Contributions from the Cryptogamic Laboratory of Harvard University. XXXIII.

Development of the cystocarp of Champia parvula.

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WITH PLATES VII AND VIII.

Champia parvula (J. Ag.) Harv. is representative of a type of carposporic reproduction remarkable for the phenomenon of cell fusion which takes place previous to the formation of the glomerule of spores. This genus together with Chylocladia and Lomentaria form a group agreeing with each other, according to Hauptfleisch,[1] in the essential points of the development of the cystocarp. The steps in this process, as described by Hauptfleisch, are very interesting and, as the subject is complex, the writer thinks that he cannot better introduce the matter which treats of his own observations than by giving first a brief summary of the results obtained by the first investigator of the fruit development of these forms.

The following four paragraphs will then constitute a brief sketch of Hauptfleisch's conclusions:

(1) The procarpic branches (Carpogonäste) are found near the tips of the branches of the frond. Each procarpic branch is attached to an ordinary thallus cell and the latter is united to one of the internal filaments (Markfaden) that traverse longitudinally the interior of the hollow fronds. The procarpic branches consist of three or four cells (three in the case of Champia), the terminal one being the carpogonium and bearing a delicate trichogyne which projects through the outer wall of the frond.

(2) After or at the time of the formation of the procarpic branch there is developed an auxiliary cell (two in Chylocladia). An ordinary thallus cell, neighbor to the cell which bears the procarpic branch, becomes richer in cell-contents and then divides into an upper and a lower cell. The upper cell is the auxiliary cell.

(3) When the carpogonium is fertilized the trichogyne withers. The cells of the procarpic branch then gradually

[1] Hauptfleisch, Die Fruchtentwickelung der Gattung Chylocladia, Champia, und Lomentaria. Flora **75:** 306. 1892.

fuse together, beginning at the carpogonium end and there results a large "fusion cell."

In Chylocladia and Champia the fusion of the cells of the procarpic branch extends so far that it finally includes the cell which bears the procarpic branch. The very large "fusion cell" then unites with the auxiliary cell which usually sends out a process for the purpose and this auxiliary cell becomes the "central cell" from which the glomerule of spores is developed. Slight modifications of the process as stated above are found in some species, but this is the phenomenon as described for Champia parvula and the main principle of a union between a fusion cell and an auxiliary cell is true in all cases. Hauptfleisch states that in *Chylocladia kaliformis* the fusion cell contains one large nucleus resulting from the union of all the nuclei in the cells of the procarpic branch. The auxiliary cell also contains a single nucleus and when the fusion cell unites with it the two nuclei approach each other and coalesce.

In Champia parvula the hook-shaped process from the fusion cell, that is put out towards the auxiliary cell, contains a single large nucleus.

(4) The wall of the cystocarp is formed in the same manner in all the genera.

Filaments spring from the cells neighboring those concerned in the process of fertilization and spore formation, and by their growth and branching the wall of the cystocarp is formed. The interior of the young cystocarp is more or less filled with a loose network of filaments that are pushed against the side of the sporangium wall by the development of the glomerule of spores.

The material with which the writer worked was collected at Woods Hole, Mass., during the summer of 1894. The observations were made chiefly from sections, as it was not easy to crush out preparations, particularly of older stages of the fruit. If care be taken the tissues of the plant may be imbedded in paraffin and sectioned without material shrinkage of the cells, such serial sections being very desirable for the study of certain stages. The writer also employed a method of sectioning suggested by Mr. W. J. V. Osterhout, in which the tissues were frozen in a solution of gum arabic. Such sections were mounted in glycerin, the method proving satisfactory and a time-saver. The specimens for the most part were stained *in toto* with Mayer's acid haemalum.

A number of antheridial plants were found during the summer, and in one instance the same plant bore both antheridial and cystocarpic branches. The antheridia form patches on the frond, indefinite in extent and variable in position, sometimes appearing as caps at the ends of the branches but more often as bands around older portions of the frond (fig. 1). The structure of the antheridium is somewhat similar to that of the genus Lomentaria described by Mr. Webber.[2] The very small antherozoids are borne singly on the tips of short filaments, which arise in branching clusters from the thallus cells. Fig. 2 shows three of these clusters and there it may be seen that each cluster consists of several short filaments, the younger being branches from the older.

