid type from the latter. With this view I cannot at all agree. Considering the canal system alone, we have cogent reasons for opposing it, and when we come to discuss the skeleton we shall find others.

III. The Skeleton of the Calcarea Heterocœla.

The Spicules.—So much has been written about the spicules of calcareous sponges, and their variations in minute details of shape are of so little interest from a morphological point of view, that I propose to say very little about them in this place, and only to recapitulate those facts which it is necessary to consider in discussing the arrangement of the skeleton.

In calcareous sponges, whether Homocœle or Heterocœle, three principal types of spicules are met with:

(*a*) Triradiate,

with three rays diverging from a common centre and lying typically in one plane, though frequently curved more or less out of that plane.

(*b*) Quadriradiate,

resembling the triradiate but with an additional ray, known as the apical ray, coming off from the centre in a plane at right angles to the plane of the other three (facial) rays.

In both triradiate and quadriradiate spicules we can distinguish three chief varieties:—(1) Regular, the three facial

rays being all alike, with the angles between them equal. (2) Sagittal, when two of the facial rays or two of the angles form a pair differing in some respects from the remaining ray or angle. In this case the paired rays are termed oral, the odd ray is termed basal, and the odd angle between the oral rays is also termed oral. (3) Irregular, when the three facial rays conform to neither of the above plans.

(*c*) Oxeote,

or uniaxial spicules (oxea), in which there is only a single axis. These spicules vary greatly in details of shape, from symmetrically fusiform, with two sharply pointed ends, to nail-shaped, with one end blunt and swollen.

As in the Homocœla, so in the Heterocœla, the mere presence or absence of one or other of these three types of spicule is of very slight—in my opinion, of not more than specific—value for purposes of classification. With the arrangement of the spicules I believe the case to be totally different, and I find, in the structure of the skeleton as a whole, characters of family value to the systematist.

The Arrangement of the Spicules.—Here, as in the case of the canal system, we shall find it most convenient to take the various genera one by one and deal with them separately. We shall find that, up to the Grantia stage, the arrangement of the skeleton follows, and appears to be to a large extent controlled by, that of the canal system. But on reaching the Grantia stage the development of a strong dermal cortex introduces new possibilities with regard to the skeleton, which commences to vary independently of the canal system, and branches off along three lines corresponding to the families Grantidæ, Heteropidæ, and Amphoriscidæ. The genus Leucascus appears to occupy an isolated position.

Leucascus (fig. 1).

In this genus (fig. 1) the arrangement of the skeleton is extremely simple, and exhibits no trace of that radial symmetry which is so characteristic of the Heterocœla. It

resembles, on the other hand, the arrangement of the skeleton in such simple Homocœle sponges as Leucosolenia protogenes, excepting that there is a true dermal skeleton in the pore-bearing dermal membrane. In both species of Leucascus (4) the skeleton consists of small, regular triradiates, irregularly scattered in the walls of the elongated chambers and exhalant canals, and in the dermal membrane. In Leucascus simplex these are the only spicules present, but in L. clavatus we find in addition some large, club-shaped, uniaxial or oxeote spicules, partly projecting from the dermal surface.

Sycetta.

Here, in accordance with the arrangement of the canal system, we can distinguish between two main parts of the skeleton,—(1) the gastral skeleton, supporting the wall of the gastral cavity; and (2) the tubar skeleton, supporting the walls of the radial chambers. The gastral skeleton consists of triradiate or quadriradiate spicules, whose three facial rays lie in the thickness of the wall of the gastral cavity, while the apical ray, if one happens to be developed, projects into the cavity. These spicules may be sagittal, as in Sycetta (Sycaltis) conifera (5), and then the basal ray is found to be directed downwards, away from the osculum and towards the base of the sponge, a position which is so constant in this and other genera as to have given rise to the term "basal ray." The tubar skeleton consists exclusively of triradiate spicules, which lie in the thickness of the chamber walls, and which always have the basal ray directed along the length of the chamber and away from the gastral cavity. Hence the oral or paired rays are spread out in a direction at right angles to the length of the chamber, and as several spicules generally lie at the same level, the tubar skeleton forms a series of more or less definite joints or rings, and is hence said to be articulate. This articulate arrangement, however, which prevails in most genera with a Syconoid type of canal system, is usually very irregular.

Sycon (figs. 2—8).

Here, again, we meet with distinct gastral and tubar skeletons, as shown in fig. 2, and the general plan of the skeleton is the same as in Sycetta. Quadriradiates are usually, if not invariably, present in the gastral skeleton, the apical ray projecting freely into the gastral cavity (figs. 2, 4, 7), and doubtless serving as a protection against the ingress of parasites. The gastral skeleton may be very strongly developed so as to form a thick cortex, which may be continued inwards along the exhalant canals, as in Sycon boomerang (fig. 7). Where this is the case—but it is very rare—it seems to me to indicate a folding of the wall of the gastral cavity. The tubar skeleton is always "articulate," and the number of "joints" which it exhibits depends upon the length of the chambers. Usually the spicules composing it are more or less strongly sagittal and triradiate, but occasionally apical rays may be developed, as in S. boomerang (fig. 7). The position of the spicules is always the same as in Sycetta, with the basal ray pointing away from the gastral cavity; where an apical ray is developed it projects freely into the cavity of the chamber. Usually a special set of spicules, known as "subgastral sagittal triradiates" are developed, as is well shown in Sycon Carteri (fig. 2). These have the oral rays extended very widely in the outer part of the wall of the gastral cavity, and thus forming a part of the gastral cortex, while the basal ray is usually very long, and points towards the distal end of the chamber in whose wall it lies. These spicules, or at any rate their basal rays, form the first "joint" of the articulate tubar skeleton, which is commonly a good deal longer than any of the succeeding joints (fig. 2). The subgastral sagittal triradiates may, however, be almost, if not quite, indistinguishable from the ordinary tubar triradiates of the sponge. Usually the three rays of the tubar triradiates do not lie all in one plane, but the oral rays are curved or inclined towards one another, so as to partially embrace the chamber in the thickness of whose wall they lie (fig. 5).

In this genus we always find, at the end of each radial chamber, a more or less dense tuft of oxeote spicules (figs. 2, 3, 6—8). The shape of these spicules varies greatly, and influences in a remarkable degree the character of the surface of the sponge. They may be enormously elongated and project far beyond the surface, which thus becomes covered with a coating of long silky hair, as in Sycon Ramsayi; or their outer ends may be swollen and nail-shaped and project but very slightly, so as to form a dense crust, as in some specimens of Sycon gelatinosum (fig. 6). All conditions intermediate between these two may also be met with. These tufts of uniaxial spicules, which are extremely characteristic of the genus Sycon, doubtless serve to protect the surface of the sponge generally, and also to filter the water before it passes into the "inter-canals." The entrances to the "inter-canals," between the tufts of oxeotes, may also be protected by the basal rays of the more distal tubar triradiates, which may curve outwards from the chamber wall, as in Sycon ensiferum (4).

In Sycon boomerang, as I have already had occasion to point out, we meet with the first indication of a true dermal skeleton distinct from that of the chambers. It consists of a few scattered triradiate and oxeote spicules lying in the thin, pore-bearing membrane, which stretches across and protects the entrances to the intercanals (fig. 8).

In this genus we frequently meet with a more or less specially developed "oscular skeleton," which when present, either in this or any other genus, always consists of a fringe of oxeote spicules, projecting more or less markedly around the osculum. Usually the fringe is vertical, or inclined only at a slight angle to the long axis of the gastral cavity; but occasionally a second, almost horizontal, fringe is developed, which projects almost at right angles all around the base of the first one. A beautiful illustration of such a horizontal fringe is given by Haeckel in the case of his Sycarium elegans (5, pl. lviii), and I have also met with it in a variety of Sycon gelatinosum from Port Jackson. The oscular skeleton is, however, a very variable structure, and of very little import-

ance from the point of view either of the morphologist or the systematist.

Sycantha.

The skeleton of this genus appears to conform exactly to the normal Sycon type, which appears to favour my view that the canal system is but a slight modification of the Sycon type.

Grantia (figs. 9, 10).

In Grantia we find the skeleton built upon the same essential plan as in Sycon, but there is, in addition, a well-developed dermal skeleton lying in the dermal cortex, which covers over the ends of the radial chambers and inter-canals, while we no longer find each chamber surmounted at its distal extremity by a tuft of uniaxial oxea. The gastral skeleton and the articulate tubar skeleton are precisely similar to what we found in Sycon, as will be at once evident on referring to fig. 9, representing the anatomy of Grantia extus-articulata.

The skeleton of the dermal cortex in this genus consists principally of triradiate spicules lying parallel to the dermal surface. These spicules may be sagittal, with the basal ray directed, as in the gastral cortex, towards the base of the sponge. A good example of this arrangement is seen in Grantia labyrinthica (9).

In addition to the triradiate spicules we also find in the dermal cortex of Grantia, in most if not all species, a number of oxeote spicules placed at right angles to the dermal surface. These may either be very small and numerous, as in Grantia extusarticulata (fig. 9), or they may be large and fewer, as in G. Vosmaeri (fig. 10). In the former case they form a kind of crust, and are spoken of by some writers as "mortar-spicules:" their inner ends only penetrate the dermal cortex for a short distance. In the latter case their inner ends may penetrate through nearly the entire thickness of the sponge wall. In no case in this genus do they form tufts at the ends

of the radial chambers, but they are always arranged entirely without regard to these.

In Grantia labyrinthica (9) we find minute surface oxea in the gastral as well as in the dermal cortex. This is a very unusual occurrence, but is paralleled in Ute Spenceri (4).

In Grantia Vosmaeri (fig. 10), where we have a marked shortening of the radial chambers and a corresponding elongation of the exhalant canals, together with a strong development of the mesoderm surrounding them, we find the skeleton in the inner portion of the sponge wall losing its regular radially symmetrical character, and becoming diffuse and scattered. This is an illustration of a general law, that the skeleton of the chambers varies with the chambers themselves, which will be found to hold good throughout the group, with few exceptions. As the chambers lose their radial symmetry and regularity of form and arrangement, so the skeleton loses its radially symmetrical articulate character, and becomes diffuse and scattered. This will be seen to follow as a natural consequence, if we remember that the position of the spicules is to a large extent determined by the position of the layer of mesoderm (in the chamber wall) in which they are developed. Hence it is that irregularity in the skeleton generally accompanies thickening of the mesoderm, for when this is effected the spicules are free to take up a variety of positions which, while embedded in a very thin layer of mesoderm, they are unable to assume.

Grantiopsis (fig. 11).

In Grantiopsis cylindrica (4) we meet with a slight modification of the Grantia type of skeleton, as shown in fig. 11. The dermal cortex is enormously developed, but its skeleton still consists of triradiate and oxeote spicules arranged as in Grantia. In the thin gastral cortex quadriradiates are present as usual, but of somewhat peculiar shape, with small facial and enormous apical rays. The subgastral sagittal triradiates of the ordinary Sycon and Grantia types are here replaced by subgastral sagittal quadriradiates. The position of

these spicules agrees with that of the subgastral sagittal triradiates of Sycon and Grantia, but an apical ray is developed which projects into the gastral cavity, almost in a line with the centrifugally directed basal ray. Hence these spicules are not homologous with the subgastral quadriradiates of some Amphoriscidæ, their position being different.

The articulate tubar skeleton of Grantiopsis cylindrica is very remarkable, owing to the peculiar form of the spicules of which it is composed. These spicules are the most extreme modifications of the sagittal triradiate type which I have ever seen or heard of. They consist almost entirely of the strangely developed centrifugally directed basal ray, which is straight, fusiform, gradually sharp-pointed at the distal end, and at the proximal end provided with a pair of minute, widely divergent, conical teeth, which represent the extremely reduced oral rays. The basal ray measures about 0·3 by 0·008 mm., while the oral rays are only about 0·003 mm. long. The entire tubar skeleton is made up of these spicules and of the basal rays of the subgastral quadriradiates, arranged usually in single series, but with overlapping ends, each series comprising only about three spicules (fig. 11).

Ute (figs. 12—14).

In this genus we find the skeleton arranged as in Grantia, only with the addition of a number of very large oxeote spicules disposed longitudinally in the dermal cortex. The gastral skeleton is exactly like that of Grantia and Sycon, and so also is the tubar skeleton in most species. In Ute argentea, however, there is, as Polejaeff points out (8), a tubar skeleton composed only of a single joint, i. e. of the rays of the subgastral sagittal triradiates. To this tubar skeleton the term "inarticulate" has been applied, but this appears to me to be a mistake, for it is very different from the so-called "inarticulate" tubar skeleton of the Heteropidæ and Amphoriscidæ. As I shall show later on, however, the distinction between "articulate" and "inarticulate" tubar skeletons is not altogether satisfactory.

The development of the dermal skeleton varies much in different species as regards its extent, but always follows the same pattern. The large longitudinally arranged oxea always form the most conspicuous feature, and frequently give to the surface of the sponge a very characteristic striated appearance. Nearly always, however, triradiates and minute surface oxea are also present, arranged as in Grantia. In Ute spiculosa and U. Spenceri (4) the triradiates are very numerous indeed, while in U. glabra (5), U. argentea, and U. syconoides (4) they are very scarce.

The presence of the longitudinally disposed oxeote spicules in the dermal cortex, although often giving the sponge a very characteristic appearance, is by no means peculiar to the genus Ute, for the same character is found in Leucandra alcicornis (5) and in two species of Homocœla Simplicia, viz. Leucosolenia asconoides (4, 12) and L. uteoides (16); and it is also characteristic of the genus Heteropia (4).

In Ute spiculosa (4), where the mesoderm is very strongly developed, we find, in accordance with the rule laid down above, that the skeleton of the chamber layer is dense and irregular, though showing traces of the normal articulate arrangement in the usually centrifugal direction of the basal rays of the triradiates.

In Ute Spenceri (4) we find one or two slight peculiarities in the skeleton. Thus we find, as in Grantia labyrinthica, a number of minute oxeote spicules on the gastral as well as on the dermal surface; and we find also that the exhalant canals are protected by quadriradiates of special form. The tubar skeleton is distinctly articulate, though becoming confused as it approaches the dermal cortex.

Synute (fig. 15).

In this sub-genus the dermal cortex and its contained spicules are enormously developed, so as to bind together all the individuals of a branching colony into one continuous whole (fig. 15). Here, as in other cases where the dermal cortex is very strongly developed, the cortical triradiates lose

their parallelism with the dermal surface and become irregularly scattered. In other respects the arrangement of the skeleton follows the ordinary Ute plan.

Utella.

In this genus, of which the type species is Haeckel's Sycandra hystrix (5), we find a very remarkable modification of the Grantia type of skeleton, for a layer of longitudinally disposed oxeote spicules is developed in the gastral cortex, instead of, as in Ute, in the dermal one. For a description and illustrations of Utella hystrix I must refer the reader to Haeckel's great work (5).

Anamixilla.

Here, again, the skeleton is very peculiar, as will be seen at once on referring to Poléjaeff's drawing thereof (8). The flagellated chambers are elongated and radially arranged. The gastral and dermal cortex, each with its skeleton, is developed as in Grantia. There is, however, no articulate tubar skeleton, although it is important to notice that subgastral sagittal triradiates are still present, as in Ute argentea. The most remarkable feature of this sponge is the presence, in the chamber layer of the wall, of a number of large triradiate spicules, out of all proportion to the size of the chambers and arranged without regard to the direction of these, but generally lying across them and more or less parallel to the dermal surface. It looks as if the chamber layer had first lost the greater part of its own skeleton, all except the subgastral sagittal triradiates, and had then been invaded by large spicules from the dermal cortex.

Sycyssa.

