Development of the Frond of Champia parvula, Harv. from the Carpospore.

BY

BRADLEY MOORE DAVIS.

With Plate XXI.

THE investigation, the results of which are set forth in this paper, was begun at the suggestion of Dr. William A. Setchell, at the Marine Biological Laboratory, Woods Holl, Massachusetts, in the summer of 1891. The greater part of the work, however, was done in the botanical laboratory of the Leland Stanford Junior University at Palo Alto, California. To Dr. Setchell, and Dr. Douglas H. Campbell I wish to express my thanks for many helpful suggestions which they have given me in my work.

But little was known about the minute structure of this interesting alga, representative of a very curious group, until 1886, when a memoir by Prof. F. Debray [1] appeared. In 1887 a paper by Robert P. Bigelow [2] was published upon the same subject, written without knowledge of Prof. Debray's memoir. Previously to this time, papers bearing upon the subject of

[1] Debray, F., Recherches sur la Structure et le Développement du Thalle des *Chylocladia*, *Champia* et *Lomentaria*. Bull. scientif. du Départ. du Nord, ix. pp. 253-266, 1886.

[2] Bigelow, R. P., On the Structure of the Frond of *Champia parvula*, Harv. Proc. Amer. Acad., vol. xxiii. p. 111, 1887.

[Annals of Botany, Vol. VI. No. XXIV. December, 1892.]

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

the structure and manner of growth of this alga and allied species had been published by Nägeli, Berthold, and Wille. It will be of interest to compare later their views with those of Debray and Bigelow. Debray and Bigelow arrived independently at the same conclusions in regard to the apical growth and the development from the growing-point of the structures characteristic of the adult frond of this species. My own observations are in accordance with their conclusions, and a brief *résumé* of their investigations had best be given here.

They found that the tip of the adult frond was occupied by a group of actively growing cells. These cells were often disposed in three distinct circles. The inner circle was composed of four to six cells, which met at a point at the apex. Each of these cells gives rise to a file of segments, which is cut off behind it, and which can be traced for some distance from its proper initial cell. These are the primary files of segments. Just behind the initial cells of the first circle is a second circle of initial cells, which usually have their pointed ends wedged in between the initial cells of the first circle. Each initial cell of the second circle gives rise to a file of segments. These are the secondary files. Again, just behind the second circle and between the primary and secondary files of segments, is a third circle of initial cells, double the number of the first or second circle. Each of these cells also gives rise to a file of segments.

The segments cut off from the initial cells soon undergo a very important division. This usually occurs when the segment is separated from its generating cell by one sister-segment. A cell-wall is formed across the segment perpendicular to its greatest diameter and parallel to the surface of the frond. The segment is thus divided into an inner and an outer cell.

The cortex of the frond is developed from the outer cells of the segments. These divide irregularly by cell-walls perpendicular to the surface of the frond. This division first begins when the segment is separated from its initial cell by from

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

two to four segments. This division of the outer cells of the segments breaks up the files of cells which radiate from the group of initial cells at the apex of the frond. The files of cells are not distinguishable after the division of the segments. The division of these cortical cells tends to lengthen the frond.

As the frond thus grows in length, the cells which were cut off on the inside, when the segments divided in the plane parallel to the surface of the frond, lengthen into internal filaments or hyphae. The inner cells lengthen to keep pace with the growth of the frond. Every segment adds a cell to a hypha when it divides into the inner and outer cell. The frond increases in length by the division of the outer cells, and the inner cells lengthen as the frond grows. These inner cells form the long hyphae which traverse the length of the hollow frond on the inside. The hyphae begin near the apex of the frond, under the files of segments, which are cut off from the initial cells. Of course there are as many hyphae as there are initial cells.

The cells of the hyphae are often attached to the inside of the frond by one or more small cells, and usually have upon them, on the side nearest the axis of the frond, one large pear-shaped cell, the bulb-cell. The bulb-cells develop when very near the summit of the frond, and when several of them upon different hyphae meet and touch, they become fastened together, and by farther growth form the transverse diaphragms, so characteristic of the species.

Some of the botanists who have published papers on the structure of this alga and allied species have held views as to their manner of growth which differ widely from the view of Debray and Bigelow. Carl Nägeli [1] believed that *Lomentaria kaliformis* had an apical cell at the tip of each branch, and that this divided by oblique partitions to form the frond.

Dr. G. Berthold [2] described and gave a diagram of the tip of *Champia parvula.* He pointed out that there was a group

[1] Carl Nägeli, Die neuern Algensysteme, p. 246, 1847.

