XVIII.—*On the Cell-structure of Griffithsia setacea* (Ellis), *and on the development of its Antheridia and Tetraspores.* By EDWARD PERCEVAL WRIGHT, M.A., M.D., F.L.S., F.R.C.S.I.; Professor of Botany in the University of Dublin. [With Plates XII. and XIII.]

[Read, April 8, 1878.]

THE true morphology of the various structures to be met with among the Algæ cannot be decided upon until the first beginnings as well as the final forms of these structures be fully known; and as there must yet be a great deal of investigation before the history of their evolution is fully worked out, it happens that there is at the present moment a good deal of uncertainty as to the meaning of the names given to the various parts to be met with in any one species. In this matter the many important works on Systematic Phycology will not help one very much.*

Professor Agardh† divides the large order of the Ceramieæ into two sub-orders, the first of which, Callithamnieæ, is characterised as having the Sphærospores formed by the alteration of the ramuli or out of free articulations, and this sub-order contains such well-known genera as Callithamnion, Ballia, Halurus, Griffithsia, &c., &c. Of this last-named genus there is, perhaps, no more common species than that one first figured and described by Ellis in 1767,‡ and now known as *Griffithsia setacea.* In the Atlantic

* "Entwicklungsgeschichte und wissenschaftliche Morphologie scheinen nun einmal dem Systematiker ein wahrer Horror zu sein." C. Nägeli: "Morphologie und Systematik der Ceramiaceæ." *Sitzungsberichte der konigl. bayer. Akademie der Wissenschaften zu Munchen,* 1861, Bd. 11, p. 317. This is, however, being a little hard on the Systematists.

† J. G. Agardh. *Epicrisis Systematis Floridearum.* Lipsiæ, 1876, p. 2.

‡ *Philosophical Transactions* of the Royal Society, vol. 57, 1767.

Ocean it is found not only all round the shores of Great Britain and Ireland, but also along the west and south shores of Europe, along the northern shore of Africa, and apparently on its north-western coast—at least at the Canary Islands. In the South Pacific Ocean it is found on the Tasmanian shore and around the North Island of New Zealand.

A residence by the sea side has enabled me for some time past to keep an almost daily watch over the evolution of several common species of marine algæ, such as grow on a rocky coast. One of the main objects of my investigations was to satisfy myself as to the general phenomena of cell development and cell growth.* During these researches I have constantly referred to Professor Carl Nägeli's most excellent account of his observations "On the Formation and Growth of Vegetable Cells."† Indeed this memoir has been to me as a text-book. So happy and truthful are Professor Nägeli's descriptions of the phenomena he has witnessed, that in attempting in what follows to describe some of those which I have seen, it may appear to some as if I were often but repeating his phrases. In some instances the results here recorded in reference to an individual algal form may seem incompatible with some of his more general conclusions; but I remember how that he himself has written, "Even now, in spite of all my efforts, I have only, as to the results on many points, arrived at probabilities—their further development and establishment I must leave until a happier time."‡

The frond in Griffithsia is described as "filamentous; filaments jointed throughout; articulations cylindrical, all containing bags of endochrome surrounded by a narrow border" (Harvey); or "filiformis, subdichotome ramosa articulata monosiphonia" (Agardh). It seems difficult to attach any

* "In ordinary speech, *Development* is often used as synonymous with *Growth*. It hence seems needful to say that Development as here and hereafter used *means* increase of structure and *not* increase of bulk. It may be added that the word *Evolution*, comprehending Growth as well as Development, is to be reserved for occasions when *both* are applied."—Herbert Spencer: *Principles of Biology*, Volume i.

† I have used and throughout quote from Professor Henfrey's Translation of this Memoir of Nägeli's, which is published in the Ray Society's Volumes for 1845 and 1849. The original Memoir appeared in Schleiden und Nägeli's *Zeitschrift fur Wissenschaftliche Botanik*, 1840–46.

‡ Ray Society's Volume for 1845, p. 95.

very definite morphological values to several of the terms here employed: what are these bags of endochrome? of what does their narrow border consist? how are they formed? and if the filaments consist of a number of these bags of endochrome, all placed in a series of distinct articulations, how is the whole frond one siphon?

If a frond of *Griffithsia setacea* be carefully detached under water, as can easily be done when the plant is found growing on the steep wall of some rock pool, and be at once floated into a bottle well filled with sea water, and this be as tightly as possible corked, the frond or collection of fronds will continue to grow for days and weeks together. The bottle may be opened from time to time, so that individual fronds may be examined, but it ought to be quickly re-corked. The bottle should not be kept exposed to direct sunlight nor in too warm a position, otherwise the evolution of the fronds will be unduly accelerated, and so may not be quite normal in form. If the bottle be not tightly corked there will be an undue evaporation of the water, the residuum will become too salt, and the health of the fronds will in several ways be interfered with. Professor Harvey* mentions that he at one time in this way kept a tuft of this species in good condition for upwards of two years.

If the growing tip of a frond be floated on to a glass slide in a drop of salt water, and covered with a thin glass cover (it should not be subjected to any other pressure), and then be examined under a one-fourth inch objective, it will be seen to consist of a well-marked cell wall which will act as its boundary, and the upper terminal portion of which will present a more or less nipple-shaped form; occupying the cavity within this will be seen the more or less pink-coloured cell contents; often towards the very apical portion of these will be found a portion in which the pink colour will not be very apparent: gradually, indeed, this will merge into a quite colourless morsel which will be found just under the apex of the outer cell wall. From a prolonged watching of this same gradually growing tip, or from the aggregate of a series of such observations on such growing tips, selected at various stages

* W. H. Harvey. *Phycologia Britannica*, 4to Edit., Volume iii. Description of Plate CLXXXIV.

of growth, it would seem that a true growth takes place (at times somewhat rapidly) in the outward cell wall, which thereby increases not only in length but also in width and general bulk; and quite cotemporaneously with this there is a proportionally well-marked increase to the cell contents; and this increase might be roughly compared to the stuffing of a bolster-case, where the tightest packed portions would be towards the bottom, and the loosest portions would be towards the top, only of course the bolster-case is quite open at the top where it receives the contents, and in the Griffithsia frond the top is closed and the contents get in by a sort of atomic transfusion.