In this very remarkable genus, for our knowledge of which we are entirely indebted to Haeckel (5), the canal system appears to be arranged upon the regular Grantia plan, but we are told that the skeleton is made up solely of oxeote spicules, there being no radiate spicules present of any kind. The skeleton of the gastral cortex consists of (1) a gastral layer of

irregularly arranged bundles of very slender oxea, and (2) a subgastral layer composed of regularly arranged, parallel, longitudinal bundles of large, stout oxea: this is comparable to the similar layer in Utella. The tubar or chamber skeleton is composed of the inner ends of enormous radially arranged oxeote spicules, comparable to those found in Grantia Vosmaeri, but larger and apparently more regularly arranged. The outer ends of these spicules project far beyond the dermal surface. The skeleton of the dermal cortex is composed of (1) a layer of very slender oxea, arranged irregularly but parallel to the dermal surface, and (2) a layer of very slender oxea, arranged radially and forming a kind of pile over the outer surface, as in so many Heterocœle sponges.

This genus, of which the only known species is Sycyssa Huxleyi, from the Adriatic, must be regarded as possessing a very aberrant type of skeleton, and occupying a very isolated position in the group.

Leucandra (figs. 16, 17).

To understand the structure of the skeleton in this genus we must return to that of Grantia, of which it is evidently a modification. We saw how in Grantia Vosmaeri (fig. 10)—where the exhalant canals have begun to elongate and the chambers to shorten, and where the mesoderm is very strongly developed in the inner half of the sponge wall—the skeleton has begun to lose its regular articulate character. The same thing is carried to a much greater extent in Leucandra, where the canal system has lost its symmetry and the skeleton has followed suit (figs. 16, 17). The skeleton of the gastral and dermal cortex, however, retains the same structure as in Grantia; it is only the skeleton of the chamber layer which is affected by the changes in the canal system. Hence we find that in a typical Leucandra (fig. 16) the skeleton of the gastral cortex is made up principally of quadriradiate spicules whose apical rays project into the gastral cavity, while the skeleton of the dermal cortex is made up of triradiates, lying parallel to the dermal surface, and longer or

shorter oxeote spicules usually projecting more or less at right angles therefrom. The skeleton of the chamber layer, on the other hand, consists of irregularly scattered triradiates or quadriradiates.

In some species, e.g. L. phillipensis and L. australiensis, the quadriradiates of the gastral cortex are continued inwards along the larger exhalant canals, which possibly indicates a folding of the wall of the gastral cavity, though I do not think it necessarily does so.

In some species, e.g. L. phillipensis, we find many of the triradiates of the chamber layer retaining their primitive sagittal character, and with the basal ray pointing towards the dermal surface. This may be a reminiscence of the time when they formed part of an articulate tubar skeleton. Subgastral sagittal triradiates may also still be present (figs. 16, 17).

Lelapia.

In this genus of a single species the canal system is unknown, and the skeleton is peculiar. The skeleton of the gastral cortex is composed of ordinary radiates; while that of the dermal cortex is composed of triradiates, quadriradiates, and minute oxea. The skeleton of the chamber layer is composed of large, longitudinally arranged oxea, crossed at right angles by bundles of tuning-fork shaped triradiates whose basal rays point towards the dermal surface. For further particulars I must refer the reader to Mr. Carter's description of the sponge (12), as I have never had an opportunity of examining it myself.

I should, perhaps, mention that Mr. Carter describes the occurrence of small quadriradiate spicules "on the surface," presumably in the dermal cortex. Triradiate spicules are very apt to develop an apical ray, often so small as to be of no conceivable use, and apparently indicating a mere "sport," if one may use the term. Therefore, unless the feature could be shown to be constant, well established, and characteristic, I should not be inclined to attribute any great value to it. It

certainly appears to be a difficulty in the way of utilising the presence of subdermal quadriradiate spicules as a family characteristic in the Amphoriscidæ, but in the latter case the apical rays are so constant, and form, in most cases, such an important part of the skeleton, that we must treat the question from a different standpoint.

Leucyssa.

In the skeleton of this genus we meet with a parallel case to that of Sycyssa, only associated this time (presumably) with a Leuconoid canal system.

The genus is very imperfectly known, and what we do know about it we owe chiefly to Haeckel (5). Two of the three species (L. spongilla and L. cretacea) are described from single specimens, and a third (L. incrustans) is extremely rare. In all, the skeleton appears to be quite irregular, consisting of a felt-work of oxeote spicules. In L. spongilla the spicules are spindle-shaped, straight, and smooth. In L. cretacea they are swollen at one end and pierced like a sewing-needle; and it is interesting to note that similar spicules are found in Leucandra ochotensis (5). In Leucyssa incrustans (Carter's Trichogypsia villosa), a European species which, thanks to the kindness of Mr. Carter, I have had the opportunity of partially examining (in the dry state), the skeleton consists of a very dense, irregular felt-work of spinose oxea.

Grantessa (fig. 18).

In this genus we have an entirely new element introduced into the composition of the skeleton, in the form of subdermal sagittal triradiate spicules. The existence of these spicules in certain species has long been recognised, but their importance from a systematic point of view appears to me to have been under-rated. They never appear, so far as my experience goes, in sponges without a dermal cortex, and they seem to be first introduced as additions to the ordinary Grantia type of skeleton. Thus in Grantessa sacca (4, 11) we find all the parts of a typical Grantia skeleton present,

including the skeleton of the dermal and gastral cortex and a normal articulate tubar skeleton; but in addition to these parts we find also a well-developed layer of sagittal triradiates, whose oral rays are extended in the dermal cortex parallel to the surface, while the elongated basal ray projects inwards for some little distance into the chamber layer. The position of these spicules is thus exactly the reverse of that of an ordinary tubar triradiate, the basal rays pointing in exactly opposite directions in the two cases.

In Grantessa intusarticulata (4), the anatomy of which is represented in fig. 18, we find a precisely similar condition, but the chambers are shorter, and the number of joints of the articulate tubar skeleton correspondingly fewer. In this species, also, it is highly interesting to notice that in the youngest portions of the sponge, nearest the osculum, where the chambers are shortest, the skeleton of the chamber layer consists solely of the basal rays of the subdermal and subgastral sagittal triradiates, so that we have here a typical example of the so-called "inarticulate" tubar skeleton. In other words, we find the two types of tubar skeleton, articulate and inarticulate, existing side by side in the same sponge. In Grantessa poculum, an excellent figure of which, under the name Amphoriscus poculum, is given by Polejaeff (8), the skeleton is almost exclusively "inarticulate," but I find from my own examination of the sponge that the inner triradiates are not always strictly subgastral, but may be situate some little distance beneath the gastral cortex.

The dermal and gastral skeleton in this genus agrees so closely with that of Grantia as to require no further comment (compare figs. 9 and 18), unless we specially mention the fact that in some species of Grantessa the oxeote spicules of the dermal surface are collected into tufts, which, however, bear no relation to the radial chambers. This character, which is well shown in Grantessa sacca, first gave origin to von Lendenfeld's genus Grantessa (11). I do not believe it one of great systematic value; and I do not hesitate to include in the same genus species like G. intusarticulata and G.

poculum, in which the oxeote spicules are not collected into tufts.

Heteropia.

This genus bears precisely the same relation to the genus Grantessa as Ute does to Grantia, the skeleton being of the ordinary "inarticulate" Grantessa type, but with the addition of large longitudinally arranged oxea in the dermal cortex. For further details I must refer the reader to Mr. Carter's description of Heteropia (Aphroceras) ramosa (15).

Vosmaeropsis (fig. 19).

All three species included in this genus (4) exhibit, like Grantessa and Heteropia, a well-developed layer of subdermal sagittal triradiates; but as the other parts of the skeleton vary somewhat in the three cases, it will be advisable to consider them separately.

Vosmaeropsis macera, the anatomy of which is represented in fig. 19, shows least deviation from the ordinary Grantessa type. There are, however, no quadriradiates in the gastral cortex, but I do not consider this a very important character. The oxeote spicules of the dermal cortex are also very variable in their development, and may be almost, if not quite, absent; but this, again, is not an important character. Otherwise, the skeleton agrees closely with that of an ordinary Grantessa in which no distinct articulate tubar skeleton is developed.

In Vosmaeropsis depressa (4) the skeleton is modified, in accordance with the massive form of the sponge and the arrangement of the canal system. The bulk of the skeleton is made up of fairly large, subregular, or slightly sagittal triradiates, scattered without definite order throughout the thickness of the sponge, many having one slightly longer ray pointing towards the dermal surface. Beneath the dermal surface, but apparently only on the upper surface of the cushion-shaped sponge, is a distinct layer of subdermal sagittal triradiates, with inwardly directed basal rays. The

dermal skeleton is made up principally of subregular triradiates of various sizes, placed horizontally, but with no definite arrangement; amongst these very minute slender oxea are scattered, especially numerous around the osculum.[1] Around the main exhalant canals is a layer of small sagittal triradiates, forming what must probably be regarded as the gastral skeleton. No quadriradiates are present, and I have not detected any special subgastral sagittal triradiates. The skeleton of this sponge bears much the same relation to that of Grantessa as that of Leucandra does to that of Grantia.

Vosmaeropsis Wilsoni is remarkable for the enormous development of the cortex and its contained skeleton on both gastral and dermal surfaces. The skeleton of the chamber layer is like that of Vosmaeropsis macera (fig. 19), but the sagittal triradiates are of unusually large size. A well-developed oscular skeleton, in the shape of a fringe of oxeote spicules, is also present, but this is not a feature upon which much stress need be laid in any case.

Heteropegma (fig. 20).

We have seen how, in Grantessa, the very characteristic skeleton is derived from the ordinary Grantia type by the mere addition of a layer of subdermal sagittal triradiate spicules. The skeleton of Heteropegma is also derivable from the Grantia type by an analogous change, only the subdermal spicules are quadriradiates and not triradiates. Moreover it is important to observe that the subdermal quadriradiates of Heteropegma and other Amphoriscidæ are not modifications of subdermal sagittal triradiates, such as are found in the Heteropidæ. If they were so, we should expect to find the basal ray still pointing inwards towards the gastral cavity, and the additional apical ray lying in a plane more or less parallel with the dermal surface. As a matter of fact, however, the three facial rays of the subdermal quadriradiates lie parallel

[1] Oxeote spicules are sometimes developed around the osculum when they cannot be found anywhere else in the sponge.

with the dermal surface, and it is the apical ray which is directed inwards through the chamber layer. Hence the position of these spicules is quite different from that of the subdermal sagittal triradiates of the Heteropidæ, while in the one case it is the basal ray in the other it is the apical one which plays such an important part in the support of the chamber layer.[1]

The anatomy of Heteropegma nodus-gordii is represented in fig. 20. It will be seen that the dermal cortex is strongly developed, and has the ordinary Grantia structure, except that there are no oxeote spicules. The gastral cortex is extremely thin and its skeleton greatly reduced, consisting of a number of very small quadriradiates arranged in the usual manner. The articulate tubar skeleton is also very much reduced, consisting of very minute spicules, chiefly quadriradiate. This reduction in the skeleton of the chamber layer is partly compensated for by the presence of very large subdermal quadriradiates, whose facial rays are extended in the inner part of the dermal cortex, while the apical ray penetrates through the chamber layer almost to the gastral surface.

The skeleton of the Victorian Heteropegma latitubulata (4) resembles that of H. nodus-gordii, except in certain very minute details of spiculation, the tubar and gastral spicules being still further reduced in size.

Amphoriscus.

In this genus the articulate tubar skeleton, which was still clearly recognisable in Heteropegma, has disappeared, although the radial Syconoid character of the canal system remains. In one species, however (Poléjaeff's Amphoriscus elongatus [8]), the subgastral sagittal triradiates still persist. We always find, as in Heteropegma, a layer of subdermal quadriradiates with inwardly directed apical rays; and we also find, in addition to these, in nearly all species, a layer of subgastral quadriradiates with outwardly directed apical rays.[2]

[1] The subdermal quadriradiates are probably derived from the ordinary triradiates of the dermal cortex by the development of an apical ray. Compare my remarks on the skeleton of Lelapia.

[2] These spicules are not homologous with the subgastral quadriradiates of

Hence the chamber layer is usually supported solely by the apical rays of quadriradiates, which pierce it from opposite directions. In Amphoriscus cylindrus and A. cyathescus (4, 5) we learn from Haeckel that the dermal cortex is composed entirely of the facial rays of quadriradiates, there being no triradiates left. This fact supports the view that the subdermal quadriradiates of the Amphoriscidæ are merely modifications of the ordinary dermal triradiates, which have developed an apical ray without changing their position. In the case of the subdermal sagittal triradiates of the Heteropidæ, on the other hand, the position of the spicules is quite different from that of ordinary dermal triradiates.

Syculmis.

The skeleton of Syculmis synapta (5), the only known species of the genus, agrees in the main with that of Amphoriscus, but is further complicated by the addition of a root-tuft of oxea and anchoring quadriradiates, which is, I believe, without parallel amongst the Calcarea. For further details I must refer the reader to Haeckel's monograph.

Leucilla (figs. 21, 22).

In this genus, again, we always find dermal or subdermal quadriradiates with inwardly directed apical rays. These form the most constant feature of the skeleton, the other parts being somewhat variable in different species. A gastral cortex, constructed as in Grantia, is probably always present, and sometimes, as in Leucilla uter (fig. 21) and L. australiensis (fig. 22), subgastral sagittal triradiates are still recognisable, indicating probably the derivation of the skeleton from the Grantia type. All the triradiates of the dermal cortex may be converted into quadriradiates by the development of a long inwardly directed apical ray, as in Leucilla uter (fig. 21); or some of them may still retain their primitive triradiate character, as in L. australiensis (fig. 22).

Grantiopsis, or of Polejaeff's Grantia tuberosa (8), which are only slight modifications of the ordinary subgastral sagittal triradiates.

Dermal oxea, like those of Grantia, may also be present (fig. 21). The chamber layer is generally further supported by other quadriradiate spicules, which may have a more or less definite subgastral position (fig. 21), or be irregularly scattered through the chamber layer (fig. 22), or by irregularly scattered triradiates, as in Leucilla prolifera (4).

The skeleton of Leucilla (Leucandra) cucumis, Haeckel (5), exhibits a further complication of the Leucilla type. The skeleton of the dermal cortex is made up of an outer layer of triradiate spicules, as in Grantia, and an inner layer of quadriradiates with inwardly directed apical rays. These quadriradiates help to form a framework for a remarkably regular series of subdermal cavities, and are assisted in so doing by a second, deeper layer of quadriradiates with outwardly directed apical rays. Within this deeper layer of quadriradiates comes the chamber layer of the sponge wall, supported by irregularly scattered quadriradiates; and within this comes the gastral cortex, composed of triradiate spicules. In addition to the spicules mentioned, large oxeote spicules are found arranged longitudinally between the dermal triradiates. Illustrations of the skeleton of this remarkable sponge will be found in Haeckel's great work.

Summary.

We find, from our survey of the various genera of Heterocœla, that the starting-point for the development of the skeleton throughout the group (leaving out of account Leucascus, which may have originated independently from the Homocœla) is the radially symmetrical skeleton of Lycetta. This primitive radial symmetry is highly characteristic of the group, and is obviously dependent upon the primitive radial symmetry of the canal system. The first great change in the structure of the skeleton is brought about by the development of a dermal cortex, in which a special skeleton is formed. The skeleton of the chamber layer of the sponge wall now begins to vary. This variation is in some cases obviously dependent upon the gradual change of the canal system from the

Syconoid to the Leuconoid condition. This change brings about a loss of radial symmetry in the chamber skeleton, which is transformed from the regular "articulate" type of Sycetta, Sycon, Grantia, to the irregularly scattered condition of Leucandra. Other modifications, however, also take place, which are obviously not dependent on the variation of the canal system, and which are consequently of the utmost importance for systematic purposes. These modifications consist in the development of subdermal sagittal triradiate or of subdermal quadriradiate spicules, which characterise the two families Heteropidæ and Amphoriscidæ respectively. Both these modifications are first instituted (in the genera Grantessa and Heteropegma respectively) while the canal system still retains its primitive radial symmetry and its articulate tubar skeleton (figs. 18, 20), and in both cases they are retained, while the canal system gradually changes from the Syconoid to the Sylleibid or Leuconoid type, and the primitive articulate tubar skeleton disappears (figs. 19, 22). Thus the primitive centrifugal radial symmetry of the skeleton is lost as the canal system changes from the Syconoid to the Leuconoid type, but in the Heteropidæ and Amphoriscidæ it is to a certain extent replaced by a kind of secondary centripetal radial symmetry, due to the development of subdermal radiates with inwardly directed basal or apical rays. Indications of the primitive radial symmetry are sometimes found in the presence of subgastral sagittal triradiates after all other traces of the articulate tubar skeleton have disappeared. The gastral cortex, as might be expected, is subject to less modification than any other portion of the skeleton, and does not vary to any great extent throughout the group. A striking exception to this rule is, however, found in the genus Utella. Very startling exceptions to the ordinary rules of skeletal structure are found in the genera Sycyssa and Leucyssa, apparently due to the loss of all radiate spicules, and the development in their stead of oxea.