[2] Dr. G. Berthold, Beiträge zur Morphologie und Physiologie der Meeresalgen. Jahrbücher f. wiss. Botanik, Bd. xiii. p. 686, 1882.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

of apical cells, which he thought were arranged in the following definite manner. At the apex of the frond were four apical cells which formed a cross. In the angles of the cross were four more apical cells, and behind these two sets and between the apical cells were eight more. Each apical cell gave rise to a file of segments. His view is similar to that held by Debray and Bigelow, although the latter do not find such extreme regularity in the arrangement of the apical cells. Berthold also showed that there was a hypha for every apical cell.

N. Wille [1] has described a conical apical cell in *Lomentaria kaliformis*, which divides by walls in several directions and thus gave rise to segments. By the division of these segments into inner and outer cells, and the continued division of the outer cells, the cortex and internal hyphae are developed. Debray has also studied *Lomentaria kaliformis*, and believes that there is a group of initial cells in this species as well as in *Champia parvula*. Debray has written a second memoir [2], in which he treats at length of the structure of the fronds of the allied genera of *Chylocladia*, *Champia*, and *Lomentaria*.

All the publications upon the subject treat only of the adult frond, and the development from the spore has not been carefully studied in any of the three allied genera above mentioned. It was in the hope that the careful study of the development of the spore of one of these curious algae might throw some light upon the relationship of these three genera, that this investigation was undertaken.

The Carpospore; its Germination and Segmentation.

Fruiting plants of *Champia parvula* are found throughout the middle of summer, and towards the latter part of the

[1] N. Wille, Beiträge zur Entwickelungsgeschichte des physiol. Gewebesystems bei einigen Algengattungen. Bot. Centralblatt, vii, xxvi. p. 86, 1886.

[2] Debray, F., Sur la Structure et le Développement des *Chylocladia*, *Champia*, et *Lomentaria*, 2me mémoire. Bull. scientif. de la France et de la Belgique, Tom xxii. p. 399, 1890.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

season reach a large size, the tufts being four to five inches in diameter. On these plants the older portions of the frond bear empty cystocarps, and the younger portions cystocarps which are just mature or in process of development. The ripe spores may be easily obtained in large quantities by leaving the fruiting plants over night in a dish of sea-water. In the morning the bottom of the dish will be sprinkled with the reddish spores, which have been thrown out during the night. This ejection of the spores occurs only at night, as was proved by experiment. Many of the spores, when they escape from the cystocarps, settle down on the mother-plant and develop there into young plants, not unfrequently reaching the length of an inch and a half. Most of the stages in the segmentation of the spore (Plate XXI, Figs. 4–10) were obtained from the parent plant, and all of the young plants come from the same source. There could be no doubt about the identity of these small plants with the mother-plant, for one could find them in all stages of development, from the newly-shed spore to the plants showing all the characteristics of the adult frond, with diaphragms and hyphae.

Several attempts were made to grow the spores, but they never developed beyond a 4-celled stage. The method of sowing was to place the spores on a glass slide in the bottom of a dish of sea-water, and then to keep a small stream of sea-water constantly running through the dish. The spores are heavy, and readily remain on the slide. Those which germinated attached themselves to the slide, so that they could be killed, hardened, stained, and mounted in balsam, by simply dipping the slide into the various fluids. There was silt suspended in the salt water, which settled over the spores, and probably prevented their farther development.

The spores, which measure ·05–·08 mm. in diameter, are spherical, and filled with dark red chromatophores (Fig. 1).

The nucleus lies in the centre, making that portion of the spore appear lighter and brighter in colour. It was noticed that the smaller spores germinated more readily and appeared

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

more mature, being provided with a firmer wall, and with denser cell contents.

The first sign of germination is the formation of a thick hyaline wall around the spore. In the adult plant the cell-walls on the outside of the frond are thickened into a hyaline layer. This layer is developed directly from the hyaline coat of the spore. The formation of the hyaline coat serves to attach the spore to the substratum, and the cell-division then begins almost immediately.

The first division of the spore takes place in a plane perpendicular to the substratum (Fig. 2), and this is followed soon after by another division, at right angles to the first, but also perpendicular to the substratum (Fig. 3). The spores enter the 2-celled stage about twenty-four hours after their ejection from the cystocarps, and then enter almost immediately into the 4-celled stage. Many examples of these two stages were found on the adult cystocarpic plants. The youngest stages were usually to be found towards the end of the branches of the frond, especially around those cystocarps whose contents had but a short time before been discharged. All the stages more advanced than the 4-celled condition were obtained from the parent cystocarpic plant.

