

Sphaerococcus coronopifolius, Stackh.

BY

T. JOHNSON, B.Sc. (London),

*University Scholar in Botany, Demonstrator of Botany in the Normal School
of Science, Kensington.*

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With Plate XVIII.
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VEGETATIVE THALLUS.

THE red sea-weed *Sphaerococcus coronopifolius*, Stackh., occurs, in England, along the south-west coast from the Isle of Wight to Land's End, being found attached to rocks at extreme low-water and deeper levels, by means of a disc-like 'root,' from which one to three main 'stems' arise. The main stem produces irregularly placed branches, from which very numerous short upwardly directed branchlets spring. These alternate or subdichotomously formed branchlets are flattened and relatively wide, and have the whole length of their two edges closely beset with small cylindrical filaments, often themselves slightly branched (Fig. 1). The whole plant may be a foot long, and as broad as it is long. Each cylindrical filament repeats on a smaller scale the structure of its parent branchlet, and this of its parent branch (Fig. 2). Running through the middle of the filament is a central axis consisting of a uniseriate row of large tubular cells in which the usual Floridean characters are well-marked. From the distal end of each joint-cell of this central axis two lateral uniseriate cellular branches are given off right and left, obliquely inclined in an upward direction to the surface of the thallus-filament. Each lateral cellular branch forms a number of short secondary lateral branches arranged at right angles to the surface of the thallus, and closely

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applied to one another, side by side, so as to produce a compact cortex, the thickness of which is increased by the apical growth of these cortical secondary lateral branches (Fig. 7). Each member of the branch-system of the thallus thus consists of three layers; a medulla formed by the central axis, a middle layer formed of the loose lateral cellular branches of the central axis, and a cortex formed as just described. The 'midrib' (central axis) and the 'lateral ribs' (lateral cellular branches) were first observed and described by Sowerby, according to Harvey¹, but their relation to one another and to the rest of the thallus in the way with which Schmitz² has made us familiar in the Florideae generally, was not known. Up to the present the central axis and its lateral branches have not been figured. Most of the figures of the thallus branches published are life-size, and taken from living or dried specimens. Examination however of spirit-material treated with clearing reagents and magnified four or five times brings out the central axis and its branches well (Figs. 1 and 2).

THE PROCARPIMUM.

As it is in the cylindrical filaments, the ultimate branches of the thallus, and in them only that the female sexual organs—the procarpia—occur, I shall speak of them as *procarpium-branches*. It is no doubt in a great measure owing to the opacity of these branches, the absence of any external indication of the presence, not to say the exact position, of the buried procarpia, the smallness of the cells, and the number of different planes in which the various parts of the procarpium lie, that they have not hitherto been even mentioned. Their number somewhat atones for their general obscurity. We have seen that the whole margin of the thallus-branchlet is beset right and left with cylindrical filaments. These are all

¹ Harvey, *Phycolog. Brit.* ii. pp. 182–184, Pl. 61. 1846–1851.

² F. Schmitz, *Untersuchungen über die Befruchtung der Florideen* in *Sitzungsber. d. k. Akad. d. Wiss. Berlin*, 1883. Translation by W. S. Dallas, F.L.S., in *Ann. Mag. Nat. Hist.*, vol. xiii. 1884, in which any following references will be found.

