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"................. per litora spargite muscum,
Naiades, et circùm vitreos considite fontes:
Pollice virgineo teneros hìc carpite flores:
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo."
N. Parthenii Giannettasii Ecl. 1.

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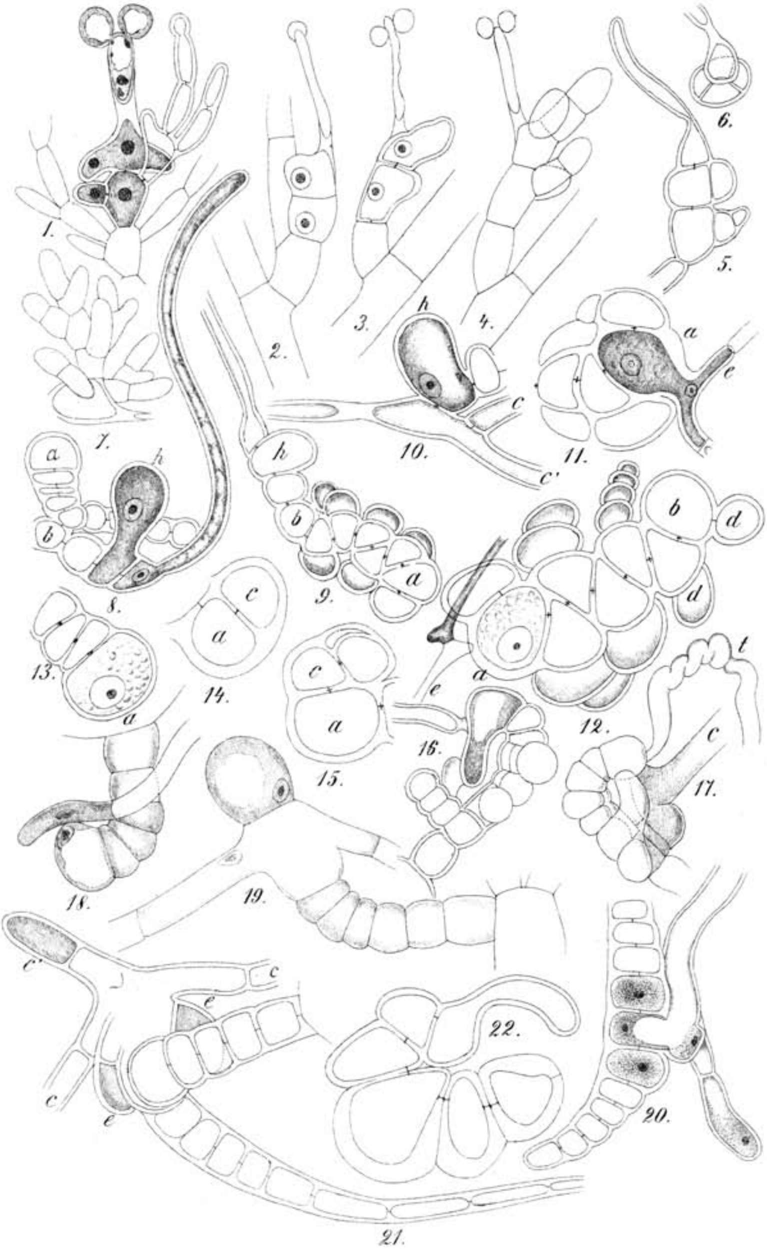
I.—*On the Fertilization of the* Florideæ. By Prof. F. Schmitz*.

[Plates I. & II.]

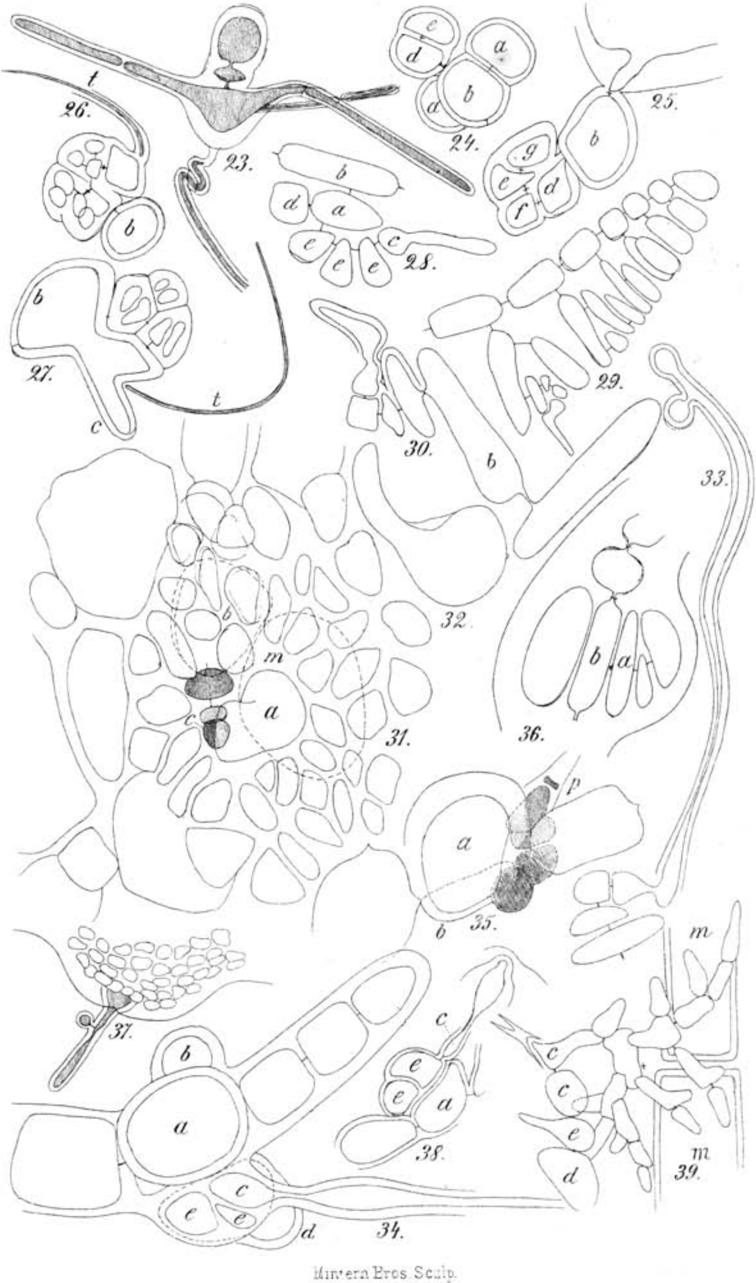
Recent botanical investigations have proved, in more and more numerous cases, that in sexual fertilization a direct union of two sexually differentiated cells takes place, the product of which, as a fertilized ovicell, becomes developed into the germ of a new plant. At the same time it appeared that the most essential point in this union of the two sexual cells was the union of the nucleus of the male cell, which sometimes constitutes almost the entire mass of this male cell, with the nucleus of the female cell, in precisely the same way as also occurs in the fertilizing processes of animals†. Nevertheless several processes of fertilization not satisfactorily explained have hitherto stood in the way of a generalization of these

* Translated by W. S. Dallas, F.L.S., from the 'Sitzungsberichte der kön. pr. Akademie der Wissenschaften zu Berlin,' 1883, p. 215.

† See also Strasburger, "Ueber den Befruchtungsvorgang," Sitzungsb. niederrhein. Gesellsch. für Nat.- und Heilkunde zu Bonn, 4th December, 1882.



Mintern Bros Sculp.



Mintern Bros. Sculp.

results. The Florideæ, especially, in which the union of the two sexual cells usually has as its consequence the further development of a third more or less distinct cell, present great difficulties to a general theory of sexuality.

My own observations upon the development of the Squamarieæ* had led me to the discovery of peculiar processes in the formation of the fruit in that group of Florideæ, which joined on to the previous observations of Thuret and Bornet on the fructification of *Dudresnaya* and *Polyides*. This induced me to extend my investigations further, and to attempt the general solution of the question of the mode of sexual fertilization and fructification in the Florideæ. The solution of this problem was rendered remarkably difficult by the circumstance that in my dwelling-place (situated far inland) the procuring of the requisite material for investigation was attended with the greatest difficulty. Hence I feel it to be my duty to offer my special thanks to the Royal Academy of Sciences in Berlin, for having enabled me to make a long sojourn on the sea-coast in the autumn of 1881. And I also express my most grateful thanks to Dr. Bornet of Paris for his liberal and always ready assistance with material for investigation.

This difficulty of procuring suitable material for examination, in order to complete and conclude the studies that I had commenced, may also justify me in bringing together in what follows† the results obtained, as a report upon my investigations up to this time, without at present going much into detail. I propose still further to continue this investigation of the Florideæ, and, if possible, to complete it by the examination of all the types of the European seas.

I.

The thallus of the Florideæ is generally composed of branched cellular filaments. These individual branched cellular filaments are sometimes free (*Chantransia*, *Callithamnion*), sometimes held together by a more or less dense jelly (*Batrachospermum*, *Crouania*, *Nemalion*), sometimes so firmly and closely involved by a very dense and tenacious intercellular substance as to represent a parenchymatous cellular

* Sitzungsb. niederrhein. Gesellsch. für Nat.- und Heilkunde zu Bonn, 4th August, 1879, pp. 376, 377.