As a result of this growth of the cell wall, and of the increase to its protoplasmic contents, it happens that the lower, denser, and more highly coloured portion of the protoplasm is greatly added to, and this apparently at the expense of the upper, less dense, and nearly colourless portion; but in reality, by its conversion into the more formed material, which thus is becoming more and more advanced forward, until gradually it acquires its supply of chlorophyll, and becomes fully organised. The upper portion of the protoplasm is not only less dense and less mucilaginous, but at the very growing tip it seems to fade into a colourless granular material, which seems as if it had not got its full complement of water of organization. To return, however, to the consideration of the older first-formed portion, which at a certain time and when a certain length thereof seems to have reached a certain stage of its existence, becomes separated into two—an upper and a lower portion—of which the upper is by far the smaller, being often not more than a mere convex-shaped lens-like mass—the top, as it were, of the coloured thimble-shaped body which is included within the nipple-shaped cell wall. This separation can only be at this stage detected by the most careful adjustment of the light, which will show some slight difference at the line where the two surfaces meet. It is not, however, an absolute separation into two perfectly distinct parts, for there still remains a well-marked central portion which connects the upper with the lower part, and which ceases to form a connecting link between them only at a very much more advanced period of time.

These structures will be the better seen, and their peculiarities will be the better understood, if a portion of a frond just at the stage now described be gradually immersed in weak glycerine (it is a good plan to allow a drop of glycerine placed at the edge of the glass cover to drive the salt water out before it: this will be greatly helped if the exit of the less dense fluid be assisted by a piece of blotting-paper, and when the substitution of the glycerine is successfully accomplished there will not be a single air bubble entangled). The cell contents will now very slowly indeed contract, and the different portions will be then more distinctly seen: first, there will be the lowermost cylinder of protoplasm, with its flattened poles, of a lovely and uniform pink hue (some specimens kept in glycerine for more than six months have not yet lost their colour, though in the process of time it does fade); secondly, the delicate tube of pink protoplasm, stretching from the upper portion of this lower mass to the under portion of the upper; and thirdly, this upper mass itself, often flat on its own lower surface, and irregularly convex on the upper surface—though it is noteworthy that this, its outer margin, is often radiate in outline as well as uncoloured, as if it had been torn away in its contracting from the inner surface of the outer cell wall.

Resuming our study of the living organism—the lower cylindrical mass will be found, when carefully watched, and after it has grown to a certain size, to gradually differentiate a cell wall. As a mean of many observations I believe that this is not laid down all at once, but in greatly varying densities, the peripheral portions being much more strongly laid down at first, towards and including the basal portions, and the wall surrounding the portions of the moiety of the lower tube of connexion not being for some time apparent. The upper and necessarily conical portion cannot be said to be fully formed until, in its turn, it separates from itself anew a convex lens-shaped mass, when it will then complete the upper and apical portions of its cell.

At each throwing off thus of a mass of protoplasm, the mass of protoplasm so thrown off is an item of development, the result of a previous growth. Though the penultimate portion may and does increase its bulk (grow), yet its capability of development in an apical direction ceases; further on, it will be seen that its development in a lateral direction is not interfered with; but even then it is not without interest to find that its lateral outgrowths invariably have some relation with its last-formed portion.

Often at a very early stage, after the separation of an apical portion of the cell contents from the mass immediately below them, a very faint line of demarcation will be perceived in the centre of the connecting tube of pink protoplasm: as growth advances this becomes more and more apparent, and the halves now seem, though touching each other, not to be absolutely joined. If reagents are used, these halves will be at once drawn asunder, and each fully-formed inner mass has then got an apical and a basal opening or pore in its cell wall, and in a long series of such masses there will be formed a more or less continuous communication, which will represent the pore-area-system of Nägeli.

These openings are alluded to by my friend William Archer as pits; and in his excellent memoir* on the structure of the cells in *Ballia callitricha* he calls attention to the novel fact, that in this alga these pits or pores are closed by very characteristic little bodies which he calls "stoppers" or "lids." "In every joint of the plant (except the apical joints) there occurs a 'pit,' with its 'stopper' at *each end of each joint,* that is, at least two such in each cell: in the apical joints there occurs but one (at the base). . . . . Why these pits are formed at all, or what special function they subserve, is not apparent; but the marvel is, that no sooner are they in existence than the openings seem to be thereupon again methodically plugged up." I venture to think that these pits or pores are formed in the process of development of the inner row of cells (at least in Griffithsia, to which genus Ballia is, however, very closely allied), in which process the individual cells are for a considerable time not completely separated from each other. When these same cells, in the process of growth becoming gradually more and more separated, at last become completely so, then, at the point of detachment and in the middle of what was a string of protoplasm, but at this period is a tube, the walls of which have been formed out of the protoplasm, which tube is also filled with protoplasm, there will remain an opening plugged up with protoplasm: this plug will soon differentiate from its outer margin a cell wall, which may be continuous with the cell wall of the tube

* W. Archer, F. R. S., "On the Minute Structure and Mode of Growth of Ballia callitricha." *Transactions* of the Linnean Society. Second Series. Vol. i., Botany, p. 211.

(which in Griffithsia is generally the case); or this cellulose plug may not become incorporated with the cell wall at the bottom or top of the cell, as is the case in Ballia, and then it will constitute the "stopper" of Archer. There is also this difference, that in Griffithsia the plug seems to be formed with its convexity towards the outside, not towards the inside of the cell, as in Ballia, and it will be remembered that there are no necks to the cells in the latter genus. It will also be remembered that such structures must present a very different appearance when observed in a dried or macerated frond and in a fresh or living frond; and whether my interpretation of the formation and function of these bodies be the right one or not, the marvel is, that Archer has made out as much as he has of the complicated structure of Ballia from the morsel at his disposal, which was first macerated in fresh water and after that in spirits.