procarpium-branches potentially. In each of them the procarpia, the number of which varies from one to six or more, occur at intervals throughout its length, close to the central axis, above, below, right or left of this as seen from above. In fact any primary lateral cellular branch of the central axis may develop a procarpium. From the second (proximal) joint-cell, rarely from the basal cell, of such a cellular branch, a usually three-celled secondary lateral branch arises. The three cells are so related to one another as to form a curved branch (Fig. 3); they are full of highly refractive minutely granular nucleated protoplasm, and constitute a carpogenous branch, the apical cell of which is the carpogonium and develops the trichogyne. This carpogenous branch is readily distinguishable from the other secondary lateral branches by lying deeper within the procarpium-branch and by the characters of the contents of its cells (Fig. 7). The procarpium is completed by the formation of a number of small secondary lateral branches of limited growth, from the basal and next joint-cell of the lateral branch bearing the carpogenous branch. These small cells, having similar but less refractive and dense contents than the cells of the carpogenous branch, are the 'carpogenous cells,' and have an important part to play in the formation of the fruit. In a longitudinal section of a procarpium-branch seen under an inch objective, the procarpia, situated close to the central axis in the middle layer of the procarpium-branch, stand out by the brightness of one or more of the cells of the carpogenous branch and by the closeness of aggregation of the small carpogenous cells. It is possible only under a higher power to make out the details of structure of any individual procarpium. Thus in Fig. 7, in the procarpium p' , only one cell of the carpogenous branch could be observed under an inch objective, though under a $\frac{1}{8}$ -inch objective all the cells of the carpogenous branch as well as part of the trichogyne were recognisable. The trichogyne is unusually variable in its course in *Sphaerococcus*. It reaches the surface of the thallus after curving in different cases in almost every imaginable direction, sometimes creeping for a long way in the

interior of the thallus as if searching for a weak spot in the cortex, there to project on to the external surface. It is only rarely that it passes almost directly to the surface (Fig. 4). It was not until I had spent a long time in examining some hundreds of sections under a $\frac{1}{8}$ -inch objective that I could satisfy myself that the coiling filament I saw in connection with the carpogenous branch was really the trichogyne, and that it projected at the thallus surface. I was constantly cutting it across. Indeed, in making thin sections of a procarpium-branch, it is almost sure to be so cut even if the rest of the procarpium is left intact. I found it very useful to place a piece of a thallus-branchlet bearing several procarpium-branches for twenty-four hours or more in a mixture of pure glycerine and alcohol until it became semi-transparent, then to examine each procarpium-branch on both sides with a high power until one was seen in which the procarpia were likely to yield useful results, and taking this particular procarpium-branch, after noting the exact position of its procarpia, to cut it longitudinally between thumb and finger. The sections, though sometimes lost or spoilt, were usually thin enough to allow examination of the procarpia and yet thick enough to prevent injury of them. Subsequent staining with various reagents often rendered the parts, in the usual way, more distinguishable.

THE CYSTOCARP.

I did not clearly see the contact of a spermatium with the trichogyne, but judging from changes in the procarpium it is highly probable that fertilisation takes place in the normal way. More than once I found the trichogyne cut off from the rest of the carpogonium by a constriction at its base (Fig. 5), the contents of the carpogonium being thus divided into a useless non-nucleated part (compared by Schmitz to the polar body of *Vaucheria*), and a more important nucleated part, the fertilised ovicell, the foundation of the fruit. In one case in which the trichogyne had been cut off I found two nuclei in the 'fertilised ovicell,' but whether they were the

male and female nuclei about to fuse, or were due to the division of the nucleus of the fertilised ovicell, I cannot say (Fig. 6). In another case the wall of separation between the carpogonium and the middle cell of the carpogenous branch had broken down, the contents of the two cells were completely fused together, but the nuclei were still separate. A fusion of this fused cell with the basal cell of the carpogenous branch I did not observe with certainty. There is, I think, little doubt that it occurs. Investigations of later stages of development gave some very interesting results which show the necessity of the examination of each genus of the Florideae. The course of events in the development of the cystocarp in *Sphaerococcus* is briefly as follows. The carpogonium (after fertilisation) fuses with the hypogynous cell, and this apparently fuses with the basal cell of the carpogenous branch. The common cell so formed next fuses with the mother-cell of the carpogenous branch, the second (proximal) joint-cell of a lateral branch, and this cell then fuses with the basal cell of the same branch. Fusion however does not cease at this point, for the basal cell of the lateral branch fuses with the cell bearing it, a joint-cell of the central axis of the procarpium-branch, and this joint-cell fuses with the next joint-cell below it. By this means a large common conjugation-cell is obtained, from the greater part of the surface of which (not from that part formed by the two joint-cells of the central axis) ooblastema-threads arise even before the process of fusion is completed. These threads are short radiating, branching, and of few cells, the end one or two cells becoming carpospores. It has been seen that each procarpium is completed by a cell-complex of carpogenous cells borne by the two basal cells of the primary lateral branch concerned. These carpogenous cells do not remain sterile here. They become more directly connected with the common fused cell, the central cell of the cystocarp, and produce at their free ends chains of carpospores just as do the ooblastema-threads directly sprouting from the central cell. Carpogenous cells similar to these have been described in other genera, and have had ascribed to them a similar