† The numerous statements in literature which are opposed to various individual points in the following statement cannot here be entered upon in detail. This must remain for a future special elaboration of the different groups of the Florideæ.

body*. Sometimes in this case the main branch of a system of ramification projects particularly in the midst of its numerous lateral branches (*Batrachospermum*); sometimes, by rapid growth of the lateral branches which arrange themselves beside it in equal development and strength, it becomes concealed and unrecognizable.

The individual filaments increase in length by apical growth with acropetally advancing division of the terminal cell, which sometimes exceeds the rest in size, and is then easily distinguished as the apical cell, and sometimes does not differ from the other cells. Hence the individual branches of the thallus are sometimes seen to be provided with a distinct apical cell at the apex of the main branch of the whole system of ramifications, and sometimes, if neither the main shoot of the system of ramifications nor the terminal cells of the individual branches stand out distinctly, they grow in length apparently with an apical surface, while in all cases the same mode of apical growth takes place.

The apical growth of the cellular filament is generally followed by a frequently *very* abundant intercalary growth by extension of the individual cells. In this case, however, no (orthogonal or oblique) transverse division of the individual joint-cells ever takes place, any more than a longitudinal division, with a divisional wall occupying the organic longitudinal axis of the cell†. The only divisions which break

* From this dissimilar structure of the thallus the differences in habit of the different forms of thallus appear much greater than the differences of the general mode of growth really are. These essentially consist in a different behaviour of the older lamellæ of the mother-cell membranes. Thus if these older lamellæ of the mother-cell membranes are perforated locally during the outgrowth of a branch-cell, the branch-cell grows into a free filamentous branch. On the other hand, if these lamellæ are only stretched and lifted up by the growing branch-cell, the branch-cell remains united with the neighbouring cells in a more or less closely packed so-called parenchymatous cell-union, and held together by a common external membrane. If these common cell-membranes then swell up gelatinously the thallus assumes the form of a system of branched cellular filaments, which are enclosed and enveloped by a more or less dense jelly.

This heterogeneous development of the thallus consequently never precludes a near relationship of two Floridean genera, however different they may be in habit at the first glance.

For the same reason, however, a near relationship of two genera cannot any more be excluded because the spore-forming mass of tissue, the so-called nucleus of the cystocarp, forms, in the one case, a closed cellular body, and in the other a branching tuft of filaments (compare, for example, *Helminthora* and *Nemalion*, *Callithamnion* and *Seirospora*, *Cruoria* and *Cruoriopsis*, *Chylocladia* and *Lomentaria*, &c.).

† For the establishment of this fact, in many cases, very wearisome and troublesome investigations are necessary, so that it may easily be

up the individual filament cells, rather cut portions of the margins off*, which then become developed into longer or shorter lateral branches.

These marginal cells are formed on the individual joint-cells, sometimes singly, sometimes in plurality, sometimes simultaneously, sometimes one after the other, and, according to their number and their earlier or later development, they produce a very heterogeneous habit of the cell-division and of the ramification of the individual filaments. A very widely spread mode is that at the upper end of a newly produced joint-cell a branch-cell is at once separated off which extends itself by the side of the terminal cell of the filament almost as rapidly and strongly as the latter itself, and thus readily produces the appearance of a regular dichotomous branching; in what follows this mode of ramification is characterized as *subdichotomous* as by Bornet.

At each division of a Floridean cell a peculiar pit is formed in the organic central point of the dissepiment formed; this maintains the two sister cells in communication so long as they remain alive†.

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overlooked. In literature therefore there are many contradictory statements (by Nägeli, Kny, Reinke, &c.). In all cases, however, that I have hitherto been able to investigate I have been unable to confirm these statements; and now, after very numerous investigations, I believe I am justified in establishing the above propositions as generally applicable to the Florideæ. Should exceptions really occur here and there, they certainly take place extremely seldom.

* Upon the circumstance that in the Florideæ a joint-cell is *never* divided by a transverse wall, or by an (organically) median longitudinal wall, but that rather lateral marginal cells only are cut off from such joint-cells, depends also the fact that the cellular tissue of the Floridean thallus is *always* to be referred back to a system of branched cellular filaments, even when the thallus is solid and the individual cells are held together without gaps. Every cell-body constructed under this condition must show the same behaviour; and it is due only to the cessation of this condition that the roots, stems, leaves, &c. of the Archegoniata and Phanerogamia also cannot be referred back to a system of simple branched cell-filaments.

The Ascomycetes, however, show an exactly similar behaviour to the Florideæ; in the great majority of them a transverse division of the individual joint-cells of vegetative cell-filaments takes place but rarely. In consequence of this the construction of the thallus out of branched cell-filaments usually appears just as distinctly in these Ascomycetes also as in the Florideæ; and the occasional occurrence of parenchymatous cell-bodies (*e. g.* in the foundation of the perithecia of *Pleospora herbarum* [*cf.* Bauke in the 'Botanische Zeitung,' 1877, pp. 315 *et seqq.*]) is probably due, just as in the Florideæ, only to a close firm conglobation of the very short-jointed branched cell-filaments.

† Such a pit consequently occurs both in the lower and in the upper septum of each joint-cell. Between the two pits of these two transverse

In any subsequent division of the cell, by which, as already mentioned, marginal cells alone are always separated, this pit never occurs in any such marginal cell, but is always preserved in the joint-cell itself. The same thing is repeated at each cutting off of a marginal cell, so that from the number and distribution of these pits, even in the quite unequally extended cells of full-grown branches of the thallus, the genetic connexion of the individual cells with the whole of their neighbour-cells may be recognized, at all events so long as the occurrence of secondary pits does not produce difficulties. Such secondary pits, however, frequently occur, especially in species with a small-celled thallus, developed in such a manner that the individual thallus-cells are placed in connexion with all the neighbouring cells by *subsequent* development of one or more pits in the separating septa, indifferently whether they are or are not separated by these septa from sister-cells. Nay, even the cells of the secondary rhizoidiform medullary-filaments of the thicker Floridean stems are sometimes brought into close connexion with individual cells of the tissue through which they grow, by such secondary pits.

These pits (which are generally circular) are closed by extremely thin membranous lamellæ. But on each side of these closing membranes there always lies a thick lamina of a very dense substance (very easily and intensely coloured* by hæmatoxyline and analogous staining materials), and this so closely and firmly that it can rarely be separated, and only by swelling up of the closing membrane†. The two plates are

walls runs the organic longitudinal axis of the joint-cell. As already stated, no transverse division nor any (organically) median longitudinal division ever occurs in a joint-cell, and consequently no dissepiment is ever formed in the joint-cells which either cuts their organic longitudinal axis or includes it; hence it follows that the joint-cell must *always* retain the two original pits in the two end-surfaces, as indeed is the case.

* With regard to this behaviour with colouring agents the substance of these closing plates of the pits shows a very close analogy with the so-called mucilage of the sieve-tubes, which, however, I think, on the ground of repeated investigations (on Cucurbitaceæ), must be regarded quite otherwise than is now commonly the case.

Thus, while this mucilage is generally regarded as lifeless, and supposed to travel in the sieve-tubes from cell to cell, I am quite unable to find in the facts any support for such a migration of the mucilage. In my judgment this "mucilage" rather remains in a *definite* form (which, however, is exceedingly easily destroyed in preparation) in the individual cells in which it was produced. In the more complicated cases (*e. g.* in the Cucurbitaceæ) the formed mucilage-masses (closing plates of the sieve-plates and uniting hollow cylindrical cords) of the individual joints of the sieve-tubes (cells) all remain in connexion with each other, and thus form in the plant a connected system of peculiar cords.

† I succeeded in effecting this in a very instructive manner in speci-

directly connected by numerous cords, which principally (sometimes apparently exclusively) perforate the closing membrane at the periphery of the pit, and here often coalesce laterally into hollow cylindrical bands*.

On the other hand, however, these plates are directly and firmly coherent with the parietal protoplasm of the cell, and apparently form only the completion of the parietal protoplasmic sac † along the surfaces of the pits; in reality, however, they are probably, at least towards the lumen of the cell, coated with a very thin layer of protoplasm. In dead material, the cell-walls of which usually swell up more or less in a gelatinous form, the pairs of laminæ remain united, and in accordance with this we see the contracted plasma-body of all the individual cells more or less drawn out into cord-like processes towards the neighbouring cells, connected together by means of these pairs of laminæ.

Thus by means of the cords which traverse the closing membranes of the pits and unite the two laminæ of the different pairs, a direct connexion of the neighbouring cells with one another is established, and thereby a direct union of all the cells of the thallus is attained ‡, enabling these thallus-cells, notwithstanding their extraordinarily great number, by unitary cooperation to form a single whole, a single individual plant §.

mens of *Griffithsia Schousbœi*, J. Ag., and *Pterothamnion plumula*, Näg., which had been hardened with picric acid.

* How far analogous closing-plates also belong to the pits of other Algæ (Fucaceæ, Dictyotaceæ, Volvocaceæ, &c.) can only be decided by further investigation. The fact that, on the contraction of the plasma, plasma-cords remain pretty regularly attached to these pits, leads one to expect similar conditions in the structure of these pits. But the small size of most of these structures greatly increases the difficulty of deciding the question with certainty.