When the evolution of the frond has advanced thus far, there will be found to exist within a common and undoubtedly a cellulose cell wall a series of organisms, all but the ultimate one, more or less intimately attached by both ends to each other, and it itself attached to the penultimate one. At this stage the frond might be compared to a glass tube closed at both ends, through which there ran a single row of pink oblong beads, threaded on a string of the same colour, each of the lower beads being about the same size, but the upper ones being smaller, as not yet grown adult, and all being so arranged as to allow the connecting thread to be seen; but in such a frond, where are the articulations? what is the single siphon? and what are the bags of endochrome? The answer to the last question is apparent—these bags are the organisms the development and growth of which have just been described, and which I cannot any longer hesitate to call cells.

One fact in reference to their structure I have never been able to satisfy myself about, and that is, of the presence of cellulose in their cell walls, when these are *enclosed* within the original and first-to-grow cell wall. When treating of the development of the cells which bear the antheridia and tetraspores—cells absolutely the same in their genesis to those now alluded to—the behaviour under reagents of their cell walls will be found to in no way differ from the behaviour of the originally formed cell wall; so that I am even, from this fact, forced to conclude that, when under an outer layer, the cell walls are either atomically different in their constitution, or that the denseness of this outer layer prevents the full action of reagents.

If by the monosophonous nature of the frond is meant the continuation from one of these inner cells to all the others—if this describes in other words Nägeli's pore area, which ceases to exist on the formation of the "stoppers," or on the more complete covering over of the pores—then it does not appear to me a characteristic appellation; for as the fronds become in a manner articulate, then the very dividing of them into sections seems to me to do away altogether with the appositeness of the term monosophonous.

As to the so-called articulations. In process of growth and in proportion as the outer cell wall is the further removed from the point of development, so it (the outer cell wall) thickens, and sometimes the striæ of growth will be most beautifully apparent. These additions to its thickness are of course on its inner surface, and they would appear to be laid down with great evenness and regularity; but as these thickenings go on, those in the older and lower portions of the frond will be seen to be laid, not only thus, but, as it were, also on the outer portion of the cell walls which have been laid down by the inner separated masses of protoplasm; and these layers of thickening will go on increasing until they penetrate into and quite surround the delicate connecting tube between these cells. While I describe these secondary layers as laid down upon the outer portion of the inner cell walls, I must not be taken as meaning that they are incorporated with these, as the secondary layers are with the outer cell wall, but rather that they consist of, as it were, a series of bulgings out from these very secondary layers, which bulgings force themselves in between the newer and inner cells; and once having done so, the same line of direction of deposit is adhered to, but the layers of secondary deposit are always laid down in the usual way upon one another. After these deposits have become sufficiently numerous, then these portions of the frond will be by them divided into a number of false joints or articulations, as it may perhaps be convenient to call them. But I cannot see that this peculiar method of deposit can in itself constitute each of these divisions, into which the outer wall of the frond is now divided, a true cell. To my apprehension these cannot answer the definition of such a structure. In the case of the frond of *Griffithsia setacea*, it will be found not to break across at these divisions with that peculiar fracture so characteristic of a true joint between two vegetable cells: on the contrary, the frond is often at these portions very tough, and will allow of a good deal of manipulation ere breaking, nor is there any true breach of continuity between the outer circumferential layer.

A frond growing as above described would of course give rise to a filament, the length of which would depend in a great measure upon its power of development, while its breadth would obviously depend upon its power of growth, and the total product of its evolution would be its sterile self. It, however, does give origin also to lateral prolongations which arise as follows:—After one of the central cells has become so far differentiated as to have constituted itself a separate entity, though still in communication with the cells below and above it, it will sometimes be seen to increase in thickness at its upper surface, where, in fact, a slight bulging out will appear; at the same time or previously the outer cell wall, just opposite to this bulging, will also be seen to become thinner, and it too will bulge out; and after a short time as the growth goes on, and the bulging has assumed the form of a little bud-shaped body, a process of development commences, whereby the bud-shaped portion of the protoplasm, the greater part of which will be of a pink colour, will separate itself from the protoplasm behind it, retaining a connexion thereto by the little string of protoplasm as before described for the primary axial cells, and will commence to form one of the lateral prolongations of the frond: its further progress will be carried on just as in the main growth previously described. To me it would appear, 1, that the outer cell wall took the first step in this lateral cell development—that it became first thin, then by intussusception grew outwards, the outgrowth being in this case slightly upward as well as outward; 2, that as it grew it added to the protoplasm beneath it, sending back as it were fresh material to the already existing nutrition in its rear; and 3, that there was no evidence of the origin of a growing force from the rear, but only in the front. I will not insist on any of these propositions here; they seem forced upon me when I attempt to account for the various phenomena which I have witnessed. In only one or two instances out of several hundreds of observations have I seen these lateral growths proceed from any other portion of the frond (in *Griffithsia setacea*) than that just described, viz.: the outer cell wall in the region of the upper peripheral margin of the inner pink-coloured cell. Between such lateral exogenous outgrowths (ramuli of the Phycologist) there is an equally well marked continuity of the outer cell wall, as we have seen existing in the main axis of the frond, so that these ramuli are not to be easily detached from the stem. Why they should take their origin from the region described, and why they should grow from some parts of the frond and not from others, may be put down as characteristics of this species. In their growth there is no true dichotomy—indeed in this species the terminal cell never divides into two: there is, however, a decided tendency to these ramuli being given off in a verticillate manner, though the verticil is a long drawn-out one, except, indeed, when it is formed in connexion with the organs of reproduction, when, as we will immediately proceed to describe, all its twigs arise from the one plane.

The Antheridia.—Harvey describes* the antheridia as "minute oval bodies composed of dense whorls of exceedingly minute glassy filaments, frequently occupying the place of tetraspores in the involucres," while he describes the tetraspores as "spherical, attached to the inner faces of the dichotomous involucral ramuli with wide borders. The involucres containing tetraspores are found on different plants from those containing favellæ. The tetraspore-producing plant is the commoner of the two."

This is, perhaps, the best place to mention that there is in the Herbarium of Trinity College (Dublin) a drawing by Miss Biddulph, of *Griffithsia setacea*, which is evidently the one thus referred to in Hooker's "British Flora," vol. ii. p. 338. "Mr. Borrer informs me (W. H. H., 1833) that a similar appearance was observed and drawn by Miss Biddulph many years ago, and communicated by her to Mr. Sowerby. This consists of minute ovate bodies, apparently composed of whorls of extremely slender filaments, invested with jelly, and attached, like the capsules (*i.e.*, the tri-sporous capsules), to the interior faces of the involucral bracteæ."