function. Schmitz states that a closer investigation of their fate shows them to be sterile and not connected with spore-formation. This conclusion will throw doubt on the accuracy of my statement. Still all the observations I have made in *Sphaerococcus* support my view, and in addition it should be stated that in no other genus of the Florideae (*Gracilaria* excepted) is a fusion of the individual cells of a procarpium known to take place to such an extent¹.

As the development of the fruit proceeds its size increases until there is a clear indication to the naked eye of its presence, in the form of a spherical swelling. As a fruit may arise from any one of the procarpia scattered through the whole length of a procarpium-branch, and as this branch may be quite short when fertilisation occurs, it is easy to explain the earlier descriptions of the cystocarp of *Sphaerococcus* taken from an external examination of the plant. 'Fructificatio, tubercula minutissima, modo sessilia, modo pedunculata, in ramulis extremis sita, atro-purpurea².' The fruit-sheath (pericarp or involucre) is derived from the cortex of the procarpium-branch, and is thus present before the fruit begins to form. The fruit-cavity is a result of the arching of the pericarp and of an increase in the distance between the lateral cellular branches of the joint-cells of the central axis. Lysigeny does not occur, schizogeny strictly speaking occurs to only a limited extent; the fruit-cavity is due rather to the increase of the space between the cellular branches which have been free from one another at their

¹ Schmitz, op. cit., p. 23, says, 'Perhaps, also, in some of these forms (Rhodomeleae) a plurality of auxiliary cells may be formed in the individual procarpium; but I have hitherto never been able to demonstrate such a case with certainty.' Again, in a footnote on p. 20, Schmitz says: 'This point [the conjugation of the fertilised ovicell with the nearest auxiliary cell] in the development of the fruit of the Corallineae (the exact investigation of which is, as is well known, rendered remarkably difficult by the small size of the cells), I have hitherto been unable to establish directly. Moreover, not only in the Corallineae, but also in many other Florideae with small-celled, closely packed cellular tissue, there are special difficulties opposed to the exact ascertainment of the fate of the fertilised ovicell which render these investigations extremely troublesome and tedious, and greatly hinder any certain decision.'

² Good. and Woodw., in Trans. Linn. Soc. iii. p. 185.

proximal ends from the first. The carpospores escape from the ripe fruit through an irregular slit in the pericarp, not through a definite pore. On account of the frequent formation of a fruit-cavity of large size, especially towards the apex of the procarpium-branch before there is any indication of carpospores, the size of a swelling is not a safe guide as to the stage of development of the fruit. Each cystocarp is the product of one procarpium and of one only, close as the procarpia are to one another and loose as is the middle layer of the procarpium-branch. The carpogonium has in its immediate neighbourhood a number of cells, some of which are specialised, and with all of which it fuses to produce the central cell of the cystocarp. All these cells are auxiliary cells, and being close to the carpogonium do not need any ooblastema-thread (connecting-tube) to place them in connection with the fertilised ovicell. I am not able to throw much light on the fate of the nuclei in these auxiliary cells, and cannot say how far their fusion with one another, following on that of the hypogynous cell with the carpogonium, should be regarded as a second act of fertilisation (granting this may happen), here many times repeated. Looking at the development of the cystocarp from another point of view, *Sphaerococcus* exhibits the phenomena of fecundation as seen in the Florideae at their best. In no other genus in which one cystocarp results from one procarpium is the possibility of the abundant supply of nutriment from a number of different regions in the thallus to the central cell of the cystocarp and so to the sporiferous filaments insured to such a degree. In *Sphaerococcus*, not only does the carpogonium fuse with the other cells of the carpogenous branch, but with the two basal cells of a lateral branch and with two joint-cells of the central axis of the whole procarpium-branch. The nearest approach to this (after *Gracilaria*) is seen in *Chondria tenuissima*, Ag., one of the Rhodomeleae. In this species¹, after fertilisation, the