In Leucascus the skeleton appears never to have

reached the radially symmetrical condition, but to have remained in the scattered one found amongst the reticulate Homocœla.

IV.—The Histology of the Heterocœla Calcarea.

All my observations upon the histology of the Heterocœla Calcarea have been made upon spirit-preserved specimens, and I cannot therefore claim for them the same value as attaches to the recent observations of Bidder (21—24) and Minchin (25, 26), who were able to study the sponges in the living condition. Nevertheless even a cursory examination of my figures 23 to 64 will, I hope, show that there is a good deal of histological detail to be made out even in spirit-preserved specimens of calcareous sponges.

With regard to the classification of the tissues, I still maintain the opinion which I expressed in my memoir on the anatomy of Grantia labyrinthica (9)—that is to say, I still follow Schulze (27) in considering that the ectoderm of the larval sponge (at any rate in the Calcarea) furnishes not only the epithelium of the dermal surface, but also that of the entire inhalant canal system; that the endoderm lines the remainder of the canal system (including, of course, the flagellated chambers) from the prosopyles to the osculum, and that the mesoderm furnishes all the remainder of the sponge body.

As to the homology of the three layers in sponges with the similarly named layers in higher animals, I do not presume to offer an opinion. It is sufficient for our present purposes that three layers exist in sponges; and as the names ectoderm, mesoderm, and endoderm have come into general use for these layers, and serve admirably to express their relations one to the other, I naturally adopt them in this place.

The Ectoderm.

This forms a single layer of epithelial cells which lines the external surface of the sponge, and also the whole inhalant

canal system, from the dermal pores to the prosopyles. If we consider the manner in which the inhalant canal system of the more highly developed Heterocœla has been derived from the Sycetta condition, by the closing in of a space which originally lay altogether outside the sponge, it is obvious that Schulze's view as to the extent of the ectoderm must be correct.

I also believe that Schulze was perfectly correct in his opinion (7) as to the structure of the ectoderm. In the case of Grantia labyrinthica I stated that the ectoderm resembles exactly what Schulze has described in Sycon 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" (9).

Since the above was written I have also described and figured very carefully the ectodermal epithelium of a Homocœle sponge, Leucosolenia Wilsoni (1). "It consists of thin, flattened, plate-like cells, polygonal in outline, and each with a swelling in the centre where the nucleus is situate. The cell itself averages about 0·0136 mm. in diameter, and the nucleus, which is very distinctly outlined and more or less spherical (or perhaps somewhat flattened in the same manner as the cell), has a diameter of about 0·0034 mm. Within the nucleus appear a few small, deeply staining granules. Around the nucleus the protoplasm is highly granular, exactly as described by Schulze, while towards the periphery of the cell it becomes gradually hyaline. Adjacent cells are in contact at the edges,

and all together form a single-layered, continuous epithelium over the outside of the Ascon-tube. As a rule, in ordinary preparations, although the nuclei and granules of the ectoderm-cells may be clearly enough visible, it is very difficult to distinguish the outlines."

In writing the above I regret to say that I overlooked Metschnikoff's very precise and clear account (28) of the ectoderm of Leucosolenia (Ascetta), published long before, in which he describes and figures an ectodermal epithelium precisely similar to that previously described by Schulze in Sycon raphanus, and subsequently by myself in Grantia labyrinthica and Leucosolenia Wilsoni. In the same paper (28) Metschnikoff also states that the ectoderm of Leucandra aspera has the same structure.

Metschnikoff's latest views on the subject of the ectoderm in sponges in general are contained in the following very interesting passage from his recent work on "Inflammation" (29). After pointing out that the body of the sponge is composed of three characteristic layers, he observes: "La couche superficielle, ou l'ectoderme, revêt le corps entier de cellules épithéliales plates, limitées entre elles par des contours qui deviennent très nets après l'application d'une solution de nitrate d'argent. Les cellules mêmes sont visiblement contractiles, ce qui s'observe surtout aux bords libres des jeunes individus, où on aperçoit des prolongements amiboïdes appartenant aux éléments ectodermiques. La contractilité de ces cellules joue certainement un rôle dans le phémomène remarquable de l'ouverture des pores nombreux, éparpillés sur la surface de l'éponge entière, et apparaissant entre deux ou plusieurs cellules plates."

Minchin also (25, 26) concludes that the normal condition of the ectoderm in Leucosolenia clathrus, the form specially studied by him, is flattened and plate-like, and he also ventures upon the generalisation that "the contractile elements in all cases are the flattened ectodermal epithelium." The contractile nature of the ectoderm-cells I do not doubt; I believe it to be an important character, and I shall presently

offer some slight evidence of a similar contractility amongst the Heterocœla.

Taking into consideration all the above evidence, I think we may regard it as an established fact that the ectoderm, at any rate in all calcareous sponges, like that of Sycon raphanus, normally consists of flattened plate-like polygonal cells with centrally placed nuclei. I shall presently have to bring forward fresh evidence in support of this view.

A peculiar "flask-shaped" condition of the ectodermal cells has, however, been described from time to time in various sponges, and has recently received a good deal of attention from Bidder and Minchin.

This condition was first described by Metschnikoff (28) in an Olynthus form of Leucosolenia, and the peculiarity appears to consist in the nucleus being suspended, as it were, in an envelope of protoplasm from the under surface of the plate-like cell. Bidder (21), in criticising my description of the flattened ectoderm of the Homocœla, observes, "Although this form occurs in the Homocœla, it is, in my experience, rare. The typical ectoderm (e. g. Ascetta clathrus) I find composed of onion-shaped gland-cells containing a nucleus and granules, and provided with a usually fine duct, the expanded end of which forms the hexagonal area whose boundaries are, in the case of most sponges, all that has been observed."[1] Bidder identifies his "onion-shaped gland-cells" with the cells above referred to as described by Metschnikoff in an Olynthus form, and gives a list of species in which he has observed this condition. In his later papers he brings forward additional evidence for believing "that in all groups of sponges the flask-shaped epithelium does occur" (24). He also identifies (24) the "pendent cell body" of his flask-shaped cells with the subdermal gland-cells which have been described by von Lendenfeld in the Keratosa and by myself in Grantia labyrinthica. This identification is probably correct, but I

[1] It appears to me that it is generally much more easy to see the nuclei than it is to see the outlines of the cells.

do not think that Bidder has by any means proved that the "pendent cell body" belongs to the ectoderm at all. It seems quite as reasonable to believe that it is the presence of subdermal gland-cells, in many cases at any rate, which has led Bidder to believe in the general occurrence of flask-shaped or onion-shaped glandular ectoderm-cells. Until we have more light on the subject I prefer to retain my old belief in subdermal gland-cells, but I am quite open to conviction on this point, which, with the material at my disposal, I am incapable of deciding for myself.

The observations of Minchin (25, 26) are also very noteworthy in this connection. This author explains the flask-shaped condition as due simply to contraction of the normal, flattened, plate-like cells, and his observations upon Leucosolenia certainly support this view. Subdermal gland-cells do not appear to occur, at any rate as a rule, in the Homocœla, and so far as these sponges are concerned I am inclined to accept Minchin's explanation.

I must now describe what few additional observations I have myself been able to make on the ectoderm of the Heterocœla. These observations support the view that the ectoderm is composed of a single layer of flattened plate-like cells, which retain to a greater or less extent the power of contraction. I believe that the character of this epithelium is, usually at any rate, the same throughout, from osculum to prosopyles, although it is much more difficult to detect on the exposed outer surface of a dermal cortex than on the protected surface of an inhalant canal. I have observed it most satisfactorily in a specimen of Vosmaeropsis Wilsoni (4) which I took the precaution to kill with osmic acid. This sponge is provided with a very distinct oscular sphincter, which has much the same structure as that described by Minchin in Leucosolenia clathrus (25). It is composed of two layers of epithelial cells with probably a very thin layer of gelatinous mesoderm (ground substance) between them. Both layers of cells are regarded by Minchin in Leucosolenia as ectodermal, and (as a mere matter of convenience, for we must draw the line between

ectoderm and endoderm somewhere) I follow him in this respect, and regard both layers of epithelial cells in the oscular diaphragm of Vosmaeropsis Wilsoni as ectodermal also. As there is no structural distinction between the flattened endodermal cells which line the gastral cavity in Heterocœle sponges and the ectodermal cells, it is impossible to say exactly where one begins and the other ends.

A portion of the epithelium which covers the upper surface of the oscular diaphragm in the sponge in question is represented in fig. 63, drawn from an osmic acid preparation mounted in glycerine. The cells are mostly polygonal, and fit tightly together by their edges. Each has the form of a flat plate, with usually a single nucleus situated in about the centre. The nucleus is small, and in osmic acid preparations looks clearer and more transparent than the surrounding protoplasm. The latter contains numerous granules, larger and more abundant towards the centre of the cell, which are stained very darkly by the osmic acid. The majority of the cells are about as broad as they are long, but some of them are fusiform, like those of the Leucosolenia diaphragm figured by Minchin in his fig. 12. On the under surface of the diaphragm a similar layer of cells occurs, but these are not so deeply stained by the osmic acid, doubtless owing to want of penetration.

I do not doubt that these epithelial cells are contractile, and that their contractility serves to open and close the diaphragm.

If we trace this epithelium from the oscular diaphragm up over the lip of the osculum and on to the outer surface of the sponge, we find that it maintains exactly the same character throughout, covering the whole outer surface of the sponge with a layer of flattened cells. The dermal cortex is penetrated by very numerous inhalant pores (fig. 23), and on reaching the margin of one of these the ectodermal epithelium turns in, and is continued as a lining to the inhalant canal system, a lining which resembles minutely the epithelium of the oscular diaphragm, and the component plate-like cells of which are

extremely conspicuous in sections of osmic acid specimens (fig. 23).

Sometimes in sections of ordinary spirit-preserved material, cut by the paraffin method, the flattened cells of the ectodermal epithelium appear separated from one another by considerable intervals, as is shown in fig. 29, representing a portion of the epithelial lining of the inhalant canal system of Grantessa intusarticulata, and in fig. 59, representing epithelium from a corresponding situation in Sycon Ramsayi. This appearance is evidently due to contraction of the cells, which may still remain connected in places by strands of protoplasm which stretch across from one to the other. Both ectodermal and endodermal epithelial cells appear to be very subject to such contraction, and it appears to me very possibly to indicate a normal contractility in life, such as is described by Metschnikoff (29).

It has been recently maintained by Bidder (23) and Minchin (26) that the prosopyles which pierce the walls of the flagellated chambers are formed each by the perforation of a single nucleated cell; but, while Bidder attributes to these cells an endodermal origin, Minchin regards them as derivatives of the ectoderm. For my own part I am disposed to regard the prosopyles as inter-cellular and not intra-cellular in nature, and Schulze's admirable drawings of the anatomy of Sycon raphanus (7) point to the same conclusion. My own drawings of the anatomy of Grantia labyrinthica show exactly the same condition, and in the very numerous sections of calcareous sponges which I have examined, I have met with no evidence to cause me to doubt the correctness of the view that the prosopyles are simply gaps between cells. Bidder, indeed (21), interprets the remarkable groups of yellow granules which I described in Leucosolenia cavata (1) as perforated prosopyle cells. I do not deny the possibility of this view, but I do not think that the evidence is sufficient to justify it, and, in any case, the occurrence of such structures (whatever they may be) is in my experience very rare even in the Homocœla, and altogether unknown in the Heterocœla, of

which I have examined very numerous species. Therefore, even if we admit that perforated prosopyle cells occasionally occur, there is no reason for believing that this is the usual condition, but quite the contrary. When viewed en face the prosopyles of calcareous sponges usually appear as sharply defined approximately circular spaces (figs. 25, 30). Not infrequently the nucleus of an ectodermal epithelial cell happens to lie exactly on the margin of this space (fig. 30), but I do not think there is any reason for regarding this fact as indicating that the prosopyle itself is of an intra-cellular nature; while sections such as those figured by Schulze in the case of Sycon raphanus, and by myself in the case of Grantia labyrinthica, clearly indicate the contrary.

Before leaving the question of the ectoderm I may conveniently describe in this place a very curious condition which exists in Grantiopsis cylindrica (4). This highly interesting Australian species is known only from a few fragments, probably all belonging to the same specimen. These fragments are, however, in a remarkably good state of preservation, but notwithstanding this fact it is a difficult matter to make out the epithelial cells either on the outer surface of the sponge or in the somewhat complicated inhalant canal system. On the other hand, we find in both these situations a very peculiar layer of minute granules, which, when examined under a Zeiss F objective, presents in surface view the appearance shown in fig. 57, and in sections at right angles to the dermal surface the appearance shown in fig. 56. The granules themselves appear slightly elongated and very thickly and evenly scattered over the surface. Embedded in the gelatinous ground substance of the mesoderm, at some little distance beneath the dermal surface, are found numerous very distinct subdermal gland-cells, connected by thread-like processes with the granular layer, as shown in fig. 56. The granules themselves do not stain with borax carmine, and present, under the Zeiss F obj., a very striking resemblance to bacteria. So great is this resemblance that I submitted a fragment of the sponge to Mr. Thomas Cherry, Demonstrator in Pathology in

the Melbourne University, who kindly made a careful examination of it for me, with the following results. The granules were scraped into a glass, dried, stained with fuchsin, mounted in Canada balsam, and examined under a $\frac{1}{12}$-inch oil immersion objective (Leitz) with a No. 5 eye-piece. We then found that they presented the appearance shown in fig. 58, being usually each somewhat dumb-bell shaped, or composed of two ovoid segments placed end to end, though sometimes the shape was irregular. They averaged about 0·004 mm. in length, and consisted of a fairly darkly stained, sometimes slightly granular body, with a round very darkly staining structure, presumably a nucleus, in each end of the dumb-bell, or, when the shape was irregular, with several such nuclei. It thus appears that, though probably not bacteria, the bodies in question are micro-organisms of some kind which live upon the surface of the ectoderm. Nuclei, presumably belonging to the epithelial cells, are still visible amongst the granules, at any rate in the inhalant canals, and I am inclined to think also on the outer surface of the sponge; but we have here an excellent illustration of the way in which the structure of the ectoderm is sometimes obscured by the accumulation of foreign bodies.

Bidder would possibly interpret the subdermal gland-cells of Grantiopsis cylindrica as representing the true ectodermal epithelium. But they do not look like it (fig. 56). They appear to be but very slight modifications of the ordinary stellate mesodermal cells, and as such they will be described on a future page.

The Endoderm.

I have little to add concerning the histology of the endoderm to what I have already written on the subject. As already stated, I consider as endoderm not only the collared cells which line the flagellated chambers, but also the flattened pavement epithelium which lines the gastral cavity and exhalant canals of the Heterocœla. It is, of course, quite conceivable that this pavement epithelium is formed by an

ingrowth of the ectoderm from the region of the osculum, replacing and, as it were, pushing back the collared cells. I do not, however, consider that there is any reason for supposing this to be the case. In the case of the Homocœla I have shown (1) that the lining of the gastral cavity is not always composed entirely of collared cells, but that the apical rays of the quadriradiate spicules which frequently project into this cavity are clothed with a layer of flattened epithelium. I suggested at the time that this epithelium might possibly be derived from the mesoderm; but, on the other hand, it might with equal justice be regarded as indicating a transformation of collared cells into permanent cells, and we are quite at liberty to suppose that a similar transformation, only on a much larger scale, has taken place in the gastral cavity and exhalant canals of the Heterocœla.