Derbès and Solier† state that the tetrasporic ramuli in Griffithsia do not

* *Phycologia Britannica,* loc. cit.

† A. Derbès et A. J. Solier: "Mémoire sur quelques points de la physiologie des Algues." *Supplément aux Comptes Rendus des Séances de l'Académie des Sciences.* Tome 1er, p. 70.

produce antheridia, "ces trois sortes d'organes (favellæ, antheridia and tetraspores) sont toujours placés sur des pieds distincts." All three take their origin in the terminal cell of a small ramulus of two or three articulations, which itself rises from the main frond. "Cette cellule, d'abord petite, à peu près sphérique, grandit peu à peu, en prenant une forme spathulaire ou ovalaire: quelquefois elle devient arquée par une inégalité de développement dans quelqu'une de ses parties. Bientôt dans son intérieur et vers le sommet, apparaissent de petites cellules, d'abord un peu diffuses, puis se dessinant avec plus de netteté, et prenant l'aspect de fils moniliformes. Ces fils croissent, se développent par dichotomie, et finissent par rompre l'enveloppe membraneuse qui les a protégés jusqu' alors. C'est là l'involucre du jeune gloiocarpe déjà bien reconnaissable, qui ne tardera pas à se compléter par l'adjonction, soit de tétraspores, soit de favelles, soit enfin d'anthéridies."

Of the two species examined by Derbès and Solier, one—*Griffithsia spherica* = *G. setacea*—is figured as having antheridia of a more or less globose form, and the antherozoids are figured as provided with a flagelliform appendage. I cannot, however, understand how the antheridia figured in Plate XVII., figures 6 to 8, ever develop into the adult form, figure 9 on same Plate. The second species—*G. secundiflora*—in which the antheridia are figured as oblong, almost conical, has by Thuret* been placed in a distinct genus, Bornetia. Professor Agardh scarcely more than alludes to the antheridia in Griffithsia, but places the genus in the section "sphærosporis intra ramulos involucrantes fronde nuda . . . ramis involucri invicem liberis."

Professor Nägeli writes†:—"Die tetrasporentragenden Aeste bestehen aus 1–2 sterilen unteren und aus 1 seltener 2 oder 3 oberen Gliedern, welche Quirlzweige erzeugen. Die Scheitelzelle ist verkürzt und zwischen den Quirlzweigen versteckt. Die letztern sind meist nur einmal oder zweimal gabelig-getheilt und einwärts gebogen; der Hauptstrahl besteht aus drei oder vier Gliedern. Auf der innern Seite der Gliederzellen, 90° von

* Gust. Thuret. "Note sur un nouveau genre d'Algues, de la famille des Floridées." *Mémoires de la Soc. Imp. des Sciences Naturelles de Cherbourg*, vol. 3 (1855), p. 157.

† *Morphologie und Systematik der Ceramiaceæ*, loc. cit., p. 390.

dem Seitenstrahl oder der Dichotomieebene entfernt, stehen verzweigte Stiele, welche auf jedem Glied eine Tetraspore tragen. Die Entwicklungsgeschichte zeigt, dass die Sporenmutterzellen die Scheitelzellen von zweizelligen Strahlen sind, und dass sie durch sympodiale Verzweigung in eine seitliche und scheinbar sitzende Stellung geschoben werden.

"Die antheridientragenden Zweige sind etwas einfacher gebaut als die sporentragenden; sie zeigen nur eine Gabelung und der primäre Strahl is bloss dreizellig. An der Gabelung steht auf der innern Seite, einen rechten Winkel mit der Dichotomie bildend, ein kurzer Zweig mit quirlständigen verzweigten Seitenstrahlen, welche ganz mit Antheridien bedeckt sind. Die Antheridienzweige bilden einen Quirl um die oberste Gliederzelle des begrenzten Astes; zwischen denselben ist die Scheitelzelle des letztern mehr oder weniger verborgen. Abbildungen und Beschreibungen lassen glauben, die Quirlzweige, welche Tetrasporen und Antheridien tragen, seien an der letzten Zelle des Astes befestigt. Diess ist unrichtig; die Tragzelle ist immer die vorletzte (d. h. die letzte Gliederzelle) und die eigentliche Scheitelzelle wurde übersehen."

I cannot tell what species of this genus Professor Nägeli had under investigation for the purposes of this description, which is the only one I have met with that in the slightest degree seems to mention the phenomena which I now proceed to describe, as they occur in *Griffithsia setacea*.

One of the lateral prolongations (ramuli) of the main axis having grown out in the manner just described, until one, two, three, or four (perhaps most often three) of the inner cells have become developed, the terminal portion of the outer cell wall will be seen to begin to expand, and it becomes more and more globular, and then elongating itself, becomes at last somewhat pear-shaped. Just at this period, the most attentive observation, assisted by reagents in every way that I could think of, revealed nothing peculiar in the behaviour of the inner mass of protoplasm, except that as the expansion of the outer cell wall increased, so also did the inner mass of protoplasm, the upper portion being much wider than the lower portion, where, by means of the connecting tube of protoplasm, it would be in contact with the penultimate joint cell; presently, however, a small, often rather conical, mass of protoplasm is detached in front; this detached mass being just under what to this has been the growing tip of the ramulus. As will be seen by-and-bye, this in a short time will become an outer cell, and will constitute the crowning or summit cell of this ramulus, which now becomes a reproductive twig. In this I confirm the statement of Professor Nägeli; for not only is this a terminal cell, but it is also not an ordinary articulation cell, and it is also remarkable in that it never gives rise to any further articulations. This upper wedge of protoplasm, which is then the basis of the terminal cell, soon becomes hidden away amid the new growths that will surround it. Some may think it too fanciful to trace a resemblance between it and the apical cell in the ordinary caulome; but, like this, it is always the advance cell, though the cells that may arise in an exogenous manner around it soon surpass it in size, these, too, growing around and in advance of it, and, with other functions to perform, soon completely putting it out of sight; but we must investigate how these latter arise.