The cystocarpic plants, from which the later stages were taken, were prepared for study by fixing the plants in ½ per cent. hot chromic acid, and were preserved finally in 70 per cent. alcohol. Very little difficulty was experienced when this material was imbedded in paraffin for sectioning. There was but little cell-shrinkage, but some care was necessary to keep the chamber inside the frond from collapsing.

The early stages in the segmentation of the spore were studied while on the adult frond. Small pieces of the frond, which contained the young plants, were cut off and mounted in 50 per cent. glycerine. By turning the piece of the frond over and over it was a simple matter to get both top and side views of the different stages. In drawing the figures, all sketched with the camera lucida, I have disregarded the substratum, which in every case, except Figs. 1, 2, and 3, was the

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

parent plant. The boundary of the outside hyaline layer, which is simply the thickened outside cell-walls, has been indicated in the figures. This layer is perfectly homogeneous, showing no striations, which is also true of the other cell-walls. The measurements were all made with a Zeiss micrometer eye-piece.

The third division in the segmentation of the spore seems to be in a plane parallel to the substratum, making an 8-celled stage out of the 4-celled stage. Fig. 4 gives a side view of the 8-celled stage. The fourth stage, 16 cells, Fig. 5, is not a common one, and probably does not last long, but changes quickly into the fifth stage, represented in Fig. 7, which consists of 28 cells.

As shown in Fig. 5, the 16-celled stage develops from the 8-celled stage, by each of the eight cells being cut by cell-walls parallel to the substratum. The cell-walls are probably slightly oblique, inclining towards the centre of the embryo. Optical sections of later stages seem to indicate this (see Fig. 14). In the 16-celled stage the first indication of the formation of an organ of attachment appears. This is indicated by a slight bulging of the four bottom cells of the embryo. Fig. 6 represents a top view of the 16-celled stage, and shows the four cap-cells with the four cells just below them. The fifth stage, Fig. 7, is but slightly different from the one preceding it, Fig. 5. Each of the eight cells, arranged in a zone between the two groups of four cells at the top and bottom, divides by a perpendicular cell-wall. The slight processes, which appeared at the bases of the four bottom cells, have now been cut off as four separate cells, from which are to arise the four organs of attachment.

With the next stage (Fig. 8) we may consider the segmentation of the spore complete. In the two figures, 7 and 8, numbers have been given to the cells, which seem to be the same or to have had the same origin. It will be seen that the only change that has occurred has been at the base of the embryo.

The four cells, numbered 5 in Fig. 7, have each given rise

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

to three cells, while the four cells directly above them (numbered 4) have been divided first into eight cells by walls parallel to the substratum, and then each of the four upper cells have been divided by a perpendicular wall.

Disregarding the thick gelatinous coat, it is probable that the segmented spore is about the same size as the freshly discharged spore. This is illustrated by the series, Figs. 1–9, all made under the same magnification, namely 450 diameters. The ripe spores themselves vary from ·05 to ·08 mm. in diameter, and one would expect a corresponding variation among the different stages. Up to this time there has been no forward growth of the young plant, and all the cell-division has been concerned with establishing the young plant firmly upon its support by means of the four small holdfasts. There has been nothing like that apical growth which is peculiar to the adult.

Professor Debray [1], in his second memoir, mentions having germinated the tetraspores of *Chylocladia kaliformis*, but he did not follow their development carefully. He remarks that they divide in an irregular manner, while preserving their spherical shape. In my own experience I have found the earlier stages (Figs. 2–7) very common and with the greatest symmetry of form, but, of course, with later stages there is much greater likelihood of irregular cell-division. I have found in the few examples of stages five and six (Figs. 7 and 8) that I have examined (for these stages are passed over quickly, and are consequently rarer and are also more difficult to manipulate), that there are sometimes slight irregularities in cell-division. Often some of the cells, by their more rapid growth, have crowded their neighbours a little out of the proper symmetrical arrangement. However, these irregularities were usually at the base of the plant, and in all cases there were four cap-cells at the top of the young plant. It is from these four cap-cells that the apical growth begins, and from them that the group of initial cells arises.

[1] Debray, Bull. scientif. de la France et de la Belgique, Tom xxii. p. 415.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

Development of the Growing-Point.