The epithelium which lines the gastral cavity and exhalant canals resembles minutely the ectodermal epithelium which clothes the outer surface of the sponge and lines the inhalant canal system. This will be evident from a comparison of figs. 59 and 60, representing respectively the epithelium from an inhalant and from an exhalant canal of Sycon Ramsayi, the differences which exist between the epithelium in these two situations being obviously very slight and insignificant. Similarly fig. 64 represents the epithelium from an exhalant canal of Vosmaeropsis Wilsoni, which, if we allow for the contraction of the cells due to difference in the method of preparation, is practically identical with the ectodermal epithelium from the same sponge represented in fig. 63. Indeed, unless specially prepared, as with osmic acid, the ectodermal epithelium, as already pointed out, exhibits a precisely similar contraction, and in both cases this is such a constant and well-marked feature that I am inclined to think that it betokens a normal contractility during life. The appearance of the endodermal pavement epithelium, as seen in section, is shown in figs. 27, 28, and 61. The swelling in the centre of the cell, where the nucleus is situated, is frequently very strongly marked, and causes the epithelium to

be very conspicuous in sections taken at right angles to its surface.

In an undetermined specimen of Leucandra, from Port Jackson, the epithelial cells lining the gastral cavity just within the osculum are so much swollen out as to be almost as thick as they are broad, and they also present a vacuolated blister-like appearance, as shown in fig. 32. Lower down in the gastral cavity the epithelial cells have the normal flattened form.

The flagellated chambers of most, if not all Heterocœle sponges, whether they be of the elongated Syconoid or of the rounded Leuconoid form, are separated from the exhalant canals into which they open by very distinct membranous diaphragms (figs. 25—27, 31). When viewed en face these diaphragms have usually the appearance shown in fig. 31, consisting of a thin, transparent membrane, in which are visible spindle-shaped cells arranged concentrically. The actual outlines of the cells I have not succeeded in distinguishing, but their elongated character and concentric disposition are usually clearly indicated by the arrangement of the granules which surround the nucleus. Collared cells are never found on either surface of this membranous sphincter, and whether it consists of one or two layers of cells is a very difficult question, which I have not been able definitely to decide. The concentrically arranged, spindle-shaped cells are obviously muscular, and as such I described them in my memoir on Grantia labyrinthica. In that paper, however, I classed them as mesodermal elements. I am now convinced that they are simply modifications of the cells which line the exhalant canals, comparable to the muscular cells of the oscular diaphragm described by Minchin in Leucosolenia, and by myself in Vosmaeropsis. Fig. 27 shows how the epithelial cells of the exhalant canal are continued on to the surface of the chamber diaphragm. Usually they appear very much elongated in this situation, as shown in fig. 31, but sometimes the elongation is scarcely visible at all, as shown in figs. 25 and 26. Probably the exact form of the cells depends upon their state of contraction. The epithelial cells of the exhalant

canals themselves may exhibit elongation and concentric arrangement around these canals, but not to the same degree as in the chamber diaphragms.

The chamber diaphragms, then, I regard as being composed of endodermal muscular cells, formed by modification of the ordinary endodermal pavement cells. Whether they consist of one or two layers of these cells is doubtful; probably of two layers, with a small amount of gelatinous ground substance between.

It thus appears that, if Minchin is right in regarding the muscular cells of the oscular diaphragm in Leucosolenia as ectodermal, and if Schulze is right in regarding the lining of the exhalant canals in Heterocœle sponges as endodermal, then both the ectoderm and endoderm may give rise to strikingly similar muscular structures. Possibly this may be an argument for regarding the muscular cells of the oscular diaphragm in Leucosolenia as endodermal and not ectodermal; but it appears to me that this is a question which cannot be decided in the present state of our knowledge.

Concerning the remaining endodermal cells, the collared cells which line the flagellated chambers, I have little to say. I may, however, call attention to fig. 25, representing half of a flagellated chamber of an undetermined species of Leucandra, in which Sollas's membrane and the collars of the collared cells are remarkably clearly seen. This figure also shows the exhalant aperture with its membranous diaphragm, and two prosopyles. Whether or not Sollas's membrane is continuous over the prosopyles I have been unable to determine, and it appears to me that the point can only be decided by the examination of living specimens.

I quite agree with Bidder (21) that the endoderm is not only multiform, but also "most proteic," as, indeed, was long ago shown by Carter (30) from observations on the living Sycon (Grantia) compressum, in which he observed the collared cells becoming amœboid, and moving about the field of the microscope. I am therefore quite prepared to believe that the existence of Sollas's membrane may be only a transitory condition, due to special circumstances, of which we are as yet

ignorant. That it does exist in many cases is beyond dispute, and it is extremely interesting to learn that Bidder (21) has observed in the living Sycon raphanus the coincidence of the flagella of the collared cells with Sollas's membrane, just as I described it in Halichondria panicea (31).

A curious illustration of the polymorphic nature of the collared cells, is afforded by the peculiarly contracted chambers which I described in my memoir on Grantia labyrinthica, and indicated in my drawings of the anatomy of that sponge by the letter *x*. I have now observed the same phenomenon in other Heterocœle sponges—viz. Ute syconoides and Leucandra phillipensis—and am very glad to be able to give some more exact details as to the form and arrangement of the collared cells in these cases. Fig. 24 represents a contracted chamber of Ute syconoides shown in transverse section, and surrounded by four ordinary chambers and four intercanals. It will be seen that the layer of collared cells has shrunk away from the tubar skeleton, drawing the mesodermal tissue after it. The collared cells themselves have become radially elongated, and, owing to their having a smaller area to spread themselves over, very much crowded. It was doubtless this crowded condition which caused me to describe them as being arranged in more than one layer in the case of Grantia labyrinthica. Each cell is more or less pyramidal in form, and the nucleus is situated in the apex of the pyramid towards the lumen of the chamber.

In my earlier paper (9) I endeavoured to explain the occurrence of these contracted chambers (which exhibit a very different appearance from chambers in which contraction has been produced by the action of the preserving fluid) by supposing them to represent old and exhausted chambers in process of dying, and destined to be replaced by the development of new chambers.

Bidder, in his very interesting "Note on Excretion in Sponges" (23), has suggested a different explanation. After describing the accumulation of "spherules" in the bases of collared cells, he adds, "I believe these basal spherules to be

stores of nutritious matter. In Leucandra aspera and Sycon raphanus .... the collar cell, after it has accumulated a certain quantity of spherules in its base, splits off this base by a transverse fission as a non-nucleated mass of protoplasm, which we may term a 'plinth' (fig. 4); the plinth then lies between the nucleated distal part of the cell—the 'column'—and the mesodermal jelly in S. raphanus, or the thin basement membrane which is all that usually divides the epithelia in L. aspera. I have observed in the mesoderm of S. raphanus large wandering cells, which I believe to be generative elements, with pseudopodia attached to these plinths, and spherules of the same character as the basal spherules, both in the wandering cells and in their pseudopodia. There can be little doubt that they were feeding on ths reserve stores of the collar-cells. The division into column and plinth takes place as a rule at the same time in all or most of the cells of a chamber. The 'columns' or distal parts appear as small, columnar, nucleated cells, provided with a small amount of clear protoplasm, rudimentary collars not united, and flagella (fig. 4A)." Later on, in the same paper, Bidder observes that he interprets the peculiar structures met with by me in Grantia labyrinthica as column-and-plinth chambers violently contracted in alcohol. There is certainly a good deal to be said in favour of this view, and, examining the structures in question in the light of Bidder's remarks, I have seen in Leucandra phillipensis appearances which might be taken as indicating the formation of "plinths." The abundant occurrence of small nucleated cells in the mesoderm which surrounds the contracted chambers, as shown in fig. 24, is certainly suggestive either of the congregation of amœboid cells to feed on the collared cells, or of the collared cells or segments thereof becoming amœboid and wandering away into the mesodermal jelly. The occurrence of such cells in the surrounding jelly is characteristic of the contracted chambers, and their small size appears to me to be an argument in favour of regarding them as metamorphosed collared cells rather than as ordinary amœboid ones.

In Leucandra phillipensis the ordinary amœboid cells are very much larger than the cells in question in the same sponge; in fact, compared to the latter and to the collared cells they are as giants. Curiously enough, I observed one of these large amœboid cells, shown in fig. 50, apparently feeding, by means of pseudopodia, on the collared cells. The chamber to which the collared cells belonged was, however, in the ordinary uncontracted condition, and I could not see any indication of the division of the collared cells into "column and plinth."

On the whole, the peculiar contracted condition, such as is shown in fig. 24, and which occurs in chambers both of the Syconoid and Leuconoid types, is perhaps to be regarded as indicating not so much a process of death as one of rejuvenescence, and this is, after all, but a slight modification of my former view. We may suppose that, after perhaps taking in a large supply of food, the chamber passes into a resting condition. The collared cells then undergo certain changes which are not fully understood, but which finally result in the formation of a new chamber with ordinary active collared cells. The contraction of the chamber during this process appears to me to be normal, and not due to the action of reagents.

The Mesoderm.

The transparent gelatinous ground substance which forms the bulk of the mesoderm in all calcareous sponges, appears to vary only in the extent to which it is present and the proportion which it bears to other parts of the sponge. It is most strongly developed in the dermal and gastral cortex (figs. 10—12). It may also be fairly abundant in the walls of the flagellated chambers, as in Sycon gelatinosum (figs. 3—5), but it is usually very sparingly developed in this situation, so as to be distinctly recognisable only at the points where the chambers touch one another (fig. 13). Hence in very many cases the walls of the chambers appear in thin sections to be made up of two contiguous layers of cells, the collared cells on the inside and the pavement epithelium of the inhalant canals on

the outside. I do not doubt, however, that there is always a thin layer of mesoderm between the two, a fact which is indicated by the development of spicules in the chamber walls. It is certainly continued into the endogastric septa of Grantessa erinaceus, which consist of a layer of gelatinous ground substance, with an occasional stellate cell, covered on each side by a layer of flattened epithelium (fig. 62).

Concerning the spicule sheaths, which are formed by a slight concentration of the structureless mesodermal jelly around the spicules (fig. 53), I have nothing to add.

In my memoir on Grantia labyrinthica I classified the mesodermal cells which lie embedded in the gelatinous ground substance as follows:—(1) Amœboid, (2) Stellate, (3) Glandular, (4) Endothelial, (5) Muscular, (6) Nervous, and (7) Reproductive. I am still prepared to abide by this classification so far as the amœboid, stellate, glandular, and reproductive cells are concerned. The only muscular cells which have yet been observed in calcareous sponges I now regard, as already indicated, as ectodermal or endodermal. The supposed nervous cells I am now extremely doubtful about, in all cases, and I am strongly inclined to think that the appearances described as such are due to the presence of subdermal gland-cells. This point, however, can only be settled by a very careful re-investigation of living material. The endothelial cells I still retain provisionally amongst the mesodermal elements, although I shall presently give reasons for believing that they need not necessarily be regarded as such.

Amœboid and Stellate Cells.—I have observed most beautiful examples of amœboid cells in Leucandra echinata (fig. 33) and L. phillipensis (figs. 48—50). They are found scattered here and there in the mesodermal ground substance between the flagellated chambers, and, in these two sponges, are conspicuous by their enormous size. The amœboid cells are typically distinguished from the stellate cells by their more uniformly granular protoplasm, their larger nuclei, and the absence of the slender, thread-like, radiating processes, which characterise the stellate cells; the latter are very different in appear-

ance from the blunt, rounded pseudopodia which characterise a typical amœboid cell. Nevertheless it is often very difficult to say whether a particular cell should be classed as stellate or amœboid, especially when that cell is of small size; and I am inclined to think that no hard-and-fast line of distinction can be drawn between the two. Thus figs. 39—42 represent a number of cells from the dermal cortex of Leucandra phillipensis, which I personally should class as stellate, but it would be very difficult to prove that they are not amœboid. Similarly fig. 55 represents four mesodermal cells from the dermal cortex of Grantiopsis cylindrica, which may be classified as stellate or amœboid, according to the taste of the observer. For my own part I am inclined to believe that even the most typical stellate cells may be, to a greater or less extent, amœboid, and capable of a certain amount of movement. What appears to be division of the "stellate" cells by fission is very clearly seen in the cortex of Leucandra phillipensis, in which many of the cells have two nuclei, and also show signs of division in the form of the cell body (figs. 39, 40, 42).

Glandular Cells.—These, as I have already pointed out (9), are of two kinds, calcoblasts and subdermal gland-cells. I can only confirm the account of these structures which I gave in the case of Grantia labyrinthica. I have recently observed some very beautiful examples of calcoblasts. They appear to be most easily recognisable on the inner portions of projecting dermal oxeote spicules. Figs. 44—47 represent portions of such spicules from the dermal cortex of Leucandra phillipensis. Each spicule has a single nucleated calcoblast attached to its inner half, and I do not hesitate to regard these cells as the manufacturers of the material of which the spicules are composed. At the same time it will be sufficiently obvious, on comparing figs. 44—47 with figs. 39—42, that the calcoblasts are very similar in appearance to the ordinary "stellate" cells, which are found embedded in the gelatinous ground substance in their immediate neighbourhood.

In Grantiopsis cylindrica I have found very large cal-

coblasts[1] attached to the rays of the large triradiate spicules in the dermal cortex. Three of these cells are shown in figs. 52—54, and their characters certainly justify the assumption that they are but slight modifications of ordinary stellate cells. It appears to me that the calcoblasts, at any rate in the case of large spicules, must be amœboid, for, unless they be so, I cannot understand how the spicules can increase uniformly in thickness. I have already suggested (9) that there are probably primary and secondary calcoblasts, the former being mother-cells within which spicules are formed, and the latter cells which apply themselves to the surfaces of already formed spicules and increase the thickness of the latter. The cells represented in figs. 52—54 are probably secondary calcoblasts; those represented in figs. 44—47 may be primary.

Minchin (32), in the case of Leucosolenia, found the triradiate spicules to have a nucleus at the extremity of each ray, and a fourth one at the confluence of the rays. As there are four of these nuclei they probably indicate the presence of secondary calcoblasts, for we can hardly suppose that the spicule is originally formed by more than one cell.

We come now to the subdermal gland-cells, which Bidder (24) regards as the "pendent cell bodies" of flask-shaped ectoderm-cells. These cells may occur beneath both the gastral and the dermal surfaces of the sponge. In Grantia labyrinthica they are more plentiful beneath the gastral than beneath the dermal surface, a fact which I associate with the peculiar shape of the gastral cavity, which causes its surface to be almost or quite as much exposed as the dermal surface. A situation beneath the dermal surface, however, appears to be their normal one, and they are rare elsewhere. To my description of these structures in Grantia labyrinthica I have little to add. I have found them especially well developed in Grantiopsis cylindrica (fig. 56), where the connection with the surface is very long and slender. In Leucandra phillipensis I have detected them around the inhalant

[1] Compare with these the "conjectural calcoblast," figured by Poléjaeff (8) in his Leuconia multiformis.

canals as well as beneath the dermal surface (fig. 43). In all these cases they closely resemble the ordinary stellate mesoderm-cells, and as modifications of such I am for the present disposed to regard them. That they secrete a slime which covers the surface of the sponge in life, I do not doubt.

Vesicular Cells.—I propose this name for certain large rounded cells which occur scattered singly, but in considerable numbers, immediately beneath the gastral epithelium of Ute syconoides. The general appearance of these cells is shown in fig. 37. The body of the cell stains uniformly and fairly darkly with borax carmine. It is not granular, but hyaline. The nucleus is small, darkly staining, and situated at one side of the cell. It appears to have been pushed aside by the accumulation of fluid in the cell body, as in fat-cells. I am not aware that cells of this kind have been noticed before in calcareous sponges, and they appear to me to be most nearly comparable to the "cystenchyme" cells of Silicea and Keratosa—as, for example, Stelospongus (33).

Reproductive Cells.—The only reproductive cells upon which I have made any observations are the ova, and these have been so frequently described that I need say little about them here. Figs. 34 and 36 represent typical calcisponge ova, consisting each of a large naked body of highly granular protoplasm, with a large, very sharply defined nucleus and a distinct nucleolus.