If the remaining mass of the protoplasm—to wit, that portion which is to be found between the summit portion and the penultimate joint-cell—be carefully examined, it will be found to undergo a wonderful series of changes, and these so rapidly that it is only by the study of many specimens that they can be clearly understood. The upper surface of this mass is more or less flattened: joined to it by a central tag of protoplasm is the ultimate cell. Around its upper margin seven to nine minute morsels of protoplasm become detached (though still as usual attached to it each by its tiny string of protoplasm); at first they are like pink pearls set around the margin of a coronet; each little pearl elongates itself, in time detaches off in front another small morsel, and becomes then much more elongated. The direction these detachments will take is moulded as it were by the inner outline of the outer common cell wall, so that these tiny embryo branchlets are necessarily, as they are produced, curved in an arched manner over the single central ultimate cell. Growth still goes on: there is often one further process of development, and then a third addition is made to each branchlet; so that, while still within the now very transparent outer pear-shaped cell wall, there can be seen seven to nine minute twigs, forming a well-marked involucre, each of the rays starting from around the upper margin of the single central mass. After a little further advance in growth, the outer cell wall will be burst asunder, and gradually the enclosed rays begin to unfold themselves. The growth is now most rapid; the cell walls around every separate mass of protoplasm seem ready formed; the cells speedily enlarge; each of the three of which every single ray consists soon increases in bulk, the lower ones more obviously, and the outer portion of their walls more rapidly than the inner, so that they still bend themselves well over the central cell: the little tags of protoplasm connecting cell with cell can be traced to the very minutest twig endings.

For distinctness sake these rays, which themselves are formed on the same pattern, though not at all in the same way, as the ramuli which bear them, may be called the "involucral ramuli." The cells which compose them, it will be agreed, are in no way genetically different from those already described as forming the inner row of cells in the main frond or ramuli of Griffithsia, except, inasmuch as that by the rupture of the common investing outer cell wall they have come into direct contact with the medium in which they live. Their cell walls, it will now be found, answer to the reagents for cellulose; and in their form and appearance, especially where they join on to the ruptured portion of the old cell wall, no difference between the two series is to be detected.

Sometimes, even before these involucral ramuli become free, minute protuberances will be seen projecting from the upper and innermost portions of the first-formed cells of each ramulus. These seem to arise exactly in the same manner as the cells, but always assume and retain a quite globular form: at other times secondary ramuli will arise from the same spot; these will be in their turn also finally three-celled, and from the upper and inner portion of the two lowermost of these cells will arise the same minute protuberances, each ending in a well and distinctly formed globular-shaped cell. These globular-shaped cells have two very different destinies: one set will develop into antheridial cells, and the other set into tetrasporic cells, both being found in the same involucre.

The antheridial cells are much more universally found in the involucres than the tetraspores; but it is quite possible that further observation may show that this is not always the case. Already I have some reason to think that the first involucres to open, namely, those formed on the twigs nearest to the base of the frond, chiefly develop antheridial cells, while those nearest to the apex of the same frond are found to have a smaller number of antheridial cells and a larger proportion of tetrasporic cells; so that it is possible that the last to be formed fruiting twigs might develop an immense preponderance of tetrasporic cells, and so might account for the statement so often made that the antheridia and tetraspores are found on separate plants. At the very first appearance of the mother antheridial cell it is evident that its protoplasm, unlike that entering into the formation of the other cells of the thallome, is at once quite isolated; there is no string or tag uniting it with the protoplasm of the cell that gave it origin. It is also sessile, and very densely filled with pink-coloured protoplasm. By the growth of these cells—of which each ray of the involucre may carry as many as seven to nine—the basal portions of the rays are pushed outwards, though these never lose completely their arched-over appearance. I have never detected the presence of nuclei, but after a short time the protoplasm of the cell divides into a number of separate masses, which very soon assume the appearance of a number of little balls; these quickly develop cell walls, and now an interesting phenomenon presents itself; for a small thread of protoplasm from each of the newly-formed daughter-cells is seen to project from it, and to stretch out to the inner periphery of the mother cell wall, and this thread is now equally enclosed with the rest of the masses of protoplasm in the mother-cell by a wall of cellulose, which in process of growth seems to penetrate through the wall of the mother-cell, sometimes in a straight, sometimes in a curved direction. At this stage there is nothing that I know of which these daughter-cells so much resemble as the cells of *Olpidium tumefaciens* (Magnus), specimens of which, parasitic in the trichomes of *Ceramium acanthonotum* (Carm.) I happened to have at the time constantly under examination. The resemblance, though great, is, however, only superficial; in each daughter-cell of the antheridial cell of Griffithsia the protoplasm, losing its pink colour, becomes nearly colourless, and gives origin to several antherozoids, which make their escape from the daughter-cell through the tube-like canal, and after their exit are not to be distinguished from the ordinary motionless antherozoids of most Florideæ—motionless I write, in conformity with usage—but at this stage an antherozoid is a mass of protoplasm unincumbered with a cell wall; and I feel sure that with an eighth of an inch objective I have seen obscure amœboid movements in them—movements quite sufficient to enable such bodies to cling to or even enter a trichogyne. The antherozoids do not all make their exit at the same time from the daughter-cells of one mother-cell; but each daughter-cell, when it has lost its contents, shrivels up, the tube-like portion remaining projecting from the outer wall of the mother-cell. There is not a trace in the mother-cell of any sterile central cell, nothing that could be compared to the axis, for example, in the antheridium of Polysiphonia.

The difference between this form of development of globular antheridia and that to be met with in other Florideæ, Lejolisia for example, may not be as great as at first sight appears. In many points it appears to me to resemble somewhat that figured by Professor Pringsheim* as occurring in his *Spermothamnion roseolum*, where "Die zwei bis drei letzten durch die Theilungen in der Endzelle gebildeten Zellen eines Fruchtzweiges verlängern sich nicht, sondern theilen sich rasch hintereinander durch mehrere erst den übrigen Scheidewänden parallele, dann auf diesen senkrechte Wände und bilden einen fast farblosen, kleinzelligen Zellkörper, in dessen einzelnen Zellen die Körper, die man jetzt als Samenkörper der Florideen betrachtet, je einer in jeder Zelle entstehen. Diese haben die bekannte, allen Florideen gemeinsame Form farbloser, kleiner Bläschen und werden einzeln aus ihren besondern Mutterzellen durch eine seitlich in der Wand entstehende Öffnung entleert."