† Whether these laminæ are produced by local differentiation (chemical transformation) of the parietal protoplasm, may for the present remain an open question. I regard this, however, as not improbable.

‡ The direct connexion of all the cells of the thallus by means of these pits has already been indicated by Bornet ('Etudes Phycologiques,' p. 100), who, however, regards these pits as perfectly open canals. He even endeavoured, through this direct connexion of all the thallus-cells, to explain how, from the fecundated female cell, the fertilizing influence propagates itself to that cell which grows into the spore-fruit.

§ In my opinion these connecting cords between the two closing plates of the pit serve essentially for the transference of dynamic influences from cell to cell; the corresponding pores of the cell-membrane, however, at the same time render possible a readier exchange of dissolved substances between the two neighbouring cells. A migration of protoplasm itself from one cell to another by means of these open communications I regard as inadmissible.

Various facts indeed seem to me to favour our regarding the two

An open communication, so that an interchange of formed protoplasmic portions, cell-nuclei, or chromatophores could take place between the two neighbouring thallus-cells, is, however, not established by these pits. Such an open communication is indeed formed only in a few cases (Corallineæ*) by the development of large open pores which are produced subsequently in the common dissepiment of neighbouring thallus-cells, analogous to the widely diffused H-shaped connexions of the hyphæ of Ascomycetes and Basidiomycetes.

II.

On this thallus the sexual cells originate by the differentiation of certain terminal cells of the entire system of branched cell-filaments.

The *male cells* are usually formed in great numbers together. Close to the generally small terminal cell of a shorter or longer branch-filament (one or) several small branch-cells are formed by the uppermost joint-cells, and these, like the terminal cell itself, become developed into male cells. The same thing is repeated in the second and often in the third joint-cell (sometimes also in the following joint-cells), or short, one- or more-celled lateral branchlets issue from these joint-cells, the terminal cells of which, as well as the branch-cells of the superior joint-cells, become converted into male cells. Hence the male cells are placed several together at the apex of the uppermost cell and at the upper end of the next following joint-cells of a simple or ramified branch-filament. Such branches are distributed sometimes singly, sometimes united in groups on the thallus of the different species of Florideæ, and thus form so-called *antheridia* of very multifariously variable structure.

Such antheridia sometimes present the form of separate larger or smaller tufts of filaments (*Callithamnion*, *Scinaia*, &c.); but generally a greater or less number of such tufts

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closing plates of the pits as those organs of the individual cells which receive and use up the stimuli transmitted from neighbouring cells. And likewise, for various reasons, I would regard it as not impossible that the above-mentioned "mucilaginous masses" of the sieve-tubes (which, in my opinion, agree in substance with the closing plates) possess a function perfectly analogous to that of these closing plates and their connecting cords, namely, essentially the using up and conduction of dynamic influences, so that Hanstein's idea ('Protoplasma,' p. 172), that possibly the sieve-tubes of plants are comparable to the nerves of animals, would be confirmed.

* See Schmitz in 'Sitzungsb. niederrh. Gesellsch. für Natur- und Heilkunde,' 1880, p. 122.

are collected into groups covering larger or smaller portions of the surface of the thallus (*Nitophyllum*, *Peyssonelia*, *Polyides*, *Ceramium*, &c.). Sometimes these groups are immersed and line depressions of the surface of the thallus, or these depressions may even be converted into pitcher-like receptacles, which, in their development, present the greatest resemblance to the spermogonia of the Lichens and Ascidiomycetes (*Gracilaria*, *Galaxaura*, and many Corallineæ). In all cases, however, the male cells originate exclusively (I have never observed an exception) from the terminal cells of longer or shorter branches of the thallus-filaments, never from their joint-cells*.

In all exactly investigated cases the individual male cell appeared colourless from its first origin onwards; formed chromatophores were never to be recognized in it. On the other hand, a pretty large nucleus was everywhere to be detected in the protoplasm, which usually contained some small shining granules. At the complete maturity of the male cell its membrane ruptures at the apex and the plasma-body issues forth as a solid spherical or elongated body, which is sometimes drawn out into a tail-like point at the inferior extremity (*Cruoria purpurea*, *Corallina*, *Amphiroa*). In the interior of this escaped *spermatium*, however, a tolerably dense protoplasm with some small shining granules always encloses a pretty large cell-nucleus, which is sometimes central, sometimes rather excentrically placed.

The development and emission of the individual spermatia of an antheridium takes place gradually. Very frequently, however, after the evacuation of a spermatium-mother-cell, its supporting cell grows through it and develops, within the empty envelope of the spermatium-mother-cell, a new male cell (*Batrachospermum*, *Chantransia*), until the contained masses of the supporting cell are used up.

The individual escaped spermatia represent small membraneless cells, which, according to the prevailing opinion, are destitute of any spontaneous mobility. My own observa-

* Some few contradictory statements in literature (on the formation of the spermatia of *Melobesia deformans*, in Solm's 'Corallinenalgen des Golfes von Neapel,' p. 53, and of *Hildenbrandtia rivularis*, in Borzi 'Rivista Scientifica,' i. no. 1, Messina, 15 May, 1880) I must leave out of consideration for the present, as I have not myself been able to investigate the cases referred to. But as I have found the above-given rule confirmed in all carefully investigated Florideæ, even when the first glance at the antheridia gave one the impression of a quite different mode of development, I must regard it as not improbable that on more exact investigation the above-mentioned exceptional cases may also be referred to the same rule.

tions have also hitherto failed in detecting, *with certainty*, in these cells either any locomotive organs, or, indeed, a striking spontaneous mobility of any kind. But one series of observations* leads me to think that the prevalent supposition, according to which the spermatia only reach the female cells passively by the movement of the surrounding water, by no means entirely exhausts the facts; and I would therefore prefer, for my own part, to leave the question of the mobility of the isolated spermatia still undecided.

III.

The female sexual cells of the Florideæ originate without exception from the terminal cells of longer or shorter lateral branches of the whole system of ramification of the filaments of the thallus. These branches are frequently formed only as secondary lateral branches after the formation of all the other ramifications. Sometimes they are confined to a very small number of cells (two or three, rarely one), sometimes they attain a greater length; and while sometimes they do not differ in structure from the other neighbouring sterile branches, in most cases they may easily be distinguished by their form†, the size of their cells, or the different branching of their joint-cells. In all cases, however, their terminal cell finally be-

* For example, when observing living spermatia of *Polysiphonia elongata*, Grev. (at Heligoland), I quite distinctly saw a single spermatium travel slowly through the field of the microscope, while the other spermatia lay quite still.

Several times I also saw spermatia of the same *Polysiphonia* attached in such a manner that the globular spermatium stood off from the supporting surface about twice the length of the diameter of its body, although still firmly adhering to it, as it accompanied all (even the smallest) movements of the supporting body with pendulum-like oscillations. It was natural to see in the filamentous connecting cord which, from what has been said, it must be assumed attached the spermatium to the supporting body, the cilium of the spermatium which has hitherto been sought in vain. But, unfortunately, notwithstanding all my endeavours, I was unable *clearly* to detect this supposed cilium, often as I thought I could discern it.

A further indication of spontaneous mobility in the spermatia of the Florideæ is to be found in the fact that in *Batrachospermum* the spermatia must penetrate through the gelatinous envelope of the branches of the thallus in order to reach the apex of the completely immersed carpogonia. They can hardly be capable of such penetration without some proper (perhaps amœboid ?) mobility.

† These branches appear to be particularly noteworthy on account of their similarity to the "procarpia" of the Collemaceæ, as in *Batrachospermum Julianum*, Arcangeli, according to the description of Arcangeli (Nuov. Giorn. Bot. Ital. xiv. 1882, pp. 160 *et seqq.* tav. v. figs. 1–8), in which species the female cell occupies the apex of a short-jointed spirally-contorted branch.

comes converted into the female sexual cell by allowing a diverticulum to issue from its apex, which elongates into a longer or shorter hair-like or clavate process, the *trichogyne*, which has sometimes one or more spiral contortions (figs. 17, 23) or is bulbously dilated (fig. 33) at the base. This female cell may be here described as the *carpogonium* * (by analogy with the oogonium of the Chlorophyceæ).

At the period of fertilizable maturity the carpogonium contains, in its usually ovate ventral portion, a very abundant protoplasm with a large distinct cell-nucleus. Sometimes also well-developed more or less intensely coloured chromatophores are contained in this protoplasm (*Nemalion*, *Helminthocladia*, *Batrachospermum*); but in other cases the protoplasm of the carpogonium is perfectly hyaline. The trichogyne into which this bellied part of the carpogonium is continued by means of a short neck-like constriction, is filled with colourless protoplasm, which is usually free from vacuoles in the apex itself, but pervaded by more or less numerous vacuoles in other parts, and also contains some larger or smaller shining granules of variable number and distribution (fig. 8), which behave towards staining agents like the chromatine granules of the cell-nucleus.