We must refer at the outset to an interesting point in the structure of the older cells of the frond. The young cells at the apex of a branch contain only one nucleus but cells somewhat removed from the growing point are multinucleate. This character is very striking and is shown in most of the figures (see figs. 2, 7, 9, 14, etc.).

The writer has observed similar conditions in the older cells of several genera of Florideæ, for example Callithamnion, Griffithsia, Spermothamnion, and Polysiphonia, and in some cases, as in the older cells of Griffithsia, the number of nuclei becomes very large indeed. Apparently a multinucleate structure of the older cells of Florideæ is likely to prove a very general fact.

My preparations have shown that the procarpic branch may consist of two or three cells. It is a small structure (figs. 3 and 4), and is always attached to one of the large thallus cells. As a rule the thallus cell (*t*, in the figures) is joined to one of the internal filaments, *f*, that traverse the frond, but this is not always the case, and procarps and young cystocarps have been found quite removed from it.

The trichogyne is a very delicate structure arising from an extremely small cell, the carpogonium, *c*. The whole structure is so small that even under such high magnification as 1,500 diameters, it is very difficult to determine the structure of its cell contents. There is granular matter in the carpogonium (fig. 4) that stains rather deeply and may be nuclear substance.

In one case (fig. 3) a trichogyne was found with what ap-

[2] Webber. On the antheridia of Lomentaria. Ann. of Bot. **5**: 226. 1891.

peared to be an antherozoid at its tip, but the trichogyne was so very delicate and the antherozoid so small that the relation between the two structures could not be satisfactorily studied. Even if such stages as are shown in fig. 3 were common their small size seems to the writer to preclude the possibility of determining what takes place at the time the antherozoid is applied to the trichogyne.

The single cell or each of the two cells of the procarpic branch below the carpogonium contains a single well defined nucleus. The thallus cell (fig. 3 and 4, *t*) to which the procarpic branch is attached is larger and contains rather denser cell-contents than the neighboring cells of the frond, but like them is multinucleate. It is probably always united to neighboring thallus cells by strands of protoplasm, although such connections may not always appear in sections which are necessarily cut in a single plane. The attachment to the internal filament is usually by a broad strand of protoplasm, and not infrequently one of the bulb cells found along the internal filaments occurs opposite this point (fig. 3, *b*).

The trichogyne withers quickly and the upper portion disappears very rapidly. The swollen portion at the base (carpogonium) remains somewhat longer (figs. 5 and 6) but takes the stain very faintly and finally disappears, and the lower cells of the procarpic branch are left attached to the thallus cell. The condition of the procarp is then either that shown in fig. 7 or fig. 8; that is, it consists of one or two cells, each probably containing as a rule only a single nucleus, attached to a thallus cell which is multinucleate. At this time the protoplasm of the thallus cell and of the cells of the procarpic branch above has become very dense and stains heavily, so that these stages appear very conspicuous in the sections. The nuclei in the thallus cell multiply in number and increase in size at this period when the cell is becoming gorged with protoplasm.

At this point we had best consider the changes which take place in the tissue around the cells of the procarp after the trichogyne has disappeared. The contents of the thallus cells directly around that which bears the procarpic branch gradually assume a different character. The protoplasm becomes very much denser and the nuclei increase in number and grow larger in diameter. These thallus cells are evidently what Hauptfleisch has called the auxiliary cells. There are frequently several of them but there may be only one. They are exactly similar to the thallus cell, bearing the procarpic branch, in the appearance of their cell contents, and we can only identify the latter by its attachment to the procarpic branch on the outside and as a rule to an internal filament on the inside of the frond.

Coincident with the gradual change in the character of the cell-contents which precedes the differentiation of the auxiliary cells, a number of short filaments begin to grow up over the procarpic branch. The filaments arise from the thallus cells around the procarpic branch, meeting at a point above it, and form a sort of dome over that structure. This is the beginning of the wall of the cystocarp. In the early stages it is perfectly evident that these filaments arise from ordinary thallus cells which afterward become auxiliary cells. So the auxiliary cells are not special structures developed separately from the vegetative tissue, but they are cells of the vegetative tissue directly around the procarp that become modified as to their cell-contents in a manner quite similar to those of the procarp.