Immediately after the segmentation of the spore, the growth of the young plant is more or less irregular. The cells at the base of the plant frequently divide very irregularly, and serve to strengthen the four organs of attachment. The space between the four small holdfasts becomes sooner or later filled in with cells, and a disc-shaped base is formed. One specimen was noticed in which the four holdfasts were present unaltered in a plant half a millimetre long.

A plant, ·15 mm. long, is figured in Fig. 9. The cells which probably agree in origin are numbered to correspond with Fig. 8. The apex of the young plant at this stage is very small, and is almost completely covered by the four cap-cells. At this time the growth of the young plants is very rapid.

Because of the size of the young plants it soon became evident that it would be impossible to get satisfactory top and side views of the apex that would show how the groups of initial cells arise. Further study was carried on by means of microtome-sections.

The plants had been well fixed in chromic acid, and very little difficulty was experienced in preparing them for sectioning. The young plants were very small, so for convenience they were always left attached to a short piece of the old frond on which they had grown. They could be much more easily handled when thus attached to a short piece of the mother-plant.

The specimens were all stained in alum-carmine; the colour given them enabled the specimens to be oriented in the paraffin blocks more easily. They were treated with absolute alcohol in the usual way, and prepared for the paraffin by treatment with turpentine and solutions of paraffin in turpentine. In some cases the stain produced by alum-carmine was sufficient to show all the points, but usually it was necessary to stain again on the slide, and no stain was found so satisfactory for this purpose as Bismarck-brown. The

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

sections were cut serially on a Minot microtome ·01 mm. in thickness. There was no cell-shrinkage, when care was taken not to let the paraffin get too hot, but with large specimens there was always danger of the hollow frond collapsing.

Transverse sections of the young plants will first be considered, for it is these alone that show how the group of initial cells arises. The smallest plant sectioned was ·10 mm. long, and there were ten sections in the series. Eight of these sections are shown in Fig. 10, in the order in which they were cut. This plant was more advanced than that shown in Fig. 6, although it was not so long. Its base was disc-shaped, and was not raised on four organs of attachment, as the case figured in Fig 9.

The first section, Fig. 10 *a*, shows the four initial cells at the apex of the frond, arranged in the form of a cross. They are numbered 1, 2, 3, 4, and appear also in the second section, Fig. 10 *b*. The four initial cells are the same as the four cap-cells of the segmented spore. They have divided several times, giving rise to daughter-cells behind them, and are now smaller than they were at first.

The other sections are very interesting, because there is an apparent division of each section into four parts. In the stained specimen this division was very noticeable, much more so than can be represented in outline-drawings, for the older cell-walls between the four divisions stained much more heavily. I have drawn in each figure two straight lines to mark the extent of the four divisions. It will be remembered that in the later stages of the segmentation of the spore there were always present four clearly marked divisions, each of which had a cap-cell at the top, and at the bottom was terminated by an organ of attachment. It is interesting to find this division into four parts present for so long a time in the young plants.

Fig. 11 shows the first two sections from another slide of a plant ·15 mm. long, and Fig. 12 is the first section of a plant ·17 mm. long. In both of these plants the four initial cells derived from the four cap-cells are distinct. They are num-

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

bered 1, 2, 3, and 4 in these figures, as in all the other figures of cross-sections.

Now it will be apparent that as the young plant grows, the top, which was at first small enough to be covered by the four cap-cells, would finally become so broad that it would include some of the daughter-cells derived from the four initial cells.

The four initial cells become smaller in size, and as the apex increases in area they become slightly separated behind. This allows some of the cells behind to crowd in between them, and then they assume the functions of initial cells, and daughter-cells are cut off behind them.

If one or two of the four primary initial cells are not quite so large as the others, they are very likely to be pushed aside by this crowding forward of the cells behind them, and thus the apex will be occupied by five or six initial cells. If the four primary initial cells are of equal size and are symmetrically arranged, the cells behind them will not be able to displace them, but will take up their position just behind them, but with their points wedged in between them.

It is interesting in this connection to notice Berthold's[1] views as to the arrangement of the apical cells. He thought that they were always arranged in a regular manner. There were four initial cells at the apex; behind this group was a second group consisting of four cells placed in the angles of the cross formed by the first group of four cells. Behind the second group were eight more initial cells, arranged between the files of segments, derived from the eight initial cells in front of them. Such a case might happen if the development were perfectly symmetrical, although usually the growth is irregular, and results in there being a circle of 5–6 initial cells at the apex.