This type of development is, taking into account the absence of a central axis, more like that in Polysiphonia, as Professor Pringsheim himself suggests. That observed in Griffithsia has this peculiarity, in addition to the others mentioned, that while in both Spermothamnion and Polysiphonia the antheridial cells do not terminate an axis of growth, (being indeed very probably metamorphosed trichome-cells), for certainly in the latter, and apparently in the former after the antheridial mother-cell has performed its function, the cell below it continues the growth of the axis

* N. Pringsheim: "Beiträge zur Morphologie der Meeres-Algen." *Abhand. der Konigl. Akad. der Wissenschaften zu Berlin*, 1862, p. 18. (Plate VI., Figs. 4, 5, 6.)

outwards—in Griffithsia nothing of the kind is to be met with; the antheridial cell is neither an inter-cellular cell, as in Polysiphonia, nor is it ever thrown off and a new growth begun below it, as in Spermothamnion.

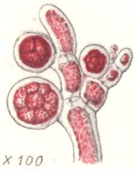
In leaving this part of the subject, it may be as well to quote Professor Nägeli* on the structure in Ceramiaceæ:—"The structure of the frond on the species of Ceramiaceæ is made up of apical cells (primäre Zelle des n^{ten} Grades), lateral cells (primäre Zelle des $n + 1^{ten}$ Grades), and joint cells (n^{te} secundäre Zelle)." "The joint cells no longer divide either through transverse or longitudinal division, so that the filament only increases by cell formation in the apical cell." "These joint cells possess, however, the power of growing out and producing thereby branch cells, by which the accessory filaments are formed." "The partition walls between two secondary (secundäre) cells of a primary axis, and also those between the secondary cells of such an axis and the first secondary cells forming its accessory filaments (Tochterachsen) contain each a central pore. The membrane is not in contact over the whole plane of the pore, but only so around the circumference, leaving way for a narrow elliptical space. The pores of the stem cells are considerably larger than those of the leaf-cells."

The Tetraspores.—The cells bearing the tetraspores take their origin much after the same fashion as the mother-cells of the antheridia; but one fact will speedily announce that the cell is proceeding in a tetrasporic rather than in an antheridial direction, namely, that the mass of protoplasm, which in the latter separates itself into an isolated mass, previous to developing the daughter-cell in the former, remains attached by a little pedicel of protoplasm—the existence of which I find also in every species of Polysiphonia in which I have watched the development of the tetrasporic fruits. After the mass of protoplasm is well formed it divides into four parts, as it appears to me, and as shall be more particularly referred to in the following memoir on Polysiphonia. These are at first on two planes, forming, as it were, a flat verticil of three globular pins' heads proceeding out of the upper margin of an also globular mass of protoplasm occupying a lower plane, and from the base of which depends the little stalk or pedicel of protoplasm

* C. Nägeli: *Die Neuern Algensysteme*, 1847, p. 196, *et seq.*

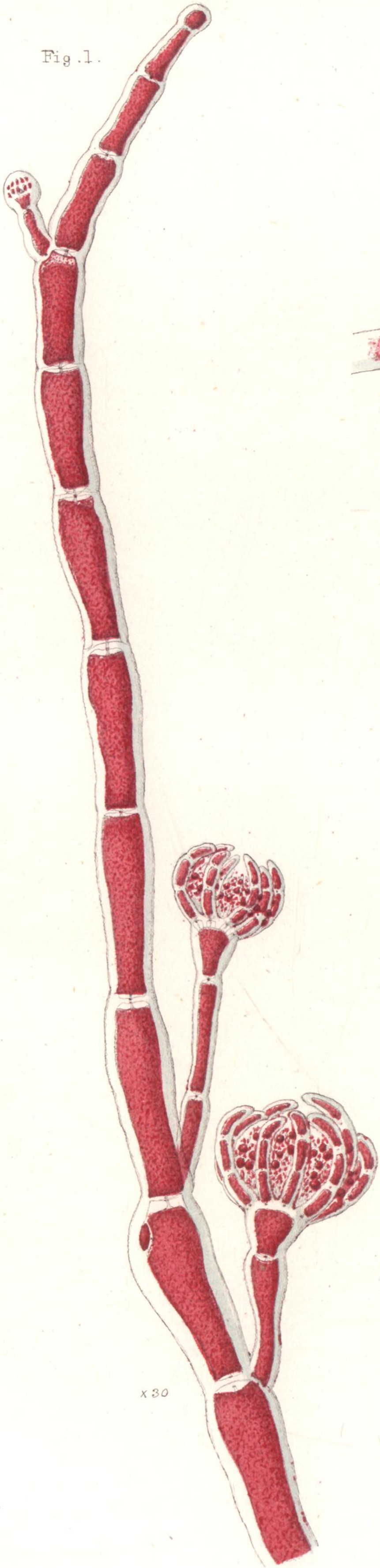
referred to. By the gradual expansion of the lower one, one of the upper three is forced backwards and upwards, while the other two mount up, as it were, but under it, into a position partly above the lower mass and partly on either side of it, the uppermost one partly mounting upon them, and thus rounds off the mass. If we regard the lower spore as giving us the front view of the tetrasporic capsule, a back view would show the two side spores and the upper spore, but not the lower spore, while a front view would show the two side spores and the lower spore, but not the upper spore. As the spores reach a certain size, the little stalk of protoplasm seems to disappear, or at most it only leaves traces of its existence in the pore opening to be seen in the common cell wall, which is, under reagents, apparent; each of the four spores also now forms its own cell wall, and their development is then complete.

Fig. 7.