¹ Schmitz, op. cit., p. 28.

auxiliary cell which is the mother-cell of the carpogenous branch and bears in addition a cell-complex, fuses with the carpogonium, and with the nearest cells of the cell-complex, giving a large multinucleate cell from which sporiferous filaments sprout out. In *Sphaerococcus* there is a combination of the three chief types of fruit-formation of the Florideae; for the ooblastema-threads arising from the surface of the carpogonium are comparable to the sporiferous filaments of the Helminthocladiaceae (*Nemalion*, *Batrachospermum*, etc.), and those from the surface of the fused auxiliary cells and from the carpogenous cells (secondary auxiliary cells) are comparable to the sporiferous filaments of the Rhodomeleae and other Florideae with more or less compact thallus, and to the sporiferous filaments (meta-ooblastema-threads) of the Squamariae and Cryptonemiaceae. A comparison of the course of development of the fruit in *Sphaerococcus* with that in *Gracilaria* will show how very similar these two genera are in this respect. Comparison of the vegetative thallus of the two shows *Sphaerococcus* to be the less modified form. In *Gracilaria* the central axis of the thallus branch is no longer evident, since its lateral branches are as well-developed and have applied themselves closely together and to its sides, forming a central medulla of large cells in which the joint-cell of the central axis is obscured. The absence of a clearly marked central axis in *S. australis* Harv. caused Harvey¹ to exclude this plant from the genus *Sphaerococcus* and to place it nearer *Gracilaria*. Opinions differ as to the other genera to be included in the Sphaerococcaceae. Schmitz² considers *Nitophyllum* to be a member of the family and describes its procarpia as being the simplest. Its thallus is very different from that of either *Sphaerococcus* or *Gracilaria*, and its fruit, judging from the brief account of Schmitz, is not at all like that which I have described in these two genera. Hauck³ considers *Chondrymenia* to be the third genus of

¹ Harvey, op. cit.

² Schmitz, op. cit., p. 24.

³ Hauck, Rabenhorst's Krypt.-Flora, Die Meeresalgen, 1885, p. 184.

the family. Its thallus is readily conformable with that of *Sphaerococcus*, though its procarpia and fruit-development are not yet known. Kützing¹ describing *S. coronopifolius* as mentioned under the name *Rhynchococcus*, places *Rhynchococcus* with *Calliblepharis* in the family Rhynchococceae. If the latest view, that of Schmitz, be followed and the genus *Nitophyllum* be regarded as one of the Sphaerococcaceae, this family presents a striking example of the difficulty of determination of the exact systematic position of a genus from a consideration of the structure of its thallus; for in these three genera we have examples of three of the four main types of thallus-structure met with in the Florideae:—

1. In the simplest Florideae (many of the Helminthocladiaceae) there is a uniseriate cellular central axis with apical growth and bearing numerous free lateral radiating branches. This type is not represented in the Sphaerococcaceae.

2. The lateral branches (also uniseriate, cellular, branching, and apically growing) have become more or less closely applied to one another so as to form a loose cortex to the distinct central axis. This type, seen in the Gelideae and Rhodomeleae (e.g. species of *Polysiphonia*), is represented by *Sphaerococcus*.

3. The lateral branches are closely applied to, and as well-developed as, the central axis, which is no longer distinguishable as such (Corallineae). Represented by *Gracilaria*.