Fig. 11 shows the first two sections of a plant ·15 mm. long. In this plant there are four initial cells, numbered 1, 2, 3, 4, at the apex. Another cell, numbered 5, by its shape and posi-

[1] G. Berthold, Beiträge zur Morphologie und Physiologie der Meeresalgen. Jahrbücher f. wiss. Botanik, Bd. xiii. p. 686, 1882.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

tion seems about to push its way into this group of four initial cells. In Fig. 12, the first section of a plant ·17 mm. long, the four original initial cells are not symmetrically arranged, and it is evident that the cell numbered 5, and perhaps also 6, would soon have become members of the first circle of initial cells. The first four sections of a plant ·30 mm. long are shown in Fig. 13, and in that plant the tip may be said to have five initial cells. Probably the cells numbered 1, 2, 3, and 4 are the original four. Here the position of the cells numbered 6, 7, 8, and 9 indicate that they will be, if they are not already, initial cells in the second circle.

The young plant starts out with four initial cells. These were the cap-cells of the segmented spore. The initial cells cut off segments behind them, which divide rapidly and by their growth increase the area of the apex of the frond. The cells at the apex of the frond crowd one another, and some of them are forced to take position between the four apical cells. One or two of them usually wedge their way in between the four initial cells and finally become part of the first circle of initial cells. Other cells remain with their points placed between the cells of the first circle and take on the functions of initial cells and become the second circle of initial cells. A third circle of initial cells will be developed in a similar manner when the area of the apex of the frond becomes large enough to allow of its formation. After the groups of initial cells are well established the segments derived from each initial cell form files of cells radiating from the apex.

The development of the hyphae and diaphragms will now be considered. I was very much surprised to find that they were the last structures of the frond to develop. It certainly seems that in *Champia parvula* they are developed some time after the initial cells have been differentiated and have assumed their function. The cells that are derived from the initial cells form a continuous tissue with the cells at the base of the plant, a tissue that is continuous with the cortex of the adult frond. This fact would seem to indicate that the hyphae

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

are secondary structures developed to strengthen the cortex. The usual view has been to consider the initial cells morphologically as the ends of the hyphae, and the cortex as a tissue developed from the hyphae.

Longitudinal sections of young plants ·36 mm. long were cut, which were without a trace of hyphae and of course without diaphragms, as the latter are developed from hyphae. Sections of plants ·28 mm. long were also cut and these had both hyphae and diaphragms.

The figures 14–18 tell the story of the development of the hyphae. Fig. 14 is an optical section of the fully segmented spore, shown in Fig. 8. Fig. 15 is a longitudinal section of a plant ·20 mm. long, and it would probably appear in cross-section in about the stage of Fig. 12. The comparative length and breadth of the initial cells lettered × is shown. In Fig. 16, which is a section of a plant ·25 mm. long, we have the first beginnings of two hyphae: × and $\times^1$ are the two initial cells, and just behind them may be seen the segments which have been cut off from them. Segments 1^1, 2^1, 3^1 have each been divided by a wall parallel to the surface of the cortex, cutting off the cells of the hyphae lettered h^1, h^2, h^3. Segment 1 on the left-hand side of the figure has not divided, but from segment 2 a hypha (*h*) has started. It is worth noticing that the segments 1^1, 2^1, and 3^1 and 1 and 2 are part of the same tissue, which extends to the base of the plant, and that the cells below them have no connection with the hyphae. From the appearance of the ends of the hyphae it is probable that they creep down a little on the inside of the frond, see Figs. 16 and 17.

Fig. 17 is a figure of a longitudinal section through a plant ·32 mm. long. The first diaphragm (lettered *d*) has been formed, but the section was cut a little obliquely and does not show the relation of the cells of the hyphae to the cortex as well as does Fig. 18. It is interesting, however, on account of the two hyphae lettered *h*, both of which seem to have grown down along the inside of the frond from the apex. The series of four transverse sections shown in Fig. 13 are

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

probably of a plant in about this same stage of development. The sections *b*, *c*, and *d* of this figure show on the inside cross-views of the hyphae.

Perhaps the most instructive figure is Fig. 18. The plant from which this was taken was ·28 mm. in length. In this the initial cells are lettered x and x^1, and the segments derived from each initial cell are numbered to correspond. The typical arrangement of the segments and of the cells which are cut off from them to form the hyphae is, I think, apparent. Segment 1^1 has not cut off its hyphal cell; all the rest have. In the older segments (4, 5, 3^1 and 4^1) the cortical portion of the segments has again divided, and this illustrates very beautifully the manner in which the cortex grows.