At this time the cells of the *carpogonial branch* (*i. e.* of that branch the apical cell of which becomes converted into the carpogonium) present a very different development in the different genera and species. In many instances (*Batrachospermum*, *Lemanea* sp., *Naccaria*, *Chondria*, &c.) they are furnished with more or less numerous lateral branches, while in other cases they are unbranched. Sometimes the whole of these cells are somewhat enlarged, and filled with more or less numerous plasma-masses; in other cases only certain joint-cells of the carpogonial branch are enlarged and abundantly furnished with contents (*Calosiphonia*); but the uppermost of these joint-cells, the hypogynal cell, is particularly often distinguished from the other cells by its stronger development (*Glœosiphonia*, figs. 8–10, *Scinaia*, &c.).

These fertilizably mature carpogonia then in most cases extend the apex of their trichogyne beyond the surface of the thallus and into the surrounding water. In certain cases,

* The terminology of the organs of fructification of the Florideæ is at present rather uncertain. The expressions "carpogonium," "procarpium," "carpogenous cell," "trichogyne," "trichophore," "fructifying tube," &c. are used by different authors in very different ways. I have therefore found myself for my present purpose compelled to settle this terminology, which, moreover, frequently was not suited to modern conceptions, quite independently, although still, as far as possible, employing previously established terms.

however, the apex of the trichogyne remains concealed in the interior of the thallus, that is to say, enclosed within its gelatinous envelope (*Batrachospermum*). But in both cases the isolated spermatia (by spontaneous movement?) reach the apex of the trichogyne and attach themselves to it, at the same time (hardly previously) surrounding themselves with a membrane. Then the membrane of the spermatium and apex of the trichogyne is resorbed at the point of adhesion, and through this opening the two masses of contents are placed freely in connexion. In this way the plasma-bodies of the carpogonium and spermatium unite to form a single coherent cell, which at first still contains two different cell-nuclei.

In the next developmental stage the cell-nucleus of the spermatium has disappeared from its previous place and is nowhere to be discovered in the interior of the conjugation-cell, but in the bellied part of the carpogonium there is, as before, a single cell-nucleus. A fusion of the two original cell-nuclei to form this latter cell-nucleus could nowhere be directly perceived. Nevertheless, from the analogy of other cases, it may with the greatest probability be assumed that the cell-nucleus of the spermatium travels through the trichogyne into the bellied part of the carpogonium, and here amalgamates with the cell-nucleus of the carpogonium.

The cell-wall then thickens in the neck of the trichogyne and narrows the central opening more and more until finally this is completely closed in the middle (figs. 1, 2–4, 6, 7, 10, 16, 23, 35). In this way the connexion between the bellied part of the carpogonium and the trichogyne with the spermatium is interrupted by means of a more or less thick membranous plug, and the whole conjugation-cell divided into two independent cells.

These two division-cells, however, are of quite different value, inasmuch as only the lower cell possesses a cell-nucleus and now commences a rapid further development; the upper one, on the contrary, is quite destitute of a formed cell-nucleus, and remains inactive until its earlier or later disappearance. The former represents the fecundated female cell, the *fertilized ovicell*; the latter, on the contrary, forms a useless part of the conjugation-product of the two sexual cells, which is now divided off and thrown aside, while the fertilized ovicell prepares for further development.

In the interior of the separated trichogyne-cell there are frequently, varying in number and form, larger or smaller granules which behave towards colouring-agents like the chromatine corpuscles of cell-nuclei, but never belonged to formed cell-nuclei (fig. 1). I have not been able to ascertain whether these granules, which are already present within the trichogyne in the fertilizably mature carpogonium, are given off by the cell-nucleus of the carpogonium; but it seems not improbable that they really originate from the chromatine corpuscles of that cell-nucleus. The described process of fecundation would then have to be explained as follows:—that in the female cell, the carpogonium, the separation of the directive body (*i. e.* a portion of protoplasm with the separated useless portions of the cell-nucleus) does not take place until after the union of the male cell with the female cell, and the fusion of the male cell-nucleus with the nucleus of the female cell. I have no hesitation * in fact about interpreting the processes described in this manner †.

Fecundation is effected in the manner just described in all the Florideæ hitherto exactly investigated by me, however different the form of the trichogyne may be in the individual cases. Everywhere this trichogyne, after fecundation had taken place, was divided off as a non-nucleated cell from the fecundated ovicell by the closure of the short neck of the trichogyne, and abandoned to destruction. The fecundated ovicell, however, then immediately commenced a very active new growth.

IV.

In this recommencing growth the fertilized ovicell by no means separates from its previous tissue-connexions (as in the oogonia of the green Algæ or the archegonia of the Archegoniata), but rather remains afterwards as before in unaltered connexion with the neighbouring hypogynous cell and retains the old cell-membrane of the carpogonium as its own cell-membrane, extending and strengthening it as required. Nay,

* In most instances, certainly, in plants (as in animals), the directive corpuscle is separated before the fecundation of the female cell (see Strasburger, 'Befruchtung und Zelltheilung,' pp. 79, 80), as, for example, among the Algæ in *Œdogonium*, *Coleochæte*, and *Vaucheria* (in the last-named alga the directive corpuscle contains numerous small fragments of nucleus which have been separated off from the numerous cell-nuclei of the young oogonium). But an expulsion of the directive corpuscle only *after* fecundation has taken place cannot be regarded as at all inconceivable if we consider that in the expulsion of the directive body only an evidently useless part of the cell-nucleus with some protoplasm is separated and thrown off from the female cell, but that such a rejection of the separated part of the cell-nucleus may just as well take place before as after the conjugation of the two sexual cells.

† The portion of the female cell destined to be expelled as a directive body was consequently employed before its separation as an extended trichogyne to intercept the spermatium, and thus to facilitate the access of the male cell-nucleus to the nucleus of the female cell.

even the pit which united the carpogonium-cell with the hypogynous cell also continues its function, and places the fertilized ovicell in direct connexion with the hypogynous cell, and through this with the general cellular tissue of the parent plant. Hence the requisite nutritive materials can be transmitted to the growing ovicell in the simplest and most convenient manner. Nay, this connexion of the fertilized ovicell with the tissue of the thallus of the parent plant is so complete, that this fertilized ovicell easily produces exactly the impression of an ordinary thallus-cell, from which, in fact, it can sometimes be distinguished almost solely by its perfectly peculiar further development (*Chantransia corymbifera*, Thur., figs. 2, 3, 4).

This further development of the ovicell is, however, very different in the individual cases.

1. *Helminthocladieæ.*

In the simplest case the ovicell pushes forth one after the other numerous offshoots, *ooblastemas* as they may here be called (fig. 1), which grow into short-jointed cell-filaments of greater or less length, and abundantly subdichotomously branched. The number of these ooblastema-filaments is, however, very variable; sometimes they are produced in great numbers on the whole periphery of the ovicell except the basal surface and the vertex (*Batrachospermum*); sometimes their development on the ovicell is only one-sided (*Chantransia*, figs. 2–4, *Scinaia*, fig. 7); sometimes the ramifications of these ooblastema-filaments are perfectly free (*Batrachospermum*, *Chantransia*, *Helminthocladia*, *Nemalion*, *Scinaia*), and sometimes they are united by a common gelatinous envelope into a nearly globular closed cell-body (*Helminthora*, according to Bornet *). Sometimes also the fertilized ovicell first of all arches upwards and cuts off a large upper daughter-cell, and the ooblastema-filaments then push forth from the whole free surface of this daughter-cell (*Nemalion multifidum*).

In the genus *Lemanea* several ooblastema-filaments grow forth from the fertilized ovicell at the apex of a carpogonial branch, which may be unramified (*L. fluviatilis* and *ciliata*, according to Sirodot's figures †) or furnished with short lateral branches (*L. torulosa*, and, according to Sirodot's figures, also *L. catenata* and *parvula* ‡), and these filaments growing ob-

* Thuret-Bornet, 'Etudes phycologiques,' p. 64.
† Ann. des Sci. Nat. sér. 5, tome xvi. pl. iii.
‡ *Ibid.* pls. iv. and v.

liquely downwards extend into the cavity of the tubular thallus, and here become abundantly ramified.

In all these cases, however, by ramification of the ooblastema-filaments a more or less abundantly and closely compressed tuft of threads is formed, and this sometimes remains naked (*Chantransia, Lemanea*), but in most cases is furnished with a more or less dense envelope of cell-filaments proceeding from the carpogonial branch or the neighbouring filaments of the thallus (*Batrachospermum, Nemalion, Helminthocladia*), which sometimes even close together to form a solid fruit-wall (*Scinaia*). Sometimes also certain of these sterile envelope-filaments grow through the ramification of the fertile tuft of filaments, and become interwoven, as sterile paraphyses, among the branched ooblastema-filaments (*Batrachospermum*).

In certain cases (*Batrachospermum, Chantransia, Nemalion, Helminthocladia*) these ooblastema-filaments finally develop single carpospores from the terminal cells of their ramifications. These terminal cells swell up and become filled with an abundance of contents. At last the membrane at the apex of the cell bursts, and the whole plasma-body escapes as a single naked spore. These spores are successively evacuated from the different terminal cells of the same tuft of filaments; but after the evacuation of the individual terminal cell its supporting cell grows through it and produces within the evacuated membrane a new spore-forming terminal cell, until finally all the nutritive substances of the whole tuft of filaments are used up. In other cases, besides the terminal cells of the ramifications of the tuft of ooblastema-filaments, the upper joint-cells also develop single carpospores in greater or less number, so that these become developed into longer or shorter, simple or branched chains (*Scinaia, Lemanea*).