4. The lateral branches are closely applied to one another, and occur right and left of the parent axis in one plane, essentially giving the thallus a flattened parenchymatous character (some of the Rhodymenieae). Represented by *Nitophyllum*.

Supposing the accounts of the structure of the procarpia and of the development of the cystocarp in *Sphaerococcus* and *Gracilaria* to be correct, I still refrain from any attempt to assign to them any other position than that they at present occupy, hoping that when more genera have been examined

¹ Kützing, Phyc. Gen., p. 403 (1843).

and the systematic arrangement of the Florideae is undertaken afresh, the results of the present investigations may prove useful.

It remains for me to compare the present account of *Sphaerococcus coronopifolius* with that of previous observers. According to Harvey¹ the plant was first noticed by Ray and described by him in his Synopsis². Sowerby, as already noted, was the first to observe, with the aid of the simple microscope, the 'midrib' and faint veins of the thallus-branches. Goodenough and Woodward in a paper read before the Linnean Society in 1795, 'Observations on the British Fuci, with particular descriptions of each species,' described *S. coronopifolius* as *Fucus coronopifolius*³. Their description of the fruit has been already quoted. In 1801 Stackhouse's work on Marine Plants⁴ was published. In this treatise Stackhouse objects to the wide range of forms included in the genus *Fucus*, and suggests amongst other new genera *Sphaerococcus*, the generic diagnosis being 'external globular pericarps adnate or immersed; sessile or pedunculate; containing seeds as above.' Stackhouse continues: 'This forms a very numerous genus, as many of the larger shrubby species and almost all the minuter kinds are found to be tubercled, and it does not appear to me that the tubercles being sometimes *internal* is a sufficient reason to separate them from this genus, as it may arise either from accident or from the plant not being sufficiently advanced in maturity.' The latter theoretical alternative is seen to be practically true. Speaking of the fructification, Stackhouse says: 'The fructification of this species is subject to vary; in its luxuriant state the margin is fringed with soft forked branching spinules, among which the orbicular seed-bearing tubercles are intermixed like berries. It seems however at times to have simple pedunculate tubercles on the margins.' The description is accompanied by a colored illustration of

¹ Harvey, op. cit.

² Ray, Synopsis.

³ Good. et Woodw., op. cit. p. 185.

⁴ Stackhouse, Nereis Brit. 1801, p. 83, Pl. XIV.

the fruiting thallus (natural size). Harvey¹ describes the branches as 'multifid ending in acute laciniae [branchlets] fringed with cilia [procarpium-branches], tubercles [cystocarps] immersed in the cilia.' The first biologist who gave any details of the internal structure of the cystocarp was J. Agardh², and in these words: 'Coccidia . . . nucleum simplicem foventia; placenta basalis cellulis strati medullaris contexta, a vertice et lateribus fila gemmiferi ima basi subfasciculata.' Kützing³ in 1843 was the first and only observer who figured the internal structure of the cystocarp. In this figure, repeated in Kützing's 'Tabulae Phycologicae'⁴ and in Hauck's⁵ 'Die Meeresalgen,' taken from a transverse section of the fruit, the sporiferous filaments are represented radiating from a central placenta of numerous small cells. There is no indication of the very large fused 'central cell' which I have described. It looks very much as if Kützing's figure was made from a transverse section of the fruit beyond the point of origin of the sporiferous filaments from the central cell and in the region of the 'carpogenous cells.' The procarpia have not hitherto been observed.

I am very much indebted to Dr. D. H. Scott for the suggestion of the investigation, for the supply of the material, and for opportunities of examining it.

¹ Harvey, op. cit.

² J. Agardh, Sp. Alg., iii. p. 395.

³ Kützing, Phyc. Gener., p. 403, Tab. 61. I.

⁴ Kützing, Tab. phyc. xviii. Tab. 10.

⁵ Hauck, op. cit., p. 179, Fig. 76 b.

EXPLANATION OF FIGURES IN PLATE XVIII.