In my memoir on Grantia labyrinthica I adduced evidence for believing that the ova, at a certain stage of their existence, migrate through the epithelium of the inhalant canals and hang freely from its surface, so as to be bathed by the inflowing stream of water, and I regarded this as a special contrivance for securing fertilisation. In Ute syconoides I have had the good fortune to observe a very beautiful instance of the manner in which the ovum hangs suspended from the wall of an inhalant canal, as represented in fig. 35. I was particularly glad to obtain this confirmation of my previous observations, as the inhalant canals of Ute syconoides are much more sharply defined and easily recognisable than those

of Grantia labyrinthica, and there is no possibility of doubt as to the exact position of the pendent ovum. Fig. 36 represents an ovum of the same sponge which has presumably been fertilised, and has taken up the normal position for development, just behind the layer of collared cells which lines one of the flagellated chambers, as shown in figs. 5 and 13.

For an account of the spermatozoa of the Heterocœla I must refer the reader to Poléjaeff's work on the subject (34).

Endothelial Cells.—Under this name I have previously described (9) the more or less flattened cells which line, in a single layer, the cavities in which the embryos develop. Fig 38 shows a typical example of an embryo lying in a cavity lined by such cells. Schulze (7) attributes to these cells a mesodermal origin. For the present I adopt this view; but I would like to point out that they may possibly be ectodermal, for it is easy to imagine that an ovum, after migrating through the wall of the inhalant canal, in returning into the mesoderm may push before it a portion of the ectodermal epithelium, from which the embryo capsule might be derived. This, however, is, in the present state of our knowledge, mere speculation.

V.—The Classification of the Heterocœla Calcarea, with Diagnoses of the Families and Genera.

We are now in a position to apply the results of our anatomical investigation to the classification of the group. I have found it necessary to forestall to a certain extent what I have to say here about the classification, in order to satisfactorily arrange my notes on the anatomy, but this was obviously unavoidable. In the present section I propose not only to set forth the classification of the group, and to give brief diagnoses of the families and genera, but also to discuss, so far as appears necessary, the questions of synonymy and nomenclature.

Order HETEROCŒLA, Poléjaeff (8).

Diagnosis.—Calcareous sponges in which the collared cells are confined to more or less well-defined flagellated chambers.

Family 1.—Leucascidæ, Dendy (4).

Diagnosis.—Flagellated chambers very long and narrow, copiously branched; communicating at their proximal ends with exhalant canals, which converge towards the oscula; their blind distal ends covered over by a dermal membrane pierced by true dermal pores, which lead into the irregular spaces between the chambers. Skeleton consisting principally of small radiates, irregularly scattered in the walls of the chambers and exhalant canals, and in the dermal membrane.

Genus 1.—Leucascus, Dendy (4), fig. 1.

Diagnosis.—The same as that of the family.

Remarks.—Leucascus, the sole genus of the family, appears to occupy a very isolated position amongst the Heterocœla, both as regards skeleton and canal system. Its skeleton, as already pointed out, has not yet attained to the typical radiate condition of the Heterocœla, but retains the irregular scattered character of the reticulate Homocœla. The genus might, indeed, be easily confounded with the reticulate section of the genus Leucosolenia (1), but differs in several very important particulars; viz. (*a*) The possession of a distinct pore-bearing dermal membrane, which is found in no Homocœle sponge with which I am acquainted, and is not even developed amongst the Heterocœla until we reach the most advanced Sycon condition. The pseudoderm of many reticulate Homocœla (1) is by no means an homologous structure. (*b*) The absence of collared cells from the exhalant canals, which there is no reason for believing to be of a "pseudogastral" nature, as in my type D of the reticulate Homocœla. (*c*) The flagellated chambers, although, owing to the massive form of the sponge and the absence of a single central gastral cavity, they cannot be truly radial, nevertheless show a marked tendency to become so.

The genus may, perhaps, be best regarded as derived independently from a lowly organised type of radiate Homocœla.

It might, perhaps, be regarded as a degenerate Heterocœle which has lost its radial symmetry, but the facts do not appear to me to warrant this hypothesis.

Family 2.—Sycettidæ, Dendy (4).

Diagnosis.—Flagellated chambers clongated, arranged radially around a central gastral cavity, their ends projecting more or less on the dermal surface, and not covered over by a continuous dermal cortex. Tubar skeleton articulate.

Remarks.—This family is equivalent to van Lendenfeld's (10) two sub-families Sycanthinæ and Syconinæ taken together. As I have already pointed out, his genus Sycantha is probably but a slight modification of the ordinary Sycon type. The name Sycettidæ is adopted partly because the genus Sycetta is the simplest of the three included in the family, and partly to avoid confusion with the much more comprehensive Syconidæ of previous writers, such as Polé-jaeff (8).

Genus 2.—Sycetta (Haeckel [5], emend.).

Diagnosis.—Radial chambers separate from one another, and without tufts of oxea on their distal ends.

Remarks.—This genus, as here maintained, is much less comprehensive than was originally intended by its author (5). Haeckel included in the genus all Syconoid species in which triradiate spicules alone entered into the composition of the skeletons, and thus was obliged to group together such structurally different species as S. primitiva and S. stauridia; while he had to exclude S. conifera simply because some of the triradiates develop an apical ray, and thus become quadriradiate. Von Lendenfeld also confined his diagnosis of the genus to the character of the spiculation (10), but modified it so as to include S. conifera. Poléjaeff (8) merged the genus into Sycon. If, however, we include in the genus only those species which, like Haeckel's Sycetta primitiva and S. (Sycaltis) conifera, conform in skeletal characters and canal system to the diagnosis given above, we shall have left a

very natural and well-characterised genus, comprising only three species, viz. S. primitiva, S. sagittifera, and S. conifera, all of which are described by Haeckel in his great monograph.

Genus 3.—Sycon (Risso, emend.), figs. 2—8.

Diagnosis.—The radial chambers are usually more or less united at places where they come into contact with one another, and they are always crowned at their distal extremities with tufts of oxeote spicules.

Remarks.—The most characteristic feature of this genus is afforded by the tufts of oxeote spicules which crown the distal ends of the radial chambers. In some species, such as Sycon boomerang (4) and S. gelatinosum (4, 5), we find a transition to the genus Grantia, in the presence of a pore-bearing dermal membrane stretched between the distal ends of the radial chambers; but this never forms a cortex which completely covers over the chambers as in the Grantidæ, and it in no way interferes with the characteristic tufts of oxeote spicules.

The genus as here constituted includes most of Haeckel's species of his genus Sycandra (5), but I follow Poléjaeff (8) in giving priority to the old name Sycon. Familiar European examples are S. raphanus and S. ciliatum, and I also include S. (Grantia) compressum, on account of the tufts of oxeote spicules which crown the ends of the chambers. Poléjaeff's genus Sycon is, as already pointed out, more comprehensive, and includes our Sycetta, while von Lendenfeld (10) adopts the genus Sycandra in almost the same sense as Haeckel.

Genus 4. Sycantha, von Lendenfeld (10).

Diagnosis.—Radial chambers united in groups, with freely projecting distal cones surmounted by tufts of oxeote spicules.

Remarks.—It appears to me that the only character which can be relied upon for distinguishing this genus is the grouping

of the chambers. I have already given my reasons for coming to this conclusion in discussing the canal system.

Family 3.—Grantidæ, Dendy (4).

Diagnosis.—There is a distinct and continuous dermal cortex, completely covering over the chamber layer, and pierced by inhalant pores. There are no subdermal sagittal triradiates, nor conspicuous subdermal quadriradiates. The flagellated chambers vary from elongated and radially arranged to spherical and irregularly scattered ones, while the skeleton of the chamber layer varies from regularly articulate to irregularly scattered.

Remarks.—This family does not nearly correspond with any which has hitherto been proposed; for, disregarding differences in canal system, I include therein some genera with a Syconoid and others with a Leuconoid type, and rely upon the structure of the skeleton for thus uniting them. I believe myself to be justified in this course of action by the great variation of the canal system which has been shown to exist in closely related forms and even in the same species, and which I have already discussed in a previous part of this paper.

The family, as here constituted, is distinguished from the Sycettidæ by the positive character afforded by the development of a strong dermal cortex, and from the Heteropidæ and Amphoriscidæ by the negative characters afforded by the absence of subdermal triradiates or quadriradiates. It is very difficult to diagnose the family, which is a very comprehensive one, so as to exclude the Leucascidæ, but the latter present a peculiar combination of skeleton and canal system which is not to be found amongst the Grantidæ, and appear never to have passed, as I believe all the Grantidæ have, through a primitive Syconoid stage with radially symmetrical skeleton.

Genus 5.—Grantia (Fleming, emend.), figs. 9, 10.

Diagnosis.—The elongated flagellated chambers are ar-

ranged radially around the central gastral cavity; they are not provided with tufts of oxea at their distal ends, but are covered over by a dermal cortex composed principally of triradiate spicules, and without longitudinally disposed oxea. An articulate tubar skeleton is present.

Remarks.—The genus Grantia, as here defined, is very nearly co-extensive with the same genus as employed by Poléjaeff (8). It appears to me, however, that the genus must be limited to those species in which no tufts of oxea are developed on the ends of the radial chambers, in order to define it with desirable sharpness from Sycon; for, as I have already shown, we meet with the first indications of a dermal cortex in the latter genus. Hence I cannot agree with Poléjaeff in including Sycon (Grantia) compressum. Nor can I agree with von Lendenfeld's diagnosis (10), for he expressly states that a crown of radial "Thabden" may be present on each chamber, and his diagnosis is so worded as to exclude Haeckel's G. (Sycetta) strobilus and G. (Sycetta) cupula, which, as was recognised by Poléjaeff (8), undoubtedly belong to the genus Grantia.

Sub-genus Grantiopsis, Dendy (4), fig. 11.

Diagnosis.—The sponge has the form of a greatly elongated hollow tube, whose wall is composed of two distinct layers of about equal thickness. The outer (cortical) layer is provided with a very strongly developed skeleton of radiate spicules, and is penetrated by narrow, ramifying, inhalant canals. The inner layer is formed by elongated radial chambers, arranged very regularly side by side. The skeleton of the inner layer is very feebly developed. The tubar skeleton is articulate, and composed of very abnormal sagittal triradiates whose paired rays are greatly reduced.

Remarks.—This genus is obviously only a very special modification of the well-known Grantia type, although at first sight, especially as regards external form, it appears very distinct. The only species known is the Victorian Grantiopsis cylindrica (4).

Genus 6.—Ute (Schmidt, emend.), figs. 12—14, 24.

Diagnosis.—The ends of the elongated radial chambers are covered over by a well-developed cortex, composed in great part of large oxeote spicules arranged parallel to the long axis of the sponge. The tubar skeleton is articulate, or else composed entirely of the basal rays of subgastral triradiates.

Remarks.—This genus I maintain in the same sense as Poléjaeff (8) and von Lendenfeld (10). It now includes five species, viz. the original European type, Ute glabra, Schmidt (17), and the Australian U. argentea, Poléjaeff (8), U. syconoides, Carter (12), U. spiculosa, Dendy (4), and U. Spenceri, Dendy (4). The spiculation of the dermal cortex, upon which the genus is founded, is paralleled in two species of Leucosolenia, L. asconoides, Carter (12), and L. uteoides, Dendy (16); and also in Leucandra (Aphroceras) alcicornis, Gray, and Heteropia (Aphroceras) ramosa, Carter (15). Indeed, this character gave rise to Gray's family "Aphrocerasidæ" (18), which, like other families founded upon an insufficiency of characters, has had to be abandoned.

The genus appears to be a natural one, but is obviously very closely related to Grantia, and, had it not been already well established, I should have hesitated in attributing generic importance to a character which is found in so many very distinct sponges.

Sub-genus Synute, Dendy (13), fig. 15.

Diagnosis.—Sponge compound, consisting of many Ute-like individuals completely fused together, and invested in a common cortex, composed largely of huge oxeote spicules arranged longitudinally.

Remarks.—I at first thought that my Synute pulchella (13) should stand as the type of a new genus, but I have since come to the conclusion that the complete fusion of the Ute individuals, though perhaps unparalleled amongst sponges

with a Syconoid type of canal system, is scarcely a character of generic importance, and I have therefore reduced the species to the rank of a sub-genus.

Genus 7.—Utella, Dendy (4).

Diagnosis.—Flagellated chambers elongated, arranged radially around the central gastral cavity. There are no longitudinally arranged oxea in the dermal cortex, but a layer of oxeote spicules, longitudinally arranged, lies beneath and parallel to the gastral surface. The tubar skeleton is articulate.

Remarks.—This genus was proposed for the reception of Haeckel's remarkable Sycandra hystrix (5), and Schmidt's Ute utriculus (19) may perhaps also be included in it. The genus is obviously a special modification of the Grantia type. It is, as I have already pointed out, very unusual to find oxeote spicules in the gastral cortex of any calcisponge.

Genus 8.—Anamixilla, Poléjaeff (8).

Diagnosis.—Flagellated chambers elongated and radially arranged. There is no special tubar skeleton, the skeleton of the chamber layer consisting of large radiate spicules, arranged without regard to the direction of the chambers, and of the outwardly directed basal rays of the subgastral sagittal triradiates.

Remarks.—The derivation of this remarkable genus from the Grantia type is still indicated by the presence of the subgastral sagittal triradiates. It may be compared to a Grantia in which the ordinary articulate tubar skeleton has been almost entirely replaced by the invasion of large triradiates from the dermal cortex. The only species as yet known is the Australian Anamixilla torresi, Poléjaeff (8), to the account of which given by Poléjaeff I have nothing to add. I have, however, ventured to slightly alter the original diagnosis.

Genus 9.—Sycyssa, Haeckel (5).

Diagnosis.—The flagellated chambers are elongated and

arranged radially around the central gastral cavity. The skeleton consists exclusively of oxeote spicules.

Remarks.—The only known species of this genus is Haeckel's Sycyssa Huxleyi, from the Adriatic (5). The genus occupies a very isolated position. The remarkable skeletal characters upon which it is based have been discussed on a previous page.

Genus 10.—Leucandra (Haeckel [5], emend.), figs. 16, 17.

Diagnosis.—The flagellated chambers are spherical or sac-shaped, never arranged radially around the central gastral cavity, with which (or with the main exhalant canals derived therefrom) they communicate by a more or less complicated exhalant canal system. The skeleton of the chamber layer is composed of irregularly scattered radiate spicules, but it may still present traces of its derivation from a radially symmetrical type, in the presence of a few subgastral sagittal triradiates.

Remarks.—This genus, as here maintained, is still a very comprehensive one, and does not correspond exactly to any which have hitherto been proposed. It includes many species which would fall under Poléjaeff's Leuconia (8), but that author frankly admits that his Leuconia requires sub-dividing; and, moreover, Vosmaer (14) has shown that Bowerbank's name Leuconia, adopted by Poléjaeff, was previously occupied by a genus of Mollusca. I therefore agree with Vosmaer in adopting Haeckel's name Leucandra, but as that genus was based entirely upon the presence of certain forms of spicules, without regard to their arrangement, I cannot accept it in the sense originally intended. On the same principle, I include in the genus Haeckel's species of Leucetta, as I do not believe the mere absence of quadriradiate or oxeote spicules, or both, to be of generic significance. Indeed, I was strongly inclined to adopt the name Leucetta, on grounds of priority, for the genus as now constituted; but considering that Leucandra, as employed by Haeckel and Vosmaer, makes the nearest approach to the genus as now characterised, and considering also that the name Leucetta has been adopted by Poléjaeff

(8) and Vosmaer (14) in a very different sense, I have thought it desirable to make use of the name chosen.