In all these instances, however, the developed fruit, the *cystocarp*, constitutes a more or less richly branched tuft of filaments, sometimes naked, sometimes covered with enveloping filaments, sometimes surrounded by a closed fruit-wall, and either immersed in the thallus or attached externally.

2. *Gelidieæ.*

In the cases hitherto referred to, the spore-forming ooblastema-filaments are nourished during their development from the thallus-tissue of the parent plant by the intermediation of the ovicell, which remains persistent (usually as the central cell of the whole tuft of filaments). This, however, is no longer the case in a group of genera which come nearest to these.

In these forms the fertilized ovicell usually develops only a single ooblastema-filament (*Caulacanthus*, fig. 39, *Pterocladia*), which, ramifying abundantly, turns towards the middle of the branch of the thallus to which it belongs, and with its ramifications clings round the central cord of cells, the so-called *central axis* of the branch, which at this part is frequently (*Pterocladia*, *Wrangelia pectinata*, Ag.) enveloped by a special small-celled tissue with abundant contents. Through the cell-masses of this tissue the ramifications of the ooblastema-filament twist about and frequently attach themselves firmly to individual very full cells of this tissue (*Pterocladia*), or, when it is deficient, to the cells of the central cord itself (*Caulacanthus*, fig. 39), here and there also entering into direct connexion with them by the development of pits (*Wrangelia*). Being abundantly nourished through the agency of this tissue, the branches of the ooblastema-filament then ramify very considerably, and develop from each of the clavate and erected terminal branch-cells either a single spore (*Caulacanthus*) or short chains of two (or more) spores, in the same way as in the Helminthocladieæ already described.

Thus by the abundant ramification of the ooblostema-filament there is produced a tuft of spore-forming filaments, which spread out in the interior of the branch of the thallus, and give rise to a local enlargement of it. This enlargement increases more and more until the maturity of the spores, and becomes constantly more and more distinctly marked off from the remaining sterile part of the thallus-branch. This dilated part then finally constitutes the fruit, the *cystocarp*, of these Floridean genera, the peripheral tissue of the thallus becoming developed into the fruit-wall, in which an aperture of egress is produced by local separation of the cells, while in the interior the mass of the spores is produced around the central cell-cord from the ramifications of the ooblastema-filament.

In some of these forms (*Naccaria Wigghii*, Endl., and *hypnoïdes*, J. Ag.) a further complication of the course of development of the fruit occurs. Here the carpogonial branch in very different states of development is beset with several short lateral branchlets, and in this way forms a pluricellular complex of larger and smaller cells (figs. 24 and 26 *), generally with abundant contents. The sprouting ovicell now enters into open connexion with one or another of these neighbouring larger cells, with complete amalgamation of the two plasma-bodies (fig. 27), and only then does the ooblastema-

* See the explanation of the figures.

filament shoot forth from the conjugation-cell and become developed in the manner above described. In detail this conjugation of the growing ovicell with neighbouring cells rich in contents (*auxiliary cells*, as they may be called in the sequel) takes place in very different ways according to the species. In general, however, the only object of this borrowing from neighbouring cells rich in contents in connexion with the development of the ooblastema-filament is evidently to strengthen the latter, which originates from the very small fertilized ovicell, and enable it to develop more luxuriantly.

3. *Cryptonemieæ and Squamarieæ.*

In some of the last-mentioned forms, as stated, the cells of the creeping spore-producing filaments enter into close connexion with the cells of the central axis or of its enveloping tissue by the formation of pits, evidently for the facilitation of nutrition. This goes still further in a series of other forms which follow these most closely (*Dudresnaya*, *Polyides*, *Dumontia*, *Calosiphonia*, *Glœosiphonia* *, *Petrocelis*, *Cruriopsis*, and other Squamarieæ).

In these one or several ooblastema-filaments shoot forth from the fertilized ovicell, and these either become immediately diffused in the surrounding thallus-tissue (*Dumontia*, *Glœosiphonia*, fig. 10, *Calosiphonia*, fig. 23), or first of all become connected by pit-formation with neighbouring auxiliary cells (generally cells of the carpogonial branch itself), and then grow further (*Petrocelis Ruprechti*, Hauck), or, lastly, enter into a conjugation with these auxiliary cells, when the ooblastema-threads issue from the conjugation-cell singly or in plurality (*Dudresnaya*, fig. 17, *Polyides*). In all cases, however, the ooblastema-threads, branching abundantly, creep about as thin long-jointed cell-filaments in the interior of the thallus-tissue.

While thus creeping about the apices of these cell-filaments attach themselves to certain cells rich in contents, which are developed in greater or less number in the vicinity of the carpogonial branches within the branch of the thallus. Sometimes these cells are simple joint-cells of the ordinary sterile branches of the thallus-filaments, scarcely distinguished by their size from the other cells of the filament (*Calosiphonia*);

* Berthold has also observed processes similar to those occurring in the above-mentioned genera in other Cryptonemiaceæ (species of *Halymenia*, *Nemastoma*, and *Grateloupia*), but has hitherto published no detailed account of them (see Falkenberg, in Schenk's 'Handbuch der Botanik,' Bd. ii. p. 184). My own attention was called by Berthold to the occurrence of such processes in *Calosiphonia*.

in other cases these cells are easily distinguished by their remarkable size (*Petrocelis*, *Polyides*); in other cases, again, they become developed into peculiarly-formed thallus-filaments, and are thus easy to detect in the midst of the sterile tissue (*Dudresnaya*, figs. 18, 20, *Dumontia*). To these cells, which from their subsequent behaviour are also to be called auxiliary cells, the ooblastema-threads attach and unite themselves.

Sometimes (*Petrocelis Ruprechti*, Hauck) the apex of the ooblastema-thread grows directly to the auxiliary cell and attaches itself firmly thereto. By resorption of the separating membranes the apical cell itself enters into a conjugation with the auxiliary cell. In the majority of cases, however, the apex of the ooblastema-thread grows close by the auxiliary cell, not unfrequently clinging to it (fig. 18), and then separates as a growing terminal cell (fig. 20). But the newly formed joint-cell, which is now applied more or less closely to the auxiliary cell, enters into open connexion therewith by the development of a shorter or longer conjugation-process. In both cases, after the resorption of the separating membranes, the plasma-bodies of the auxiliary cell and the ooblastema-cell unite to form a single cell-body.

The further development of this conjugation-cell is, however, very different in the various individual cases. In many instances (*Polyides*, *Petrocelis*, *Dudresnaya*) the amalgamation of the two conjugating cells is limited to the union of the two protoplasm-bodies into a single cell-body, while the cell-nuclei of the two conjugating cells remain separated, and are still to be found within the two halves of the conjugation-cell. In these cases a process issues laterally from that half of the conjugation-cell which represents the ooblastema-cell, and its apex becomes segmented off as a separate cell (fig. 19), and then, by further growth, gives origin to a distinct spore-complex *. Lastly, in other cases (*Glœosiphonia*) the two conjugating cells fuse together completely, and from the ooblastema-cell the whole of the protoplasm, with the cell-nucleus, gradually passes over into the auxiliary cell until only the external membrane remains (figs. 11, 12). Then the auxiliary cell becomes separated off as an independent

* In *Dudresnaya coccinea*, Crouan, the terminal cell of this process does not grow into a spore-complex (as in *D. purpurifera*, J. Ag.), but it develops into a long-jointed cell-filament, which, as a side-branch of the ooblastema-thread, diffuses itself in the surrounding tissue. But besides this process of the former ooblastema-cell (one or) two spore-processes issue from the same cell (fig. 21), which apply themselves laterally to the former auxiliary cell, grow and close around it, and then produce a single, sometimes indistinctly bilobed spore-complex.

cell from the emptied ooblastema-cell and shoots forth laterally (fig. 13). This outgrowth, however, becomes separated off as an independent cell (fig. 14), and then, as the central cell, gives origin to a single spore-complex (fig. 15).

Thus, in the first case, the individual joint-cell of the ooblastema-thread (after preliminary conjugation with an auxiliary cell) produces a lateral branch-cell which leads to spore-formation, just as in the Gelidieæ, previously described, only that here this cell does not give origin to a single spore, but (just in consequence of the conjugation with an auxiliary cell) to a whole complex of spores, which appears to be individualized as a single fruit or cystocarp. Here the ooblastema-cell is evidently strengthened by the conjugation with the auxiliary cell, and rendered capable of the production of more numerous spore-mother-cells (*Polyides*, *Dudresnaya*). In the latter case, however, this calling in aid of the auxiliary cell passes into a complete amalgamation and union of the ooblastema-cell with the auxiliary cell, after which the resulting conjugation-cell becomes further developed in the same way as the ooblastema-cell assisted by the auxiliary cell in the former case.