Illustrating Mr. Johnson's paper on the procarpium and fruit in
Sphaerococcus coronopifolius (Stackh.).

Fig. 1. A piece of the fruit-bearing thallus. *cys.* cystocarp. *p. b.* procarpium-branch. $\times 4$.

Fig. 2. The small piece, *a*, of Fig. 1 more highly magnified. Letters as before. $\times 40$.

Fig. 3. A procarpium (except carpogenous cells). *c.* carpogonium. *h. c.* hypogynous cell. *c. l.* cells of lateral branch. *c. s.* cells of central axis. *t.* trichogyne projecting at right angles to plane of vision. $\times 1000$.

Fig. 4. A part of a procarpium-branch. *t.* trichogyne projecting. $\times 480$.

Fig. 5. Beginning of cystocarp. Carpogonium, *c.*, and hypogynous cells, *h. c.*, fusing. *t.* trichogyne cut off. $\times 1000$.

Fig. 6. Part of a procarpium just after fertilisation. In the carpogonium, *c.*, are two nuclei. Other letters as before. $\times 1000$.

Fig. 7. Longitudinal median section of a procarpium-branch. *c. s.* joint-cell of central axis. *p' p'' p'''* three procarpia; *cfg. c.* the carpogenous cells. In *p'* the cells of the carpogenous branch and a little of the trichogyne were visible under a $\frac{1}{4}$ -inch obj. In *p'''* the greater part of the trichogyne was observable, the cells of the carpogenous branch were found in another section. *c. c.* the fused central cell of the fruit, showing radiating ooblastema-threads. *pp.* pericarp or involucre (fruit-sheath). $\times 120$.

Fig. 8. Part of a procarpium (*p'*, of Fig. 7), showing some of its carpogenous cells, *cpg. c.* Other letters as before. $\times 400$.



Fig. 1.

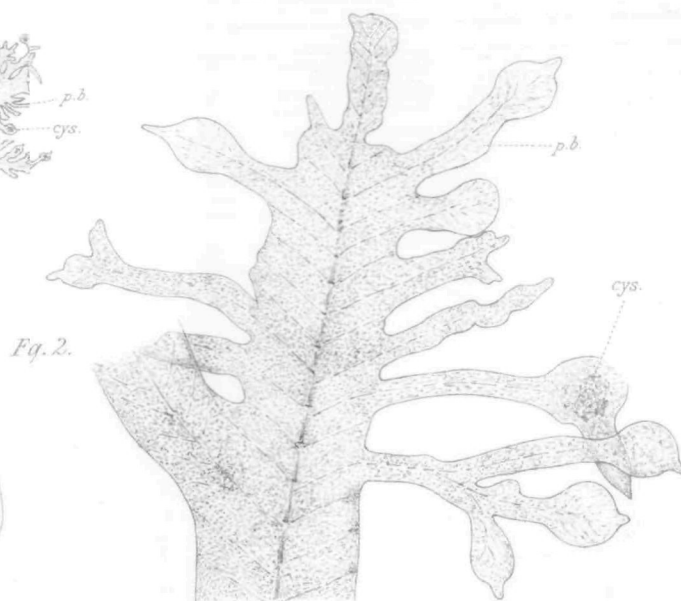


Fig. 2.

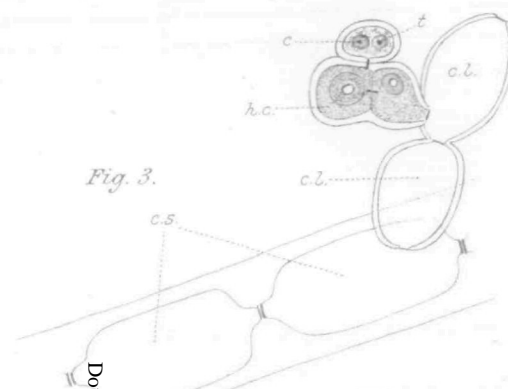


Fig. 3.