I believe that very probably the genus will still require subdividing at some future date, but it will be an extremely difficult matter to satisfactorily characterise the different subdivisions; the irregular nature of the skeleton appears to me to defy classification. It might be possible to maintain Gray's genus Aphroceras for species like Leucandra alcicornis, in which the dermal cortex is composed chiefly of longitudinally arranged oxea. Aphroceras would then stand in the same relation to Leucandra as Ute does to Grantia; but, unfortunately, we find species intermediate in skeletal characters between the typical Leucandra and the proposed Aphroceras, in which we have large oxea in the dermal cortex, but not arranged with regularity parallel to the long axis of the sponge, nor yet projecting at right angles from the surface. I have already expressed my hesitation in maintaining the genus Ute; and as the genus Aphroceras has not, like Ute, come into general use, I do not care to take upon myself the responsibility of re-establishing it.

Certain species of Leucandra, as already pointed out in dealing with the skeleton, still exhibit traces of descent from a radially symmetrical form, in the presence of subgastral and other sagittal triradiates; and for the present we may conveniently regard the genus as being descended from an ancestral Grantia type, by modification of the canal system and skeleton along the lines laid down in an earlier part of this paper.

The true relations of many species of the genus are obscured by the habit of colony formation by the fusion of many individuals, which gives rise to irregular, massive sponges, as in the case of Synute; but I do not think that we can generically separate these species from those which retain the more primitive condition, with a single central gastral cavity.

My Leucandra phillipensis (4), the anatomy of which is drawn in fig. 16, is a typical example of the simpler section of the genus, while the European Leucandra nivea (5) offers an illustration of the massive colonial habit. Numerous other

examples are given in my synopsis of the Australian Calcarea Heterocœla (4).

Genus 11.—Lelapia (Gray [18], emend.).

Diagnosis.—Canal system unknown. Skeleton of the chamber layer composed of large, longitudinally arranged oxea, crossed at right angles by bundles of tuning-fork shaped triradiates whose basal rays are directed towards the dermal surface.

Remarks.—This genus was first proposed by Gray (18) for certain remarkable tuning-fork shaped spicules described by Bowerbank, but the sponge to which those spicules belonged was then unknown. Carter (12) subsequently described some sponges, collected by Mr. J. Bracebridge Wilson in the neighbourhood of Port Phillip Heads, in which similar tuning-fork shaped spicules were present, and he gave to these sponges Gray's name, Lelapia australis. Whether Mr. Carter's species is really identical with the sponge to which the spicules described by Bowerbank and Gray belonged, must remain an open question. The fact that the spicules in question came from Australia lends an air of probability to the identification, but then similar spicules are known in the fossil condition from deposits as old as the Cretaceans, according to Carter (12). In any case, the Victorian sponges described by Carter (12) under the name Lelapia australis must stand as the types of that species, and the species thus constituted must stand as the type of the existing genus Lelapia.

Unfortunately we know nothing definite as to the canal system of Lelapia australis, although it is to be inferred, from the fact that Mr. Carter places it amongst the "Leucones," that the canal system belongs to the Leuconoid type. The structure of the skeleton as described by Mr. Carter is very peculiar, and it is upon this character alone that the generic diagnosis must, for the present, be based.

The position of the genus in the system of classification is necessarily only provisional, and it can only be finally determined by further research on the canal system. Unfortunately

Lelapia australis is extremely rare, and although Mr. Wilson has for some years past sent me the results of his dredging expeditions, so far as the sponges are concerned, I have never yet had the good fortune to meet with a specimen.

Genus 12.—Leucyssa, Haeckel (5).

Diagnosis.—Canal system presumably of the Leuconoid type. Skeleton composed solely of oxeote spicules irregularly scattered through the sponge.

Remarks.—This is another of those genera of which we know scarcely anything but the skeleton with any degree of accuracy. There can, however, be little doubt that the canal system belongs to the Leuconoid type. The fact that Haeckel included the genus amongst his Leucones, and the irregular character of the skeleton, both point to this conclusion. I have already discussed the relationship of the genus in speaking of the skeleton. For the present it may perhaps best be regarded as derived from a Leucandra-like type by loss of the radiate spicules, and their replacement by oxea. There are three very distinct species included by Haeckel (5) in the genus, viz. Leucyssa spongilla, L. cretacea, and L. incrustans. All these species are extremely rare, so that the probabilities of our obtaining a more exact knowledge of the canal system of the genus are somewhat remote.

Family 4.—Heteropidæ, Dendy (4).

Diagnosis.—There is a distinct and continuous dermal cortex covering over the chamber layer, and pierced by inhalant pores. Subdermal sagittal triradiates are present. The flagellated chambers vary from elongated and radial to spherical and irregularly scattered. An articulate tubar skeleton may or may not be present.

Remarks.—The leading characteristic of this family, by which it is distinguished from all others, is the presence of the subdermal sagittal triradiate spicules, which, to a greater or less extent, replace the primitive articulate tubar skeleton. As regards the canal system, we meet with much the same

series of variations as in the Grantidæ; and the shape and arrangement of the chambers, as in that family, can only be utilised as an aid in diagnosing the genera.

The family is evidently derived from an ancestral Grantia-like type, as is clearly indicated by the retention of the primitive radial arrangement of the chambers, and the articulate tubar skeleton, by the least modified species (fig. 18).

The family, as here maintained, is not nearly identical with any which have hitherto been proposed. No previous writers have drawn that sharp distinction between subdermal sagittal triradiates and subdermal quadriradiates which I have indicated in dealing with the skeleton, and which seems to me to be of the greatest value for purposes of classification.

I have adopted the name "Heteropidæ," not because I regard the genus Heteropia as most typical of the family, but because a family name derived from the principal genus, Grantessa, would be liable to confusion with the name "Grantidæ," already used for the preceding family.

Genus 13.—Grantessa (von Lendenfeld [11], emend.), fig. 18.

Diagnosis.—The flagellated chambers are elongated, and arranged radially around the central gastral cavity. The dermal cortex consists principally of triradiates, and does not contain longitudinally disposed oxea.

Remarks.—In working over the Australian Heterocœla I met with an extensive series of specimens, belonging to at least six species,[1] which evidently formed a very natural assemblage, characterised by essentially the same peculiarities of skeleton and canal system. Most of these species had already been described by various authors under a variety of generic names, viz. Amphoriscus (Poléjaeff), Grantessa (von Lendenfeld), Heteropia (Carter), Hypograntia (Carter), and Leuconia (Carter).

From these names I selected Grantessa for the group of species in question, for the following reasons:—The name Am-

[1] For a list of these species, with synonyms, vide 4.

phoriscus is occupied by a distinct genus of sponges, which ought not to be confounded with the one under consideration; the name Leuconia is altogether out of the question, for reasons already discussed; and the name Grantessa has priority over both Heteropia[1] and Hypograntia.

The genus Grantessa of von Lendenfeld (11), however, is by no means synonymous with the genus here maintained. The original type of the genus is Grantessa sacca, and its author bases the generic distinction upon the presence of tufts of oxeote spicules projecting more or less at right angles from the dermal surface, and arranged without regard to the radial chambers (10). In his description of G. sacca, however, he mentions the presence of "dermal" sagittal triradiates with an inwardly directed basal ray, but he evidently does not consider this character as of generic, much less of family importance. Attributing, as I do, great importance to the presence of subdermal sagittal triradiates, and very little importance to the arrangement of the dermal oxea in tufts (which bear no relation to the radial chambers), I have felt it necessary, while adopting the name Grantessa, to give an entirely new significance thereto.

Genus 14.—Heteropia (Carter [15], emend.).

Diagnosis.—The distal ends of the elongated radial chambers are covered over by a well-developed dermal cortex, consisting principally of large oxea arranged parallel to the long axis of the sponge.

Remarks.—The name Heteropia was first applied by Carter to his Aphroceras ramosa (15), and I therefore consider that species as the type of the genus. The name was also applied by the same author and at about the same time (12) to a number of Victorian sponges, but I have already pointed out that for the latter the name Grantessa must take priority. Indeed, it is perhaps doubtful whether Heteropia ramosa deserves to be generically separated from Grantessa, to which genus it bears exactly the same relation

[1] Heteropia is also in use for another genus.

as Ute does to Grantia. As, however, there appear to be no intermediate stages known between Grantessa and Heteropia, the latter genus appears to have just as much right to stand separately as Ute has, and the same objection does not hold good as in the case of Leucandra and Aphroceras previously discussed. Even should the genus have to be abandoned, still the name "Heteropidæ" may be conveniently retained for the family. The only known species of the genus is H. ramosa.

Genus 15.—Vosmaeropsis, Dendy (4), fig. 19.

Diagnosis.—Flagellated chambers spherical or sac-shaped, never truly radial. Dermal cortex composed principally of triradiates, without longitudinally disposed oxea.

Remarks.—This genus stands in much the same relation to Grantessa as Leucandra does to Grantia. The canal system of Vosmaeropsis macera (fig. 19) affords an excellent example of the "Sylleibid" type which characterises von Lendenfeld's genera, Polejna and Vosmaeria (10); but I have already expressed my opinion that the mere presence of this type of canal system cannot be utilised for purposes of classification, as it is found in several very distinct forms which we cannot unite in defiance of the great structural differences in their skeleton. It might be doubted whether Vosmaeropsis should be generically separated from Grantessa, as this separation depends entirely upon the canal system; but, although I do not consider the distinction between the Sylleibid and Leuconoid types of canal system sufficiently well marked to be utilised for generic purposes, I think we may very conveniently thus utilise the much greater distinction between the Syconoid and Leuconoid types, considering the Sylleibid one, for purposes of classification, as belonging to the Leuconoid division.

I only know of three species which can be included in the genus Vosmaeropsis, viz. V. macera (4), V. depressa (4), and V. Wilsoni (4).

Family 5.—Amphoriscidæ, Dendy (4).

Diagnosis.—There is a distinct and continuous dermal cortex over the chamber layer. Conspicuous subdermal quadriradiate spicules, with inwardly directed apical rays, are present. The flagellated chambers vary from elongated and radially arranged to spherical and irregularly scattered.

Remarks.—In this family, which does not by any means correspond to von Lendenfeld's "Amphoriscinæ" (10), the distinguishing characteristic is the presence of subdermal quadriradiate spicules with inwardly directed apical rays. These, as I have already pointed out, are not to be regarded as homologous with the subdermal sagittal triradiates of the Heteropidæ, although they appear to fulfil the same function. We find in this family exactly the same series of variations in the canal system as in the two preceding, and, as before, I have utilised this variation, so far as the Syconoid and Leuconoid types are concerned, for purposes of generic distinction, including the Sylleibid type in the Leuconoid.

The family is evidently to be derived from a Grantia-like ancestral type, by the development of conspicuous and inwardly directed apical rays by the triradiates of the dermal cortex.

Genus 16.—Heteropegma, Poléjaeff (8), fig. 20.

Diagnosis.—The flagellated chambers are elongated and arranged radially around the central gastral cavity. There is a vestigial tubar skeleton of minute radiates. The dermal cortex is very thick, composed principally of triradiate spicules.

Remarks.—This genus is extremely interesting as showing how the primitive articulate tubar skeleton, which is on the verge of disappearance, is gradually replaced by the development of the subdermal quadriradiates (fig. 20). Poléjaeff (8) makes no mention of the subdermal quadriradiates in his diagnosis of the genus, although he was well aware of their presence, and I have therefore been obliged to draw up a fresh diagnosis.

The genus was founded for the reception of Heteropegma nodus-gordii from off the Bermudas and Cape York, and

we now also know a species, H. latitubulata (4), very closely resembling the first, from Victorian waters.

Genus 17.—Amphoriscus (Haeckel [20], emend.).

Diagnosis.—The flagellated chambers are elongated, and arranged radially around the central gastral cavity. There is no articulate tubar skeleton, but, in addition to the subdermal quadriradiates, subgastral sagittal triradiates or subgastral quadriradiates may also be present.

Remarks.—In his "Prodromus" (20) Haeckel proposed the generic name Amphoriscus for a very natural group of three species, all characterised by the Syconoid type of canal system and the presence of quadriradiate spicules only in the skeleton. Of the highly characteristic arrangement of the skeleton, with subdermal and subgastral quadriradiates whose apical rays point in opposite directions, his generic diagnosis takes no notice. This arrangement, however, is exhibited by all the species referred by Haeckel to the genus, and affords, to my mind, a much more suitable foundation for a generic diagnosis. In his monograph (5) Haeckel altered the generic name to Sycilla, but retained the old diagnosis ("Sycones spiculis quadricruribus"). He also added a fourth species to the genus.

Polejaeff (8) retains the genus Amphoriscus, but extends the diagnosis to include species with subdermal sagittal triradiates, which, in my opinion, must be kept quite separate in the genus Grantessa. His Amphoriscus poculum and A. flamma both belong to the genus Grantessa. His A. elongatus, however, must be retained in the genus Amphoriscus, and is, indeed, a very noteworthy species; for, although the articulate tubar skeleton has been lost, the subgastral sagittal triradiates still persist, and have not yet been replaced by subgastral quadriradiates, as in all Haeckel's species of the genus. Von Lendenfeld (10) follows Polejaeff in including in the genus Amphoriscus species with subdermal sagittal triradiates as well as those with subdermal quadriradiates, while he separates, quite unnecessarily to my

mind, those species which happen to have oxeote spicules as a distinct genus, to which he gives the name Ebnerella.

As examples of the genus Amphoriscus as maintained by me, I may cite all Haeckel's species of Sycilla (5) and Polé-jaeff's Amphoriscus elongatus (8).

Genus 18.—Syculmis (Haeckel [5], emend.).

Diagnosis.—The flagellated chambers are elongated, and arranged radially around the central gastral cavity. The skeleton of the chamber layer is composed of the apical rays of subdermal and subgastral quadriradiates. There is a root-tuft of oxea and anchoring quadriradiates.

Remarks.—Haeckel's diagnosis (5) of the genus was based entirely upon the spiculation, without regard to the arrangement of the skeleton. As it happened, however, he only knew one species—the remarkable Syculmis synapta—which possesses only quadriradiate and oxeote spicules; and therefore, although it is necessary to alter the generic diagnosis, it is not necessary to make any change in the extent of the genus. Syculmis synapta (5) is evidently only a very special modification of the Amphoriscus type.

Genus 19.—Leucilla (Haeckel [5], emend.), figs. 21, 22.

Diagnosis.—Flagellated chambers spherical or sac-shaped, never truly radial.

Remarks.—This genus occupies a position amongst the Amphoriscidæ, analogous to that occupied by Leucandra amongst the Grantidæ, and Vosmaeropsis amongst the Heteropidæ, being distinguished by the Leuconoid (or Sylleibid) character of the canal system. Leucilla uter, as I have already pointed out, affords an excellent example of the Sylleibid type (fig. 21), while in Leucilla australiensis (fig. 22) we meet with a more typically Leuconoid modification. Even in Leucilla australiensis, however, we often find the flagellated chambers more or less elongated, thus showing how

impossible it is to draw a sharp line of distinction between the two types.

The genus Leucilla was founded by Haeckel (5) for Leuconoid sponges in which the spicules are all quadriradiate, of course without regard to the arrangement of the skeleton. The first species which he describes is Leucilla amphora, and I have taken this as the type of the genus, and constructed the generic diagnosis accordingly. The only other species described by him, L. capsula, also comes into the genus as now constituted. It thus appears that our Leucilla is a much more comprehensive genus than Haeckel's, and this is because we include in the genus species with triradiate and oxeote spicules.

Poléjaeff (8) has attached a very different significance to the name Leucilla, giving to the genus much the same character as von Lendenfeld has given to his family Sylleibidæ; indeed, the latter was founded (11) chiefly upon Poléjaeff's Leucilla. I revert, however, to Haeckel's two species, and make their characters the foundation of the genus.

In my synopsis of the Australian Calcarea Heterocœla (4) I, somewhat unnecessarily I fear, proposed the name Paraleucilla for Haeckel's Leucandra cucumis, which is characterised by the presence of distinct subdermal cavities supported by a somewhat specialised portion of the skeleton of the chamber layer. I now regret having taken this step, the more so as Poléjaeff (8) had previously proposed the name Pericharax for the same sponge. Poléjaeff, however, also included in the genus Pericharax his P. Carteri, which is a very different sponge from Leucandra cucumis, and does not even come within the limits of our family Amphoriscidæ. I do not now think that either Pericharax or Paraleucilla ought to stand as a distinct genus. Poléjaeff's Pericharax Carteri is but a slight modification of the ordinary Leucandra type, while Haeckel's Leucandra cucumis is a similar modification, only rather more marked, of the Leucilla type.