An examination of the figures will perhaps serve to make the points considered in the last two paragraphs more plain. In several of the figures previously described (figs. 5, 6, 7, and 8) it will be noticed that the thallus cells on each side of the procarp have given rise to small cells above which bend over towards the procarpic branch. These with other cells, which are developed later, become the apical cells of a complex system of branches that form the wall of the cystocarp.

Fig. 9 is of a stage not very different from fig. 7. Here the wall of the cystocarp has begun to develop, but the conditions of the procarpic cell, *p*, and the thallus cell which bears it, *t*, are not materially changed except that they are larger and their nuclei much more prominent. On the right hand side of the figure is an auxiliary cell, *a*, very similar in appearance and structure to the thallus cell which bears the remains of the procarpic branch. Above the auxiliary cell is another cell rather dense in contents which is probably about to change into an auxiliary cell.

Fig. 10 illustrates a case in which the procarpic branch was originally composed of two cells besides the carpogonium and trichogyne. The thallus cell, *t*, which bears the procarpic branch is so cut that only a portion appears in this section.

Above it are the cells of the procarpic branch and on the left are three auxiliary cells, two at the side and one somewhat behind the others. The figure is especially interesting because it is evident that the vegetative branch, *v*, is directly continued from the two auxiliary cells at the side.

Figs. 9 and 10 do not give a correct idea of the great increase in size of the auxiliary cells and the cells of the procarp at this stage of development, for the magnification is much less than in figs. 6 and 7.

The writer has never observed any evidence that the cells of the procarpic branch ever fuse with each other or with the thallus cell which bears them. After the withering of the trichogyne the cells increase in size and the strands of protoplasm connecting them become much wider, but the cell-outlines remain quite distinct and the nuclei entirely separate. There is no union of nuclei into one large fusion nucleus. The thallus cell bearing the procarpic branch continues in its multinucleate condition. Each cell of the procarpic branch contains one nucleus which may afterwards fragment into several.

The auxiliary cells always contain in the beginning a number of nuclei and in the writer's preparations nothing was ever observed that would indicate a later union into one fusion nucleus; they always remain multinucleate.

However, some very interesting cytoplasmic disturbances take place. The thallus cell bearing the procarpic branch sends out many protoplasmic processes that unite with the auxiliary cells directly adjoining it, sometimes two or three processes with the same cell. In a like manner the auxiliary cells unite with one another and with the vegetative cells around them. This cytoplasmic activity occurs while the cystocarp is developing, but the position and number of the nuclei in the cells are apparently not affected by the formation of this net-work of fused cells. Fig. 11 illustrates an instance where the thallus cell, *t*, is connected by two strands of protoplasm with the auxiliary cell, *a*, and a similar condition is shown on the left hand side of fig. 13. In fig. 13 the reader will also observe how general is the cytoplasmic union of cells in the loose tissue around the young cystocarp. It should also be noted that the cytoplasmic fusion processes are smaller than the nuclei in the cells directly concerned with the development of the cystocarp.

The development of the favellæ of spores now remains to be considered. We must start with stages such as are shown in figs. 9 and 10. It will be remembered that at this stage the trichogyne and carpogonium have entirely disappeared so that the cell lettered *p* in these two figures is the one directly under the carpogonium. This cell gives rise to the cystocarp. By several transverse divisions, which are usually somewhat oblique, it forms a short branch consisting of four or five cells, two stages of which will be seen in figs. 11 and 12. The branch is greatly bent to one side in later stages and then oblique walls are formed across the upper segments in a very irregular manner, and there results a compact mass of cells divided up into a number of lobes. The entire young cystocarp is really a very complex set of filaments consisting of angular and irregularly shaped cells, but this structure is not readily shown in sections. The cells at first contain each a single nucleus, but when the cystocarp is mature it is apparent that the spores are borne on the ends of short branches (fig. 14) whose cells are multinucleate although each spore is uninucleate.