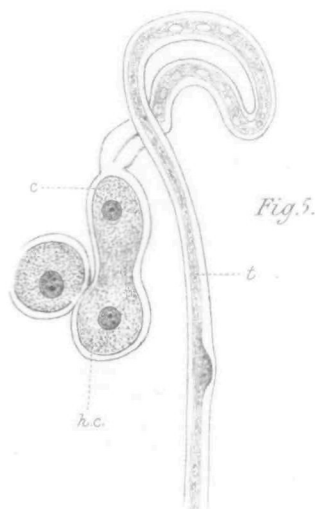


Fig. 5.

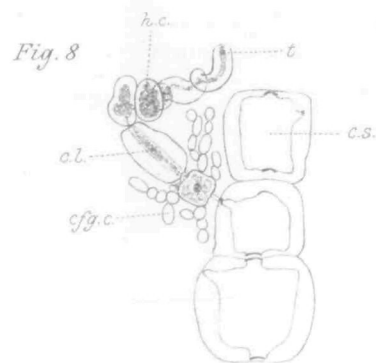


Fig. 8.

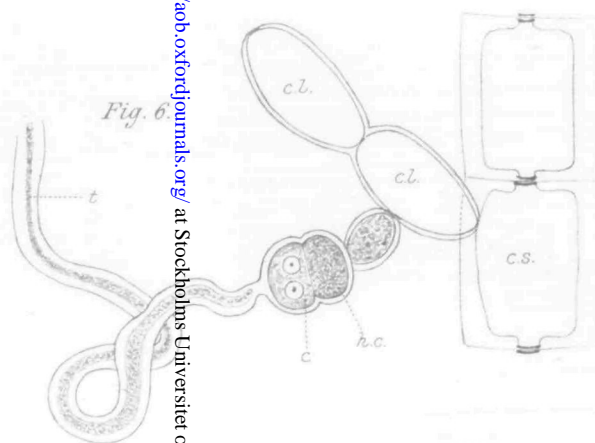


Fig. 6.

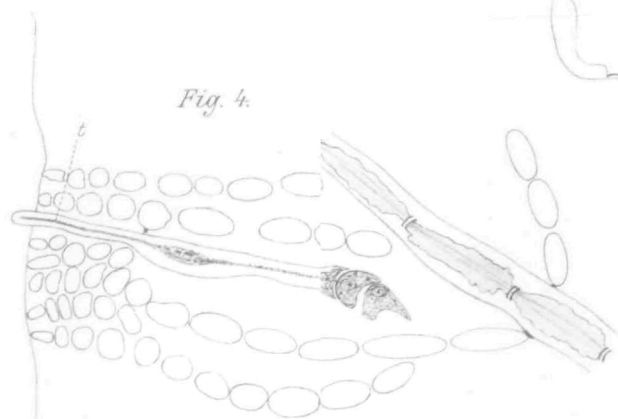


Fig. 4.

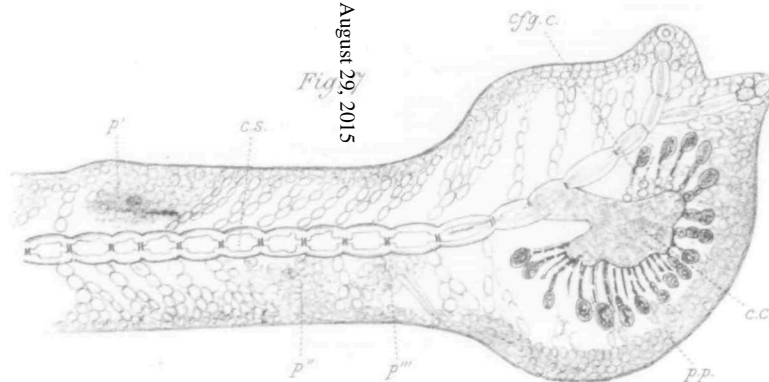


Fig. 7.

T. Johnson del.

University Press, Oxford.