VI. The Origin and Phylogeny of the Calcarea Heterocœla.

No one will probably dispute the now well-established hypothesis that the Calcarea Heterocœla are descended from some one or more ancestral Homocœla. The Homocœla are undoubtedly the more primitive of the two great groups into which Poléjaeff (8) divided the calcareous sponges, and the only question which we need discuss is the process by which the Homocœle gave rise to the Heterocœle type.

In my memoir on the organisation and classification of the Homocœla (1) I proposed to divide the sole genus, Leucosolenia, into three sections, according to the nature of the canal system, for even in the simplest of sponges the canal system exhibits a considerable amount of variation. To these sections of the genus I applied the names Simplicia, Reticulata, and Radiata. The Simplicia include such simple Olynthus types as never form colonies, and also those colonial forms in which the whole colony consists of individuals (Ascon-persons) which may branch, but which never form complex anastomoses nor give off radial tubes, so that the individuality of the different members of the colony is always recognisable. In the Reticulata the sponge colony forms a more or less complex network of branching and anastomosing tubes, and it is no longer possible to distinguish the individual Ascon-persons of which the colony is composed. The Radiata include such species as exhibit a radiate structure—the sponge consisting of a single central Ascon-tube, from which other tubes are budded off radially.

In all species of Leucosolenia it is supposed that the whole of the primitive gastral cavity is lined by a layer of collared cells, and that when, as in my type D of the Reticulata, exhalant canals exist which are not lined by collared cells, these canals (pseudogasters) really lie outside the sponge, and are probably formed by upgrowth of the colony around them.

The Olynthus type, consisting of a simple sac lined by

collared cells, and pierced by an osculum and prosopyles, is universally admitted to be the ancestral form of all calcareous sponges. If we look for a more advanced type amongst the Homocœla, from which the Heterocœla may possibly be derived, the radiate section of the genus Leucosolenia at once suggests itself. The type of this radiate section is Leucosolenia tripodifera (1); and Bidder (21) is of opinion that certain other species, notably Leucosolenia Lieberkuhnii, should also be included therein. In L. tripodifera we find a single wide central tube, with a terminal osculum, numerous prosopyles, and a thin wall lined by collared cells—so far a typical Ascon individual. From this tube, numerous radially arranged branches are given off, which themselves branch copiously, and terminate all at about the same level in blind, rounded extremities, which touch one another, and thus form an even surface to the whole sponge. Each of the radial branches repeats, on a smaller scale, the structure of the parent tube, and each is first formed as a hollow bud or outgrowth from the latter, the youngest buds lying at a little distance below the osculum. The radial tubes occasionally anastomose and inter-communicate, like the branches of a reticulate Leucosolenia, but this appears to take place only occasionally; at any rate, it is not a characteristic feature. The skeleton of this sponge consists of rather slender sagittal triradiates and quadriradiates, and of the "tripod" spicules. The latter are confined to the distal extremities of the radial chambers. The sagittal radiates are arranged in a single layer in the walls of the tubes, the quadriradiates with the apical ray projecting into the gastral cavities both of the central tube and its radial branches. As already stated, the spicules are sagittal, and in the central tube the basal rays point towards the base of the sponge; while in the radial tubes the basal rays point towards the blind distal ends, exactly as in the articulate tubar skeleton of Syconoid Heterocœla.

Here, then, we have a form which makes a very near approach, both in canal system and skeleton, to the Sycetta type amongst the Heterocœla, and it is from some such

radiate Homocœlous form as this that the Heterocœla have probably been derived. I do not by any means wish to single out Leucosolenia tripodifera itself as the ancestor of the Heterocœla, for I do not for a moment believe that it is so. The copious branching of the radial tubes, and the fusion of adjacent tubes at the points of contact, indicate a more advanced condition in some respects than is met with in the simplest Heterocœla (Sycetta). The youngest part of the sponge, nearest to the osculum, where the radial tubes are still simple and unbranched, makes a much nearer approach to the hypothetical ancestral form.

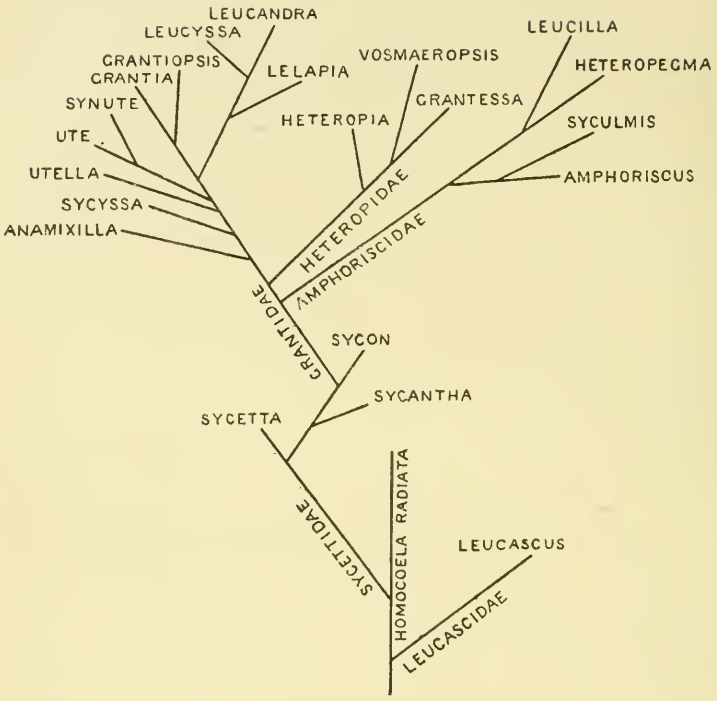
In any case, the simple radiate type of structure, though perhaps no more highly specialised than certain other types met with amongst the Homocœla, appears to form the natural starting-point for all the divers types met with amongst the Heterocœla, with the probable exception of Leucascus, to which I shall refer again later on. The simpler forms of Heterocœla still preserve the radiate character, which becomes at first even more pronounced in the structure of the skeleton. It is also a most important and significant fact, that in the ontogeny of these simple Heterocœla the radial tubes (flagellated chambers) are formed as outgrowths from a central tube, exactly as in Leucosolenia tripodifera. An excellent illustration of this mode of formation is given by Korschelt and Heider (2).

I ought, perhaps, in this place to say something about Dr. von Lendenfeld's supposed families "Homodermidæ" and "Leucopsidæ." I have, however, already expressed my views on this subject in an earlier paper (1), and those views I still maintain, for I cannot see that there is anything in Dr. von Lendenfeld's observations, including those published in "Die Spongien der Adria" (10), to justify us in accepting these families. It would take too long to argue the question here, and I am quite content to refer the reader to Dr. von Lendenfeld's own writings.

I maintain, then, that the ancestral form of the Heterocœla was a simple, radiate, Homocœle sponge, simpler even than

Leucosolenia tripodifera, and that the radiate Heterocœle type was developed from this by replacement of the collared cells of the central gastral cavity by a flattened epithelium and specialisation of the skeleton, a modification which might readily give rise to the primitive Heterocœle genus Sycetta. The manner in which I believe the majority of the remaining genera of Heterocœla to have been derived from a Sycetta-like ancestor, has perhaps been already sufficiently indicated in dealing with the anatomy and classification of the group. The genus Leucascus, however, does not appear ever to have passed through a Sycetta stage, for while the greatly elongated flagellated chambers may indicate by their arrangement (at any rate in some specimens) a certain degree of radial symmetry, the skeleton exhibits none whatever; it is quite as irregular as that of a reticulate Homocœle, or as that of the most modified Leucandra. Considering the nature of the canal system, however, I believe that the irregularity of the skeleton in Leucascus is a primitive condition, and not, as in Leucandra, a secondary one. Possibly Leucascus may be either derived directly from a reticulate Homocœle ancestor, by the formation of a true dermal membrane and dermal pores, or from a very low type of radiate Homocœle, in which the skeleton had not yet acquired any radial symmetry. I am inclined to adopt the latter view.

The opinions as to the origin and inter-relationships of the Calcarea Heterocœla which I have endeavoured to justify in the foregoing pages, may be conveniently summarised in the accompanying diagram, which naturally takes the form of a genealogical tree.



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EXPLANATION OF PLATES 10—14,

Illustrating Dr. Dendy's paper "Studies on the Comparative Anatomy of Sponges."

Note.—The majority of the drawings have been made from paraffin sections of ordinary spirit material, and in most cases a camera lucida has been employed.

In Figs. 1—22 the collared cells are diagrammatically represented by red dots, and the outlines of the spicules are drawn in blue.

Reference Letters.

calc. Calcoblast. *c. c.* Collared cell. *c. g. c.* Central gastral cavity. *ch. di.* Diaphragm of exhalant opening of flagellated chamber. *d. cor.* Dermal cortex. *d. p.* Dermal pore. *ect. ep.* Ectodermal pavement epithelium. *emb.* Embryo. *emb. c.* Embryo capsule. *end. ep.* Endodermal pavement epithelium. *ex. c.* Exhalant canal. *ex. op.* Exhalant opening of flagellated chamber. *fl. ch.* Flagellated chamber. *fl. ch. x.* Flagellated chamber in the contracted condition. *g. cor.* Gastral cortex. *g. q.* Apical ray of gastral quadriradiate spicule, projecting into the central gastral cavity. *i. c.* Inhalant canal. *mus. c.* Muscle cell. *osc.* Osculum. *ov.* Ovum. *pros.* Prosopyle. *s. d. q.* Subdermal quadriradiate spicule. *s. d. s.* Subdermal sagittal triradiate spicule. *s. g. s.* Subgastral sagittal triradiate spicule. *s. m.* Sollas's membrane. *sp.* Spicule. *sp. s.* Spicule sheath (formed from the gelatinous ground substance of the mesoderm). *st. c.* Stellate mesoderm-cell. *t. ox.* Tuft of oxeote spicules at the end of a radial chamber.

PLATE 10.

Fig. 1.—Leucascus simplex. Portion of a vertical section, passing, on the left, through the osculum. Drawn under Zeiss A, ocular 2.

Fig. 2.—Sycon Carteri. Portion of a transverse (horizontal) section, showing three of the radial chambers. Drawn under Zeiss C, ocular 2.

Fig. 3.—Sycon gelatinosum. Portion of a longitudinal (vertical) section, passing through the distal ends of the radial chambers. Drawn under Zeiss C, ocular 2.

Fig. 4.—Sycon gelatinosum. Portion of a longitudinal (vertical) section, passing through the proximal ends of the radial chambers. Drawn under Zeiss C, ocular 2.

Fig. 5.—Sycon gelatinosum. Portion of a tangential section, cutting across the radial chambers. Drawn under Zeiss C, ocular 2.

Fig. 6.—Sycon gelatinosum. Portion of a tangential section of the dermal surface showing the tufts of nail-shaped oxea which crown the distal ends of the radial chambers, and the pore-bearing membrane stretched between them. Drawn under Zeiss C, ocular 2.

Fig. 7.—Sycon boomerang. Portion of a transverse (horizontal) section, showing one much-branched radial chamber. Drawn under Zeiss A, ocular 2.

Fig. 8.—Sycon boomerang. Portion of a tangential section of the dermal surface, showing the tufts of oxea which crown the distal ends of the radial chambers, and the pore-bearing membrane (containing a few spicules) stretched between them. Drawn under Zeiss C, ocular 2.

PLATE 11.

Fig. 9.—Grantia extusarticulata. Portion of a transverse (horizontal) section. Drawn under Zeiss A, ocular 2.

Fig. 10.—Grantia Vosmaeri. Portion of a longitudinal (vertical) section. Drawn under Zeiss A, ocular 2.

Fig. 11.—Grantiopsis cylindrica. Portion of a transverse section. Drawn under Zeiss A, ocular 2.

Fig. 12.—Ute syconoides. Portion of a transverse (horizontal) section. (The majority of the spicules have been dissolved out by the action of acid alcohol, but the large oxea of the dermal cortex are shown cut across.) Drawn under Zeiss C, ocular 2.

Fig. 13.—Ute syconoides. Portion of a tangential section cutting across the radial chambers. Drawn under Zeiss C, ocular 2.

Fig. 14.—Ute syconoides. Portion of a tangential (longitudinal) section, passing above through the dermal surface and below through the dilated distal ends of the radial chambers. Drawn under Zeiss A, ocular 2.

PLATE 12.

Fig. 15.—Synute pulchella. Portion of a transverse (horizontal) section, showing the central gastral cavities of three Ute individuals, each surrounded by radial chambers and all together invested in a common cortex. Drawn under Zeiss A (with the bottom lens removed), ocular 2.

Fig. 16.—Leucandra phillipensis. Portion of a transverse (horizontal) section. Drawn under Zeiss A, ocular 2.

Fig. 17.—Leucandra australiensis. Portion of a transverse (horizontal) section. Drawn under Zeiss A, ocular 2.

PLATE 13.

Fig. 18.—Grantessa intusarticulata. Portion of a transverse (horizontal) section. Drawn under Zeiss A, ocular 2.

Fig. 19.—Vosmaeropsis macera. Portion of a transverse (horizontal) section. Drawn under Zeiss A, ocular 2.

Fig. 20.—Heteropegma nodus-gordii. Portion of a transverse section. Drawn under Zeiss A, ocular 2.

Fig. 21.—Leucilla uter. Portion of a vertical section. Drawn under Zeiss A, ocular 2.

Fig. 22.—Leucilla australiensis. Portion of a longitudinal (vertical) section. Drawn under Zeiss A, ocular 2.

PLATE 14.

Fig. 23.—Vosmaeropsis Wilsoni. Portion of the cortical inhalant canal system, as seen in a transverse section of a specimen killed with osmic acid. The space occupied by the dermal cortex, between the inhalant canals, is left blank, and the pore-bearing dermal surface is shown in perspective. Drawn under Zeiss C, ocular 2.

Fig. 24.—Ute syconoides. Portion of a tangential section cutting across the radial chambers, showing a chamber in the contracted condition, surrounded by four ordinary chambers and four inhalant canals, portions of which only are drawn. Drawn under Zeiss E, ocular 2.

Fig. 25.—Leucandra sp. One of the rounded flagellated chambers cut in half. One row of collared cells, with collars united by Sollas's membrane, is seen round the margin, while the observer looks down upon the exhalant opening of the chamber and two prosopyles. Drawn under Zeiss F, ocular 2.

Fig. 26.—Leucandra sp. Exhalant aperture of another chamber from the same specimen as Fig. 25, surrounded by the membranous chamber diaphragm, in which the nuclei and granules of muscle-cells are seen. Drawn under Zeiss F, ocular 2.

Fig. 27.—Grantessa intusarticulata. Portion of a section through the gastral cortex and proximal end of a radial chamber. On the right a portion of the chamber diaphragm, marking the junction of the radial chamber with the exhalant canal, is seen in section. On the left a portion of the inner end of an inhalant canal is seen. Drawn under Zeiss F, ocular 2.

Fig. 28.—Grantessa intusarticulata. Portion of a section through the gastral cortex, showing two of the endodermal pavement cells in section and a stellate cell embedded in the gelatinous ground substance of the mesoderm. Drawn under Zeiss F, ocular 2.

Fig. 29.—Grantessa intusarticulata. Three contracted ectodermal

pavement cells from the lining of an inhalant canal. Drawn under Zeiss F, ocular 2.

Fig. 30.—Grantessa intusarticulata. Portion of the wall of a radial chamber looked down upon, showing a number of contracted collared cells, and between them a prosopyle, with the nucleus of an ectodermal pavement cell on its margin seen at a slightly higher focus than the collared cells. Drawn under Zeiss F, ocular 2.

Fig. 31.—Vosmaeropsis macera. Exhalant opening of a flagellated chamber, surrounded by the membranous chamber diaphragm containing muscle-cells. Drawn under Zeiss F, ocular 2.