In this specimen, Fig. 18, there is one well-developed diaphragm, lettered d^1, and also the beginnings of the second diaphram, lettered d^2. At this last point some of the hyphal cells have met and become fastened together. By the farther division and growth of these hyphal cells, keeping pace with the widening of that portion of the frond, the second diaphragm would have been developed. One bulb-cell, lettered *b*, is shown in this section, attached to a hypha (*h*). The development of the bulb-cells has not been seen in these young plants, but there is no doubt, from the investigations of Debray and Bigelow, that they arise from hyphae.

I wish again to call attention to the lateness of the development of the hyphae. The cap-cells of the segmented spore often divide several times before the hyphae appear. That this is so is proven by the fact that the initial cells of a young plant are much smaller than the cap-cells of segmented spores. Compare Figs. 14 and 15, both drawn under the same magnification; the segmented spore (Fig. 14) is ·08 mm. long, the young plant (Fig. 15) is ·20 mm. long. The hyphae, when they first appear, are very small (see Fig. 16) and insignificant. If the hyphae are to be considered as structures which are directly derived from the initial cells and which give rise to the cortex of the adult frond, one would hardly expect to find them to be the last structures formed in the development of

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

the plant. They start simply and increase in size and importance as the frond has need of their support and the support of the diaphragms derived from them.

All the important structures of the adult frond are now present in the young plant, and in its farther growth the initial cells simply repeat the cell-divisions that I have already described. It will be noticed that all the stages which I have figured and described, although taken from a number of cystocarpic plants, form a complete series from the spore to a stage that is in all essentials identical in structure with the adult frond, which has been so carefully studied by Debray and Bigelow.

PALO ALTO, CALIFORNIA,
March, 1892.

EXPLANATION OF FIGURES IN PLATE XXI.

Illustrating Mr. Davis' paper on *Champia*.

N.B. All figures drawn with an Abbé camera. Figs. 1–9 magnified 450 diameters. The sections were cut with a Minot microtome, were ·01 mm. thick, and were mounted in benzole-balsam.

Fig. 1. A spore drawn soon after its discharge from a cystocarp and while in sea-water; the light spot in the centre marks the position of the nucleus; specimen ·05 mm. in diameter.

Fig. 2. First division of the spore; viewed from above; drawn from living specimens in sea-water; showing hyaline coat.

Fig. 3. Second division of the spore; viewed from above; specimen drawn when in sea-water.

Fig. 4. Third stage in segmentation of the spore; viewed from the side; glycerine preparation.

Fig. 5. Fourth stage in segmentation of the spore; 16 cells; viewed from the side; glycerine preparation.

Fig. 6. Top view of the same stage as Fig. 5; glycerine preparation.

Fig. 7. Fifth stage in segmentation of spore; 28 cells; viewed from the side; glycerine preparation.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

Fig. 8. Last stage in segmentation of the spore; 44 cells; viewed from the side; glycerine preparation, specimen ·08 mm.

Fig. 9. Side view of young plant ·15 mm. long; glycerine preparation. The cells are numbered to indicate probable homologies with Figs. 7 and 8.

Fig. 10. A series of transverse sections of a young plant ·10 mm. long; ten sections in the series, eight shown; the four divisions of the young plant included between the straight lines drawn across the sections; initial cells numbered 1, 2, 3, 4; stained with alum-carmine. × 250.

Fig. 11. First two sections of a young plant ·15 mm. long; primary initial cells numbered 1, 2, 3, 4; stained with Bismarck-brown. × 250.

Fig. 12. Tip of young plant ·17 mm. long; cells numbered 1, 2, 3, 4, the primary initial cells; 5 and 6 probably would soon be initial cells; stained with Bismarck-brown. × 250.

Fig. 13. Series of four sections of a young plant ·30 mm.; initial cells numbered 1, 2, 3, 4, 5, perhaps also 6, 7, 8, 9. In sections *b*, *c*, and *d* are seen cross-sections of hyphae; stained with Bismarck-brown. × 250.

Fig. 14. Optical section of the last stage in segmentation of spore; from same specimen as Fig. 8; ·08 mm. long. × 450.

Fig. 15. Longitudinal section of young plant ·20 mm. long; × and $\times^1$ initial cells; stained with Bismarck-brown. × 450.