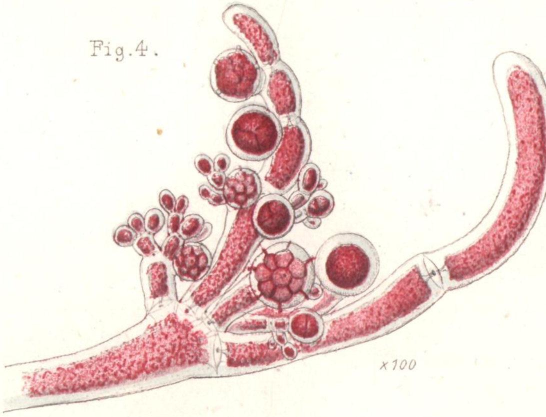
x 100

Fig. 1.



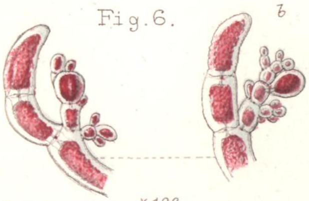
x 30

Fig. 4.



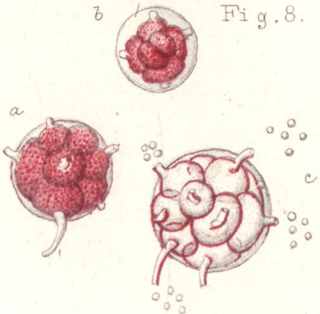
x 100

Fig. 6.



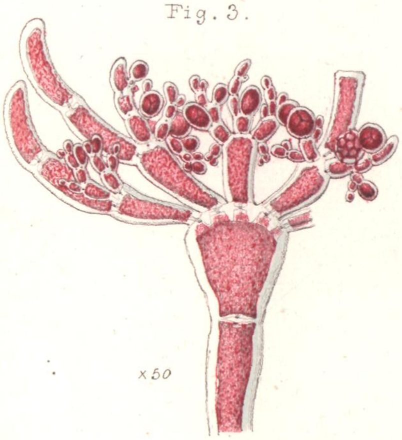
x 100

Fig. 8.



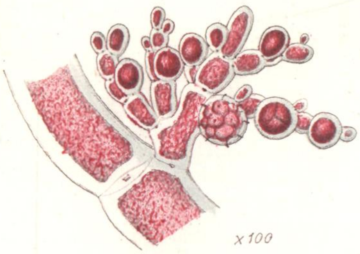
x 250

Fig. 3.



x 50

Fig. 5.



x 100

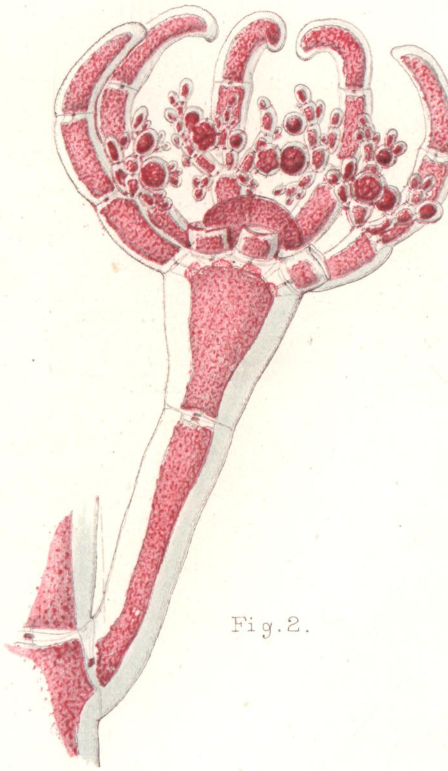


Fig. 2.

EXPLANATION OF THE PLATES.

PLATE XII.

Fig. 1. The upper portion of a filament of *Griffithsia setacea*, which has been for a short time in glycerine and water. From the left-hand upper corner of the first "joint" a fruit-bearing twig has been developed; from the right-hand upper corner of the second "joint" a protrusion of the cell wall accompanied by a detachment of a plate of protoplasm is seen; from the left-hand upper corner of the same "joint," but a little in the rear, a second fruit-bearing twig has been developed; from the right-hand upper corner of the eighth "joint" a third fruit-bearing twig is being formed. Above this last twig is the terminal portion of the filament. Magnified 30 times.

Fig. 2. A much enlarged representation of the first fruit-bearing twig from the same filament (fig. 1), with three of the now unfolded involucral ramuli cut away, so as to give a general view of the various forms of cells developed from the remaining five "involucral ramuli," the terminal cell is here seen to be the last cell of the filament, while the involucral ramuli start from the penultimate cell. This figure is slightly diagrammatic, and the ultimate cell is too conspicuous; its position will be better understood by a reference to figures 4 and 5 in Plate XIII. × 50.

Fig. 3. Several of the "involucral ramuli," to show the relative position of the secondary twigs. × 50.

Fig. 4. An "involucral ramulus," greatly enlarged. From the right-hand upper corner of its first "joint" several secondary ramuli proceed. These terminate in a sterile cell; but several of the tertiary ramuli give rise to antheridial and tetraspore cells, but few of these latter are terminal cells. × 100.

Fig. 5. A secondary twig from an involucral ramulus, showing the more minute cell-endings. × 100.

Fig. 6 *a* and *b*. Ultimate cell-endings of two twigs, showing tetraspore cells. × 100.

Fig. 7. Ultimate cell-endings, showing antheridial and tetraspore cells. × 100.

Fig. 8. *a*. An antheridial mother cell; the daughter cells with antherozoids, completely filling up the cells. *b*. The same, but the daughter cells not filling up the mother cell. *c*. The same, with the antherozoids escaping.

Plate XIII.

Fig. 1. A much-branched filament of *Griffithsia setacea.* Although the frond has reached its nearly adult size, yet fresh developments of ramuli will be seen to occur in several places. On the whole frond there was but the one fruiting twig. × 25.

Fig. 2. A side cell, apparently having reached that stage of growth in which it will next undergo development. × 150.

Fig. 3. A side cell, with commencing development; some irregular thickenings of the outer cell wall are to be seen. × 150.

Fig. 4. Terminal portion of a fruit-bearing twig, with the involucre of ramuli moulded, as it were, out of the protoplasm. As seen in life, the divisions either into ramuli or of these into joints would be scarcely perceptible; but under the influence of glycerine it presents the appearance as drawn. The ultimate cell is distinctly seen. × 150.