Fig. 32.—Leucandra sp. Small portion of a vertical section through the region of the osculum, showing four of the blister-like epithelial cells which line the gastral cavity in this region. Drawn under Zeiss F, ocular 2.

Fig. 33.—Leucandra echinata, var. An amœboid cell from the mesoderm. Drawn under Zeiss F, ocular 2.

Fig. 34.—Leucandra echinata (?). An ovum from a cavity in the mesoderm. Drawn under Zeiss F, ocular 2.

Fig. 35.—Ute syconoides. Section across an inhalant canal (intercanal), showing an ovum suspended from its wall. Drawn under Zeiss F, ocular 2.

Fig. 36.—Ute syconoides. An ovum from behind the wall of a radial chamber. Drawn under Zeiss F, ocular 2.

Fig. 37.—Ute syconoides. Two vesicular cells from beneath the epithelium of the gastral cortex. Drawn under Zeiss F, ocular 2.

Fig. 38.—Grantessa intusarticulata. Section of an embryo lying in a cavity lined by epithelial cells (the embryo capsule). Drawn under Zeiss F, ocular 2.

Figs. 39—42.—Leucandra phillipensis. Stellate mesoderm-cells from the dermal cortex. Drawn under Zeiss F, ocular 2.

Fig. 43.—Leucandra phillipensis. Subdermal gland-cell beneath the wall of an inhalant canal, which is cut through on the right. Drawn under Zeiss F, ocular 2.

Figs. 44—47.—Leucandra phillipensis. Portions of four oxeote spicules from the dermal cortex, with calcoblasts attached. Drawn under Zeiss F, ocular 2.

Figs. 48—50.—Leucandra phillipensis. Amœboid cells from the mesoderm between the flagellated chambers. The one shown in Fig. 50 appears to be feeding by means of pseudopodia upon the collared cells of a flagellated chamber. Drawn under Zeiss F, ocular 2.

Fig. 51.—Leucandra phillipensis. A group of retracted collared cells. Drawn under Zeiss F, ocular 2.

FIGS. 52—54.—Grantiopsis cylindrica. Calcoblasts from the dermal cortex. In Fig. 52 the calcoblast is lying upon a ray of a large triradiate spicule. In Fig. 53 the spicule is partially dissolved by the acid alcohol, and the spicule-sheath is visible. Drawn under Zeiss F, ocular 2.

FIG. 55.—Grantiopsis cylindrica. Four small mesoderm-cells from the dermal cortex. Drawn under Zeiss F, ocular 2.

FIG. 56.—Grantiopsis cylindrica. Three subdermal gland-cells, each connected by a long, slender process with the granular dermal surface. Drawn under Zeiss F, ocular 2.

FIG. 57.—Grantiopsis cylindrica. Small portion of the dermal surface. Drawn under Zeiss F, ocular 2.

FIG. 58.—Micro-organisms from the dermal surface of Grantiopsis cylindrica. Drawn under Leitz $\frac{1}{12}$, oil immersion.

FIG. 59.—Sycon Ramsayi. Contracted epithelium from an inhalant canal. Drawn under Zeiss F, ocular 2.

FIG. 60.—Sycon Ramsayi. Contracted epithelium from an exhalant canal. Drawn under Zeiss F, ocular 2.

FIG. 61.—Sycon Ramsayi. Sections of two epithelial cells from an exhalant canal. Drawn under Zeiss F, ocular 2.

FIG. 62.—Grantessa erinaceus. Contracted epithelium of an endogastric septum, formed by outgrowth of the gastral cortex into the gastral cavity. Drawn under Zeiss F, ocular 2.

FIG. 63.—Vosmaeropsis Wilsoni. Epithelium from the upper surface of an oscular diaphragm. From an osmic acid specimen mounted in glycerine. Drawn under Zeiss F, ocular 2.

FIG. 64.—Vosmaeropsis Wilsoni. Contracted epithelium from an exhalant canal. Drawn under Zeiss F, ocular 2.

Fig. 1.

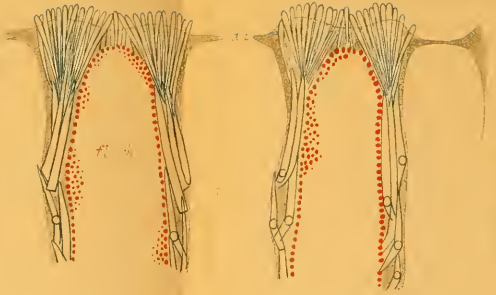


Fig. 3.

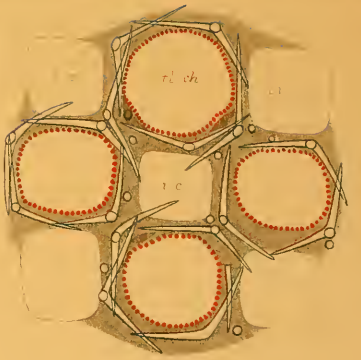


Fig. 5.

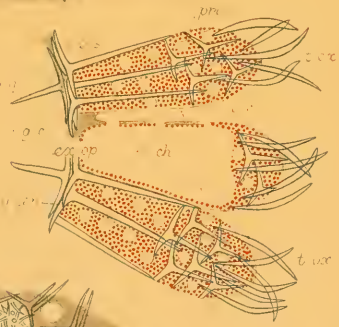


Fig. 2.

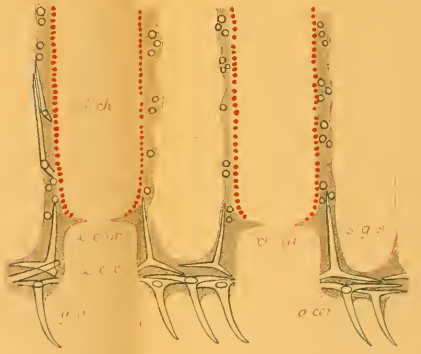


Fig. 4.

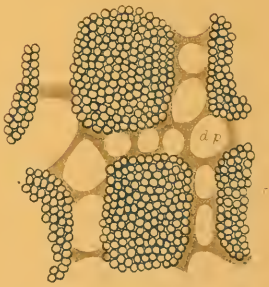
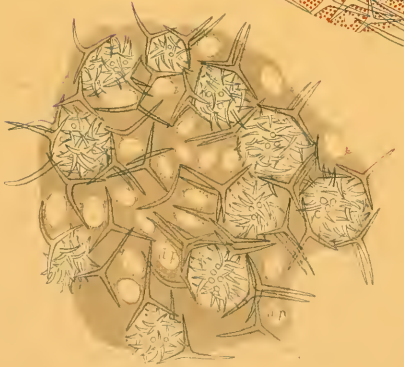


Fig. 6.



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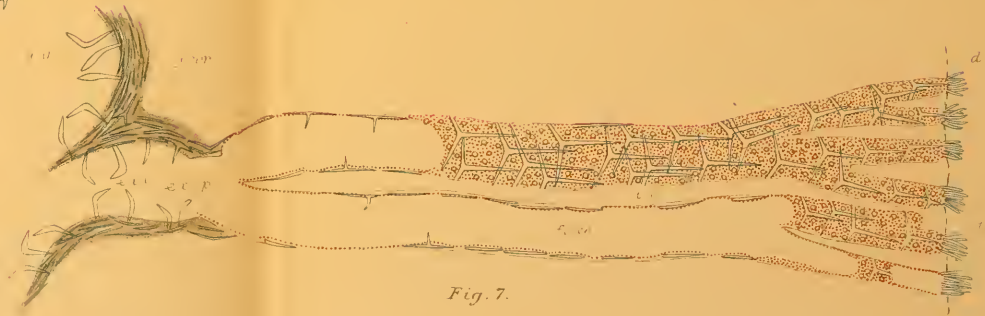

Fig. 7.

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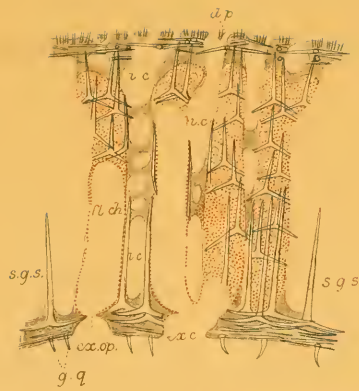

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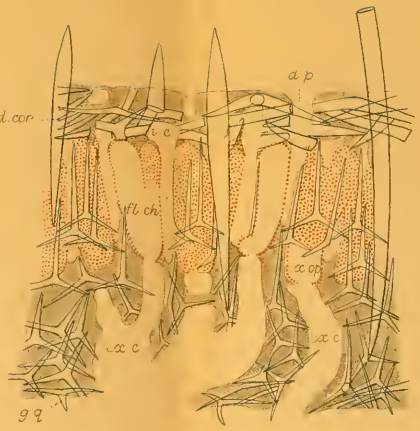

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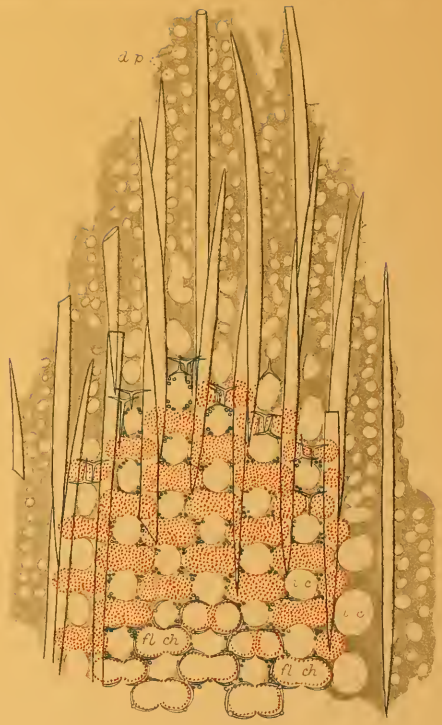

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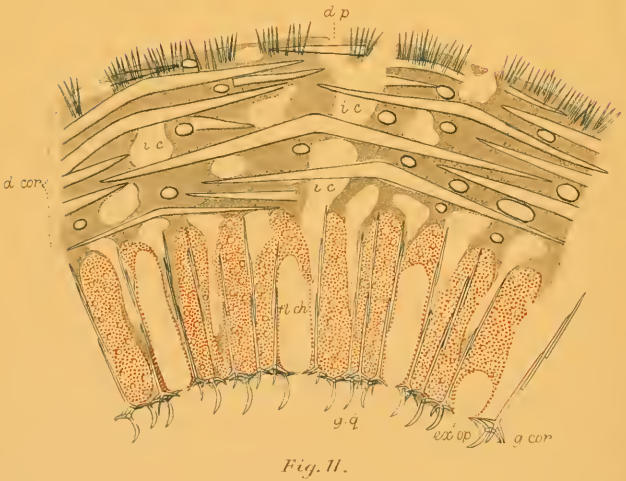

Fig. 11.

Fig. 12.

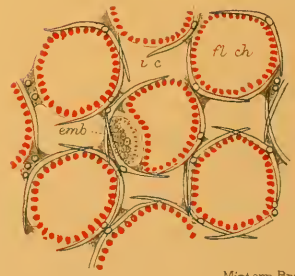

Fig. 13.

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Fig. 15.

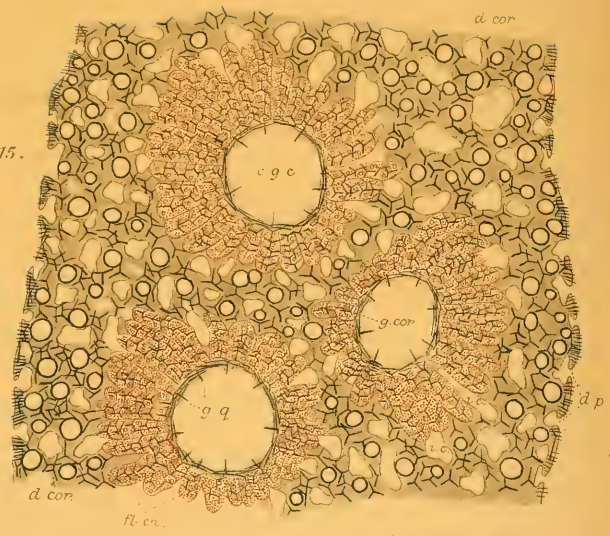

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Fig. 17

Fig. 16.

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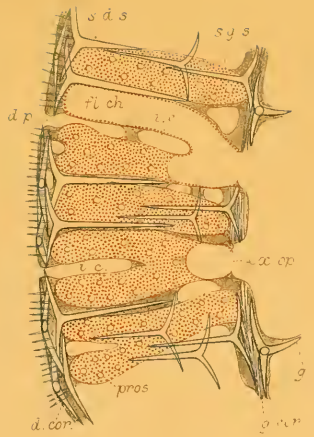

Fig 18.

Fig. 19

Fig. 22.

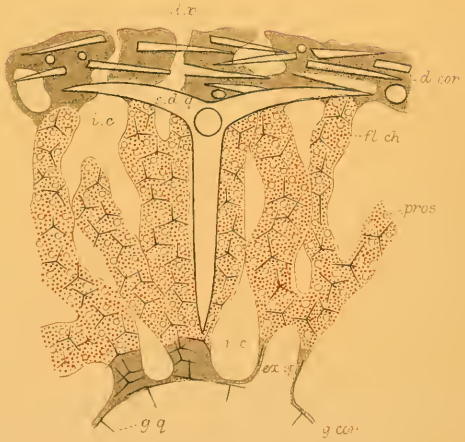

Fig 20.

Fig. 21.

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Fig. 27.

Fig. 28.

Fig. 29.

Fig. 30.

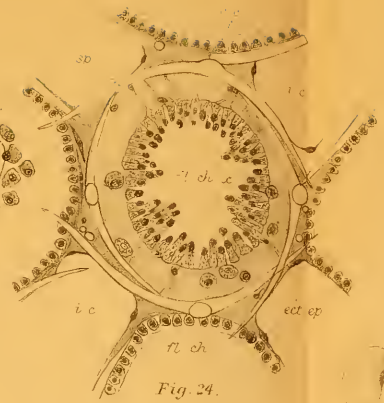
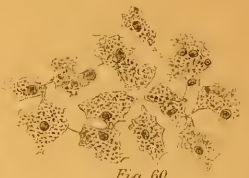


Fig. 24.

Fig. 52.

Fig. 53.

Fig. 59.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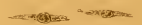
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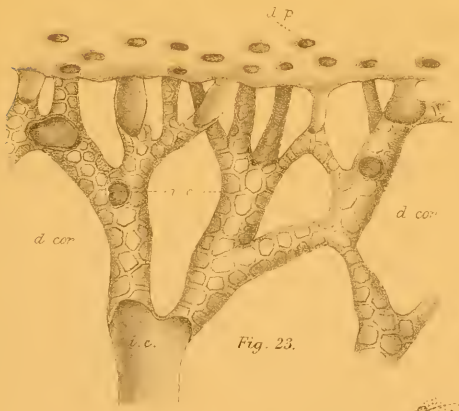

Fig. 23.

Fig. 35.

Fig. 36.

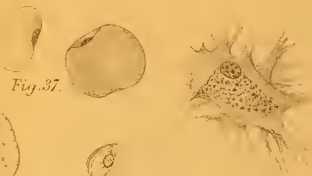
Fig. 37.

Fig. 54.

Fig. 32.

Fig. 55.

Fig. 57.

Fig. 64.

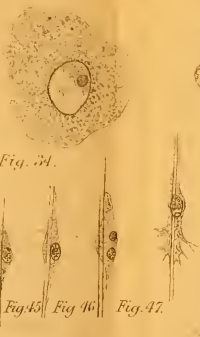
Fig. 33.

Fig. 34.

Fig. 49.

Fig. 48.

Fig. 56.

Fig. 63.

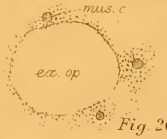

Fig. 26.

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Fig. 41.

Fig. 39.

Fig. 43.

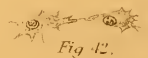
Fig. 42.

Fig. 51.

Fig. 62.

Fig. 25.

Fig. 31.

Fig. 44 Fig. 45 Fig. 46 Fig. 47.

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Fig. 50.

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