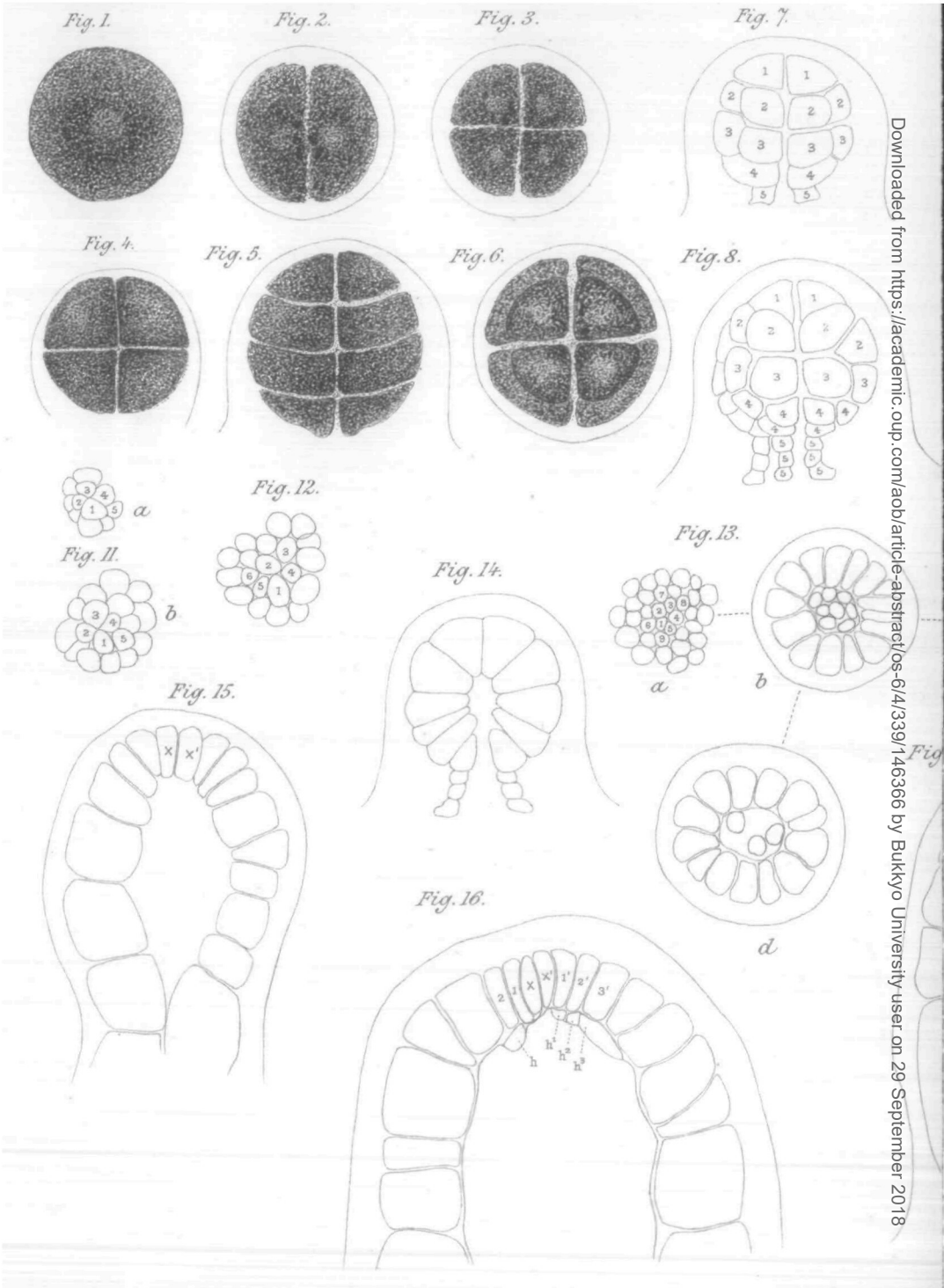
Fig. 16. Longitudinal section of young plant ·25 mm. long; × and $\times^1$ initial cells, the corresponding segments numbered; the hyphal cells lettered *h*; stained with alum-carmine. × 500.

Fig. 17. Longitudinal section of young plant ·32 mm. long; × and $\times^1$ initial cells; *h*, hyphae which have crept down on the inside of frond: *d*, diaphragm; stained with alum-carmine. × 500.

Fig. 18. Longitudinal section of young plant ·28 mm. long; segments and initial cells numbered and lettered as in Figs. 16 and 17; d^1, first diaphragm; d^2, second diaphragm just forming; *b*, bulb-cell on its hypha *h*; stained with alum-carmine. × 500.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018



Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018

Fig. 9.