Fig. 5. The same, still further advanced. The ramuli have not yet broken through the surrounding cell wall. The secondary ramuli have distinctly made their appearance. × 150.

Fig. 6. A young but fully adult cell, treated with glycerine, showing the inner delicate, somewhat contracted cell wall, and the connecting tubes, with stoppers. The protoplasm has slightly contracted from the inner cell wall. × 75.

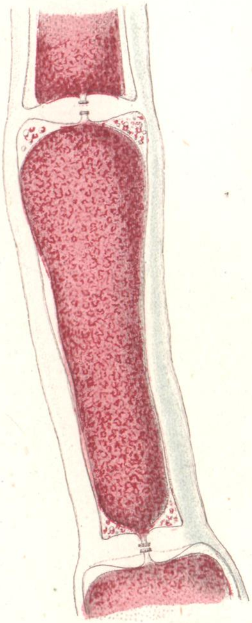
Fig. 7. The same, from an older cell, showing stoppers. The cells, owing to the action of the glycerine, have drawn away from each other, leaving at the lower stopper a little tag of cellulose membrane. × 100.

Fig. 8. The same, from a younger cell, showing the peculiar concave surfaces often seen at the ends of the inner cells. × 100.

Fig. 9. Showing formation of side cells. × 100.

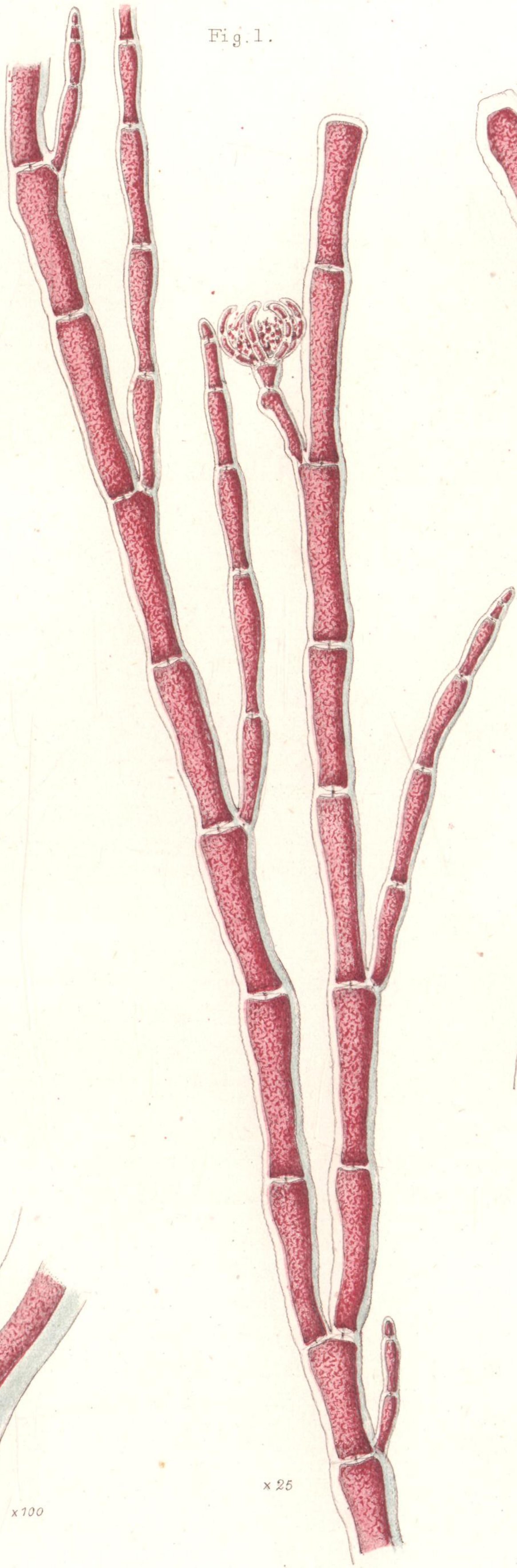
Fig. 10. Stoppers sometimes found in very old cells, considerably enlarged.

Fig. 6.



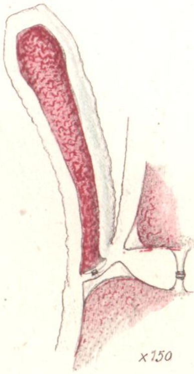
x 75

Fig. 1.



x 25

Fig. 2.

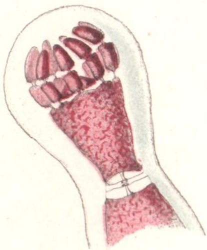


x 150

Fig. 3.

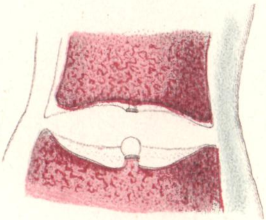
x 150

Fig. 4.



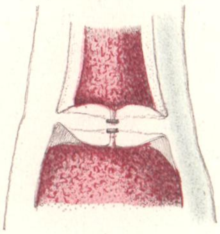
x 150

Fig. 7.



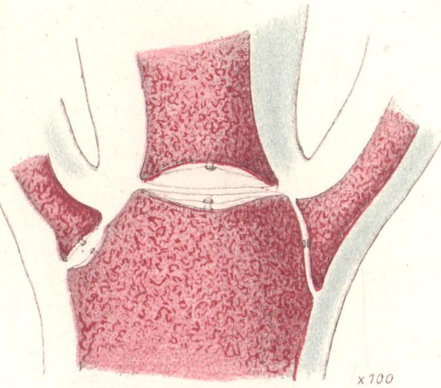
x 100

Fig. 8.



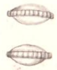
x 100

Fig. 9.



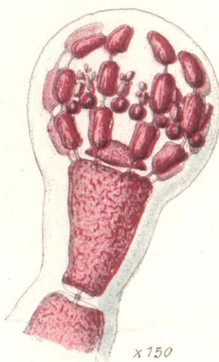
x 100

Fig. 10.



x 400

Fig. 5.



x 150