As the cystocarp arises from the cell of the procarpic branch just below the carpogonium, this is the place where we should expect to find cross fusion with auxiliary cells if such exists. The writer has observed no specimens which would indicate that an auxiliary cell ever completely fused with any of the cells directly concerned with the development of the cystocarp. Nothing was ever seen that could be compared with the "central cell" of Hauptfleisch. It is true that auxiliary cells are clustered around the cells of the young cystocarp, and it would be very easy for them to unite by protoplasmic processes, but the writer saw no clear evidence of such cytoplasmic fusion, much less of any nuclear disturbances. In some cases the cells of young cystocarps have been quite removed from auxiliary cells (fig. 14) and it was quite evident that no fusion had taken place; but when such cells are close together the protoplasm is frequently brought into such close proximity as to make it very difficult to decide the question of cytoplasmic fusion.

What is the cause of the very general cytoplasmic union of the cells at the base of the cystocarp? The phenomenon begins after the trichogyne has disappeared and the procarp has presumably been fertilized. It is concerned with the thallus cell which bears the procarpic branch and the auxiliary cells. In all these cells the protoplasm becomes very much denser and the nuclei increase greatly in size in marked contrast to the ordinary vegetative cells of the thallus. The nuclei do not fuse. It has been suggested by several investigators that cytoplasmic activity of this nature is for nutritive purposes and the writer is inclined to believe this to be true of Champia.

The auxiliary cells are then cells in the neighborhood of the procarpic branch whose protoplasm has changed in character in a similar manner to the cell contents of the latter structure. They are not specially developed organs of the frond but are at first ordinary vegetative cells at the base of the filaments that later form the wall of the cystocarp. They vary in number and they vary in the degree in which their cell contents have been modified.

How is the procarp fertilized? Unfortunately the small size of the trichogynes and antherozoids presents a very serious obstacle to the study of this point. The conditions are further complicated by the poorly defined character of the nucleus in the diminutive carpogonium and because the trichogyne withers very early and completely disappears together with the carpogonium. To explain the facts according to present accepted views of the nature of the sexual act it must be supposed that the fertilizing substance, presumably nuclear matter, passes through the trichogyne and carpogonium into the cell below. Such complexity of conditions is quite unusual for the sexual act and presents great difficulties to a clear understanding of the subject and these difficulties are made more emphatic by the insignificant appearance of the trichogynes. The trichogynes resemble somewhat degenerate cells, quite lacking the clear well defined cell structure which we usually expect of sexual elements.

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Explanation of Plates VII and VIII.

Preparations stained with Mayer's acid haemalum. All figures sketched with Abbé camera and lettered as follows: *a*, auxiliary cell; *b*, bulb cell; *c*, carpogonium; *f*, internal filament; *p*, cell of procarp just below carpogonium; *t*, thallus cell bearing procarp; *v*, developing wall of cystocarp; *x*, antherozoid. Figure 1 magnified about 5 diameters; figures 2–8 about 730 diameters; figures 9–13 about 530 diameters; figure 14 about 260 diameters.

Plate VII.

Fig. 1. Portion of frond showing distribution of antheridia.

Fig. 2. Section of frond with antheridial filaments arising from the thallus cells; *x*, antherozoids.

Fig. 3. An adult procarp attached to an internal filament; *x*, antherozoid.

Fig. 4. A procarp showing granular matter, which may possibly be a nucleus, at base of carpogonium.

Fig. 5. Procarp with withered trichogyne; two cells between carpogonium and thallus cell.

Fig. 6. Procarp with withered trichogyne, one cell between carpogonium and thallus cell.

Fig. 7. Trichogyne and carpogonium entirely gone, one cell of procarp, *p*, above the thallus cell, *t*.

Fig. 8. Trichogyne and carpogonium entirely gone, two cells of procarp above the thallus cell.

Plate VIII.

Fig. 9. Procarp with one cell above the thallus cell; auxiliary cell at the right; wall of cystocarp beginning to develop.

Fig. 10. Procarp with two cells above the thallus cell; auxiliary cells at the left; wall of cystocarp developing.

Fig. 11. Young cystocarp.

Fig. 12. Young cystocarp, next stage to figure 11.

Fig. 13. Half matured cystocarp.

Fig. 14. Group of ripe spores.

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