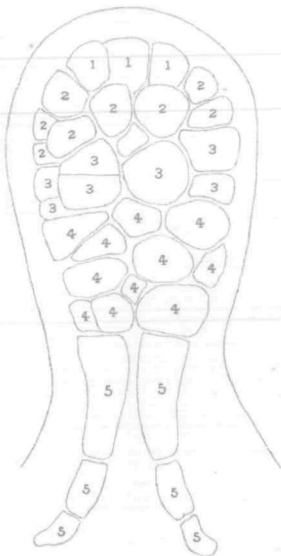
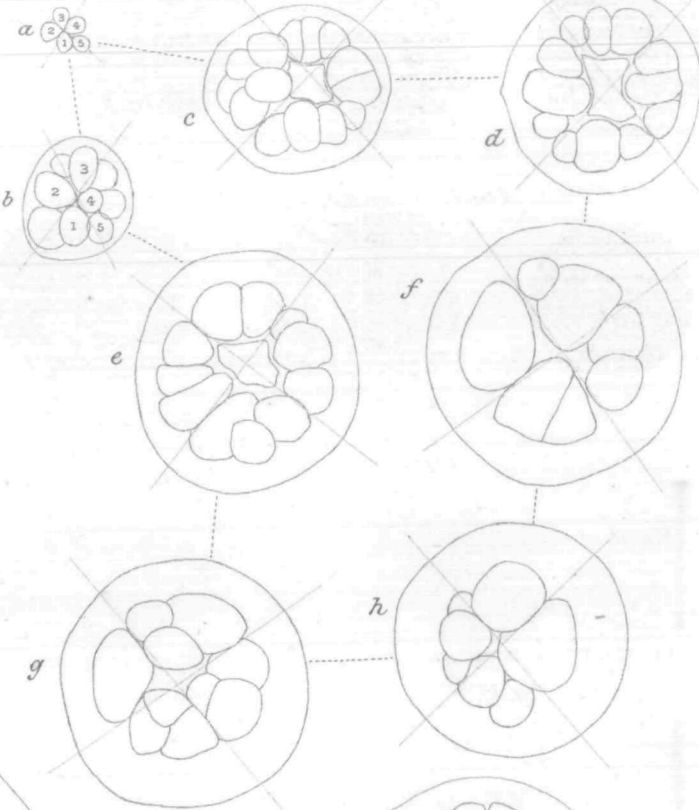
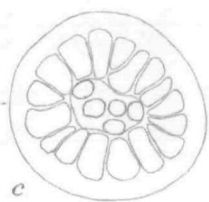


Fig. 10.





.17.

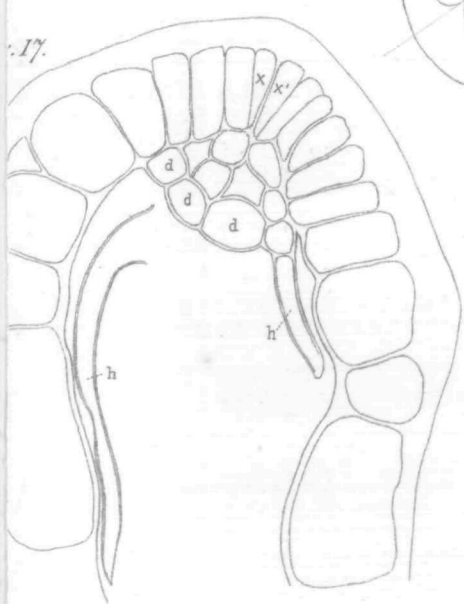
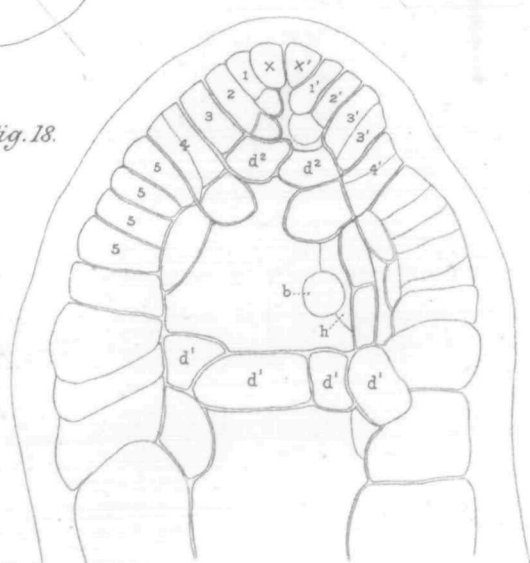


Fig. 18.



University Press, Oxford.

Downloaded from https://academic.oup.com/aob/article-abstract/os-6/4/339/146366 by Bukkyo University user on 29 September 2018