Thus, in both cases, either a lateral offshoot becomes separated off as an individual cell and then commences a very rapid growth, or, more rarely, this rapid new growth proceeds from the conjugation-cell representing the ooblastema-cell. More or less numerous marginal cells are separated off from this outgrowing cell as the central cell of the cystocarp, and grow into short-jointed abundantly-branched cell-filaments. By this means is produced a more or less highly-developed tuft of filaments, the filaments of which either remain individually free (*Peyssonelia*, *Cruoriopsis* *), or are held together

* With regard to *Cruoriopsis* I have formerly stated (Sitzungsb. d. niederrh. Gesellsch. für Natur- und Heilkunde zu Bonn, 1879, p. 377) that after the conjugation of the "fertilization-tube" of a "procarp" without a trichogyne, the other cells of the latter become directly converted into spores. I must now correct this statement in this respect, that after the conjugation of the ooblastema-cell with an auxiliary cell (the above-mentioned cell of the trichogyneless "procarp"), the former cell sprouts as the central cell of the cystocarp, and gives origin to one or two short lateral branches of from one to three cells. These lateral branches take a direction parallel to the erect thallus-filament, so that of two lateral branches, the one regularly grows upwards and the other downwards. Both together then precisely present the aspect of a trichogyneless "procarp," with the middle cell of which the "fertilization-tube" has conjugated, just as I formerly interpreted the observed facts. After I had found the key to the processes in the fructification of the Florideæ by the comparative investigation of numerous individual forms, it became comparatively easy to fathom and establish as above the development of *Cruoriopsis*, the complete elucidation of which in detail, for a time, presented many difficulties.

as a closed cell-body by a common dense and tenacious gelatinous envelope (*Cruoria*, *Polyides*, *Dudresnaya*, *Dumontia*, *Glœosiphonia*, *Calosiphonia*). The individual sections of this tuft of filaments reach maturity sometimes simultaneously, sometimes at different times; but all the filaments of these sections develop their superior cells, or even almost the whole of their individual cells, into spores, which, in the latter case, directly envelop the central cell, which alone remains sterile (*Dumontia*), but in the former case are separated from this central cell by a more or less abundant mass of sterile cells, the so-called *placenta* of systematic authors (*Glœosiphonia*, *Dudresnaya*).

Here, then, the conjugation of an ooblastema-cell with an auxiliary cell leads finally to the development of a complex of spores, which, as an independently individualized cell-body, is sometimes surrounded with a special envelope by the surrounding thallus-tissue, sometimes enclosed in the thallus-tissue without any such envelope. Such a cell-body shows exactly the habit of a distinct independent spore-fruit, and is accordingly regarded as a distinct independent cystocarp. But, in accordance with what has been stated, the origin of such a cystocarp is quite different from that of the individual cystocarp of the Helminthocladieæ and Gelidieæ. In the latter the fertilized ovicell develops into an individual spore-fruit (cystocarp), as in the Mosses; but in the present case the ovicell grows into a branched system of offshoots, which develops numerous individual cystocarps on its branches, analogous to the numerous spore-fruits of the branched ferns.

These individual cystocarps in the Squamarieæ frequently come so near together that they can hardly be distinguished from each other as independent fruit-bodies. Thus in *Cruriopsis cruciata*, Duf., numerous cystocarpia, in the form of short chains of spores, which are generally interrupted in the middle by the sterile central cell, lie close together among the erect filaments of the thallus. In *Peyssonelia* the individual closely approximated cystocarps form tufts of branched filaments, the branches of which arrange themselves among the erect parallel filaments of the nemathecia, and develop into separate chains of spores; so that here also, at the commencement of the maturity of the spores, numerous chains of spores are lodged close to each other among the erect sterile fibres. These chains of spores consequently appear as the essential, independently individualized fruit-bodies, just as in *Cruoriopsis*, and accordingly, just as in *Cruoriopsis*, they have been described as the true cystocarps, and distinguished, under the name of *cystidia*, as a special form of cystocarpia.

4. *Corallineæ.*

In the Squamarieæ parallel thallus-fibres with carpogonial branches and auxiliary cells also often stand in great numbers close together (*Petrocelis*, *Cruoriopsis*). This is the case to a far greater degree in the Corallineæ, which moreover, in other respects, closely approach the Squamarieæ.

In these Corallineæ the formation of the fruit begins with the development of a closed stratum of long parallel thallus-fibres. The penultimate cell of these threads becomes enlarged, and develops (usually in a characteristic manner) one or several unicellular lateral branches, which place themselves beside the terminal cell. But in a larger or smaller number of these parallel cell-fibres bicellular side branches are also developed on this penultimate cell, while the terminal cell becomes developed into the carpogonium and puts forth a long trichogyne. The penultimate cells of all these parallel cell-fibres, however, become auxiliary cells.

Of the numerous carpogonial branches which are in this way placed close together only a small number attain complete development and fertilizable maturity, the majority being aborted (and this is observed in the same manner also among the Squamarieæ, *e. g.* in *Petrocelis Ruprechti*, Hauck). But on the fertilization of a perfectly developed carpogonium the fertilized ovicell enters (at least as I think I may assume, from the analogy of the other Florideæ*) into a conjugation with the nearest auxiliary cell; the conjugation-cell thus formed then puts forth several processes, which immediately conjugate with the auxiliary cells in their immediate neighbourhood; and this process of conjugation is then further continued laterally to the following auxiliary cells until a tolerably extended layer of auxiliary cells is amalgamated into a distinct large disciform conjugation-cell. At the margin of this disk several offshoots are then pushed forth; these become divided by a transverse dissepiment, and thus give origin to so many separate spore-complexes.

* This point in the development of the fruits of the Corallineæ (the exact investigation of which, as is well known, is rendered remarkably difficult by the small size of their cells) I have hitherto been unable to establish directly.

Moreover, not only in the Corallineæ, but also in many other Florideæ with small-celled, closely packed cellular tissue, there are special difficulties opposed to the exact ascertainment of the fate of the fertilized ovicell, which render these investigations *extremely* troublesome and tedious, and greatly hinder any certain decision. From this also are to be explained the numerous divergent statements which occur in literature, and which differ essentially from the present explanation precisely in this point.

In detail this process shows many and various peculiar variations in the different forms of the Corallineæ; but in general its course is that the ooblastema-fibres of the fertilized ovicell conjugate successively with several approximated auxiliary cells, until, but only after the last conjugation, a sprouting forth of the conjugation-cell is set up, which develops a complex of spores (here usually a single chain of spores). The close union of the whole of the thallus-fibres, which bear auxiliary cells and carpogonial branches, has, however, as its consequence, that the whole of the spore-complexes which originate in consequence of the above repeated conjugations are placed very close together and form a connected group, which rises as a single whole upon the thallus, and therefore is to be regarded as an individual cystocarp. But according to its development this individual cystocarp is essentially different from the individual cystocarp of the Helminthocladieæ and Gelidieæ, and rather approaches more nearly to the group of isolated cystocarps which, in the Cryptonemieæ and Squamarieæ, proceed from the ooblastema-threads of a single fertilized carpogonium.

5. *Ceramieæ, Rhodomeleæ, Sphærococceæ, Rhodymenieæ, and Gigartineæ.*

Among the Cryptonemieæ already referred to, *Glœosiphonia* presents the peculiarity that a single, short branch-filament of the thallus-tissue develops its penultimate cell into an auxiliary cell, whilst the lowest cell of this branch develops laterally a short, three-celled carpogonial branch. The carpogonium and auxiliary cell are thus in this case formed as a pair, and close together*, so that it is the simplest thing possible for the ooblastema-fibres of the fertilized carpogonium to meet with the auxiliary cell belonging to it, in order to unite with the latter. In fact, in *Glœosiphonia* the single sparingly branched ooblastema-thread usually grows directly to its auxiliary cell and conjugates with it, unless the ooblastema-thread of a neighbouring earlier fertilized carpogonium has already preoccupied it.

Such a condition must, however, be greatly facilitated when the auxiliary cell is brought still nearer, or into the close vicinity of the carpogonium. The ooblastema-thread may then be reduced to a very small length or completely suppressed, as the fertilized ovicell can enter into direct union with the contiguous auxiliary cell.

* Such groups of carpogonial branches and auxiliary cells, which arise as independent wholes upon the thallus of the parent plant, are indicated in the sequel as fruit-rudiments or *procarpia*.

This is really the case in a very great number of Florideæ, nay, I believe I may assert that in the majority of the Florideæ in general (in the numerous families of the Ceramieæ, Wrangelieæ, and Rhodomeleæ, the Chylocladieæ, Rhodymenieæ, and Sphærococceæ, and lastly, the Gigartineæ) the further development of the fertilized ovicell is effected in this manner.

A short, frequently three- or four-celled carpogonial branch is attached laterally to a thallus-fibre, and is at the same time curved in such a manner that the carpogonial cell is directly applied against the neighbouring auxiliary cell, or, at least, can conveniently reach it by means of a short lateral process. Not unfrequently, also, the direct contact of these two cells is brought about by the auxiliary cell itself extending towards and closely applying to the carpogonial cell a lateral diverticulum or conjugation-process (figs. 31, 35, 38). In other respects, however, the position of the carpogonial branch and the auxiliary cell in the tissue of the thallus may be very variable.

1. These organs are most easily observed in many Ceramieæ and Wrangelieæ.

Thus in *Pterothamnion plumula*, Näg. (fig. 35), for example, one of the terminated (*begrenzte*) lateral branches of the thallus bears, inserted at one side of its basal cell, a four-celled, short-jointed carpogonial branch, which bends its apex towards the upper surface of the branch, while, on the opposite side of this basal cell, a unicellular branch develops into the auxiliary cell, which also curves its apex towards the upper surface of the whole branch of the thallus, and thus comes into direct contact with the carpogonial cell. In other cases a shorter or longer terminated cell-filament bears near the apex on a joint-cell a short (usually three- or four-celled) carpogonial branch, while from the same joint-cell several other, one- or more-celled lateral branchlets issue (fig. 34). Sometimes this joint-cell itself becomes the auxiliary cell (*Lejolisia mediterranea*, Born., according to Bornet); in other cases one of the unicellular lateral branchlets which issue, besides the carpogonial branch, from the joint-cell develops its cell into the auxiliary cell (*Ptilothamnion pluma*, Thur., and *Spondylothamnion multifidum*, Näg., according to Bornet); or an auxiliary cell originates on each side from the unicellular lateral branchlets (*Spermothamnion*, certain species of *Callithamnion*, fig. 34). In many species of *Callithamnion* the cell-filament which bears the carpogonial branch and the two auxiliary cells on one of its joint-cells is not terminated, but grows on at the apex without alteration for a longer or shorter time (*C. corym-*

bosum, Lyngb., &c.). In *Griffithsia* the penultimate joint-cell of a terminated small-celled branch-filament bears laterally two short two-celled branchlets, the lower cell of which produces laterally a four-celled carpogonial branch, and then itself becomes developed into the auxiliary cell. In *Ceramium*, on the other hand, the joint-cell of a still-growing branch develops laterally a two-celled branch, the lower cell of which becomes the rather large auxiliary cell, but also develops laterally not only one but two four-celled carpogonial branches.

2. The arrangement of these parts in the multicellular offshoots of the Rhodomeleæ is still more complicated and difficult of recognition.

In *Polysiphonia*, as is well known, the individual joint-cell first of all develops a whorl of branch-cells, which, closing together firmly at the sides, surround the central cell with a closed rind, which, by the continued division and branching of its cells, becomes more or less thickened according to the species. Here the carpogonia are now usually formed on special, terminated, lateral offshoots. On one of the superior joint-cells of such an offshoot one of the "marginal cells," and indeed the last-formed unpaired marginal cell, grows into the four- or five-celled carpogonial branch. Its lowest cell becomes the auxiliary cell, but the small-celled apex of the branch bends upwards, so that the carpogonial cell touches the auxiliary cell with the lower angle (figs. 36, 28); while, in the simplest cases, from the auxiliary cell itself a unicellular, sterile, lateral branchlet proceeds downwards. At the same time the other "marginal cells" of the above joint-cell divide and branch repeatedly, and thus produce a small cell-body, which encloses the carpogonial branch together with the auxiliary cell, and, as it rises as a whole distinctly on the thallus, may appropriately be characterized as a *procarpium*.

In other species of *Polysiphonia* and other genera of the Rhodomeleæ this procarpium appears still more complicated, because, besides the terminal carpogonial branch, one or two lateral branchlets issue from the auxiliary cell, and these sometimes branch abundantly and give origin to a many-celled cell-complex, which in the fertilizable procarpia conceals the auxiliary cell, and may easily be interpreted (as, indeed, has hitherto been generally the case) as a "group of carpogenous cells" (*Chondria tenuissima*, Ag.). Perhaps, also, in some of these forms 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.

3. Among the Chylocladieæ the carpogonial branches in *Chylocladia kaliformis*, Hook., are usually very early formed

near the still-growing apex (fig. 29). On one of the large cells composing the wall of the tubular thallus-joints a four-celled branch is developed upon the outer side, and this curves in a characteristic fashion and develops its apical cell into the carpogonium (figs. 30, 33). But over this carpogonial cell larger covering cells curve from both sides (more rarely from one side, fig. 31), which are segmented off from the two bordering cells of the thallus-wall, and bend over in such a manner that they are applied to the carpogonium by their extended margin, the conjugation-process (fig. 32). These two cells represent the auxiliary cells, of which, however, after the fertilization of the carpogonium, only a single one, as a rule, arrives at further development.

4. As the clearest example of the structure of the female sexual organs in Sphærococceæ the genus *Nitophyllum* may here be cited. In the species of this genus (e. g. *N. venulosum*, Zan.) the formation of the sexual organs proceeds from a single cell of the originally always one-layered thallus. This separates off towards the under surface of the flat thallus several branch-cells, which further branch in various ways; but superiorly it regularly forms two branch-cells, one of which develops a short sterile pluricellular branch, while the other, besides a terminal sometimes divided cell, develops a three- or four-celled small-celled branch, the terminal cell of which becomes the carpogonium. This branch bends from its point of insertion in such a manner along the supporting cell, that its terminal cell is applied to the opposite end of the supporting cell, and then from the apex of this terminal cell the short trichogyne is extended outside through a fissure between the neighbouring cells. This supporting-cell becomes the auxiliary cell.

5. Among the Rhodymenieæ, for example in *Plocamium coccineum*, Lyngb., a short three-celled lateral branch, the terminal cell of which becomes the carpogonium, is formed supplementarily upon one of the larger cells within the locally enlarging small-celled external cortical layer (fig. 37). This short branch bends along the simultaneously enlarging supporting cell and then extends the trichogyne externally from the apex of the terminal cell through the overlying cellular tissue. This mother-cell of the carpogonial branch, however, develops at its upper end a lateral diverticulum, a conjugation-process, until it comes in contact with the carpogonial cell, and forms for its part the auxiliary cell (fig. 38).

6. Finally, of the Gigartineæ, *Gigartina Teedii*, Lmx., and *Chondrus crispus*, Stackh., likewise present, within the small-celled external cortical layer of the thallus, small secon-

dary lateral branchlets, formed upon certain cells of the vegetative cell-filament, and these curve in a characteristic manner so that their terminal cell approaches very closely with one of its corners to the supporting-cell, which at the same time also greatly increases. This terminal cell becomes the carpogonium, the trichogyne of which is much enlarged, but in a variable manner, at its base *, before it extends itself exteriorly as a thin capillary process through the small-celled cortical tissue; but the supporting-cell of the whole carpogonial branch becomes the auxiliary cell.

Different as the arrangement of the carpogonia and auxiliary cells may be in all these individual cases, the forms in question nevertheless agree in the mode of further development of these organs after the fertilization of the carpogonium has taken place.

First of all the ventral part of the carpogonium becomes segmented off as the ovicell. In the next stage of development this ovicell appears emptied of protoplasm, except a very small residue (it was but seldom that I found more abundant plasma-masses retained in the ovicell, *e. g.* in *Callithamnion plumula*, Näg.), but the closely approximated auxiliary cell appears very full of contents and at once commences a new and rapid growth.

That in this case the protoplasm (with the cell-nucleus) of the fertilized ovicell (or at least a part of this protoplasm with the cell-nucleus) migrates into the auxiliary cell can hardly be doubted, as the ovicell empties itself to a greater or less extent; but the mode of this transference I have hitherto been unable to ascertain with certainty in its details.

In *Glœosiphonia* open conjugation takes place between the ooblastema-cell and the auxiliary cell; but after the migration of the protoplasm of the former cell, the latter cell completely closes the aperture of conjugation by the new formation of a portion of membrane, so that after the conjugation has been effected scarcely any trace of it is to be detected (fig. 12). If in this case the protoplasm of the ooblastema-cell passed very rapidly over into the auxiliary cell, it would depend entirely upon chance whether one could succeed in fixing the two cells during the conjugation, and so bring the latter to demonstration; but with the slower course that the process really follows it is not very difficult to find such stages of conjugation in fixed material.

In the forms now under consideration I believe we must

* Such enlargements of the base above the neck of the trichogyne also occur among many other Florideæ with densely packed cellular tissue (see figs. 33 and 38).

assume that the process of conjugation takes place in exactly the same way as in *Glœosiphonia*, but that it is effected much more rapidly than in that genus, so that direct observation of the conjugation-stages is perfectly a matter of chance. Notwithstanding all my endeavours, however, chance has not hitherto been favourable to me in the present forms (which are also difficult of investigation in other respects). Nevertheless at present I would not doubt of the occurrence of a true conjugation of these two cells.

It is true that it is quite possible that there may be a migration of the protoplasm (with the cell-nucleus) of the ovicell into the auxiliary cell *without* complete conjugation of the two cells (as in the fertilization of the Phanerogamia *, of many Peronosporeæ [*Phytophthora*, *Peronospora*†], Erysipheæ, &c.) through the separating membranes ‡, that is fine pores (*not* micellar interstices) of these membranes. But the analogy of the nearly allied Floridean genera, which distinctly show a complete conjugation of these two cells, appears to me still too weighty to allow me to decide in favour of this latter assumption so long as we have no *certain* demonstration upon a readily accessible object of the non-occurrence of conjugation §.

After this migration of the protoplasm (that is, of the cell-nucleus) of the fertilized ovicell into the auxiliary cell, the latter commences a very rapid new growth, which leads to the development of a fruit-body. This growth, however, takes place in the above-mentioned individual groups in very different manners, and the consequence of this is the very different structure and habit of the different forms of fruits ||.

* Strasburger, 'Befruchtung und Zelltheilung,' p. 58; 'Bau und Wachsthum der Zellhäute,' p. 247; Sitzungsber. d. Ges. f. Nat.- und Heilk. zu Bonn, December 4, 1882.

† De Bary, 'Beiträge zur Morphologie und Physiologie der Pilze,' 4te Reihe, pp. 72, 73.

‡ See also Pringsheim's description of the passage of amœboidal plasma-masses through the membrane of the antheridial tube of *Achlya colorata* (Sitzungsb. Akad. Wiss. Berlin, 1882, p. 870).

§ The fact that I have myself for a long time endeavoured in vain to demonstrate such a conjugation in the easily accessible species of *Callithamnion*, *Spermothamnion*, and *Griffithsia*, would certainly seem to lend support to the notion that here there is really no conjugation of the cells in question.

|| To enter in more detail into the further development of the cystocarp in the various genera of Florideæ would lead us too far. But one of these forms of fruit needs special mention, as it has been affirmed to have a parthenogenetic origin.

Thus while in the majority of the species of *Callithamnion* the spore-complex into which the single auxiliary cell grows constitutes a dense and close tuft of filaments, a close cell-body (*favella*), this spore-complex in

It is, however, a very common phenomenon that the developing auxiliary cell first of all puts forth a rather large diverticulum, and then separates it off as an independent cell. From this cell, as the central cell of the entire fruit-body, numerous side-branches then sprout forth, which ramify more or less, and finally produce, from single or numerous cells of their whole system of ramifications, individual naked carpospores. The mother-cell of this central cell, the former auxiliary cell, however, sometimes remains undivided, sometimes develops only a few side-branches, which spread out laterally and attach the developing spore-fruit to the branch of the thallus (*Callithamnion corymbosum*, Lyngb. &c.), and sometimes branches more abundantly, and forms with its

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Callithamnion versicolor, Draparnauld (according to Bornet, 'Etudes phycologiques,' p. 70, note 4, identical with *C. seirospermum*, Harv. [=*Seirospora Griffithsiana*, Harv.], *C. stipitatum*, Näg., and *C. hormocarpum*, Holmes), forms a loosely branched tuft of filaments, exactly like the tufts of *Seirospora*, which in this species originate by metamorphosis of the apices of the branches. These "seirosporiform favellæ," according to Falkenberg ("Meeresalgen des Golfes von Neapel," in Mitth. der Zool. Station zu Neapel, i. p. 253), originate by parthenogenetic development of the auxiliary cells, the carpogonia being either early aborted or not developed at all, while the auxiliary cells belonging to them continue their development notwithstanding. From my own observation, however, I cannot agree with this interpretation of the facts. Certainly in *C. versicolor*, Drap. (as in many other Florideæ), there are often aborted carpogonia, the auxiliary cells belonging to which persist. But these auxiliary cells do not grow into parthenogenetic spore-fruits, but simply become small sterile thallus-cells in the same way as in other species of *Callithamnion*; and these "seirosporiform favellæ" originate from auxiliary cells, the carpogonial branch belonging to which develops a normal carpogonium with a well-developed trichogyne. Evidently such carpogonia were accidentally no longer persistent in the specimens of the plant investigated by Falkenberg.

Moreover Falkenberg (*loc. cit.*) cites the present plant not as *C. versicolor*, Drap., but as *C. corymbosum*, J. Ag., var. ? *seirosporum*, and Berthold ("Vertheilung der Algen im Golf von Neapel," in Mitth. d. Zool. Stat. iii. p. 515) has quite recently united the same plant with *C. corymbosum*, Lyngby (J. Ag. Sp. Alg. iii. p. 40). From this latter species, certainly very similar in habit, in which seirosporæ are entirely wanting (and which, moreover, occurs with *C. versicolor* in the Bay of Naples), *C. versicolor*, Drap., is distinguished not only by the form of the cystocarps and antheridia (to which attention has already been called by Bornet, *loc. cit.*), but also by the structure of the individual thallus-cells. In *C. versicolor*, Drap., the sterile thallus-cells are always uninucleate, while in *C. corymbosum*, Lyngby (with the exception of the youngest cells) they are always multinucleate (see my statements in the Sitzungsb. d. niederrh. Ges. f. Nat.- u. Heilk. zu Bonn, June 7, 1880, p. 125 [p. 4 of the separate impressions]).

So far as I know, a parthenogenetic, *i. e.* apogamic, origin of the spore-fruits has never been described in any other Florideæ.

ramified lateral branches, in conjunction with the neighbouring thallus-tissue, a very variously formed envelope around the developing spore-tuft.

Sometimes, indeed, the auxiliary cell enters upon a perfectly different course of development; as, for example, in *Chondria tenuissima*, Ag. In this species, namely, the auxiliary cell at the period of fertilizable maturity bears, besides the terminal carpogonial branch, two very richly ramified lateral branchlets, which coalesce closely, to form an elongated cell-complex, which pushes the carpogonial branch somewhat to one side. After fertilization the auxiliary cell then increases in size, and, conjugating with the nearest cells of that cell-complex, becomes developed into a large, branched, multinucleate cell, which bears, attached to its outer surface, numerous two- or three-celled sterile cell-filaments, the final ramifications of the cell-filaments of that cell-complex. Then at the superior free extremity of this conjugation-cell, which (so far as I could make out) is not here segmented off as an independent cell, several lateral branches sprout forth, one after the other, and these, ramifying abundantly, form a short stumpy tuft of sporigerous filaments. I have no doubt that similar processes will be observable in other Rhodomeleæ.

Lastly, the Gigartineæ (*Gigartina*, *Chondrus*) call for special notice. In these forms the single auxiliary cell becomes itself the central cell of the spore-fruit. From its whole surface cell-filaments shoot forth in all directions like the rays of a star, and diffuse themselves, branching abundantly, in the surrounding thallus-tissue*.

In *Gigartina* these branched filaments finally develop single naked carpospores from the individual cells of the filaments. In *Chondrus*, on the other hand, numerous cells of these filaments enter into close connexion with individual neighbouring cells of the sterile thallus-tissue by the formation of a pit, and then, from individual cells of these filaments by repeated division, there originate complexes, each consisting of four cells, which, for their part, give origin each to a naked carpospore. Consequently, even within so natural a group as the Gigar-

* Hence the offshoots of the auxiliary cell in the present series of forms, the Ceramieæ, Rhodomeleæ, Sphærococceæ, Rhodymenieæ, Gigartineæ, and § V. appear perfectly analogous to the offshoots of the fertilized carpogonial cell, which are indicated in the preceding as *ooblastemas*. It may therefore be advisable to contrast them as *secondary ooblastemas* or *meta-ooblastemas* with those primary ooblastemas. This appears to be particularly indicated if we regard (as I believe we are bound to do, see under § V.) the action of the fertilized carpogonial cell (*i. e.* the ooblastema-cell in *Glœosiphonia* and other similar species) upon the auxiliary cell as a second act of fertilization, and interpret the fertilized auxiliary cell therefore also as a fertilized ovicell.

tineæ, there is a repetition of the same phenomenon which has been previously described in the series of forms of the Gelidieæ and Cryptonemieæ, namely, that in certain forms the ramified ooblastema-filaments produce spores directly from their cells; whilst in others these individual cells enter into connexion with the cells of the surrounding sterile thallus-tissue, and thus the formation of multicellular complexes of spores is superinduced*.

[To be continued.]

II.—*Note on the Structure of the Skeleton in the Genera* Corallium, Tubipora, *and* Syringopora. By H. Alleyne Nicholson, M.D., D.Sc., Regius Professor of Natural History in the University of Aberdeen.

Some time ago I published a short paper on the structure of the skeleton in *Tubipora*, with special reference to the relations of this genus to the Palæozoic *Syringopora* (Proc. Roy. Soc. Edinb. 1880–81, p. 219). The general conclusion to which I was led by a comparison between these two types was that, though undoubtedly similar in aspect, they were not really related to one another. The grounds upon which I based this conclusion were the following:—

(1) "In the first place, there is the very important and remarkable difference in the minute structure of the calcareous skeleton in the two types in question. In *Tubipora* the corallum is made up of fused † calcareous spicules, which are so disposed as to give rise to a universally distributed system of minute canaliculi or tubuli, which open on both the outer and inner surfaces of the skeleton by well-marked apertures. The size of these tubuli is comparatively so great that it is quite impossible that their presence could be overlooked in thin sections of *Syringopora*, if they really existed in this genus. On the other hand, the skeleton of *Syringopora*, as

* I have hitherto found among the Gigartineæ nothing analogous to the third case, namely, that the cells of the ooblastema-filaments conjugate with individual cells of the thallus, and then these thallus-cells develop into multicellular spore-complexes.

† Mr. Hickson has rightly pointed out that the term "fused" as applied to the spicules of *Tubipora* might lead to some misconception, as actual amalgamation of the spicules does not take place. The spicules, on the other hand, are united with one another closely by their sides or projecting points, and it was to indicate this union only that I employed the term "fused" in my former paper.